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# Epiphytic lichen diversity and biomass in low-elevation forests of the eastern Washington Cascade range, USA

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## Abstract

I used litterfall sampling to estimate the biomass, diversity, and community structure of epiphytic lichens in three dry forest cover types in the eastern Washington Cascade range. Cover types represented a temperature/moisture and stand structural complexity gradient. Lichen litterfall biomass increased with increasing stand complexity and moisture. Lichen litterfall biomass was 3.42 kg/ha in open pine stands, 7.51 kg/ha in young mixed-species stands, 8.55 kg/ha in mature mixed-species stands. Six species accounted for 63% of the total sample biomass: *Bryoria capillaris* (20.2%), *Hypogymnia imshaugii* (15.8%), *Letharia vulpina* (14.5%), *B. fremontii* (7.2%), *Nodobryoria abbreviata* (2.8%), and *Alectoria sarmentosa* (2.6%). *Bryoria tortuosa*, considered rare in most of its range, was relatively common in young forest. Epiphytic lichen species richness and dominance did not differ among the three forest cover types. Lichen associations differed, however, among cover types. The dominant lichen in open pine stands was *L. vulpina*, followed by *Bryoria* spp., *H. imshaugii*, and *L. columbiana*. *Vulpicida canadensis* and *L. columbiana* were weak indicator species. Young stands were dominated by *H. imshaugii*, a strong indicator species of young stands, followed by *B. capillaris* and *L. vulpina*. *Cetraria platyphylla* and *C. pallidula* also were strong indicator species of young stands. Mature stands were overwhelmingly dominated by *Bryoria* species, primarily *B. capillaris* and *B. fremontii*, both strong indicators of mature stands. *A. sarmentosa*, *H. imshaugii*, and *L. vulpina* were other moderately abundant species. *Alectoria imshaugii* was also a strong indicator species of mature forest. Impacts on epiphytic lichens of dry forest management options that reduce stand density in fire-suppressed stands might vary. Lichens associated with dry open conditions would presumably benefit. The impact on species associated with old or moist conditions, especially forage lichens, might be lessened by variable-density thinning and other practices that maintain open- and closed-canopy patchiness and large trees. That patchiness might be hard to maintain with a maintenance program of understory burning patterned after natural fire regimes. At landscape scales, however, long-term persistence of forage and other lichens associated with mature moist forest would be enhanced by restoration of stable fire regimes.
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*Keywords:* Epiphytic lichens; Litterfall; Cascade range; *Pinus ponderosa*; *Pseudotsuga menziesii*; *Abies grandis*

## 1. Introduction

Epiphytic forest lichens, particularly *Bryoria* spp., are important food for ungulates (Fox and Smith, 1988; Hanley et al., 1989; Thomas et al., 1996; Rominger et al., 1996) and small mammals (Maser et al., 1985; Rosentreter et al., 1997; Zabel and Waters, 1997), mainly during the winter when plant or fungal food sources are at low levels or unavailable under deep snow. Lichens also are important nesting material for birds and mammals (Richardson and Young,

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1977; Helle and Helle, 1989; Hayward and Rosentreter, 1994). For the northern flying squirrel (*Glacomys sabrinus*), in particular, differences in lichen diversity and abundance may explain differences in squirrel abundance among vegetation types and be a chief correlate of source habitats (Zabel and Waters, 1997; Campbell and Coxson, 2001).

Lichens, moreover, have important ecosystem functions (McCune and Geiser, 1997) and are of considerable interest for forest ecosystem management in the Pacific Northwest. Thirty species of arboreal lichens are associated with late-successional forest conditions in the Pacific Northwest: nine species are endemic and three are considered rare (FEMAT, 1993). Research on the distribution and ecology of those species, particularly those considered rare and subject to special survey requirements, is a high priority for forest ecosystem management (FEMAT, 1993, IV-100). In general, lichen diversity and biomass are thought to increase with forest structural complexity (Lesica et al., 1991; Crites and Dale-Mark, 1998; Uliczka and Angelstam, 2000; Pipp et al., 2001). Lichen species composition also varies along gradients of temperature and moisture (Eversman, 1982; Lesica et al., 1991; McCune and Geiser, 1997; Crites and Dale-Mark, 1998; Uliczka and Angelstam, 1999). Very little is known about those relationships in the relatively dry forests of the interior Columbia River Basin of the Pacific Northwest (FEMAT, 1993; Marcot et al., 1997; Rosso and Rosentreter, 1999).

I estimated biomass and diversity of epiphytic lichens by litterfall sampling (McCune, 1994) in three low-elevation dry forest types of the eastern Washington Cascades in conjunction with a study of northern flying squirrel ecology. I sampled stands of three forest types that represented a mixed structural complexity and temperature/moisture gradient: (1) dry open ponderosa pine (*Pinus ponderosa*) stands with low stand complexity; (2) mesic, young, mixed ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) stands with moderate complexity; and (3) mesic, mature, Douglas-fir and grand fir closed-canopy stands with high structural complexity. My primary objective was to quantify biomass of forage lichens, particulary *Bryoria* spp., as a potential correlate to flying squirrel abundance. A second objective was to gain knowledge of lichen community ecology in the eastern Cascades. My hypothesis was that epiphytic lichen diversity and biomass would increase along the mixed stand structural complexity and temperature/moisture gradient represented by sample stands in the three cover types.

