AN ABSTRACT OF THE THESIS OF

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Bruce McCune

With the increased recognition of moss as a secondary forest product has come an increased concern for the ecological ramifications of moss harvest. Three issues of primary concern are (1) characterizing the epiphyte communities impacted by harvest, (2) assessing the host preferences of these epiphytes, and (3) describing the availability of harvestable epiphytes. Harvestable epiphytes are generally large mats of clean, green plant material that can be easily accessed and removed from their substrate by a commercial moss harvester. Harvestable epiphytes on tree trunks and shrub stems were sampled at 10 sites in each of the Cascade and Coast Ranges in northwestern Oregon. Frequency of occurrence and biomass are reported for 50 species found in harvestable epiphyte mats, categorized as "target" (7 species), "nontarget" (37 species), and "incidental" (6 species), according to their commercial utility. Target species were more abundant in stands with relatively high hardwood basal area and densities of harvestable epiphyte hosts. Nontarget and incidental species were more abundant on hosts with relatively large surface areas and in stands with relatively high hardwood basal. All species were less abundant in stands with high conifer basal area. Eleven species of hosts, including seven shrubs and four trees, supported harvestable quantities of epiphytes, although most samples were collected from the clonal shrub vine maple (*Acer circinatum*). Epiphyte mats on tree trunks and shrub stems differed in epiphyte species composition. Relative frequency of occurence and abundance were used to determine host preference by several epiphytes, including *Orthotricum lyellii* for *A. circinatum* and *Neckera douglasii* for *Alnus rubra*. Harvestable epiphyte biomass ranged from 24 to 1469 kg/ha (dry

weight). Biomass is a function of both site quality and availability of suitable hosts. Epiphyte mat accumulation on *Acer circinatum* was more rapid, and more variable, in the Coast Range sites than in the Cascade Range sites. A model describing the factors influencing epiphyte mat accumulation is proposed and management implications for the harvestable moss resource are discussed.

Harvestable Moss: Communities, Hosts,

and Accumulation

by

JeriLynn E. Peck

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ACKNOWLEDGMENTS

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Harvestable Moss: Communties, Hosts, and Accumulation

CHAPTER 1. Introduction

For many people, "they harvest *what*?" is the first reaction when they hear of commercial moss harvest. After realizing that they too have seen moss used in the flora and craft industries, their second reaction is often, "Well, that's OK. After all, people put in long hours of hard work, and it's only moss so it can't be hurting anything." But upon closer inspection we begin to realize what a significant impact moss harvest may have on our forest ecosystems. "Moss" is rarely just moss; harvestable mats are typically composed of several species of mosses and hepatics, and often a lichen or two. In addition, these epiphytic bryophytes may play a larger ecological role than we have previously recognized.

Among the roles that epiphytic bryophytes play in forest ecosystems are nesting material for birds (FEMAT 1993), food for invertebrates (Stolzenburg 1995), hydrologic sinks (Pocs 1980, Veneklaas et al. 1990), and nutrient reservoirs (Coxson 1991, Coxson et al. 1992, Nadkarni 1981, 1984). Although the importance of the contributions these epiphytes make to the forest ecosystem has been reported, the robustness of those contributions to disturbances such as commercial harvest has not been adequately explored.

Forest management has recently begun to focus on the maintenance of rare species and species diversity in managed stands (Lesher et al. 1994, ROD 1994). A number of studies have indicated that cryptogam diversity is reduced and communities altered in managed as compared to virgin forest (Gufstaffson & Hallingbäch 1988, Lesica et al. 1991, McCune 1993, Neitlich 1993). Despite the increasing removal of bryophytes from our forests (Schlosser et al. 1992), the impacts of this disturbance on these communities are unknown.

The rate regrowth of commercially harvestable moss is unknown, making protocol-development for sustainability difficult. Most studies concerning growth of epiphytes have relied upon nondestructive measures (Pitkin 1975, Russell & Botha 1988, Tallis 1959, Vance & 20 Kirkland 1995, Vitt 1990) rather than harvesting and measuring biomass growth directly. Direct sampling of biomass (i.e. harvest methods), has been used to estimate biomass of forest floor communities (Binkley & Graham 1981, Busby et al. 1978) and a few epiphyte communities from tree canopies (McCune 1993, Nadkarni 1984, Wolf 1993). No systematic inventory of harvestable moss composition or biomass on understory tree trunks or shrub stems has been conducted in our temperate forest ecosystems, and there have been no previous descriptions of the net accumulation of harvestable epiphyte biomass.

Epiphyte communities in other regions have been evaluated for patterns of host specificity, including the northeast U.S. (e.g. Culberson 1955a, Hale 1955, Trynoski & Glime 1982), southeast U.S. (Palmer 1986), and Europe (Bates & Brown 1981, Frahm 1992). Few epiphytes have demonstrated complete host specificity (John & Dale 1995, Slack 1976), although consistent differences among hosts have been observed for epiphyte communities when contrasting conifer and hardwood species (Barkman 1958) and among certain hardwood species (Palmer 1986). Several studies currently underway (Peterson 1996, Rosso 1996) address epiphytic bryophytes and lichens on shrubs, a substrate ignored in previous studies of epiphyte communities.

This thesis fills gaps in our understanding by providing: (1) a definition of commerically harvestable epiphyte mats; (2) a quantification of species richness and abundances of harvestable epiphytes for 20 sites in the Cascade and Coast Ranges of northwestern Oregon; (3) an assessment of the relationships between harvestable epiphytes and their hosts; and (4) an estimate, from destructive harvest, of the available biomass of harvestable epiphytes and a description of the accumulation of harvestable epiphyte mats on vine maple (*Acer circinatum*) at these sites.

CHAPTER 2

Harvestable Moss Communities
in Northwestern Oregon

JeriLynn E. Peck

Abstract

In response to concern about the impact of moss harvest on the poorly known epiphytic bryophyte communities of northwestern Oregon, harvestable epiphytes were sampled on hardwood tree trunks and shrub stems from 10 sites in each of the Cascade and Coast Ranges. Of 50 species of mosses, hepatics, lichens, and vascular plants found in the epiphyte mats, only 7 were "target" species, defined as having a frequency >10% among all sites and a harvestable biomass >10 kg/ha. Six species were considered "incidental" collections due to low frequency and biomass. The remaining 37 species were "nontarget" species that would generally be avoided by commercial harvesters, but are often accidentally harvested. In the Cascade Range, *Neckera douglasii* was the most abundant harvestable epiphyte, with an average of 168 kg/ha of harvestable material across ten sites. In the Coast Range, *Isothecium myosuroides* was most abundant, with an average of 527 kg/ha of harvestable material. Harvestable epiphytes were more abundant in stands with relatively high hardwood basal area and high densities of harvestable epiphyte hosts. Nontarget and incidental species were more abundant on hosts with large surface areas and in stands with high hardwood basal areas. All species were less abundant in stands with high conifer basal areas.

Introduction

Epiphytes are a significant and diverse component of forests in the Pacific Northwest. Many species are old growth associates and are sparse to absent in young and mature sites (Lesica et al. 1991, Neitlich 1993). Epiphytes play a variety of roles in forest ecosystems, from nesting material for birds (FEMAT 1993) and food for invertebrates (Stolzenburg 1995) to nutrient sinks (Brown and Bates 1990). Epiphytes are increasingly being removed from the forest to feed a growing floral and craft trade (Peck 1990), yet little is known about the ecological impact of this harvest. While the official estimate of moss harvest on the Siuslaw National Forest, in

northwestern Oregon, is 889 m^3 (25,000 bu) per year, it is generally accepted that the annual harvest from the Forest is at least twice that (F. Duran, pers. comm., 1996).

The current study comes at a time when forest managers are required to protect rare epiphytes (ROD 1994) and manage moss harvest for sustainability (USDA Forest Service 1995). Baseline data for management have been lacking, prompting interest in species inventories and in estimating recovery rates following harvest (Wagner 1993, Peck 1995, Vance and Kirkland 1995). The objectives of this study were as follows: (1) to provide a definition of commerically harvestable moss mats, which will hereafter be referred to more generally as "harvestable epiphytes" due to the variety of organisms composing these mats; (2) to estimate species richness and abundances of harvestable epiphytes; (3) to define quantitatively categories of target species and nontarget species; and (4) to elucidate factors affecting the abundance and distribution of harvestable epiphytes in sites within the Cascade and Coast Ranges of northwestern Oregon.

Methods

Sites

Twenty sites were sampled in the Cascade and Coast Ranges of northwestern Oregon (Figure 2.1). In the Cascade Range, sites were chosen to represent lichen "hotspots" (as part of a larger study); areas presumed to have high lichen diversity based on forest composition (e.g. Neitlich and McCune 1995). Nine of these sites were within the Clackamas and Santiam Resource areas of the Salem Bureau of Land Management and one site was in the Santiam State Forest. The ten Coast Range sites were chosen to represent areas likely to be targeted for commercial moss harvest within the Hebo District of the Siuslaw National Forest. The area sampled at each site was approximately 1.5 ha. Characteristics recorded at each site included: percent slope, aspect, dominant vascular species plant, and basal area (BA) of conifers and
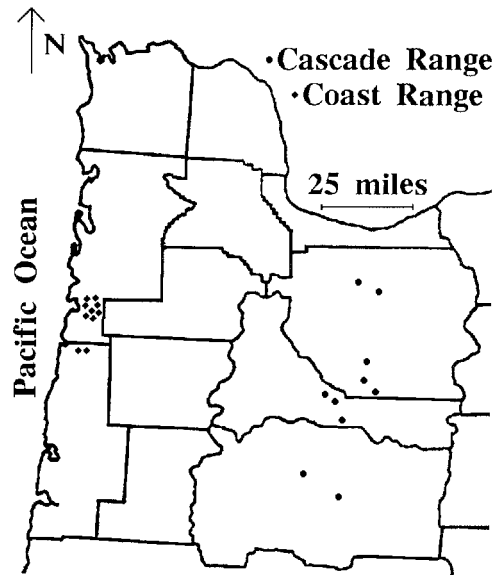
Figure 2.1. Harvestable epiphyte sampling sites, Cascade (44°30' - 45°20'N, 122°12' - 122°35'W) and Coast (45°2'- 45°13'N, 123°5' - 123°55'W) Ranges, northwestern Oregon.

hardwoods (Table 2.1). Aspect was adjusted to a 0-180° scale, with north and south at the poles (0 = north;90 = east and west). A heat-load index (McCune 1996) was calculated from aspect according to the following equation:

$$[1-\cos(\theta-45]*2^{-1} \qquad \text{Eq. 1}$$

Basal area estimates were determined using wedge prism data (BAF = m^3/ha = 10 ft^2/acre) at five points. Estimates of elevation and the horizontal andvertical distance to the nearest perennial stream or body of water were taken from topographic maps. Estimates of stand age were taken from timber records (Salem District, BLM; Santiam State Forest; Hebo District, Siuslaw National Forest). Nine of the Coast Range sites were permanently marked. Sites were sampled in July 1994.

Mat Sampling

To approximate the majority of commercial moss harvest in this region, only understory trees and shrubs with harvestable quantities of epiphytes were sampled.

Twenty or twenty-eight tree trunk or shrub stems with harvestable quantities of epiphytes were selected at each site using the point-centered quarter method (Cottam et al. 1953). This method was originally developed for sampling tree densities and stand basal areas based on tree-to-point distances from systematically located points. The first point in each transect was at least 50 m from the nearest edge (e.g. road) and points were placed at 50 m intervals. At each point, four quadrants were established. Within each quadrant, the tree trunk or shrub stem with harvestable quantities of epiphytes that was nearest the point was chosen for sampling.

Sampled tree trunks or shrub stems will hereafter be referred to as "stems." For each selected stem, the distance from the stem to the transect point was recorded (to calculate densities) as was the total length of the stem up to 2 m in vertical height (to extrapolate to the total stem level). Epiphytes were sampled below 2 m in height because few harvesters climb trees to harvest above this height and some harvest regulations restrict harvest to the lower canopy (USDA Forest Service 1995). If harvesters collect bryophytes above 2 m in height, my sampling technique will underestimate available biomass.

On each stem a one-meter-long microplot was stripped of all harvestable epiphytes (the "epiphyte mat"). Within this one-meter segment of the stem, mats varied in length, depth, and the extent of pendant growth. The midpoint of the microplot was selected randomly between 0.5 m above the ground and 0.5 m below the 2 m height cutoff. The diameter of the stem was measured at the center of the microplot. In the laboratory the epiphytes were sorted by species, their abundance estimated visually as a percentage of the total volume of material from a given stem (after McCune 1990), then oven dried (60°C for 24 hr) and weighed. Because vine maple (*Acer circinatum*) was identified as the preferred host by commercial harvesters (commercial harvesters, pers. comm., 1994), this host was chosen for additional, age-related analyses. Most vine maple stems were subsequently cored at the center of the microplot to determine stem age.

Calculations

Host surface area for the 1 m microplot was estimated from the measured diameter of the stem and the length of the microplot (1 m in all cases), assuming each stem approximated a cylinder. The density of harvestable stems at each site was estimated using calculations from the point-centered quarter method (Cottam et al. 1953, Peck & McCune 1996). Vine maple, which composed 60% of the sampled hosts, grows in aggregates (clumps) rather than individuals. Calculations based on density estimates probably underestimate the biomass of harvestable epiphytes in these sites as the point-centered quarter method has been shown to underestimate densities in aggregated populations (Persson 1971).

Epiphyte mat biomass was extrapolated from the microplot level to the site level as follows. Mat mass (g/m) was first extrapolated from the microplot to the stem level based upon the total length of the stem (m/stem) below the 2 m height cutoff, and then extrapolated from the stem to the site level based on the density of stems (stems/ha).

Gamma, mean alpha, and beta diversity indices were calculated for each of the 20 sites, for all 10 sites in each of the Cascade and Coast Ranges combined, and for all 20 sites combined. Gamma (γ) diversity was measured as the total number of species in all microplots combined. Mean alpha ($\bar{\alpha}$) diversity was calculated as the average number of species per microplot across all microplots. For matrices used in multivariate analyses, mean alpha was calculated as the average number of species per microplot for only those microplots under consideration. Beta (β) diversity, a measure of the amount of community change, was calculated as the ratio of gamma to mean alpha ($\gamma/\bar{\alpha}$). Pearson correlations (SPSS 1993) were used to evaluate relationships of environmental characteristics to gamma diversity measures. ANOVA (Statgraphics 1991) was used to compare group means between the mountain ranges, among 10-year stem age classes (for vine maple), and between tree trunks and shrub stems for $\log_e$ transformed biomass data and for the diversity measures.

