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CANOPY MACROLICHENS FROM FOUR FOREST STANDS IN THE SOUTHERN SIERRA MIXED CONIFER FORESTS OF SEQUOIA/KINGS CANYON NATIONAL PARK

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ABSTRACT

Canopy macrolichens were sampled using the "litter pickup" technique in four forest stands in the mixed conifer forests of Sequoia/Kings Canyon National Park. The purpose was to provide a basis for assessing lichen abundance trends in permanent forest plots, and to compare differences in lichen communities between four forest types typical of the southern Sierra Nevada. Each stand was characterized by a different conifer: sugar pine (*Pinus lambertiana* Dougl.), white fir (*Abies concolor* Gord. & Glend.), giant Sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.). The standing crop of lichen litterfall was estimated at 33.6 kg/ha, 14.8 kg/ha, 6.9 kg/ha, and 7.6 kg/ha respectively. Seven macrolichens were present in the litterfall, in decreasing order of overall abundance: *Letharia vulpina* (L.) Hue, *Hypogymnia imshaugii* Krog, *L. columbiana* (Nutt.) J. W. Thomson, *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw. and *Melanelia exasperatula* (Nyl.) Essl., *M. subolivacea* (Nyl.) Essl., and *Lobaria* (Schreber) Hoffm. sp. A single factor ANOVA indicated that *L. vulpina* was equally distributed throughout the four stands, while *H. imshaugii* and *L. columbiana* were not. *H. imshaugii* was the most abundant lichen in the White Fir stand, although *L. vulpina* closely approximated it there. *L. vulpina* was most abundant in the Sugar Pine, Giant Sequoia and Jeffrey Pine stands, and all other lichens were much less abundant. A complex of factors explains the differences in lichen abundance; stand density, stand structure, and tree species composition appear most important, although site environmental conditions cannot be ruled out due to the lack of replication and small sample size in this study. The White Fir and Sugar Pine stands had 2–3 times the tree density as the Giant Sequoia and Jeffrey Pine stands. Giant sequoia and incense cedar (*Calocedrus decurrens* (Torr.) Florin) shed bark and therefore do not have abundant epiphytes on branches and tree boles. White fir appears to have a generally positive effect on lichen abundance, except in extremely dense stands. The abundance of *H. imshaugii* and *L. columbiana* were highly correlated with abundance of sugar pine. Although species diversity is low, standing crop of lichen litterfall is high, and may exceed many other forests in North America.

Key Words: Sierra Nevada, lichens, biomass, litterfall, canopy.

Macrolichens of forest canopies can be used to make inferences about a variety of ecosystem characteristics, including air quality, stand structure and history, stand age, and overall forest health (Segal and Nash 1983; Wetmore 1986; Boucher and Stone 1992; Bates and Farmer 1992; McCune 1993; Rhoades 1995). The distribution of these arboreal, non-crustose lichens across the landscape reflects the dynamic mosaic of environmental conditions (Hale 1974). Within the mixed-conifer forests of the southern Sierra Nevada Mountains in California, canopy macrolichens have received limited study.

The National Park Service and other government agencies are interested in determining whether the lichens are increasing or decreasing in abundance, because lichens may have value as indicators of environmental problems (McCune 2000). Smith (1980) did a taxonomic survey of the macrolichens in Sequoia/Kings Canyon National Park and found 40 species in 13 mostly forested study sites. An air pollution impact survey of all the lichens of Sequoia/Kings Canyon National Park has identified 204 species (Wetmore 1986). Wetmore concluded that considering the dry climate, the lichen flora was diverse and healthy.

The purpose of this study was twofold: 1. To document the relative abundance of canopy macrolichens in four forest stands that are part of a permanent forest plot system in Sequoia/Kings Canyon National Park (Harmon et al. 1987; Riegel et al. 1988). These data provide a baseline for future sampling to determine temporal trends in canopy macrolichen abundance. 2. To compare the relative abundance of canopy macrolichens in four forest stands dominated by different species of conifers and representing different environmental conditions in the lower montane, mixed conifer forests of the southern Sierra Nevada Mountains.