## 2. Methods

### 2.1. Study area

The study area was in the Cle Elum Ranger District of the Wenatchee National Forest in the east-central Washington Cascades. This area is an important ecotone between the dry interior and wet coastal zones and a center of high biodiversity (Marcot et al., 1998). Study stands occurred on dry forest sites characterized by varying dominance of mostly ponderosa pine, Douglas-fir, and grand fir in the Swauk Creek drainage northeast of Cle Elum, Washington. Forest structure in this area has been extensively altered since European settlement, primarily by fire suppression (Everett et al., 1997) and selective harvest of the largest trees beginning about 1940 (S. Madden, Wenatchee National Forest, Cle Elum, Washington, unpublished data). As a result, most forest stands have an uneven age structure. Study stands ranged in elevation from 900 to 1400 m elevation.

I randomly selected four replicate sample stands of three common cover types ($n = 12$ stands): open ponderosa pine, young mixed-species, and mature mixed-species. Stands were a minimum 13 ha and of regular shape to conform to square arboreal rodent trapping grids. Open pine stands had canopy cover of 30–45% and were dominated by scattered large ($\geq$40 cm dbh) ponderosa pine (Table 1). A patchy mid-story of smaller (<40 cm dbh) Douglas-fir and grand fir was often present in mesic microsites, such as draws. Tree density averaged 815 trees per hectare (TPH), of which 10% were large trees. Trees averaged 62 years old; but large trees averaged 140 years old and the oldest trees in a stand ranged from 100 to 348 years old. Selective logging of mostly large trees occurred around 1940, 1960, and 1980 in most stands. Open pine stands were on warm dry aspects from 180° to 240°. Plant associations were mostly in the *P. menziesii* series, predominantly the dry *P. menziesii*/*Calamogrostis rubescens* plant association (Lillybridge et al., 1995).

Table 1
Mean environmental attributes and epiphytic lichen richness, dominance, and litterfall biomass of all species and *Bryoria* spp. in three low-elevation forest cover types in the eastern Washington Cascade Range[a,b]

| | Cover type | | | Mean |
|---|---|---|---|---|
| | Open pine | Young mixed spp. | Mature mixed spp. | |
| Elevation (m) | 1115 | 1092 | 1207 | 1138 |
| Aspect code[c] | 3.8 | 2.5 | 1.5 | 2.6 |
| Slope | 36 | 30 | 39 | 35 |
| Canopy cover (%) | 40 | 60 | 75 | 58 |
| Basal area ($m^2$/ha) | 20 | 24 | 32 | 25 |
| Age largest trees[d] | 129 | 112 | 156 | 132 |
| *Pinus ponderosa* density (trees/ha) | 343 | 164 | 86 | 198 |
| *Pseudotsuga menziesii* density (trees/ha) | 453 | 319 | 170 | 314 |
| *Abies grandis* density (trees/ha) | 465 | 1765 | 1565 | 1265 |
| Lichen litterfall biomass (kg/ha) | 3.42 A | 7.51 AB | 8.55 B | 6.49 |
| *Bryoria* litterfall biomass (kg/ha) | 1.12 A | 2.86 B | 6.41 C | 3.46 |
| *N* species | 5.6 A | 8.6 A | 7.8 A | 7.3 |
| Dominance[e] | 0.72 A | 0.61 A | 0.68 A | 0.67 |

[a] Sample size, $n = 4$ stands in each cover type.
[b] Different letters in rows indicate significant ($P \leq 0.10$) differences with Tukey's HSD multiple comparisons.
[c] Aspect code ranges from 1 (cool, moist) to 4 (hot, dry): 1, north (315–45°); 2, east (45–135°); 3, west (225–315°); 4, south (135–225°).
[d] Largest trees were ≥40 cm dbh.
[e] Berger–Parker dominance index.

Young, mixed-species stands had moderate canopy cover of 50–70%, with a relatively high tree density (1600 TPH), most (96%) of which were <40 cm dbh (Table 1). Dominant tree species were grand fir and Douglas-fir, with a few ponderosa pine. The average tree age was 65 years, and large trees averaged 120 years old. The structure of these sites was largely created by 3–4 entries for selective, and later shelterwood, logging of mostly large trees around 1940, 1960, 1979, and 1983. Plant associations were mostly in the *A. grandis* series, with *A. grandis/Berberis nervosa/C. rubescens* the dominant plant association.