Indirect Gradient Analyses

Global nonmetric multidimensional scaling (NMS, McCune and Mefford 1995; Kruskal 1964) was chosen to describe variation in species composition at the site level (kg/ha). The quantitative version of the Sørensen (1948) similarity index was used as a distance measure. Biomass data of harvestable epiphyte species, which spanned 4 orders of magnitude, were log_e transformed to improve normality. Because log_e transformation can only be done on non-zero data, in most cases 1 was added to the data prior to transformation. In all cases dimensions beyond the second axis provided relatively small reductions in stress (a measure of fit, after Mather 1976), and a two-dimensional solution was chosen. No outliers were identified in any of the analyses.

Ordinations were performed on four subsets of the combined Cascade and Coast Range data matrix. The "full dataset" (50 species) included all species. A reduced "frequent species" dataset (25 species) included only those species with a frequency of occurence of > 5% in at least one mountain range. Due to the similarity of results for the full dataset and the frequent species dataset, only the results from the latter are reported. A reduced "target species" dataset (7 species) consisted of species common and abundant enough to be commonly targetted for commercial moss harvest. The target species data were also analyzed for the Cascade and Coast Ranges separately. A reduced "frequent nontarget and incidental species" dataset (18 species) included all frequent species except target species. For the frequent nontarget and incidental species dataset, which consisted of species with lower abundances, 0.01 was added to the data prior to log_e transformation. A constant, the absolute value of the natural log of 0.01 (4.61) was added to make all values zero or positive (the Sørenson distance measure performs best on positive data). The data were relativized by species maxima to reduce the influence of dominant species.

Ordinations were interpreted on the basis of Pearson correlations and Kendall's tau, a measure of rank correlation useful for categorial data such as presence/absence data, between ordination axes and species and stand level characteristics. Most ordinations were rotated such that the variable with the highest initial correlation with an ordination axis was aligned with axis 1 to facilitate interpretation. The ordination

of the frequent nontarget and incidental species dataset was rotated such that the proportion of stems that were tree trunks was aligned with axis 2, for comparison with the frequent species dataset.

Differences in species composition among mountain ranges, age classes, and hosts (tree trunks vs. shrub stems) were tested with multi-response permutation procedures (MRPP, McCune and Mefford 1995; Zimmerman et al. 1985). MRPP is a nonparametric method that tests for multivariate differences among groups (p-values based on a t-statistic). Species indicative of mountain ranges, age classes, or specific hosts were discerned using indicator species analysis (Dufrêne and Legendre 1996; program INDICATE, B. McCune unpubl.), which takes both relative abundance and relative frequency into account when assigning indicator values (IV). IV's range from zero (no indicator value) to 100 (perfect indication). Significance of the IV is evaluated by a Monte Carlo procedure that randomly reassigns sample units to different groups. The resulting p-value is based on the proportion of 1000 random reassignments that result in an IV greater than the observed IV. Species with IV's 10 points higher in one group than in any other, with p-values less than 0.05, were considered indicative of that group. While a high degree of indication is important, the relative degree of indication between the groups being compared is often also biologically meaningful.

Results & Discussion

Composition of Harvestable Epiphytes

Species were divided into three categories on the basis of their commercial utility (Table 2.2). Most hepatics, and all lichens and vascular plants, were considered "nontarget" species whose collection in this study and by commercial harvesters may be considered accidental. These 37 species are neither targetted for moss harvest nor generally acceptable for harvest due to poor color or texture. Nontarget species typically had occurred in less than 5% of samples and had an

estimated biomass of less than 5 kg/ha. The nontarget species *Dicranum scoparium* and *Orthotrichum lyellii* were exceptions. Although common, these species exhibit growth forms (individual tufts) undesireable for moss harvest.

Table 2.2. Harvestable epiphyte species, Cascade and Coast Ranges, northwestern Oregon. •Denotes ROD Category 4 (ROD 1994) species. I = incidental species, N = nontarget species, T = target species. Data are frequency of occurrence and mean biomass across all microplots.

Species	Cascade Range			Coast Range			Status
	% Frequency (n=224)	Biomass kg/ha	SE	% Frequency (n=280)	Biomass kg/ha	SE	
MOSSES							
•*Antitrichia curtipendula*	45	13.1	0.6	16	16.9	0.5	T
Claopodium crispifolium	8	4.7	0.2	9	3.9	<0.1	I
Dendroalsia abietina	4	0.3	<0.1	0			N
Dicranum fuscescens	0			1	<0.1	<0.1	N
Dicranum scoparium	<1	<0.1	<0.1	5	17.3	1.0	N
Dicranum tauricum	0			<1	0.1	<0.1	N
Eurhynchium oreganum	14	4.1	0.1	17	10.4	0.2	T
Homalothecium fulgescens	2	0.9	<0.1	0			N
Homalothecium nuttallii	6	1.4	0.1	2	2.6	0.1	I
Hypnum circinale	<1	0.5	<0.1	0			N
Hypnum subimponens	1	0.1	<0.1	<1	<0.1	<0.1	I
Isothecium myosuroides	78	110.0	2.5	97	526.8	10.1	T
Leucolepis acanthoneuron	2	0.8	<0.1	0			N
Metaneckera menziesii	7	16.7	0.6	1	0.1	<0.1	I
Neckera douglasii	79	168.2	4.6	73	238.0	4.8	T
Orthotrichum affine	<1	<0.1	<0.1	0			N
Orthotrichum lyellii	8	0.5	<0.1	20	6.7	0.3	N
Orthotrichum obtusifolium	<1	0.1	<0.1	0			N
Orthotrichum pulchellum	0			1	<0.1	<0.1	N
Plagiomnium insigne	3	0.1	<0.1	1	<0.1	<0.1	N
Plagiomnium venustum	<1	0.2	<0.1	0			N
Plagiothecium undulatum	0			3	4.1	0.2	N
Rhizomnium glabrescens	0			4	2.3	0.1	N
Rhytidiadelphus loreus	8	8.1	0.4	10	42.1	1.9	T
Ulota crispa	0			3	0.3	<0.1	N

Table 2.2, continued

Species	Cascade Range			Coast Range			Status
	% Frequency	Biomass		% Frequency	Biomass		
	(n=224)	kg/ha	SE	(n=280)	kg/ha	SE	
HEPATICS							
Frullania bolanderi	5	0.2	<0.1	2	0.6	0.0	I
Frullania tamarisci subsp. *nisquallensis*	18	8.9	0.4	42	31.8	0.8	T
Lophocolea bidentata	0			<1	<0.1	<0.1	N
Metzgeria temperata	2	<0.1	<0.1	4	2.0	0.1	N
Porella cordeana	2	<0.1	<0.1	1	0.1	<0.1	I
Porella navicularis	58	19.2	0.3	35	44.7	1.7	T
LICHENS							
Cladonia	1	<0.1	<0.1	7	0.6	<0.1	N
Cladonia ochrochlora	<1	<0.1	<0.1	0			N
Leptogium corniculatum	<1	<0.1	<0.1	0			N
Leptogium polycarpum	1	<0.1	<0.1	0			N
•*Lobaria oregana*	1	0.2	<0.1	0			N
•*Lobaria pulmonaria*	2	0.2	<0.1	0			N
Menegazzia terebrata	0			<1	<0.1	<0.1	N
•*Nephroma laevigatum*	1	<0.1	<0.1	0			N
•*Nephroma resupinatum*	0			<1	<0.1	<0.1	N
Parmelia sulcata	4	0.3	<0.1	0			N
•*Peltigera collina*	2	0.1	<0.1	1	<0.1	<0.1	N
Peltigera membranacea	0			<1	<0.1	<0.1	N
•*Pseudocyphellaria anomala*	1	<0.1	<0.1	1	0.5	<0.1	N
Ramalina farinacea	2	<0.1	<0.1	0			N
Sphaerophorus globosus	<1	<0.1	<0.1	1	<0.1	<0.1	N
•*Sticta limbata*	0			<1	<0.1	<0.1	N
Usnea filipendula group	4	0.2	<0.1	0			N
VASCULAR PLANTS							
Montia sibirica	<1	<0.1	<0.1	<1	<0.1	<0.1	N
Polypodium glycyrrhiza	<1	<0.1	<0.1	5	2.2	0.1	N

Six species, considered "incidental" collections, are not generally targetted for harvest because of their low frequency of occurrence, but nonetheless are generally not discriminated against by commercial harvesters (Peck, pers. obs.). These

incidental species typically had a frequency of < 10% and had < 10 kg/ha of harvestable biomass, except for *Metaneckera menziesii*. While locally abundant, *Metaneckera menziesii* typically occurs on *A. macrophyllum* (Peck 1996), which is too infrequent a host to warrant classifying this species as a target species for general moss harvest.

The seven most common and abundant species were considered target species for commercial moss harvest. The target species had a frequency of occurrence of >10% and had > 10 kg/ha of harvestable biomass. These species are among the most common commerically harvested species (Peck, unpublished data). Together, they composed more than 90% of the total available biomass of harvestable epiphytes in these sites.

The species list overlaps considerably with other epipihyte studies in the Pacific Northwest. Nineteen out of 29 epiphytes found on *Acer macrophyllum* over five sites in British Columbia (Kenkel & Bradfield 1986) were also found in the current study. In a study of conifers in British Columbia, Peck et al. (1995) found 33 species of epiphytes, ten of which were also found in the current study. Of 44 bryophytes found in an extensive study of epiphytes on shrubs in the Oregon Coast Range (Rosso 1996), 24 were also found in harvestable epiphyte mats. Although the relative overlap among these studies may appear low, the other studies involved collections of all epiphytes whereas the current study only included species found in harvestable epiphyte mats. By definition, therefore, the current study does not include many appressed species (e.g. *Radula*). In that light, the degree of overlap suggests that harvestable epiphyte mats are composed of species that are common and abundant throughout the Pacific Northwest.

Of the less common species, the lichens listed in the "Record of Decision for Amendments to Forest Service and Bureau of Land Management Planning Documents Within the Range of the Northern Spotted Owl" (ROD 1994) are of particular interest. Of the fifty species of epiphytes found in these harvestable moss mats, eight are ROD Category 4 (ROD 1994) species requiring general regional surveys. Only one target species, *Antitrichia curtipendula*, is a Category 4 species. Harvest of these and other nontarget and incidental species may prove important if these species become

classified for active management. Their presence in these stands, and stands included in other epiphyte studies (e.g. Rosso 1996), however, suggests that some of these species may be more common than previously believed.

Diversity of Harvestable Epiphytes

In both mountain ranges a typical harvestable epiphyte mat had from three to four species, most of which were mosses or hepatics. Diversity indices for each site are listed in Table 2.3. Total cryptogamic gamma diversity across mountain ranges was 48; mean alpha diversity was 3.6 and beta diversity was 13.3. The Cascade and Coast Range sites did not differ significantly for any diversity measure for either all cryptogams, or for any component group (ANOVA, $p > 0.5$; Table 2.3).

Gamma diversity for all cryptogams increased with average mat mass ($r = 0.5$) and the presence of red alder (*Alnus rubra* Bong.; $r = 0.39$), and decreased with increased conifer basal area ($r = -0.59$). When mosses, hepatics, and lichens were considered separately, however, gamma diversity did not depend on mat mass (ANOVA, $p > 0.1$). Moss gamma diversity increased when a higher proportion of stems were tree trunks ($r = 0.49$) and with the presence of red alder ($r = 0.59$), but decreased with increased conifer basal area ($r = -0.72$). Gamma diversity for hepatics increased only with host surface area ($r = 0.49$).

Lichen gamma diversity increased in stands where salal (*Gaultheria shallon*; $r = 0.44$) and pacific yew (*Taxus brevifolia* $r = 0.30$) were present, and decreased in stands with Oregon oxalis (*Oxalis oregana*; $r = -0.44$). Although it is unlikely that the diversity of epiphytic lichens can be predicted by the presence or absence of understory vascular species, these species may reflect environmental features, such as light penetration or humidity, otherwise not represented by the measured site characteristics.

Although epiphytic bryophyte diversity has been studied within the Pacific Northwest by a number of researchers (Coleman et al. 1956; Hoffman & Kazmierski 1969; Hoffman 1971; Kenkel & Bradfield 1981, 1986; Peck et al. 1995; Rosso 1996), direct diversity comparisons between these studies and the current study are not possible as these studies included a broader range of bryophytes than only those

occurring in harvestable quantities. Diversity values in the current study were not outside the range of those found in these studies.

Table 2.3. Cryptogamic diversity of harvestable epiphytes in the Cascade (letters) and Coast (numbers) Ranges, northwestern Oregon. Alpha diversity, α, is the average number of species per microplot. Gamma diversity, γ, is the total number of species accumulated from all microplots per site and per range. Beta diversity, β, is a measure of community change, calculated as $\gamma/\bar{\alpha}$. °Indicates sites with data from 20, rather than 28, stems.

Site	α	$\bar{\alpha}$	β	Species Richness		
				Mosses	Hepatics	Lichens
°C	3.8	11	2.9	8	3	0
°D	2.5	8	3.2	5	3	0
°E	3.5	13	3.7	7	4	2
°G	3.6	13	3.6	8	5	0
L	4.0	17	4.3	5	3	9
°O	3.5	13	3.7	9	3	1
°P	3.4	18	5.3	13	2	3
Q	3.1	15	4.8	7	5	3
°S	4.0	15	3.8	9	4	2
T	3.6	12	3.3	8	2	2
CASCADE RANGE TOTALS	3.5	37	10.6	19	5	13
1	1.5	6	4.0	3	3	0
2	2.2	9	4.1	6	3	0
5	4.0	12	3.0	6	3	3
8	3.3	14	4.2	9	2	3
9	5.8	21	3.6	12	6	3
10	4.1	15	3.7	10	3	2
11	4.2	13	3.1	9	3	1
13	5.5	16	2.9	12	3	1
14	2.2	10	4.6	8	2	0
15	3.8	17	4.5	10	4	3
COAST RANGE TOTALS	3.7	32	8.6	18	6	8
OVERALL TOTALS	3.6	48	13.3	25	6	17

Variation in Harvestable Epiphyte Communities

Indirect gradient analysis indicated that target species were most abundant in low elevation, moist sites with relatively high hardwood basal area and low conifer basal area. Nontarget and incidental species were most abundant in stands with relatively high hardwood basal area and high proportions of hardwood trees. Whereas target species were most common and abundant on shrub stems, nontarget and incidental species were most common and abundant on tree trunks.