The lower montane, mixed-conifer forests of the southern Sierra Nevada Mountains of California (1,600 m to 2,300 m) are characterized by giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh.) (Cupressaceae), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) (Pinaceae), California red fir (*Abies magnifica* A. Murr.) (Pinaceae), sugar pine (*Pinus lambertiana* Dougl.) (Pinaceae), Jeffrey pine (*P. jeffreyi* Grev. & Balf.) (Pinaceae), and incense cedar (*Calocedrus decurrens* (Torr.) Florin) (Cupressaceae). Along a moisture gradient, giant sequoia occurs in mesic locations that do not dry out in the summer, white fir–mixed conifer (sugar pine and incense cedar) occurs in generally drier habitats, and Jeffrey pine occurs in the most xeric sites (Rundel et al. 1977; Vankat 1982). Fire and fire suppression play an extremely important role in stand composition and structure. In general, fire suppression results in an increase in the abundance of white fir (Rundel et al. 1977).

Appropriate sampling for canopy macrolichen studies can be challenging, particularly for studies of trends in abundance over time. Canopy access using tree climbing is the most direct means of sampling canopy macrolichens, but sampling tree crowns to determine stand level abundance (i.e. biomass) requires very large amounts of time in tall forests (Clement and Shaw 1999). As an alternative, McCune (1994) has developed a method to quantify the relative abundance of lichens in a forest stand by sampling litterfall. This "litter pick-up" technique allows one to estimate the mass of canopy macrolichens at the stand level, which can then be used to compare relative abundance to other stand types and to determine stand-level trends in abundance over time.

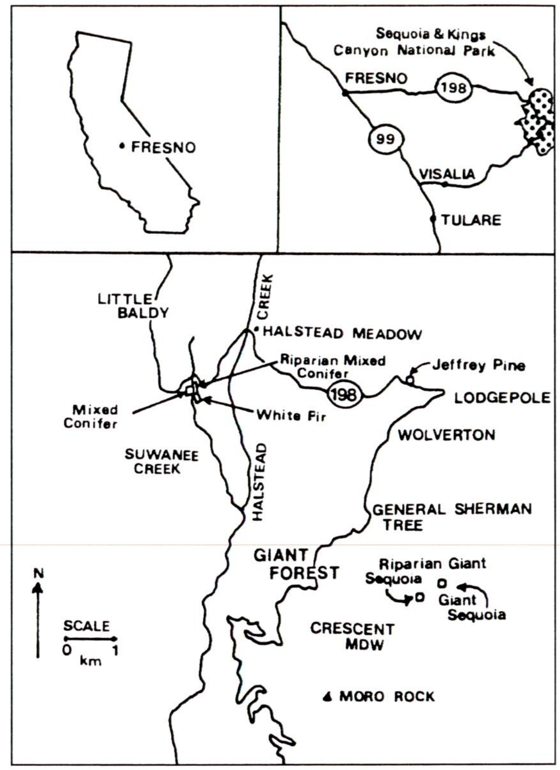

FIG. 1. Location of study site in Sequoia National Park, California (reproduced from Riegel et al. 1998). Four of these six reference stands were sampled, including White Fir, Jeffrey Pine, Riparian Giant Sequoia (Giant Sequoia) and Mixed Conifer (Sugar Pine).

METHODS

Study Site/Reference Stands

The study site is located in the northwest portion of Sequoia National Park (Latitude 36°N and Longitude 118°W) (Fig. 1). We chose four of the six reference stands described by Riegel et al. (1988), each dominated by a different species of conifer; Jeffrey pine, white fir, sugar pine (mixed conifer), and giant Sequoia (in a riparian setting). The stands are between 2,012 and 2,219 m in elevation and representative of three vegetation types: Sierran mixed-conifer (sugar pine and white fir), giant Sequoia-mixed conifer (riparian), and Jeffrey pine (Riegel et al. 1988). The reference stands were established for long-term monitoring of vegetation and are cooperatively managed by the Sequoia/Kings Canyon National Park, Oregon State University, and the US Forest Service, Pacific Northwest Research Station (Acker et al. 1998). The reference stands were established in 1984 and re-measured in June of 1994. All trees >5 cm have been tagged and mapped, and each tree has the diameter at breast height measured. Information is collected on crown ratio, crown vigor, tree mortality and damage. All data presented on stand structure comes from the 1994 measurement.

The study site has a mediterranean climate, with cool, moist winters and hot dry summers. Precipitation averages 1172 mm/year (1932–1983 mean at Giant Forest/Lodgepole, Sequoia National Park) and falls mostly as snow between November and April. The hot dry summers have a strong influence on arboreal lichen communities, which are characterized by low species numbers and dominance by a few drought-tolerant species.