Mature, mixed-species stands had relatively closed canopies (70–83% cover) dominated by a mixture of large grand fir and Douglas-fir >40 cm dbh, with some scattered large ponderosa pine, and a well-developed mid-story and understory of grand fir and Douglas-fir (Table 1). Tree density (1400 TPH) was slightly less than young mixed stands, but there were more large trees in mature stands (12%) than in young (4%) or open pine (10%) stands. These sites had no record of being logged since the late 1930s, and were considered to be "old growth" and prime spotted owl habitat (E. Forsman, US Forest Service, Corvallis, OR, personal communication). The average tree age was 100 years; but the largest trees averaged 177 years old with maximum age 180–325 years. The *A. grandis/Achlys triphylla* plant association dominated most sites.

### 2.2. Field and laboratory methods

I sampled epiphytic lichen diversity and biomass by litterfall sampling, which has been shown in southwestern Washington to be a rapid and reliable method of estimating relative abundance among different stand types (McCune, 1994). I sampled in the late summer to avoid large and variable pulses of litterfall from windy winter and spring weather during field sampling. Sampling during the late fall through early spring was impossible with the accumulation of up to a meter or more of snow. I collected epiphyte litterfall in 20, 2 m radius plots systematically distributed in the 8 ha core area of each stand. Rules for collection of lichens followed recommendations by McCune (1994). Fragments >2 cm were collected. Lichens attached to fallen branches were picked up if the branch was <10 cm base diameter. Lichen litterfall hung up in the understory at a height >2 m above the ground was not collected. Epiphytic lichens that were largely incorporated into the forest floor, i.e., attached by fungal hyphae and partly buried by other litterfall, or moldy, were not collected. Fragments were quickly cleaned and placed in a single bag in the field to speed collection, then air dried for storage.

In the lab, I dried samples at 60 °C for 24 h, then sorted samples by individual species, or by genera if samples were too mixed up to efficiently sort out individual species. Each species sample within a plot was weighed to the nearest milligram. When the lichen material was too small and mixed in the plot sample bag to efficiently separate species, I estimated the sample weight of each species as a percentage of the mixed sample weight. A ‘‘miscellaneous’’ category described a fine mix of lichen ‘‘crumbs’’ found at the bottom of plot sample bags. Keys and text in McCune and Geiser (1997) were used for species identification. Voucher specimens were retained at the Wenatchee Forestry Sciences Laboratory and the Herbarium of Central Washington University, Ellensburg, WA.

### 2.3. Data analysis

#### 2.3.1. Dependent variables

I estimated epiphytic lichen species richness, dominance, and total (kg/ha) and individual species litterfall biomass (g/ha) in each of the 12 study stands as the mean of the 20 sample plots within a stand. Richness was simply the number of species encountered. I used the Berger–Parker index (Magurran, 1988) to estimate species dominance on a scale of 0–1 (1: completely dominated by one species). Total lichen litterfall biomass (kg/ha) in each stand was the sum of individual species. I also estimated *Bryoria* litterfall biomass separately. Biomass values are for litterfall, not actual biomass in the trees. McCune (1994) found that actual epiphytic biomass in mesic Douglas-fir forests of western Oregon could be estimated by multiplying late-summer litterfall biomass by 100.

#### 2.3.2. Biomass and diversity

I analyzed cover type effects on diversity and litterfall biomass with two statistical techniques. I first used ANOVA to test for differences in richness, dominance, total biomass, and *Bryoria* biomass among cover types. Multiple comparisons of cover type means were evaluated with the Tukey’s HSD test. Exploratory analysis indicated log transformation of biomass data to meet distributional assumptions for ANOVA. Untransformed biomass means are reported in the text. Power analyses of the biomass sampling design was done with the PASS program (NCSS, 2000).

#### 2.3.3. Community structure

I examined compositional similarity among cover types and identified lichen indicator species with several non-parametric multivariate analyses of community structure, as implemented in the PC-ORD software (McCune and Mefford, 1999). The site × species abundance matrix was 12 stands × 47 species. I first used multi-response permutation procedures (MRPP) to test the hypothesis of no difference in species composition between cover types based on species frequency and biomass (Zimmerman et al., 1985; Biondini et al., 1988). An $A$ statistic measured the grouping ‘‘effect size’’, or distinctiveness of groups, on a scale of 0–1. Values of $A > 0.3$ are considered fairly high. Monte Carlo permutations calculated probabilities for differences between types. I compared those probabilities to a Bonferroni-adjusted $P \leq 0.10$ for three multiple comparisons among cover types (see rationale below for Type I error threshold).

I used canonical correspondence analysis (CCA) to analyze for gradients underlying compositional similarities among cover types and stands, and to determine which species were most strongly associated with particular cover types. I truncated the species data set to the 24 most abundant species by dropping the miscellaneous category and rare species (23 spp.) that contributed trivial biomass (<10 g/ha, or 0.05%) relative to the total collection (19.5 kg/ha). I used a compact set of five environmental variables in CCA as best proxies for representing stand (age of the largest tree, basal area, canopy cover) and environmental (elevation, aspect) conditions. Stand scores were calculated from species scores. I used a biplot to display sample stand and cover type locations in species ordination space, and their relationships with environmental variables. Monte Carlo permutations (1000 runs) tested the hypothesis that the first ordination eigenvalue differed from random expectation.