Combined datasets

The frequent species dataset consisted of 25 species, with a mean alpha diversity of 11.9 and a beta diversity of 2.2. Ordination of this dataset produced a two dimensional solution accounting for 80% of the variability in the data (Figure 2.2). Epiphytes correlated with axis 1 are shown in Table 2.4. This axis, which explained 56% of the variation in the data, represents a gradient in frequency of occurrence of epiphytes, with positive correlations for common species and negative correlations for less common species.
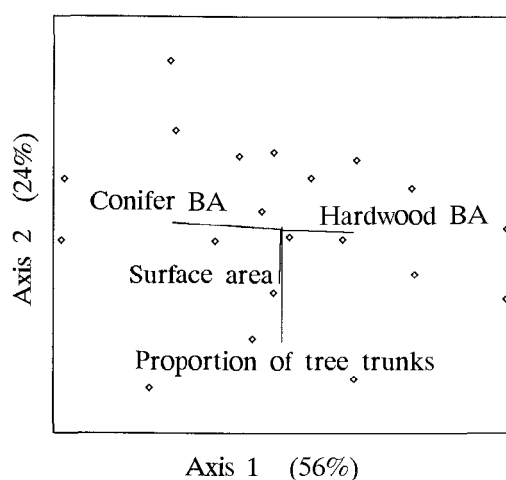
Figure 2.2. NMS ordination based on frequent species (species with >5% frequency of occurrence), Cascade and Coast Ranges, northwestern Oregon. Diamonds are sites. Line lengths represent the strength and direction of correlations of site characteristics with axes.

Axis one was positively associated with hardwood basal area (r = 0.61) and negatively associated with conifer basal area (r = -0.73) and elevation (r = -0.40). Greater harvestable epiphyte abundance in areas with high hardwood basal area (and the lower abundance in higher elevation, conifer dominated sites) supports previous indications that hardwoods are important for epiphyte communities (Neitlich and McCune 1995, Rambo and Muir 1995). The greater abundance of harvestable epiphytes in hardwood dominated sites may be due, in part, to the greater light penetration of these sites during the wet season (due to seasonal leaf abscission) relative to conifer dominated sites (King 1991). High elevation sites with high conifer basal area are probably not suitable for commercial moss harvest.

Table 2.4. Pearson correlations (r) of species with NMS axis 1 based on frequent species (species with >5% frequency of occurrence), Cascade and Coast Ranges, northwestern Oregon. Species are listed in decreasing order of positive correlation with the axis.

Species	r	Species	r
Neckera douglasii	0.85	*Porella navicularis*	0.42
Frullania tamarisci subsp. *nisquallensis*	0.77	*Metzgeria temperata*	0.42
Dicranum scoparium	0.62	*Homalothecium nuttalli*	0.40
Isothecium myosuroides	0.60	*Antitrichia curtipdendula*	0.32
Frullania bolanderi	0.55	*Ulota crispa*	0.22
Orthotrichum lyellii	0.55	*Peltigera collina*	0.10
Rhytidiadelphus loreus	0.55	*Usnea plicata group*	0.10
Rhizomnium glabrescens	0.54	*Parmelia sulcata*	0.08
Claopodium crispifolium	0.53	*Porella cordeana*	-0.02
Eurhynchium oreganum	0.52	*Dendroalsia abietina*	-0.06
Cladonia	0.48	*Metaneckera menziesii*	-0.16
Plagiothecium undulatum	0.47	*Lobaria pulmonaria*	-0.41
Polypodium glycyrrhiza	0.47		

The second axis of the frequent species dataset, which explained 24% of the variability, contrasts species more common on tree trunks with those more common

on shrub stems. *Claopodium crispifolium* (r = -0.62) and *Metaneckera menziesii* (r = -0.73), primarily found on *Acer macrophyllum*, were particularly important. Important site characteristics were the proportion of stems that were tree trunks (r = -0.77), host surface area (r = -0.58), and the presence of *A. macrophyllum* (tau = -0.40).

This second axis, then, reflects the influence of the tree trunk epiphyte communities, which are distinct from shrub stem communities. Host surface area, epiphyte mat mass (which is correlated with surface area), and species richness were all substantially higher on tree trunks than shrub stems (ANOVA, $p < 0.001$) and species composition was significantly different between tree trunks and shrub stems for both mountain ranges (MRPP, $p < 0.001$). While only target species (*Isothecium myosuroides*) indicated shrub stems, several nontarget and incidental species indicated tree trunks (Table 2.5). This suggests that shrub stems are the host for the majority of currently targetted commercially harvestble epiphytes.

Table 2.5. Indicator values for epiphytes on shrub stems and tree trunks, northwestern Oregon. Only IV's with $p < 0.05$ are listed.

Species	IV stems	IV trunks	Species	IV stems	IV trunks
Claopodium crispifolium	1	20	*Metzgeria temperata*	0	9
Dicranum scoparium	0	10	*Plagiothecium undulatum*	0	9
Eurhynchium oreganum	3	25	*Polypodium glycyrrhiza*	0	8
Isothecium myosuroides	58	26	*Porella navicularis*	17	37
Leucolepis acanthoneuron	0	6	*Rhytidiadelphus loreus*	2	14
Metaneckera menziesii	0	20			

The target species dataset consisted of 7 species, with a mean alpha diversity of 6.1 and a beta diversity of 1.2. Ordination of this dataset produced a two dimensional solution accounting for 82% of the variability in the data (Figure 2.3). The first axis, which explained 57% of the variation, was similar to the first axis of

the frequent species dataset. This axis was strongly positively correlated with all target species (r > 0.6) except *Antitrichia curtipendula* (r = 0.2), and with the basal area of hardwoods (r = 0.46), and negatively correlated with the basal area of conifers (r = -0.61). The second axis, which explained 25% of the variability in the data, was strongly correlated with *Antitrichia curtipendula* (r = 0.69), aspect (r = -0.56), and stand age (r = -0.45). *Antitrichia curtipendula* was less abundant in the older, drier stands. Although this species is typically considered an old-growth associate (ROD 1994), its presence in these younger stands suggests that its association with old-growth may be a function of general environmental conditions not specific to old-growth.
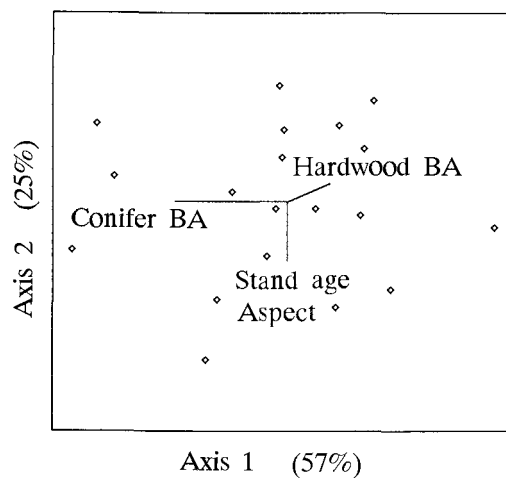
Figure 2.3. NMS ordination based on target species (seven most common and abundant species), Cascade and Coast Ranges, northwestern Oregon. Diamonds are sites. Line lengths represent the strength and direction of correlations of site characteristics with axes.

The frequent nontarget and incidental species dataset consisted of 18 species, with a mean alpha diversity of 5.8 and a beta diversity of 3.1. This dataset had a two dimensional solution accounting for 82% of the variability in the dataset (Figure 2.4). The first axis, explaining 48% of the variabilty, was positively correlated with the

abundance of *Frullania tamarisci* subsp. *nisquallensis* (r= 0.71), *Homalothecium nuttalli* (r = 0.67), and *Plagiothecium undulatum* (r = 0.58) and negatively correlated with *Porella cordeana* (r = -0.55). This axis represented a conifer/hardwood gradient in forest composition (conifer basal area r = -0.47). The second axis, which explained 34% of the variability, contrasted some shrub-stem epiphytes with some tree-trunk epiphytes. This axis was positively correlated with *Cladonia* (r = 0.52), *Orthotrichum lyellii* (r = 0.51), and *Rhizomnium glabrescens* (r = 0.62) and negatiavely correlated with *Dendroalsia abietina* (r = -0.74) and *Metaneckera menziesii* (r = -0.78). This axis showed a pattern of high epiphyte abundance at sites with higher proportions of stems that were tree trunks (r = -0.65), larger host surface areas (r = -0.50), and with older stands (r = -0.51).
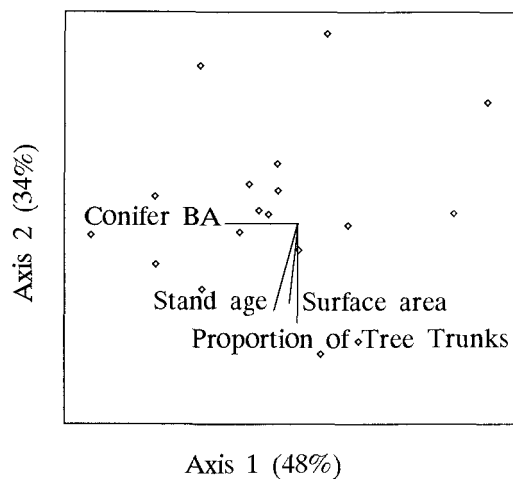
Figure 2.4. NMS ordination based on frequent nontarget and incidental species (species with >5% frequency of occurrence, omitting target species), Cascade and Coast Ranges, northwestern Oregon. Diamonds are sites. Lines represent the strength and direction of correlations of site characteristics with axes. The ordination is rotated to align the proportion of tree trunks with axis 2 to facilitate comparison with Figure 2.2.

Mountain Range Contrast

Cascade Range and Coast Range sites did not separate in the ordinations when analyzed together and separate analyses of the target species for each range revealed essentially identical patterns. In both mountain ranges, harvestable epiphyte abundance was lowest in older sites with high conifer basal area. The primary difference between ranges was the complexity of the gradients influencing harvestable epiphyte abundance, with epiphyte abundance in the Cascade Range related to aspect, slope, hardwood basal area, and the linear distance to water, which were not important in the Coast Range. This complexity, however, may simply reflect the wider geographic range, and larger spread of stand ages (from 50 to 290) of the Cascade Range sites relative to the Coast Range sites. In addition, the Cascade Range sites were chosen as areas of high lichen diversity. Although average moss and hepatic species richness was not different between the two ranges, it is impossible to quantify what effect this difference in site selection had on the comparison of the two mountain ranges.

Of all 50 species, twenty-three species were common to both mountain ranges (Table 2.2), including all target and indicental species. In the Cascade Range, *Isothecium myosuroides* contributed 31%, and *Neckera douglasii* 47%, to total harvestable biomass. Their roles were reversed in the Coast Range, where *I. myosuroides* and *N. douglasii* contributed 55% and 25% of the harvestable biomass, respectively. Species composition of harvestable epiphytes differed between the mountain ranges (MRPP, p = <0.001). Several species were indicative of a particular mountain range (Table 2.6). The Cascade indicator species occurred more frequently in the Cascades than in the Coast Range by an average of 14% with a standard error (SE) of 2%. Species more typical of the Coast Range than the Cascade Range were more frequent by 15% (SE 2%).

Table 2.6. Indicator values for epiphytes in the Cascade and Coast Ranges, northwestern Oregon. Only IV's with $p < 0.05$ are listed.

Species	IV Cascades	Coast	Species	IV Cascades	Coast
Antitrichia curtipendula	15	4	*Metaneckera menziesii*	7	0
Cladonia	0	7	*Neckera douglasii*	36	30
Frullania tamarisci subsp. *nisquallensis*	6	28	*Orthotrichum lyellii*	3	13
Isothecium myosuroides	31	58	*Porella navicularis*	43	9

Conclusions

Of 50 species found in harvestable epiphyte mats, 70% were considered nontarget or incidental species, subject to inadvertant collection by commercial moss harvesters. Although low in biomass, such a high percentage of nontarget species suggests that commercial "moss" harvest should not be managed for target species alone if sustainability of diversity and ecosystem function are management goals. Target species (e.g. *Isothecium myosuroides* and *Neckera douglasii*) were most abundant where hardwoods were present. Many nontarget and incidental species (e.g. *Claopodium crispifolium*, *Metaneckera menziesii*, and *Metzgeria temperata*) were most abundant where hardwood trees, particularly *Acer macrophyllum*, were abundant. All epiphyte species were lower in abundance in stands with high conifer basal area. Overall patterns of abundance were the similar between the Cascade and Coast Ranges.

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CHAPTER 3

Differences in Harvestable Epiphytes Among Host Species
in Northwestern Oregon

JeriLynn E. Peck

Abstract

The associations between commercially harvestable mosses and their host trees or shrubs were evaluated in 20 sites in the Cascade and Coast Ranges of northwestern Oregon. In the Cascade Range, harvestable mosses were sampled from 150 *Acer circinatum*, 15 *A. macrophyllum*, 21 *Alnus rubra*, and several *A. sinuata*, *Corylus cornuta*, *Holodiscus discolor*, *Oemleria cerasiformis*, *Rhamnus purshiana*, *Taxus brevifolia*, and *Vaccinium parvifolium*. In the Coast Range, 162 *A. circinatum*, 11 *A. rubra*, 21 *Menziesia ferruginea*, 13 *R. purshiana*, and 71 *V. parvifolium* were sampled. Host surface area, epiphyte mass, species richness, and species composition differed among hosts. In the Cascade Range, mean species richness per sample (mean alpha diversity) decreased in the order *A. macrophyllum* > *A. rubra* > *A. circinatum*. In the Coast Range, mean alpha diversity decreased in the order *A. rubra* > *R. purshiana* > *A. circinatum* > *M. ferruginea/V. parvifolium*. Decreasing mean alpha diversity parallels decreasing host surface area. Seventeen epiphyte species demonstrated host preferences based on frequency of occurrence and abundance, particularly *Orthotrichum lyellii* for *A. circinatum* and *Neckera douglasii* for *A. rubra*. Host preference was not always consistent between mountain ranges. Although there were no significant differences in epiphyte mass or species richness when accounting for surface area, species composition differed between tree trunks and shrub stems.