The Jeffrey Pine reference stand (1.0 ha) is on a moderately steep SE facing slope, (Table 1), with a glaciated granodiorite rock substrate. Exposed rock is common at the site. The canopy is open, dominated by Jeffrey pine (124 trees/ha), with California black oak (*Quercus kellogii* Newb.) (Fagaceae) (60 trees/ha) (Table 2). Dense clumps of shrubs, especially green manzanita (*Arctostaphylos patula* Greene) (Ericaceae), are present. White fir (18 trees/ha), sugar pine (2 trees/ha) and incense cedar (5 trees/ha) occur in the lower plot where the slope flattens. This is a xeric, low productivity site. Jeffrey pine is adapted to the coarse textured soil found in the fissures of the glaciated granite (Riegel et al. 1988).

The White Fir reference stand (0.9 ha) is located

TABLE 1. SITE CHARACTERISTICS OF THE FOUR REFERENCE STANDS IN SEQUOIA NATIONAL PARK.

Reference stand	Stand size (ha)	Elevation (m)	Aspect	Topographic position	Average slope (%)
Sugar Pine	1.1	2091	southeast	midslope-bench	11
White Fir	0.9	2012	southwest	bench	20
Giant Sequoia	2.0	2219	southwest/southeast	lower slope	10
Jeffrey Pine	1.0	2109	southeast	upper slope	23

on a flat area above the east-side of Suwanee Creek (Table 1). There are scattered outcrops of bedrock in the stand. The stand has a dense canopy of white fir (420 trees/ha) and California red fir (33 trees/ha) near the stream which grades into a mixed-conifer forest with scattered sugar pine (56 trees/ha) and incense cedar (177 trees/ha) on the east side of the reference stand (Table 2). White fir is most abundant in all size- and canopy-classes, while incense cedar, sugar pine and California red fir are more abundant in the intermediate and suppressed canopy classes and smaller diameter-classes (Riegel et al. 1988).

The Sugar Pine reference stand (1.1 ha) is located to the west of Suwanee Creek approximately 200 m from the White Fir reference stand on a midslope bench (Table 1). The forest is a mosaic of large old sugar pine (110 trees/ha) and white fir (473 trees/ha) trees forming a relatively open canopy in the dominant (sugar pine 20 trees/ha, white fir 19 trees/ha) and codominant (sugar pine 11 trees/ha, white fir 42 trees/ha) canopy classes (Table 2, Riegel et al. 1988). There are clumps of suppressed white fir and incense cedar (78 trees/ha) interspersed throughout the stand where white fir dominates the smaller size and canopy classes. California black oak (16 trees/ha) and California red fir (7 trees/ha) are present in low numbers. The abundance of white fir in small size classes is thought to be a result of fire suppression (Riegel et al. 1988).

The Giant Sequoia reference stand (2.0 ha) is on a lower slope, and straddles both sides of Crescent Creek (Table 1). There is a narrow corridor of herbaceous vegetation along the creek. The stand has a typical mixed conifer over-story dominated by giant sequoia (24 trees/ha), which tower above the surrounding white fir (222 trees/ha) and California red fir (64 trees/ha) (Table 2). The true firs have a reverse J-shaped size distribution with a predominance of small stems, as is typical of shade tolerant species (Riegel et al. 1988).

Macrolichen Sampling

Canopy macrolichens were sampled on June 20–24, 1994 using 2-m radius (12.57 m^2) litter pickup plots (McCune 1994). Litter refers to material (in this case lichens) fallen from the canopy. At fifteen randomly chosen grid points in each reference stand, a stake was placed in the center of the plot and a 2-m string was used to measure the radius of

TABLE 2. SPECIES COMPOSITION, NUMBER OF TREES PER HECTARE (TPH), TOTAL NUMBER OF SPECIES, DIAMETER (IN cm) CHARACTERISTICS, TREE SPECIES EVENNESS, TREE SPECIES RICHNESS BASED ON NUMBERS (KREBS 1989), TREE SPECIES RICHNESS BASED ON AREA (KREBS 1989) OF THE FOUR REFERENCE STANDS.

	Stand			
TPH by species	Sugar Pine	White Fir	Giant Sequoia	Jeffrey Pine
White Fir	472.6	420.5	221.5	18.0
Red Fir	7.1	33.0	63.5	0
Incense Cedar	77.9	177.3	0	5.0
Jeffery Pine	0	0	1.0	124.0
Sugar Pine	109.7	55.7	6.0	2.0
Ponderosa Pine	0	0	0	1.0
Cal. Black Oak	15.9	0	0	60.0
Giant Sequoia	0	0	23.5	0
TOTAL TPH	683.2	686.4	315.5	210.0
# Tree Species	5	4	5	6
median dbh	8.2	15.4	12.8	8.6
quad mean dbh	33.5	37.2	81.3	31.8
max dbh	154.1	148.7	600.0	133.1
Basal area (m^2/ha)	60	74	164	17
Evenness	0.61	0.71	0.63	0.71
Rich No.	4.9 (0.27)	4.0 (0.00)	4.6 (0.51)	6.0 (0.00)
Rich Area	5.0 (0.00)	4.0 (0.00)	4.7 (0.47)	5.9 (0.35)

TABLE 3. TOTAL STANDING CROP OF CANOPY MACROLICHENS (kg/ha) ON THE FOREST FLOOR AND FREQUENCY OF OCCURRENCE IN 2 M RADIUS PLOTS. STANDARD DEVIATION IN PARENTHESES.