Finally, I used indicator species analysis (ISA) to identify indicator, or characteristic, species found mostly in a single type and present in the majority of the sites belonging to that type (Dufrêne and Legendre, 1997). ISA combined information on both species relative abundance (i.e., biomass) and constancy to estimate indicator values for each species in each group. The maximum indicator value of an item within cover types was tested for statistical significance against the random expectation calculated by Monte Carlo permutation. I used $P \leq 0.10$ as the primary significance level for ‘‘strong indicator species’’, but also allowed a more liberal $P \leq 0.25$ to characterize ‘‘weak indicator species’’.

I accepted a significance level of $P \leq 0.10$ for all statistical analyses. Although less conservative than $P \leq 0.05$, particularly with the relatively small sample size in this study ($n = 12$ sites), I considered $\alpha = 0.10$ to be an acceptable chance of Type I error for ecological field studies that also allowed for reduced Type II error, and was well within the bounds of statistical convention (Zar, 1999). A significant difference is implied where a difference among means is reported in the text for a priori comparisons. Exact $P$-values are given for post-hoc Bonferroni-adjusted multiple comparisons among cover types.

## 3. Results

### 3.1. Biomass

Epiphytic lichen litterfall biomass increased with increasing stand structural complexity and moisture among cover types (Table 1). The relatively simple, dry, open pine stands had 3.42 kg/ha litterfall biomass. Litterfall biomass was 2–2.5× greater in the more complex and mesic young (7.51 kg/ha) and mature (8.55 kg/ha) stands than in open pine forest. Mean biomass differed significantly only between open pine and mature stands in pairwise comparisons. Six species accounted for 63% of the total litterfall biomass: *Bryoria capillaris* (20.2% total biomass), *Hypogymnia imshaugii* (15.8%), *Letharia vulpina* (14.5%), *B. fremontii* (7.2%), *Nodobryoria abbreviata* (2.8%), and *A. sarmentosa* (2.6%) (Table 2).

Litterfall biomass of *Bryoria* spp. likewise increased along the stand gradient (Table 1). Mature stands averaged 6.41 kg/ha *Bryoria* litterfall, which was 75% of the total lichen litterfall sampled in mature stands. Young stands had about half (2.86 kg/ha) and open pine stands less than a fifth (1.12 kg/ha) of the *Bryoria* litterfall of mature stands.

### 3.2. Diversity

Epiphytic lichen species diversity in litterfall, as measured by richness and dominance, did not change along the stand complexity gradient as hypothesized (Table 1). On average, lichen associations in open pine stands appeared to be less rich and more dominated by a few species than those in young or mature stands; but, variation was sufficiently high within cover types to make average differences insignificant. Relatively small sample sizes ($n = 4$) and high variation within cover types resulted in low power to detect a significant differences in richness (0.33) and dominance (0.14). About 20 samples for richness and 130 samples for dominance would be required for sufficient power (0.90) to detect significant ($P \leq 0.10$) differences among sampled cover types.

*Bryoria tortuosa*, the single epiphytic lichen species of designated conservation importance, was not abundant, but also was not very rare. It ranked in the top 28% (14) of species in biomass among the 47 species sampled (Table 2). Nevertheless, it was not abundant, contributing only 0.8% to total litterfall biomass. It was considerably more abundant and 2–3× more frequently encountered in young mixed-species stands (15% of sub-sample plots within stands), than in open pine (8%) and mature mixed-species stands (5%).

### 3.3. Community structure

MRPP analysis of community structure revealed differences in epiphytic lichen assemblages among cover types that were obscured by simple measures of richness and dominance. Epiphytic lichen assemblages in open pine and young mixed-species stands were similar ($A = 0.030, P = 0.194$), but lichens in both types differed from mature mixed-species stands ($P < 0.022$). Mature stands differed much more from open pine stands ($A = 0.215$), than from young stands ($A = 0.104$).

CCA showed a clear differentiation of epiphytic lichen assemblages among cover types along two environmental gradients ($P = 0.042$) (Fig. 1), and supported similarities and differences shown with MRPP. The primary gradient (41% variance explained) was a

Table 2

Litterfall biomass (g/ha) and indicator value of epiphytic lichen species in three low-elevation forest cover types in the eastern Washington Cascades