Introduction

Epiphytes have many ecological roles in the Pacific Northwest, including contributions to nutrient cycling (Nadkarni 1984), biodiversity (FEMAT, McCune & Antos 1982), and food webs (Maser et al. 1986, Rominger & Oldemeyer 1989, Stevenson 1978). While epiphytic lichens have received increasing attention in recent years (McCune 1993, Neitlich 1993, Sillett 1995, Sillett & Neitlich 1995), and a number of studies have documented epiphytic bryophyte communities in this region (Coleman et al. 1956; Hoffman 1971; Hoffman & Kazmierski 1969; Kenkle &

Bradfield 1986; Peck et al. 1995; Pike et al. 1975), there has been no specific investigation of the epiphyte communities subject to commercial moss harvest.

Studies of epiphytic bryophytes in other regions, including the northeast (e.g. Culberson 1955a,b; Hale 1952, 1955; Trynoski & Glime 1982), southeast (Palmer 1986), and Europe (Bates & Brown 1981, Frahm 1992), have considered host specificity. Host specificity has been variously defined as absolute restriction of a taxon to a host, of a community to a host (e.g. Barkman 1958), or of relative success on a host based on cover, fertility, etc. (Studlar 1982). Host specificity has also been described as only partially developed (Beals 1965), since epiphytes respond to many environmental variables, including localized moisture and light levels.

Few epiphytes have been identified as host specific when only methods that consider the presence or absence of a taxon on a given host have been used (e.g. John & Dale 1995, Slack 1976). A more useful method may be to identify host preferences quantitatively, rather than using presence or absence (Studlar 1982). In this study, I identify host preferences on the basis of relative abundance and relative frequency of occurrence of epiphytes on different hosts.

Differences among hosts have been observed for epiphyte communities more often than for individual species. These differences have been attributed to differences in bark texture and chemistry between conifers and hardwoods (Barkman 1958) and among different species of hardwoods (Bates & Brown 1981, Palmer 1986). Several studies currently underway (Peterson 1996, Rosso 1996) address diversity and species composition of epiphytic bryophytes and lichens on shrubs, a substrate largely ignored in previous studies of epiphyte communities. Describing epiphyte communities on hardwood shrubs is particulary important given the commercial moss harvest demands in this region (USDA Forest Service 1995) and the fact commercial moss harvesters target hardwood shrubs for harvest (D. Harrison, pers. comm.).

Since the degree of host specificity differs by region (Schmitt & Slack 1990, Slack 1976), the current study was necessary to evaluate epiphyte-host interactions in northwestern Oregon. Hosts for commercially harvestable quantities of epiphytes were identified and the host preference by individual epiphytes evaluated. No

previous studies have assessed host specificity or preference by commercially harvestable epiphytes on trees or shrubs. If the host preference of common and abundant harvestable epiphyte species is known, management may be able to direct harvest to hosts that harbor common and abundant species, while restricting harvest on hosts that harbor rarer species. In addition, a sustainable supply of harvestable epiphytes may be facilitated by silvicultural practices that favor host species.

Methods

Sites

In the Cascade Range, nine sites within the Clackamas and Santiam Resource areas of the Salem Bureau of Land Management and one in the Santiam State Forest, Oregon (44°30' - 45°20'N, 122°12' - 122°35'W) were sampled for harvestable epiphyte biomass. Cascade Range sites were chosen to represent potential lichen "hotspots," or areas presumed to have high lichen diversity on the basis of known stand composition (e.g. Neitlich & McCune 1996). In the Coast Range, ten sites within the Hebo District of the Siuslaw National Forest, Oregon (45°2'- 45°13'N, 123°5' - 123°55'W) were chosen for sampling. Coast Range sites were chosen specifically to represent sites a commercial moss harvester would select for harvest. Sites typically supported mixed conifer-hardwood stands (0 to 86% hardwood basal area). Stands ranged between 50 and 290 years in age and between 75 and 780 m in elevation (Peck 1996). Basal area of conifers, estimated using a wedge prism (BAF = 2.3 m²/ha = 10 ft²/acre) at five points, was between 2.5 and 46.5 m²/ha. The area sampled at each site was approximately 1.5 ha.

Mat Sampling

To approximate the majority of commercial moss harvest in this region, only harvestable quantities of epiphytes were sampled. "Harvestable quantities" were defined as quantities of nonadherent species that a commercial harvester would

consider worth removing (commercial moss harvesters, pers. comm. 1994; Peck 1996). Generally, harvestable mats appeared to be about 100 cm³ in volume on the stem. Tree trunks or shrub stems with harvestable quantities of epiphytes were selected using the point-centered quarter method, originally developed for sampling tree densities and stand basal area based on tree-to-point distances from systematically located points (Cottam et al. 1953, Peck & McCune 1996). For each selected trunk or stem (hereafter "stems"), below a 2 m vertical height cutoff, a one meter microplot was stripped of all harvestable epiphytes (the "epiphyte mat"). In the laboratory the epiphytes were sorted by species, their abundance estimated visually as a percentage of the total volume of material in a given mat after McCune (1990), then oven dried (60°C for 24 hr) and weighed. Nomenclature follows Anderson et al. (1990) for mosses, Stotler & Crandall-Stotler (1977) for hepatics, Esslinger & Egan (1995) for lichens, and Hitchcock & Cronquist (1973) for vascular plants. Voucher specimens are in the Oregon State University Herbarium, Corvallis.

Calculations

The density of harvestable stems at each site was estimated using calculations from the point-centered quarter method (Cottam et al. 1953) and epiphyte mat biomass was extrapolated to the site level based on these densities (Peck & McCune 1996). Vine maple, which composed 60% of the sampled hosts, grows in aggregates (clumps) rather than individuals. Calculations based on density estimates probably underestimate the biomass of harvestable epiphytes in these sites as the point-centered quarter method has been shown to underestimate densities in aggregated populations (Persson 1971).

For host species comparisons, only the most frequent hosts in each mountain Range (with at least 10 occurrences) were included. *Acer circinatum* in both ranges, and *Vaccinium parvifolium* in the Coast Range, were sampled more than twice as often as other host species. Because species richness is dependent upon sample size, a random equal sample of 25 *A. circinatum*, in the Cascade Range, and 25 *A. circinatum* and 25 *V. parvifolium* in the Coast Range, were used in comparisons with

other hosts. ANOVA (Statgraphics 1991) was used to compare group means among hosts and between mountain ranges for stem length and surface area, epiphyte mat mass, and mean alpha diversity.

Gamma and mean alpha diversity indices were calculated for each host. Gamma (γ) diversity was the total number of species in all samples combined. Mean alpha ($\bar{\alpha}$) diversity was calculated as the average number of species per sample across all samples combined and across all samples in each mountain range.

Differences in species composition among mountain ranges and hosts were tested with multiresponse permutation procedures (MRPP; McCune and Mefford 1995; Zimmerman et al. 1985). MRPP is a nonparametric method that tests for multivariate differences among groups (p-values based on a t-statistic). Species preferences for mountain ranges or hosts were discerned using indicator species analysis (Dufrêne & Legendre 1996; program INDICATE; B. McCune unpubl.), which takes both abundance and frequency into account when assigning indicator values (IV). IV's range from zero (no indicator value) to 100 (perfect indication). Significance of the IV is evaluated by a Monte Carlo procedure that randomly reassigns sample units to different groups. The resulting p-value is based on the proportion of 1000 random reassignments that result in an IV greater than the observed IV. Species with IV's 10 points higher in one group than in any other and with p-values less than 0.05 were generally considered indicative of that group. While a high degree of indication is important, the relative degree of indication between the groups being compared is often also biologically meaningful.

Results and Discussion

Mountain Range Comparisons

Although there were no significant differences in hardwood basal area, the proportion of stems that were tree trunks, the density of stems, or the average surface area or length across all hosts (ANOVA, $p > 0.09$), species composition of

harvestable epiphytes and the composition of available hosts (Table 3.1) differed between the Cascade and Coast Ranges (Peck 1996). Neither stand- nor stem-level epiphyte biomass differed between mountain ranges (ANOVA, p > 0.3). Because stands were not sampled at random, however, we cannot conclude from this that there is no stand-level difference in harvestable epiphyte biomass between mountain ranges.

Host surface area, epiphyte mat mass, and mean alpha diversity were compared for two hosts that occurred in both ranges: *Acer circinatum* and *Alnus rubra*. In the Coast Range, individual stems of *A. rubra* had 0.44 m² (95% confidence interval from 0.15 to 0.73) more surface area, 73 g/m (29 to 117) heavier epiphyte mats, and 3.2 (1.3 to 5.1) more epiphyte species per mat than in the Cascade Range. Trynoski & Glime (1982) found cover of bryophytes, but not mean alpha diversity, to increase with tree diameter (which is directly proportional to surface area in the current study). In the Cascade Range, the sampled *A. rubra* trees were smaller than is typical for mature trees, while those in the Coast Range were within the range of diameters for mature trees (Niemiec et al. 1995). Even when diameter was taken into account in the model, however, epiphyte mat mass was 50 g/m (2 to 98) higher on *A. rubra* in the Coast Range than in the Cascade Range (ANOVA, p = 0.04). Mean alpha diversity on *A. rubra*, however, did not differ between the ranges after adjusting for host surface area (p > 0.6). While epiphytes on *A. circinatum* did differ in species composition between mountain ranges (MRPP, p = 0.29), those on *A. rubra* did (MRPP, p = 0.01). Several species of epiphytes that demonstrated a preference for *A. rubra* over *A. circinatum* in the Coast Range did not do so in the Cascade Range. These included: *Antitrichia curtipendula*, *Cladonia*, *Dicranum scoparium*, *Frullania tamarisci* subsp. *nisquallensis*, and *Isothecium myosuroides* (IV's > 35 in the Coast Range, IV's < 3 in the Cascade Range).

Table 3.1. Harvestable epiphyte hosts, Cascade and Coast Ranges, northwestern Oregon. Frequency is the frequency with which each host was sampled. Gamma, γ, is the sum of epiphyte species across all samples. Mean alpha, $\bar{\alpha}$, is the average number of epiphyte species per sample.

Host	Frequency	Mean Density		Mean Length	Mean Surface area	Mean Epiphyte mat mass		γ	$\bar{\alpha}$
	(%)	(stems/ha)	SE	(m)	(m^2)	(g/m)	SE		
CASCADE RANGE N = 224									
Acer circinatum	67	3053	59	2.8	0.14	34.6	0.2	30	3.2
Acer macrophyllum	8	1136	64	2.0	1.08	157.4	9.3	16	4.7
Alnus rubra	10	3596	402	2.4	0.24	37.3	1.2	17	3.3
Alnus sinuata	2	2027	500	3.8	0.15	39.2	4.4	9	4.5
Corylus cornuta	3	6301	1438	3.3	0.12	32.0	3.5	11	3.4
Holodiscus discolor	2	307	75	1.4	0.07	36.0	5.2	7	5.0
Oemleria cerasiformis	1	659	17	2.1	0.11	30.5	6.6	3	2.5
Rhamnus purshiana	2	1684	336	2.8	0.22	20.3	4.4	5	3.3
Taxus brevifolia	2	1821	474	2.2	0.47	66.6	12.	9	3.8
Vaccinium parvifolium	4	1851	264	2.3	0.06	13.1	6.5	6	3.3
COAST RANGE N = 280									
Acer circinatum	58	7867	158	3.1	0.16	43.7	0.5	25	4.5
Alnus rubra	4	1745	173	2.2	0.68	121.0	8.6	19	6.9
Menziesia ferruginea	8	1686	113	2.7	0.09	28.4	0.2	9	1.4
Rhamnus purshiana	5	1126	135	2.0	0.32	87.3	4.7	14	5.3
Vaccinium parvifolium	25	4554	169	2.4	0.07	27.0	1.1	10	2.4

There was no difference in epiphyte mat mass between *A. circinatum* and *A. rubra* in the Cascade Range (ANOVA p > 0.05), but *A. rubra* had 83 g/m (51 to 115) heavier mats than *A. circinatum* in the Coast Range (ANOVA p < 0.001). Due to larger mats and a greater relative proportion of *A. rubra* in the Coast range (its optimal habitat, Niemiec et al. 1995), *A. rubra* makes a greater overall contribution to harvestable epiphyte biomass in the Coast Range than in the Cascade Range. There was, however, no difference in epiphyte species composition between these two hosts in the Coast Range (MRPP, p = 0.36). Although there was a difference in composition between *A. circinatum* and *A. rubra* in the Cascade Range (MRPP, p =

0.01), no epiphyte species showed distinct preferences for either host when comparing just these two host species (IV's < 10).

Cascade Range

In the 10 Cascade Range sites, six shrub and four tree species had harvestable quantities of epiphytes (Table 3.1). Comparing among the three most frequent hosts (*Acer circinatum*, *A. macrophyllum*, and *Alnus rubra*), stem length (within the 2 m height cutoff), diameter, epiphyte mat mass, and mean alpha diversity were all different (ANOVA, p < 0.02). Often prostrate or leaning, *A. circinatum* stems were on average 0.8 m (95% confidence interval from 0.3 to 1.3) longer than the typically near-vertical *A. macrophyllum* trunks within the 2 m height cutoff. *A. macrophyllum* trunk diameters were larger than *A. circinatum* and *A. rubra*, and had heavier epiphyte mats (Figure 3.1). When diameter was taken into account in the model, however, there was no difference in epiphyte mat mass between host species (ANOVA, p = 0.23). No significant differences were seen between *A. circinatum* and *A. rubra* for length, diameter, epiphyte mat mass, or mean α diversity.