| Cover type and species | Biomass (g/ha) | | | Indicator value[a] | | | | |
|---|---|---|---|---|---|---|---|---|
| | Open pine[b] | Young mixed[b] | Mature mixed[b] | Total | Open pine | Young mixed | Mature mixed | $P$[c] |
| *Alectoria imshaugii* | 3 | 4 | 185 | 192 | 5 | 7 | 80[d] | 0.07 |
| *Alectoria sarmentosa* | 4 | 131 | 361 | 496 | 5 | 42 | 52[e] | 0.21 |
| *Alectoria* sp. | –[f] | – | tr[g] | tr | 0 | 0 | 25 | 1.00 |
| *Bryoria capillaris* | 194 | 1401 | 2227 | 3822 | 17 | 31 | 51[d] | 0.02 |
| *Bryoria fremonti* | 9 | 280 | 1071 | 1360 | 1 | 20 | 69[d] | 0.05 |
| *Bryoria fuscescens* | 1 | 57 | 78 | 136 | 2 | 35 | 51 | 0.38 |
| *Bryoria* sp. | 908 | 982 | 3036 | 4926 | 18 | 27 | 55[d] | 0.06 |
| *Bryoria tortuosa* | 6 | 140 | 2 | 148 | 13 | 39 | 2 | 0.64 |
| *Cetraria chlorophylla* | tr | 7 | 2 | 9 | 5 | 53 | 9 | 0.28 |
| *Cetraria merrillii* | 6 | 3 | tr | 9 | 33 | 51 | 13 | 0.46 |
| *Cetraria orbata* | 1 | – | tr | 1 | 24 | 0 | 1 | 1.00 |
| *Cetraria pallidula* | 1 | 56 | 3 | 61 | 7 | 59[d] | 2 | 0.10 |
| *Cetraria platyphylla* | 10 | 194 | 32 | 236 | 9 | 71[d] | 17 | 0.01 |
| *Cetraria* sp. | 2 | 4 | 2 | 8 | 4 | 37 | 5 | 0.50 |
| *Cladonia fimbriata* | 9 | – | 2 | 10 | 20 | 0 | 5 | 1.00 |
| *Cladonia* sp. | 2 | 2 | 1 | 4 | 15 | 5 | 11 | 1.00 |
| *Cladonia squamosa* | tr | – | tr | tr | 1 | 0 | 24 | 1.00 |
| *Esslingeriana idahoensis* | – | tr | tr | tr | 0 | 14 | 11 | 1.00 |
| *Evernia prunastri* | – | 2 | tr | 2 | 0 | 23 | 2 | 1.00 |
| *Hypogymnia imshaugii* | 272 | 2347 | 374 | 2994 | 23 | 60[d] | 17 | 0.05 |
| *Hypogymnia inactiva* | tr | – | 11 | 11 | 1 | 0 | 24 | 1.00 |
| *Hypogymnia metaphysodes* | – | 31 | 11 | 42 | 0 | 34 | 55[e] | 0.19 |
| *Hypogymnia occidentalis* | 6 | 169 | 66 | 241 | 4 | 38 | 42 | 0.43 |
| *Hypogymnia physodes* | 1 | 22 | 9 | 31 | 1 | 42 | 29 | 0.56 |
| *Hypogymnia* sp. | 29 | 34 | 97 | 160 | 19 | 32 | 43 | 0.51 |
| *Hypogymnia tubulosa* | 1 | 24 | 37 | 61 | 2 | 13 | 17 | 1.00 |
| *Letharia columbiana* | 133 | 58 | 36 | 228 | 53[e] | 27 | 20 | 0.24 |
| *Letharia* sp. | – | – | 1 | 1 | 0 | 0 | 25 | 1.00 |
| *Letharia vulpina* | 1475 | 918 | 362 | 2755 | 46 | 32 | 21 | 0.51 |
| *Melanelia* sp. | – | tr | 1 | 1 | 0 | 14 | 36 | 0.66 |
| *Nodobryoria abbreviata* | 62 | 360 | 109 | 531 | 16 | 56 | 27 | 0.46 |
| *Nodobryoria oregana* | – | – | 2 | 2 | 0 | 0 | 25 | 1.00 |
| *Parmelia* sp. | tr | 3 | 1 | 3 | 0 | 35 | 22 | 0.73 |
| *Parmelia sulcata* | – | 1 | 2 | 3 | 0 | 29 | 10 | 0.51 |
| *Parmeliopsis ambigua* | – | – | 1 | 1 | 0 | 0 | 25 | 1.00 |
| *Parmeliopsis hyperopta* | – | tr | tr | tr | 0 | 12 | 13 | 1.00 |
| *Peltigera* sp. | 6 | 4 | 33 | 43 | 8 | 6 | 22 | 0.81 |
| *Physcia* sp. | – | – | tr | tr | 0 | 0 | 25 | 1.00 |
| *Platismatia glauca* | 3 | 106 | 137 | 246 | 5 | 38 | 55 | 0.38 |
| *Platismatia stenophylla* | – | tr | – | tr | 0 | 25 | 0 | 1.00 |
| *Ramalina farinacea* | – | – | 1 | 1 | 0 | 0 | 25 | 1.00 |
| *Usnea glabrata* | – | 1 | – | 1 | 0 | 25 | 0 | 1.00 |
| *Usnea lapponica* | – | tr | – | tr | 0 | 25 | 0 | 1.00 |
| *Usnea* sp. | – | 8 | tr | 8 | 0 | 23 | 4 | 0.82 |
| *Vulpicida canadensis* | 89 | 33 | 1 | 123 | 51[e] | 15 | 1 | 0.25 |
| *Vulpicida pinastri* | – | tr | – | tr | 0 | 25 | 0 | 1.00 |
| *Xanthoria* sp. | – | – | tr | tr | 0 | 0 | 25 | 1.00 |

[a] Indicator values are the percent of perfect indication $= (\text{relative abundance} \times \text{relative frequency}) \times 100$. Abundance was measured as biomass.