Twelve species of moss, 5 hepatics, and 2 lichens occurred more than twice in the Cascade Range on one of the three most frequent hosts (Table 3.2). Overall species composition differed among the three most frequent hosts (MRPP, p < 0.001), with host preferences evident for several species. *Isothecium myosuroides* and *Orthotrichum lyellii* were most frequent and abundant on *A. circinatum*. Typical epiphytes on *A. macrophyllum* included *Claopodium crispifolium*, *Dendroalsia abietina*, *Leucolepis acanthoneuron*, and *Metaneckera menziesii*. Only *Neckera douglasii* was consistently more frequent and abundant on *A. rubra*. *Metzgeria temperata* was the only species to occur on only one host within the Cascade Range, occurring only on *A. macrophyllum*. However, this species occurred on other hosts in the Coast Range and was observed, although not sampled, on additional substrates within the Cascade Range (e.g. logs).
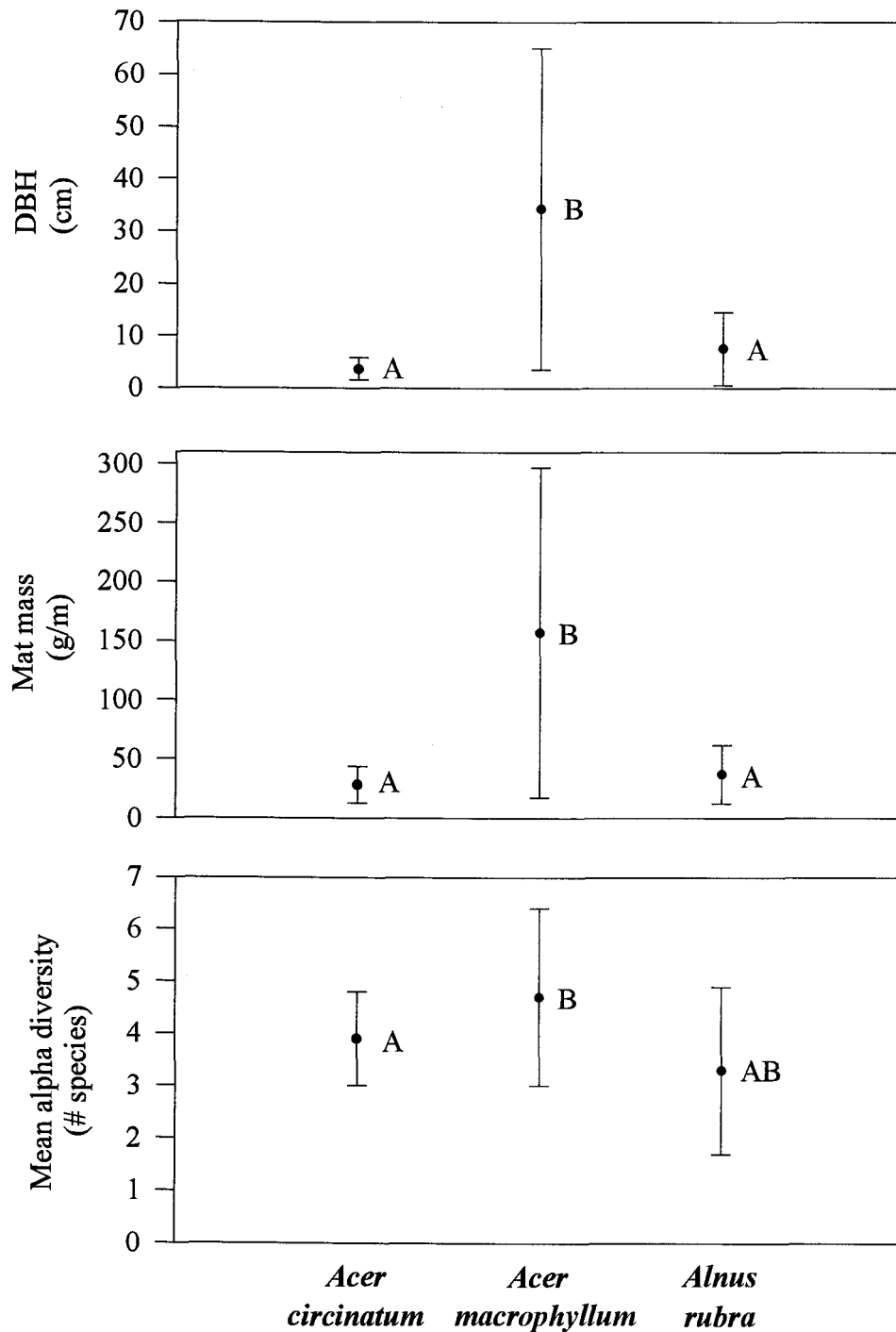
Figure 3.1. Comparison of diameter, mat mass, and mean alpha diversity among hosts of harvestable epiphytes, Cascade Range, northwestern Oregon. Dots represent means; bars are standard deviations. Letters represent group membership; common letters indicate nonsignificant differences (p > 0.05).

Table 3.2. Harvestable epiphytes for the three most frequent hosts, Cascade Range, northwestern Oregon. % = Frequency of occurrence. Mat mass is mean dry-weight g/m (standard error). IV = Indicator Value. Only species with more than 2 occurrences are shown. * Indicates IV's significantly larger than expected by chance (p < 0.05).

	Acer circinatum (n=25)			Acer macrophyllum (n=25)			Alnus rubra (n=21)		
	%	Mat mass	IV	%	Mat mass	IV	%	Mat mass	IV
MOSSES									
Antitrichia curtipendula	18	19.1 (1.0)	19	0		0	14	1.5 (0.3)	1
Claopodium crispifolium	1	<0.01 (<0.01)	0	67	25.0 (2.7)	64*	5	10.1 (2.1)	0
Dendroalsia abietina	3	<0.01 (<0.01)	0	27	4.7 (0.9)	20*	0		0
Eurhynchium oreganum	11	3.1 (0.2)	7	13	1.5 (0.3)	0	24	5.7 (0.8)	12
Homalothecium fulgescens	1	0.1 (<0.1)	0	7	4.2 (1.0)	6	5	1.7 (0.4)	1
Homalothecium nuttallii	1	0.1 (<0.1)	0	13	0.3 (<0.1)	0	19	11.1 (1.7)	16
Isothecium myosuroides	84	148.2 (19.8)	45*	47	13.6 (2.0)	10	43	7.9 (0.9)	14
Leucolepis acanthoneuron	0		0	27	11.3 (2.7)	27*	0		0
Metaneckera menziesii	1	<0.1 (<0.1)	0	80	237.6 (28.6)	73*	0		0
Neckera douglasii	80	131.1 (6.1)	25	47	25.0 (4.4)	6	81	290.4 (33.2)	46*
Orthotrichum lyellii	11	0.7 (<0.1)	17*	0		0	10	0.2 (0.0)	2
Rhytidiadelphus loreus	5	7.5 (0.6)	0	7	0.9 (0.2)	2	10	0.2 (0.0)	6
HEPATICS									
Frullania bolanderi	4	0.1 (<0.1)	0	0		0	0		0
Frullania tamarisci subsp. nisquallensis	17	10.7 (0.7)	1	0		0	24	6.5 (1.2)	19
Metzgeria temperata	0		0	20	0.6 (0.1)	18*	0		0
Porella cordeana	1	<0.1 (<0.1)	0	13	0.2 (0.1)	13*	0		0
Porella navicularis	55	18.9 (0.5)	28	80	6.6 (0.6)	20	62	39.2 (3.7)	17

Table 3.2, continued

	Acer circinatum (n=25)			Acer macrophyllum (n=13)			Alnus rubra (n=21)		
	%	Mat mas	IV	%	Mat mass	IV	%	Mat mass	IV
LICHENS									
Parmelia sulcata	5	<0.1 (<0.1)	8	0		0	0		0
Usnea filipendula group	4	0.1 (<0.1)	3	0		0	10	0.1 (<0.1)	3

Coast Range

In the Coast Range only four shrub and one tree species had harvestable epiphytes (Table 3.1). Comparing these five hosts, stem length (within the 2 m height cutoff), diameter, epiphyte mat mass, and mean α diversity differed (ANOVA, $p < 0.04$; Figure 3.2 for the latter three). There were no differences in mass among hosts when host surface area was taken into account ($p > 0.15$).

Prostrate or leaning, *A. circinatum* and *M. ferruginea* stems were on average 1.0 and 0.8 m (95% confidence interval from 0.3 to 1.7 m and 0.1 to 1.5 m, respectively) longer than the typically straight *Rhamnus purshiana* trunks within the 2 m height cutoff. No significant differences were seen between *M. ferruginea* and *Vaccinium parvifolium* for length, diameter, mat mass, or mean α diversity.

Ten moss, 3 hepatic, 1 lichen, and 1 vascular plant species occurred more than twice on one of the five most frequent hosts (Table 3.3). Species composition differed among these host species (MRPP, $p < 0.001$), with several species demonstrating host preferences ($p < 0.06$). *Antitrichia curtipendula*, *Cladonia*, *Dicranum scoparium*, *Frullania tamarisci* subsup. *nisquallensis*, *Metzgeria temperata*, *Plagiothecium undulatum*, and *Rhytidiadelphus loreus* were most frequent and abundant on *A. rubra*. *Neckera douglasii* occurred on *A. rubra* and *A. circinatum* in equal frequency and abundance. *Orthotrichum lyellii* and *Porella navicularis* also preferred *A. circinatum*. *Eurhynchium oreganum* was most frequent and abundant on

R. purshiana, while *Isothecium myosuriodes* was common to both *M. ferruginea* and
V. parvifolium.

Host preferences were not consistent between mountain ranges, despite their
relatively close proximity within the Pacific Northwest. For instance, *Neckera
douglasii* demonstrated a preference for both *A. circinatum* and *A. rubra*, in the Coast
Range, while demonstrating a preference for only A. rubra in the Cascade Range.
The only species to demonstrate absolute specificity in the Cascade Range, *Metzgeria
temperata* (Table 3.2), demonstrated a preference for a different host in the Coast
Range. Differences in host specificity have been demonstrated over a large
geographic scale (Slack 1976), with the factors considered important for host
specificity (e.g. water holding capacity, bark pH, rate of drying) influenced by climate
(Trynoski & Glime 1982).

For both ranges, *Montia sibirica* occurred as an infrequent facultative epiphyte,
indicating that some sites were extremely wet. Other studies in which typically
terrestrial species were found as facultative epiphytes cite extreme moisture conditions
as a potential cause (Frahm 1992, Peck et al. 1995). Wet sites have thicker mats and
more accumulated organic matter (Kenkel & Bradfield 1986), both of which may
provide the necessary moisture and nutrients required to sustain an epiphytic vascular
plant. Several bryophytes found as epiphytes in this study are more typical on other
substrates as well (e.g. *Eurhynchium oreganum* on humus, *Leucolepis acanthoneuron*
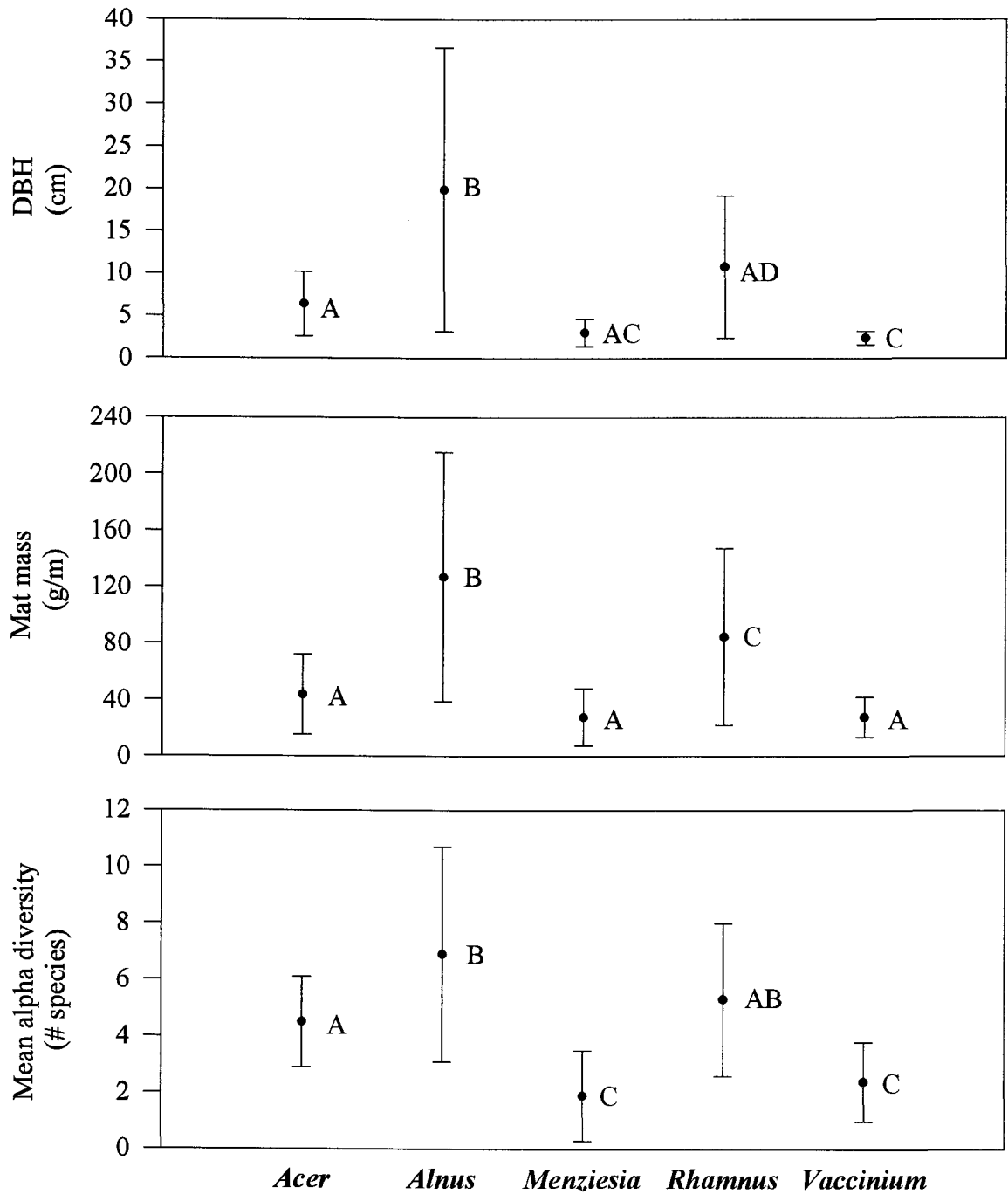and *Plagiothecium undulatum* on logs).

Figure 3.2. Comparison of diameter, mat mass, and mean alpha diversity among hosts of harvestable epiphytes, Coast Range, northwestern Oregon. Dots represent means; bars are standard deviations. Letters represent group membership; common letters indicate nonsignificant differences (p > 0.05).

Table 3.3. Harvestable epiphytes for all five hosts, Coast Range, northwestern Oregon. % = Frequency of occurrence. Mat mass is dry-weight g/m (standard error below). Only species with more than 2 occurrences are shown. * Indicates significant IV's ($p < 0.05$).

	Acer circinatum			Alnus rubra			Menziesia ferruginea			Rhamnus purshiana			Vaccinium parvifolium		
	%	Mat mass	IV	%	Mat mass	IV	%	Mat mass	IV	%	Mat mass	IV	%	Mat mass	IV
MOSSES															
Antitrichia curtipendula	15.0	24.0 (2.2)	2	36.3	17.4 (4.4)	23*	4.7	0.1 (<0.1)	0	30.8	5.5 (0.7)	5	12.7	7.9 (0.8)	1
Claopodium crispifolium	11.0	5.0 (0.3)	3	18.2	6.9 (1.4)	6	0		0	7.7	11.2 (3.0)	2	0		0
Dicranum scoparium	3.7	28.4 (10.2)	2	27.3	19.0 (3.0)	26*	0		0	15.4	2.4 (0.5)	2	2.8	0.3 (<0.1)	0
Eurhynchium oreganum	16.0	11.3 (0.4)	0	18.1	7.9 (1.7)	1	4.7	0.3 (0.1)	0	69.2	31.1 (3.0)	51*	12.7	8.2 (0.6)	3
Isothecium myosuroides	94.0	741.0 (22.9)	15	90.9	147.1 (26.7)	12	100	91.9 (5.6)	31*	100	41.8 (2.2)	16	95.8	329.1 (14.9)	25*
Neckera douglasii	91.0	402.9 (9.6)	35*	90.9	35.7 (3.3)	36*	28.6	2.9 (<0.1)	1	84.6	10.3 (0.8)	13	29.6	9.2 (0.7)	1
Orthotrichum lyellii	30.0	11.4 (1.2)	31*	18.2	0.3 (0.1)	4	9.5	0.3 (0.1)	0	15.4	0.8 (0.2)	1	2.8	0.1 (<0.1)	0
Plagiothecium undulatum	0.6	5.9 (<0.1)	0	36.4	12.2 (2.1)	25*	0		0	15.4	3.3 (0.8)	5	0		0
Rhizomnium glabrescens	5.6	3.7 (0.9)	3	9.1	1.9 (0.5)	3	0		0	7.7	3.1 (0.8)	2	0		0
Rhytidiadelphus loreus	12.0	62.4 (1.4)	3	36.4	117.9 (24.6)	20*	4.7	0.1 (<0.1)	0	23.1	21.1 (4.4)	5	0		0
HEPATICS															
Frullania tamarisci subsp. *nisquallensis*	46.0	51.1 (1.4)	6	63.6	14.7 (2.6)	22*	19.0	3.6 (0.7)	0	53.9	7.7 (1.0)	13	28.2	4.1 (0.2)	11
Metzgeria temperata	5.6	3.2 (0.9)	4	27.3	3.5 (0.8)	18*	0		0	0	0		0		0
Porella navicularis	46.0	76.3 (2.6)	23*	36.4	3.5 (0.8)	5	4.7	0.1 (<0.1)	0	53.9	4.6 (0.5)	16	11.3	1.0 (0.1)	0
LICHENS															
Cladonia	4.3	0.0	0	36.3	13.1 (2.2)	24*	4.7	0.1 (<0.1)	0	38.4	1.2 6 (0.2)	13	0		0
VASCULAR															
Polypodium glycyrrhiza	5.6	2.9 (0.5)	2	27.3	7.8 (1.4)	13*	4.7	0.2 (0.0)	0	15.4	3.7 (0.8)	5	0		0

Why Hardwoods?

Sites were chosen for sampling only if harvestable quantities of epiphytes (which were known to occur primarily on hardwoods) and *Acer circinatum* were present. Since the density of *A. circinatum* is inversely related to the density of conifers (Anderson 1969), it is not surprising that the highest abundance of epiphytes occurred in sites with relatively low conifer basal area. Nonetheless, the question still remains as to why harvestable epiphyte hosts were predominantly hardwood species. In addition to differences in bark texture (Barkman 1958) and chemistry (Palmer 1986), light regime may affect the distribution of harvestable epiphytes in deciduous forests relative to evergreen forests (Kenkel & Bradfield 1986). Greater light penetratin during the fall and early spring, typically active growing periods for bryophytes, likely promotes epiphyte growth in western hardwood forests. *Acer circinatum*, *Acer macrophyllum*, and *Taxus brevifolia* have also been noted for morphologies that enhance light interception and persistence in the understory (King 1991), which may facilitate both their own growth and regeneration and the growth of epiphytes associated with them. In addition, *A. circinatum* produces allelopathic chemicals (Moral & Cates 1971), inhibiting the growth of vegetation beneath its canopy, and subsequently reducing competition by other shrubs and trees for light for the individual and perhaps its epiphytes. *Alnus rubra* may support abundant epiphytes because its throughfall, and therefore probably its stemflow, carries higher nutrient concentrations relative to conifer species (Binkley et al. 1982). In addition, as *A. rubra* stands mature, percent canopy closure actually decreases, allowing even more light into the understory (Henderson 1978).

Summary

More than half of over 500 tree trunks and shrub stems with harvestable quantities of moss were *Acer circinatum*. Four trees and six other shrubs were sampled for harvestable epiphytes in the Cascade and Coast Ranges of northwestern Oregon. In this study, host preference was based on relative abundance and relative frequency of occurrence. Host preference was high, with eight epiphyte species

showing a preference for one of three hosts in the Cascade Range, and ten epiphytes showing preferences for one of five hosts in the Coast Range. Host preference was not always consistent between mountain Ranges, with preferences for large tree trunks over shrub stems or small tree trunks perhaps more consistent than preferences for a particular species. Silvicultural practices aimed at promoting growth of harvestable epiphytes should concentrate on the retention of mixed or pure hardwood canopies with high densities of understory hardwood shrubs.

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CHAPTER 4

Harvestable Moss Mat Accumulation
in Northwestern Oregon

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Abstract

Harvestable moss is being removed from Pacific Northwest forests in ever increasing amounts, yet no inventory data exist on the availability or sustainability of this resource. The purpose of this paper is to describe the availability and accumulation of harvestable epiphytes in 20 sites, in the Cascade and Coast Ranges of northwestern Oregon, chosen to represent sites a commercial moss harvester would consider suitable for harvest. Harvestable epiphyte biomass in the lower canopy of these sites ranged from 24 kg/ha to 1469 kg/ha. Harvestable epiphyte biomass is a function of site quality, availability of suitable hosts, and host surface area. Stand-level biomass was higher in stands with relatively higher hardwood basal area and less in stands with relatively higher conifer basal area. Epiphyte mat accumulation on vine maple (*Acer circinatum* Pursh) was more rapid, and more variable, in the Coast Range than in the Cascade Range. A model describing the factors affecting epiphyte mat accumulation is proposed. Harvestable moss can be managed as a resource not only by controlling the rate of harvest, but by promoting hardwoods and shrubs. Restricting harvest to the lower canopy should facilitate harvestable epiphyte mat recovery by retaining the source for litterfall, which may contribute significantly to mat accumulation.

Introduction

Epiphytes play a variety of ecological roles in forest ecosystems, providing nesting material and food (FEMAT 1993) and acting as nutrient sinks (Brown & Bates 1990). Ecologists have only recently begun to explore these roles, yet epiphytes are increasingly being removed from the forest to feed a multi-million dollar flora industry (Peck 1990, Schlosser et al. 1992). Poor records make estimates of historic harvest impossible, but commercial moss harvesters in this area indicate that harvest has greatly increased since 1990 (moss harvesters, pers. comm., 1996). Although most moss is harvested from publicly owned land, some agencies do not

even issue formal permits for harvest, and those that do are aware that most moss is harvested illegally (F. Duran, Siuslaw National Forest, pers. comm. 1996). In response to concerns about the impacts of moss harvest on biodiversity and forest health, some agencies have begun to impose strict regulations for moss harvest. One National Forest has set a forest-wide cap on harvest of 880 m^3 (25,000 bu) per year, which has been the average legal harvest for the past 10 years, but is generally considered to be less than half the actual annual harvest from this Forest (USDA Forest Service 1995). Although central to these regulations, the supply (available biomass) and sustainability (mat accumulation rate) of harvestable moss have not previously been estimated.

Epiphyte abundance has typically been evaluated using percent cover (Hoffman & Kazmierski 1969, McCune & Antos 1982, Pike et al. 1977, Peck 1995b, Slack 1977). There have been relatively few studies that directly estimate bryophyte biomass, in part due to the destructive nature of biomass sampling (Russell 1988). Exceptions include Wolf (1993), who directly sampled epiphyte biomass on tropical trees, McCune (1993) and Nadkarni (1984), who sampled biomass of canopy epiphytes from temperate trees, and several researchers who have estimated biomass of forest floor bryophyte communities (Binkley & Graham 1981, Busby et al. 1978, Kubicek et al. 1989). While the correlation between shoot-length growth and biomass growth is high for some species, enabling accurate biomass growth estimates from the indirect length measure (Vitt 1990), the correlations between length growth and biomass growth have not been documented for most species. To maximize accuracy of the biomass estimates upon which our descriptions of mat accumulation are based, and to mimic commercial moss harvest, biomass was sampled directly in the current study using harvest methods.

Most studies concerned with the accumulation of epiphytes have focussed on growth, reporting increases over time in length or cushion area (Pitkin 1975, Tallis 1959, Vitt 1989), cover (Vance & Kirkland 1995), or CO_2 assimilation (Aro et al. 1984, Green & Snelgar 1982, Hicklenton & Oechel 1976, Russell & Botha 1988). The focus of the current study was to estimate the net accumulation of harvestable epiphyte mats rather than growth of individual plants or populations. Net mat

accumulation involves processes such as growth, mortality, and herbivory, but also includes gains and losses to the mat from litterfall or stochastic events. The objectives of this study were to estimate the available biomass of harvestable epiphytes, and to describe the variation in epiphyte mat accumulation on vine maple (*Acer circinatum*), at 20 study sites in the Cascade and Coast Ranges of Oregon. Epiphyte mat mass is described here as a function of site quality and host density, enabling a kind of "site index" for harvestable epiphytes in western Oregon.

Methods

Sites

In the Cascade Range, nine sites within the Clackamas and Santiam Resource areas of the Salem Bureau of Land Management and one in the Santiam State Forest, Oregon (44°30' - 45°20'N, 122°12' - 122°35'W) were sampled for harvestable epiphyte biomass. Cascade Range sites were chosen to represent potential lichen "hotspots," or areas presumed to have high lichen diversity on the basis of known stand composition (e.g. Neitlich & McCune 1996). In the Coast Range, ten sites within the Hebo District of the Siuslaw National Forest, Oregon (45°2'- 45°13'N, 123°5' - 123°55'W) were chosen for sampling. Coast Range sites were chosen specifically to represent sites a commercial moss harvester would select for harvest. Sites typically supported mixed conifer-hardwood stands (0 to 86% hardwood basal area). Stands ranged between 50 and 290 years in age and were between 75 and 780 m in elevation. Basal area of conifers, estimated using a wedge prism (BAF = 2.3 m^2/ha = 10 ft^2/acre) at five points, was between 2.5 and 46.5 m^2/ha (Peck 1996). The area sampled at each site was approximately 1.5 ha.

Mat Sampling

The objectives of the mat sampling were to (1) approximate potential harvest by commercial moss harvesters in this area, in order to (2) obtain an estimate of

harvestable biomass at the site, at an order-of-magnitude level of precision, that (3) can be measured in one day of sampling. Only "harvestable quantities" of epiphytes were sampled, defined as quantities of nonadherent species (i.e. no tiny appressed liverworts [e.g. *Radula*], firmly attached species [e.g. *Dendroalsia*], or individual tufts [e.g. *Ulota*]) that a harvester would consider worth removing. This definition resulted from numerous conversations with commercial moss harvesters in this region from 1991 to 1994, and continues to be consistent with current harvest standards (D. Harrison, pers. comm. 1996). Generally, mats of at least 100 cm^3 were considered harvestable quantities.

Twenty or twenty-eight tree trunks or shrub stems (typically hardwoods) with harvestable quantities of epiphytes were selected at each site using the point-centered quarter method (Cottam et al. 1953). This method was originally developed for sampling tree densities and stand basal area based on tree-to-point distances from systematically placed points. Within each site, a 200 m (7 sites) or 300 m (13 sites) transect was established, 50 m from the nearest road. Every 50 m along each transect a point was established, such that there were five points on the 200 m transects and seven on the 300 m transects. At each point four quadrants were established, using the transect line and a line perpendicular to it as boundaries. Within each quadrant the nearest hardwood tree trunk or shrub stem with harvestable quantities of epiphytes was sampled. Since most samples were taken from shrub stems rather than tree trunks, all hosts will hereafter be referred to as "stems."

For each selected stem, the distance from the stem to the transect point was recorded as was the total length of the stem up to a 2 m vertical height cutoff (Figure 4.1). On each stem, below the 2 m cutoff, a one meter microplot was stripped of all harvestable epiphytes (the "epiphyte mat"). The midpoint of the microplot was selected randomly between 0.5 m above the ground and 0.5 m below the 2 m height cutoff. An increment core or cross-section was taken from the center of the microplot on all vine maples (*Acer circinatum* Pursh) to determine stem age. Most cored vine maple stems were then stripped of all remaining epiphytes and permanently tagged to enable future regrowth measurements.