[b] Open pine is dominated by ponderosa pine with canopy cover <60%. Young mixed-species ponderosa pine and Douglas-fir stands with canopy cover 40–70%. Mature mixed-species stands with ponderosa pine, Douglas-fir, and grand fir >70% canopy cover.

[c] $P$-value calculated as the proportion of 1000 randomized trials with indicator value equal to or exceeding the observed indicator value. $P = (1 + \text{number of runs} \geq \text{observed})/(1 + \text{number of randomized runs})$.

[d] "Strong" indicator value ($P \leq 0.10$).

[e] "Weak" indicator value ($P < 0.25$).

[f] Not detected in cover type.

[g] Trace values <1 g/ha.

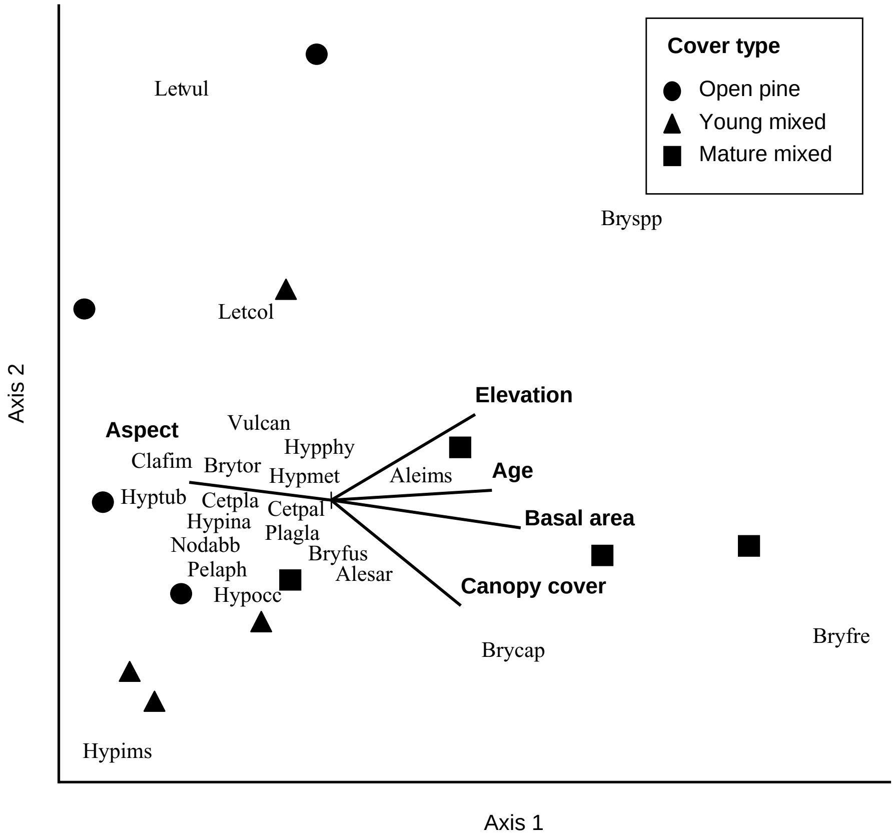

Fig. 1. Ordination of epiphytic lichen species and sample stand scores from CCA of lichen litterfall biomass in dry forest cover types in the eastern Cascade range. Species codes are the first three letters of the genus and species names listed in Table 2.

complex of stand development (basal area interset, $r = 0.88$; dominant tree age, $r = 0.75$), and associated temperature and moisture regimes (elevation, $r = 0.67$; aspect, $r = 0.65$). In support of the MRPP group analysis, mature stands stood quite separate from open pine and young mixed-species stands along Axis 1. The second gradient (17% variance explained) was most strongly correlated with canopy cover ($r = 0.59$), which also was moderately correlated with Axis 1 ($r = 0.61$). Open pine stands were relatively distinct from young and mature stands in having relatively open canopies and low stand density, and occupying warm, dry, south-facing slopes (Table 1 and Fig. 1). Canopy cover effects among open pine stands were highly variable along Axis 2, however. The dominant epiphytic lichen in open pine stands was *L. vulpina*, followed by *Bryoria* spp., particularly *B. capillaris*, then *H. imshaugii* and *L. columbiana* (Table 2). Open pine stands had no strong indicator species, but *L. columbiana* and *Vulpicida canadensis* were weak indicators species (Table 2).

Young stands had slightly higher average canopy cover and basal area, and occupied cooler and more mesic sites than open pine stands (Table 1 and Fig. 1). Young stands were dominated by *H. imshaugii*, which was a strong indicator species (Table 2). The other abundant lichens were *B. capillaris*, other *Bryoria* spp., and *L. vulpina*. Although not particularly abundant in young stands, *Cetraria platyphylla* and *C. pallidula* were strongly indicative of young stands.