2 m height cutoff

2 m

s m

s m

1 m microplot

s m

m g/m

s m

Length of stem
= s m

Mass of mat
= m g/m

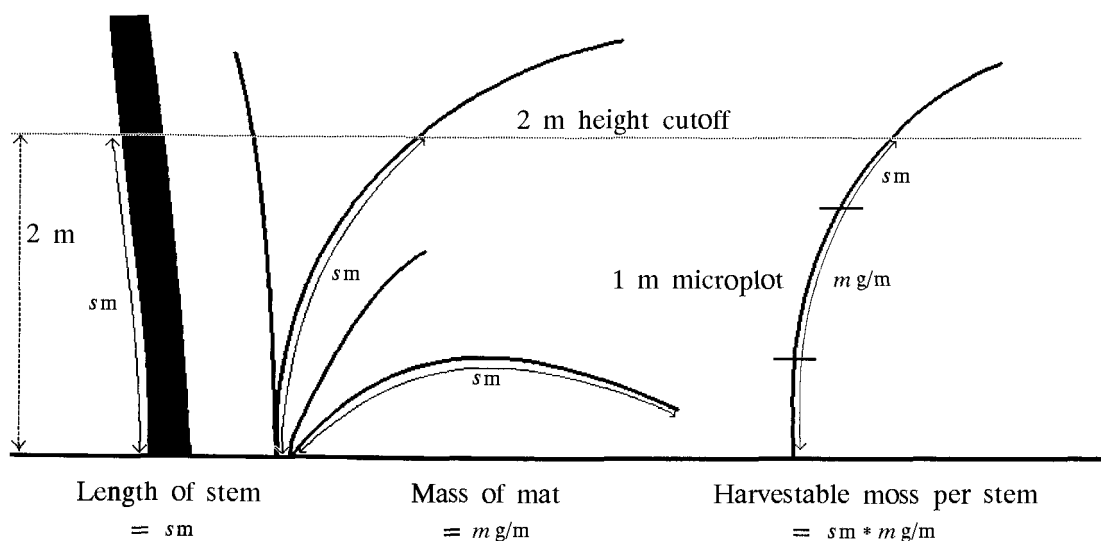Harvestable moss per stem
= s m * m g/m

Figure 4.1. Harvestable epiphyte mat sampling schematic. Microplots were randomly placed between 0.5 m above the ground and 0.5 m below the 2 m height cutoff.

In the laboratory the epiphytes were sorted by species, their abundance estimated visually as a percentage of the total volume of material in a given mat (after McCune 1990), then oven dried (60°C for 24 hr) and weighed.

Calculations

The density of harvestable stems at each site was estimated using calculations based on the point-centered quarter method. Density is the number of individuals per unit area. It follows that the inverse of density is the average area for a single individual (Cottam et al. 1953). The inverse of the average of all four distances is taken to be density (D) in stems per unit area. Subsequently, the distances from the transect point to the sampled stem (d, measured in meters) were averaged over all points ($\bar{d}$ m), and squared ($\bar{d}^2$ m^2) to obtain an area per individual stem. A simple conversion results in the number of stems per hectare: $10,000/\bar{d}^2 = D$. The point-centered quarter method is known to underestimate density in aggregated populations (Persson 1971). Because many of the sampled shrubs grew as aggregates rather than

individuals, this method probably underestimates the biomass of harvestable epiphytes in these sites. Despite this known bias, the point-centered quarter method was chosen as a practical means for efficiently selecting samples to estimate harvestable epiphyte biomass. Given the large variation in harvestable biomass, over several orders of magnitude, the variability contributed by this bias is probably relatively low.

Epiphyte mat biomass was extrapolated to the site level based on these density calculations. Mat mass for a given one-meter sampling unit was first extrapolated to the entire stem, by multiplying the mat mass (m g/m) by the total length of the stem below the 2 m height cutoff (s m/stem) (Figure 4.1). For example, the total mass for a 5 m stem (m/stem) with a sampled mat of 10 g/m would be 50 g/stem ($m*s$ g/stem). This mass was then extrapolated to the site level by multiplying the average epiphyte mat mass per stem by the number of stems per hectare, yielding a biomass in g/ha. If harvesters collect bryophytes above 2 m in height, this sampling technique would underestimate available biomass. The relationships among stem- and stand-level biomass and site characteristics were evaluated using Pearson correlations (SPSS 1993).

Mat Accumulation

We describe moss mat accumulation using a two-parameter hyperbola derived from the Michaelis-Menten equation for enzyme kinetics (Cornish-Bowden 1995). Originally proposed to describe "substrate saturation" in enzymatic chemical reactions, the analogy of substrate saturation is appropriate for the development of epiphyte mats as well. The degree to which a substrate of known age is colonized by an epiphyte mat represents the level of saturation of that substrate at the current time. Using known stem ages and mat masses, nonlinear regression (SPSS 1993) was used to solve the following equation: Mass = $a*t/(t+b)$, where "a" is the asymptote of the curve in mat mass (dry weight g/stem), "t" is the stem age in years, and "b" is the stem age at which mass = $a/2$.

This study considered only stems with harvestable amounts of epiphytes, by current harvester standards. As restrictions on moss harvest change, the definition of what is worth harvesting may also change.

Results & Discussion

Biomass Estimates

The estimated biomass of harvestable epiphytes at these sites, which ranged up to 1469 kg/ha (Table 4.1), is only a small proportion of the total biomass of epiphytes at these sites. Estimates from big leaf maple (*Acer macrophyllum* Pursh) alone put biomass of epiphytic bryophytes at over 6000 kg/ha in a mature Coast Range temperate rain forest (Nadkarni 1984), while Rhoades (1981) estimated an epiphyte standing crop of 4220 kg/ha in a Pacific Northwest *Abies lasiocarpa* forest. Old growth conifer stands in the Cascades are estimated to have over 700 kg/ha (McCune 1993) to 900 kg/ha of bryophyte biomass (Pike et al. 1977). Most of the sites chosen specifically for harvestable moss had a greater biomass of epiphytic bryophytes in the lower canopy than has been found in the entire canopy of conifer stands of comparable age. McCune (1993) estimated that 95 year old conifer stands in the Cascade Range had approximately 165 kg/ha of epiphytic bryophytes.

Estimated biomass was highly variable among sites (Table 4.1), which partially reflects the differences in site selection criteria between the two mountain ranges. However, even within the Coast Range sites, chosen specifically to represent stands with harvestable quantities of moss, between-stand variability is high. This variability can also be attributed to the variability in site quality for growing harvestable moss and in part to the variability in the amount of suitable substrate among sites. Average epiphyte mat mass is our most direct indicator of site quality, with the "best" site having 81 g/m and the "worst" site still having harvestable quantities of moss having only 19 g/m on average. Site quality for harvestable epiphytes depends on the relative basal area contributions of conifers and hardwoods, as well as factors such as

elevation and distance to water (Peck 1996). The amount of suitable substrate may depend upon not only the density of hardwood trees and shrubs, but also on the surface area of those shrubs (Peck 1996).

Table 4.1. Biomass estimates (oven dry weight) of harvestable epiphytes in the Cascade (letters) and Coast (numbers) Ranges, northwestern Oregon. ° Indicates sites with 20, rather than 28, samples per site. Stem level values are means.

| Site | Stem Level | | Site Level | | | |
	Mat mass (g/m)	Stem length (m/stem)	Stem density (stems/ha)	SE	Biomass (kg/ha)	SE
°C	19.0	2.6	6090	870	288	40
°D	37.0	3.6	2920	425	1068	200
°E	29.0	2.9	3220	325	612	113
°G	81.0	2.3	1010	65	195	22
L	64.0	2.2	340	20	37	2
°O	54.5	3.5	5030	465	379	29
°P	50.5	2.3	4130	435	519	44
Q	22.0	2.4	610	20	24	1
°S	54.0	2.6	1710	75	211	16
T	27.0	2.8	4630	275	501	56
CASCADE RANGE	44	2.8	3050	300	385	60
1	38.0	2.6	3140	290	329	30
2	30.0	3.1	4620	480	339	35
5	40.5	2.2	2710	95	210	10
8	50.0	2.5	2790	250	597	87
9	77.5	2.7	4440	415	712	50
10	39.5	3.0	7300	565	1469	194
11	38.0	2.7	1260	60	119	6
13	65.0	2.7	3040	260	558	54
14	22.5	2.9	3210	115	227	21
15	38.0	3.4	7450	380	947	53
COAST RANGE	44	2.8	4000	300	550	55

Mat mass was positively correlated with host surface area (r = 0.74), so sites with more large-surface area hosts had higher average mat masses. In keeping with this, stand-level epiphyte biomass was positively correlated with hardwood basal area (r = 0.45) and negatively correlated with conifer basal area (r = -0.60). Lower harvestable epiphyte biomass in sites with high conifer basal area may reflect a lower density of vine maple stems in those stands instead of, or as well as, lower epiphyte abundance on the suitable hosts that are present. The density of vine maple in some stands is inversely related to the density of conifers (Anderson 1969). Other factors influencing the density of suitable hosts may also be important, but require further investigation. Forest management activities, from thinning to slash burning, influence the regeneration rates of vine maple (O'Dea et al. 1995). For instance, while vine maple is known to have higher germination rates in unthinned stands, seedling survival is higher in thinned stands (Tappeiner & Zasada 1993).

The variability in stand-level harvestable epiphyte biomass is illustrated in Figure 4.2. This figure models harvestable epiphyte biomass as a function of average epiphyte mat biomass and stem density. The isolines indicate the total dry-weight harvestable moss resource (kg/ha). The range of stem densities in this study (Figure 4.2) are in accordance with previously reported shrub densities. In the Coast Range, densities from 104 to 4144 stems/ha have been estimated for vine maple alone (O'Dea et al. 1995), which was the host for 60% of our samples. In our sites, vine maple densities averaged 3053 stems/ha in the Cascade Range and 3940 stems/ha in the Coast Range.

Mat Accumulation

The accumulation of epiphyte mat mass as a function of stem age is highly variable within and between the Cascade and Coast Range sites (Figure 4.3). The Coast Range sites had a more rapid increase in accumulation over time, as well as higher median biomass accumulation at all stem ages. Although this may relate to differences between *A. macrophyllum* and *A. rubra* canopies, the generally moister climate may explain the greater accumulation in the Coast Range. The variability in
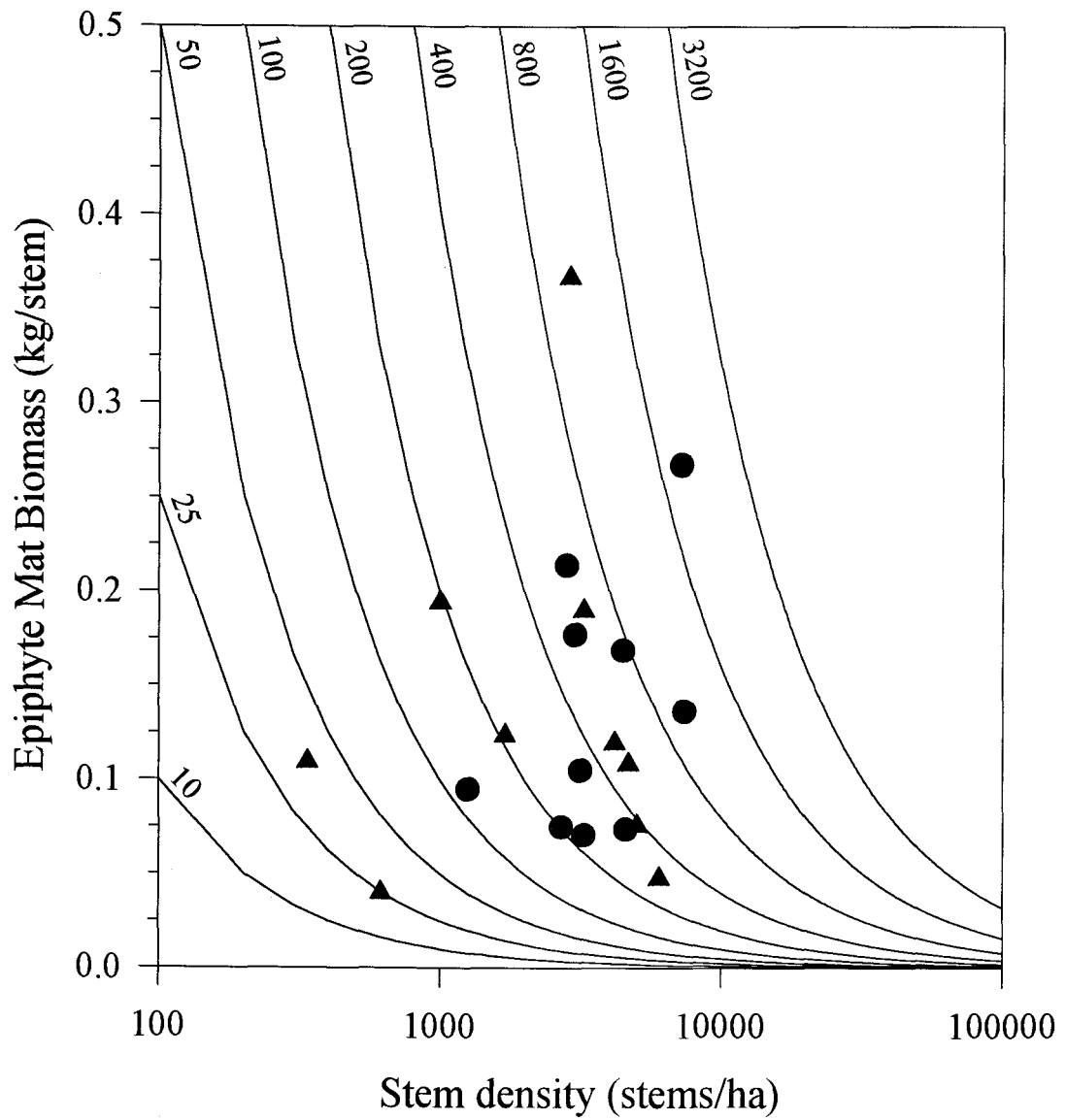
Figure 4.2. Harvestable epiphyte biomass (kg/ha) as a function of epiphyte mat mass per stem and stem density. Diamonds are Cascade Range sites; dots are Coast Range sites.

accumulation is also greater for the Coast sites. Due in part to this variability, stem density, average stem surface area, stem-level epiphyte mat mass and stand-level biomass were not statisticlaly significantly different between mountain ranges ($p > 0.3$; Table 4.1).