Mature stands had the greatest overstory development in terms of tree basal area, canopy cover, age of largest trees, and were generally cooler and moister than other cover types (Table 1 and Fig. 1). They were overwhelmingly dominated by *Bryoria* species, particularly *B. capillaris* and *B. fremontii*, which were all strong indicators of mature, or the oldest, stands (Table 2). Although not particularly abundant, *A. imshaugii* and *H. metaphysoides* also were strong and weak indicator species, respectively, of mature stand conditions. *A. sarmentosa*, *H. imshaugii*, and *L. vulpina* were other moderately abundant species.

## 4. Discussion

### 4.1. Diversity

Gradient analysis supported the hypothesis that lichen associations vary with forest stand structural complexity and temperature/moisture (McCune, 1993). Likely driving factors are differences in the age and height in the canopy, stratum development, bark vs. wood substrates, and degree of sheltering (McCune et al., 2000). Conifer tree species composition may (McCune, 1993; McCune et al., 2000; Eversman et al., 2002) or may not (Sillett and Goslin, 1999; Sillett and Rambo, 2000) influence lichen compositional differences among types. Community differences associated with host tree species would be partly derived from environmental differences associated with site environment (Eversman et al., 2002) or canopy age, height, and structure (McCune et al., 2000).

Simple measures of lichen diversity (richness and dominance) did not differ among the forest cover types that were meant to represent those gradients: several explanations are possible. One reason could be high variation within cover types along the gradient. The cover types were initially described and stands typed based on tree species composition, tree size, and canopy cover for a small mammal study. Although mean conditions in the sample stands for each type showed distinct structural differences, variation in environmental conditions that affects lichens was high enough within open pine and young mixed stands to make statistical inference difficult. Even the tentative deletion of two potential outlier stands from the analysis did not reduce the variation sufficiently to detect differences. The types were not a perfect representation of the gradients, i.e., there was too much within-stand variation of stand complexity and temperature/moisture gradients among the types. Diversity in plant associations within cover types, as determined by the number of plant associations that characterized individual vegetation plots within stands, was a good overall indicator of the within-type variation in environmental gradients. Finally, simple measures of diversity based on counts of species, such as richness and dominance, are highly variable and difficult to consistently measure within cover types (McCune et al., 1997, 2000; Peterson and McCune, 2001), or may incorporate too little information to be meaningful. Although richness did not change among types, composition did change among types and may be a more meaningful measure of community differences than richness-based measures (McCune et al., 1997).

Despite the findings of similar richness and dominance among types, species richness and evenness (i.e., the inverse of dominance) likely do decline with tree density and canopy cover, or increasing warm and dry conditions, in ponderosa pine forest (Eversman, 1982). Estimated richness and evenness, although not statistically significant, were nominally lower in open pine than in young and mature mixed-species types, which were very similar. Based on data for study stands WG and TW (upper-most open pine stands in Fig. 1) and for the type in general (Table 2), increasingly warm dry conditions facilitate dominance of the epiphytic lichen community by *L. vulpina* and *L. columbiana*. Patchiness of open pine stands likely maintained a diversity of lichens in many ways similar to young mixed-species stands as seen by the location of the other two open pine stands in the gradient analysis (Fig. 1). Patchiness consisted of closed-canopy patches of grand fir and Douglas-fir in moist microsites, such as draws and shallow slope concavities, in a matrix of warm, dry open pine.

### 4.2. Biomass

Litterfall biomass increased as hypothesized along the stand complexity and environmental gradient represented by the three cover types. If McCune's (1994) 100:1 ratio of canopy to litterfall biomass applies to this area, then epiphyte biomass is typically about 850 kg/ha in the mature stands and about 2.5× higher than in open pine stands. That pattern would seem to be a function of increasing structural complexity for lichen colonization sites, cool and moist conditions favoring hydration and growth of dominant

*Bryoria* spp., and increasing stand age that allowed for longer colonization and growth period of lichens (Pipp et al., 2001; Lesica et al., 1991; Esseen et al., 1996; Peterson and McCune, 2001; Price and Hochachka, 2001). Hence, the structural basis for classification of cover types, although a poor predictor of epiphytic lichen diversity, worked well as a predictor of total lichen litterfall and *Bryoria* spp. biomass.

### 4.3. Management implications

Forest management in the dry forest zone represented by the study area is focused on conservation of habitat for the northern spotted owl (*Strix occidentalis caurina*) and on the maintenance or restoration of stable fire regimes and healthy dry forest ecosystems that have developed under nearly a century of fire suppression and past timber harvest (Okanogan and Wenatchee National Forests, 2000). Management in spotted owl habitat, represented by the mature mixed-species type in this study, is primarily custodial with little active manipulation of forest structure. However, active management of dry forest types represented by the open pine and much of the young mixed types is being designed and implemented to restore healthy ponderosa pine ecosystems from current anomalous conditions. Management objectives for dry forest may be to: (1) reduce stand density; (2) alter species composition in favor of early-seral species such as ponderosa pine; (3) reduce ground and crown fuel loads to levels consistent with low-severity fire regimes; and (4) reduce susceptibility to insects and disease outside of endemic levels (Okanogan and Wenatchee National Forests, 2000). The primary management options for achieving those objectives are pre-commercial or commercial thinning and prescribed fire. The upshot is that managed open pine and young mixed-species stands would have a less complex and more open canopy structure with some likely warming and drying effects on stand microclimate.