We suspect the rapid accumulation of mat mass at early stem ages to be a result of the re-establishment of mat litterfall from higher in the canopy. Many of the mats on young stems with extremely high mass may have resulted from this mechanism. Litterfall from the canopy is evident on the forest floor, logs, and shrubs in these stands, several species of which commonly re-establish on the forest floor (Peck et al. 1995) and probably other substrates. Furthermore, many of the mats with extremely low mass may have resulted from the loss of mat mass as litterfall to the ground or to lower substrates. Disturbances such as tree fall often scrape moss mats from trunks and branches, stripping them bare and displacing them to below.

For those mats occuring on vine maple, it was possible to compare mat species composition among different stem age classes. For ten year age classes (0-10, 11-20...71-80), species richness did not differ between age classes ($p = 0.46$) even though older stems had heavier mats on average (ANOVA, $p < 0.001$). Older mats are not more diverse than younger mats. Although species composition varied by age class (MRPP, $p < 0.01$), no differences were seen between most age classes ($p > 0.1$). Given this, and the inability to assign reliable indicator species to any individual age class (IV's < 8), there is no clear indication of an influence of stem age on mat composition.

Studies of bryophyte growth have found highly variable rates of growth among sites and among species (e.g. Pitkin 1975) and have implicated a myriad of stand characteristics (Hosokawa et al. 1964). In this area, stand charactersitics of importance may include canopy cover (relating to light availability), distance from each sampled stem to the nearest dominant conifer or hardwood tree (light and/or propagule supply), and density of host shrubs in the immediate vicinity of the sampled stem (host availability).

To better understand the mechanisms behind epiphyte mat accumulation, a number of additional factors will need to be examined. We propose a simple model

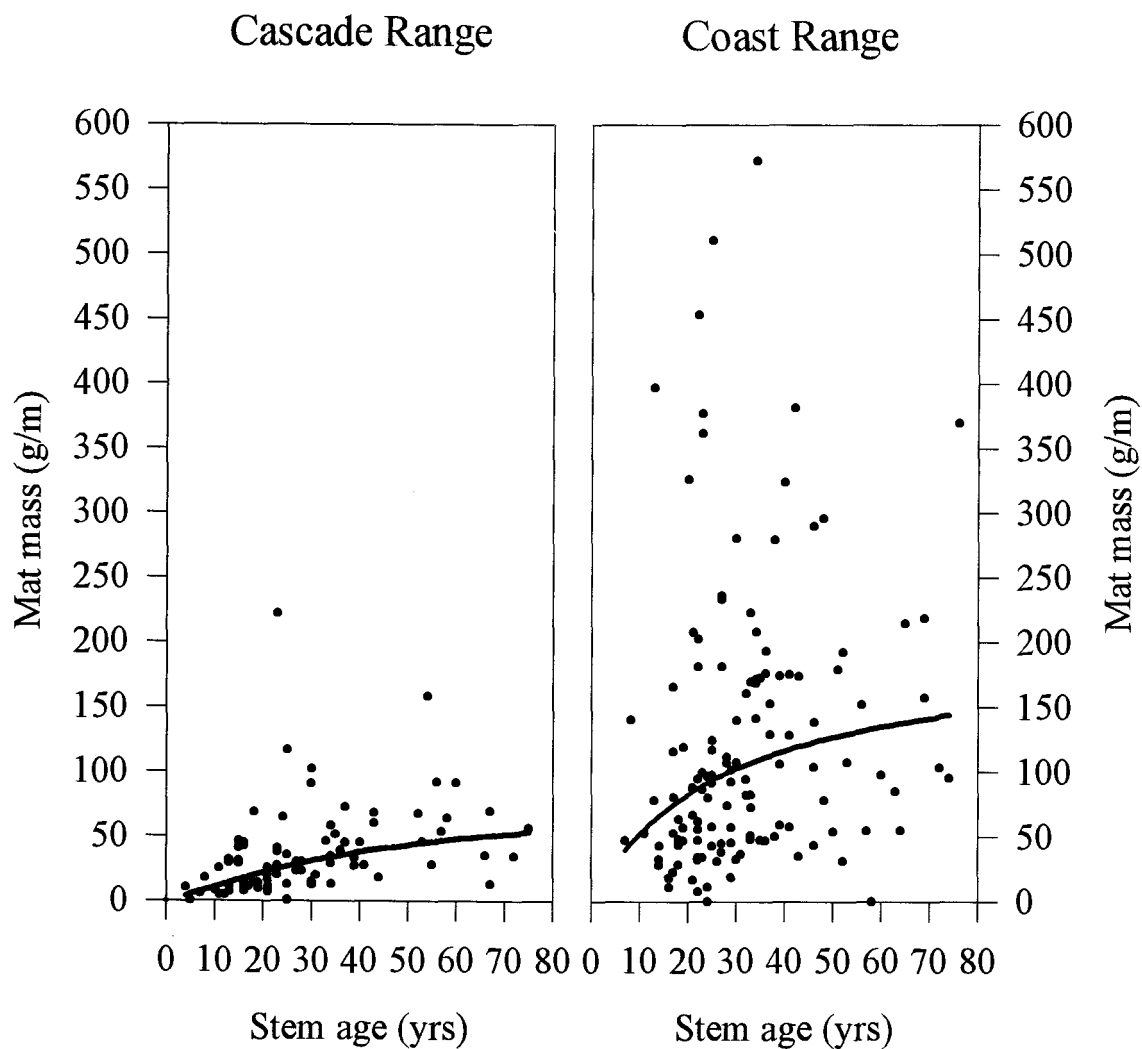Figure 4.3. Harvestable epiphyte mat accumulation on *Acer circinatum*, Cascade and Coast Ranges, northwestern Oregon. Dots represent individual epiphyte mats. Curve represents median epiphyte mat mass accumulation.
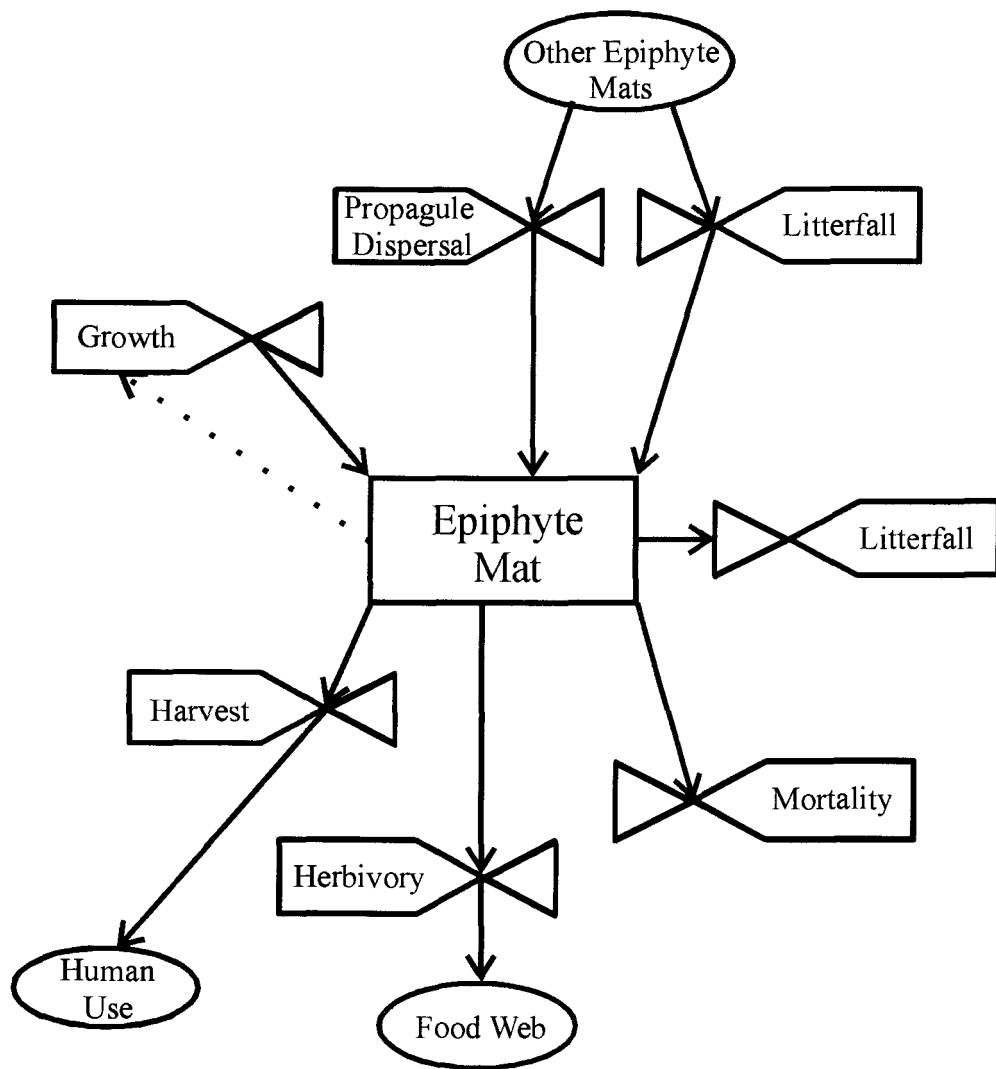
Figure 4.4. Harvestable epiphyte mat accumulation model. ◇ = driving influences, ◯ = sources or sinks, and ⋈ = processes. Solid lines are material flows; dotted lines are information flows.

for net harvestable epiphyte accumulation (Figure 4.4) incorporating possible inputs, outputs, and processes. Calibrating the model will require experimental evaluation. Processes adding to epiphyte biomass include the creation of new mats from propagules and the re-establishment of litterfall growth, both of which are influenced by climatic and microclimatic features and may depend on stand composition and structure and topography. Outputs include herbivory, litterfall from the mat, and decomposition, which may be influenced by climatic features, stand composition and structure, and perhaps the size of the epiphyte mat. The most significant loss of epiphyte biomass in this region may now be commercial harvest.

Management Recommendations

The results from this study have important implications for management for moss harvest. Protecting the harvestable moss resource is important if we wish to sustain moss harvest into the future and preserve ecosystem functions of epiphytic bryophytes. While it is obvious that regulating the rate of moss harvest is essential, it is clear from this study that we also need to maintain the supply of appropriate substrates, i.e. hardwoods and shrubs. This goal is contrary to the traditional emphasis in the Pacific Northwest of suppressing hardwoods and shrubs in favor of conifers. Given the potential importance of litterfall in accumulating epiphyte biomass, it may be important to restrict moss harvest to the lower 2 or 3 meters of the forest to preserve the supply of litterfall from higher in the canopy.

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CHAPTER 5. Summary

The harvest of moss as a secondary forest product, with it's long history and newfound government support, is here to stay. Now that managers are required to ensure the sustainability of ecosystem functions that may depend on epiphytic bryophytes, they will need to evaluate the impacts of moss harvest. The products of this thesis facilitates the initial understanding of the affected epiphyte communties and the sustainability of these resources. Considerable further research is necessary to ensure that moss harvest is regulated for sustainability of harvest, epiphyte community continuity, and ecosystem function.

This thesis provides the foundation for further investigation of the impacts of commercial moss harvest. I have characterized the community most likely affected by harvest, including many species not targetted for harvest but removed from their habitat nonetheless. I have suggested possible relationships between the overall abundance of harvestable epiphytes and the most commonly measured, and databased, site and stand characteristics. Host preferences by these epiphytes have been evaluated in both mountain ranges, and the available biomass of harvestable epiphytes has been roughly estimated. Most importantly for ensuring the sustainability of this resource, the patterns of accumulation of harvestable epiphyte mats on vine maple have been described and some of the factors affecting accumulation have been noted.

This information is useful, not only because it is the first attempt to quantify aspects of the moss harvest industry, but because it has immediate direct or indirect use for management. For instance, managers at the Hebo District of the Siuslaw National Forest will be able to use these biomass estimates to gauge how many bushels of moss they have available for harvest. They will be able to direct harvest toward stands with high densities of vine maple and away from stands dominated by conifers. The results of this thesis should also bring increased urgency to the completion of surveys for ROD (1994) listed species.

This thesis, however, dealt only with a small portion of the knowledge gap about this industry. The single largest obstacle to effective management of

commercial moss harvest is illegal harvest, whether it be by moss thieves or cheating permittees. To confound management, however, even legally permitted harvesters will harvest above 2 m in height (such that this thesis provides underestimates of the total available biomass). Current regulations also often permit by the pound, but assume 5 lbs of moist moss to a bushel, a volume measure that varies by how tightly you pack the moss and the moisture level of the moss.

Current standards and guidelines for moss harvest will need to be evaluated for sustainability of species richness, composition, and biomass availability. A nondestructive measure of biomass, which will be useful for monitoring regrowth of epiphytes following harvest, can be used if the relationship between mat thickness and biomass is established. Pike et al. (1977) estimated biomass of epiphytes on the basis of the nondestructive measure of cover. Given the three-dimensionality of bryophyte mats, as compared to relatively two-dimensional lichens that lend themselves well to direct cover-to-biomass extrapolations (McCune 1993), an additional measure of thickness appears necessary. Wolf (1993) found that epiphyte mat thickness and biomass followed similar patterns along an altitudinal gradient. This, combined with my observations, indicates that establishing a relationship between mat thickness and biomass would enable highly accurate biomass estimates without destructive sampling.

Perhaps more importantly, however, we know virtually nothing about the impact of harvest on nutrient cycling, hydrology, invertebrate communities, etc. We also do not know the extent of the industry and, therefore, whether or not it warrants promotion and careful regulations, or strict restriction. We've begun new explorations of the impacts of an old industry, and in the process we'll learn about the functional role of epiphytes in general and fill in gaps in our knowledge that can be applied to bryology as a whole.

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APPENDIX.

3 1/4" IBM Disk

Site and Stem locations, Word Perfect 5.1 format
LOCATE.DOC

Primary matrix, 504 stems X 50 species, original proportion data, Lotus 123 format
BOTH.WK1

Secondary matrix, 504 stems X 21 site variables, Lotus 123 format
2NDBOTH.WK1