The stand-scale effects of that management on epiphytic lichens might be estimated from the gradient analysis (Fig. 1). Reducing the density and basal area, thus opening the overstory and creating drier conditions in open pine and young stands, would in effect shift stands to the low (left) end of the overstory development gradient (*x*-axis) and to the open canopy end (up) of the canopy cover gradient (*y*-axis). Reducing the overstory and creating warm dry conditions likely would have the greatest impact on *Bryoria* and *Alectoria* forage lichens: biomass of most species would likely decline with the reduction in canopy complexity and moisture, but *B. tortuosa* would appear to benefit. Other species more typical of open pine forest would increase, particularly *Letharia* spp., *V. canadensis*, and *Cladonia fimbriata* in dry conditions and to a lesser extent *H. imshaugii*, *Cetraria* spp. and *N. abbreviata* if the temperature/moisture regimes is little changed.

Impacts on forage lichens might be ameliorated if some patchiness of canopy cover is maintained in thinned stands by variable-density thinning and retention of structural and compositional variation within stands (McCune, 2002). Open pine stands show many compositional affinities with the young mixed-species stands (MRPP comparisons) because of the patchiness of closed-canopy Douglas-fir patches, which have conditions similar to young mixed-species stands, in the open pine matrix. Maintenance of patchy stand configurations at all scales can be an important practice to maintain or promote lichen diversity (Neitlich and McCune, 1997; Dettki and Esseen, 1998; Dettki et al., 2000). Those patches, however, might be targets for thinning if the goal is to reduce stand density and shift species composition to ponderosa pine. Thinning prescriptions might be designed to maintain or promote patchiness to lessen impacts on lichens, particularly forage lichens. Thinning young mixed-species stands to promote ponderosa pine and open canopies might favor dry site lichens such as *B. tortuosa* while maintaining moist-site species like *Bryoria* if thinning patterns were not homogeneous. Maintaining such patchiness could be problematic, however, if thinning is followed by a maintenance program of prescribed understory burning at regular intervals (∼10 years) that is patterned after pre-settlement fire regimes (Everett et al., 2000).

Retention of the largest or oldest trees also will maintain lichen diversity and biomass of forage lichens in particular (Neitlich and McCune, 1997; Dettki and Esseen, 1998; Hazell and Gustafsson, 1999). Whereas retention of patchy stand structure might maintain stand diversity, a dispersed distribution of remnant trees in thinned areas might better facilitate persistence of dispersal limited species

(Neitlich and McCune, 1997; Dettki and Esseen, 1998; Hazell and Gustafsson, 1999; Sillett et al., 2000).

Prescribed fire in open pine and young mixed-species stands could have different effects on epiphytic lichen diversity and biomass depending on stand density, the amount of ground fuels, burning weather, burn intensity, and flame length. Typical cool burns with short flame lengths in areas with sparse fuel and open canopies likely would have few effects on epiphytic lichens. Large trees are mostly unaffected by prescribed fire, and important forage lichens are of relatively low abundance in those types of stands or would be most abundant at mid- to upper levels in the canopy of large trees (Sillett and Rambo, 2000; McCune et al., 1997; Sillett and Goslin, 1999; Lyons et al., 2000) beyond typical flame lengths. Typical prescribed fires thin dense stands of small trees, but in a patchy configuration that could enhance short-term within-stand diversity and lichen habitats similar to variable-density thinning (Marcot et al., 1997). Negative effects of fire on within-stand diversity might occur in open pine or young mixed-species stands where closed-canopy patches are eliminated by regular prescribed burns or relatively hot fires, and stands become homogenous in density and species composition of open pine with associated warm, dry microclimate. Ground and shrub lichens may be negatively affected by prescribed fire (Rosso and Rosentreter, 1999). Fire is an unlikely management tool for the mature mixed-species stands like those in this study.

The possible negative stand-scale effects are tempered, however, by potential gains in long-term landscape-scale stability and resistance to large stand-replacement fire. Current dry forest conditions largely are anomalous, outside natural ranges of variation, and unsustainable over the long-term (Everett et al., 1997; Hessburg et al., 1999). Dry forest management holds the promise of reestablishing low-intensity, high-frequency fire regimes that will restore or sustain dry forest ecosystems and the associated moist mature mixed forests that are the stronghold of forage lichens, spotted owls, and other mature forest species.

Beyond variable-density thinning, McCune (2002) provides a comprehensive review of other recommendations to promote lichen diversity in management forests. In addition to retention of green trees, especially old trees, retain hardwoods, wolf trees with large old branches, and old shrubs. Avoid cutting in ‘‘hotspot’’ habitats (Neitlich and McCune, 1997) that include talus and outcrops, riparian areas, ridge tops, and infertile sites with thin and coarse-textured soils.

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