	Stand			
	Sugar Pine	White Fir	Giant Sequoia	Jeffrey Pine
Total Lichens				
Kg/ha	33.6 (27.7)	14.8 (18.5)	6.9 (12.9)	7.6 (16.5)
Frequency (%)	100	100	100	100
Letharia vulpina				
Kg/ha	15.04 (13.3)	6.5 (12.3)	4.8 (1.5)	7.35 (16.2)
Frequency (%)	100	73	93	100
Letharia columbiana				
Kg/ha	4.4 (5.4)	0.95 (1.3)	0.2 (0.4)	0.15 (0.18)
Frequency (%)	93	100	73	80
Hypogymnia imshaugii				
Kg/ha	14.1 (15.4)	7.3 (12.0)	1.8 (2.5)	0.08 (0.18)
Frequency (%)	93	93	80	33
Bryoria fremontii				
Kg/ha	0.01 (0.03)	0	0.08 (0.3)	0.01 (0.030
Frequency (%)	20	0	20	13
Melanelia spp.				
Kg/ha	0	0	0.06 (0.1)	0
Frequency (%)	0	0	33	0

the plot. Flagging was located in four directions to denote the boundaries of the litter pickup plot. All fresh macrolichens (i.e., had not decayed beyond an identifiable state) were collected and placed in paper bags. Litter attached to wood was also collected, as was litter caught in shrubs up to 1 m off the ground that was not attached to the shrubs.

Macrolichens were transported to the lab, cleaned, and sorted to species. The lichens were then dried at 60°C for 24 hours and weighed. Lichen identifications were made using Hale and Cole (1988), and names follow Brodo et al. (2001). Species identifications were verified and unknown samples were identified by Bruce McCune, Oregon State University. Reference specimens are deposited in the University of Washington Herbarium.

Analysis

Biomass on each 2-m radius plot was transformed to g/ha for data analysis. The mean for the 15 plots in each reference stand was used to represent stand level abundance and reported as kg/ha with standard deviation. Total lichen biomass and biomass of *Letharia vulpina* (L.) Hue (Parmeliaceae), *L. columbiana* (Nutt.) J. W. Thomson (Parmeliaceae), and *Hypogymnia imshaugii* Krog (Parmeliaceae) were compared between reference stands using a single factor Analysis of Variance (Zar 1999), (d.f. = 3 between groups, and 56 d.f. within groups, $\alpha = 0.05$).

Although the study included only four stands, we explored various descriptors of forest structure and composition as potential predictors of total lichen litterfall biomass and biomass of each lichen species. Variation in lichen biomass was compared to variation in stand-level tree density and basal area, stem density of individual tree species, and tree species evenness and richness (from the rarefaction method (Krebs 1989)).

RESULTS

Species

Seven species were found in the macrolichen litterfall of these four reference stands: *Letharia columbiana, L. vulpina, Hypogymnia imshaugii, Bryoria fremontii* (Tuck.) Brodo & Hawksw. (Parmeliaceae), *Melanelia exasperatula* (Nyl.) Essl. (Parmeliaceae), and *M. subolivacea* (Nyl.) Essl. (Parmeliaceae) and a *Lobaria* (Schreber) Hoffm. (Lobariaceae) sp. fragment. The *Lobaria* fragment was unidentifiable to species, and is not discussed further. The *Letharia* species and *H. imshaugii* were present in all four stands, while *Bryoria fremontii* was absent from the White Fir stand. The two *Melanelia* species were present only in the Giant Sequoia stand which at six species, had the highest macrolichen litterfall species diversity. The other stands had four species, including the *Lobaria* sp. fragment at the White fir stand.

Abundance

The Sugar Pine stand had the highest standing crop of lichen litterfall (33.6 kg/ha) (Table 3). The White Fir stand had about ½ as much (14.8 kg/ha) and the Giant Sequoia (6.9 kg/ha) and Jeffrey Pine

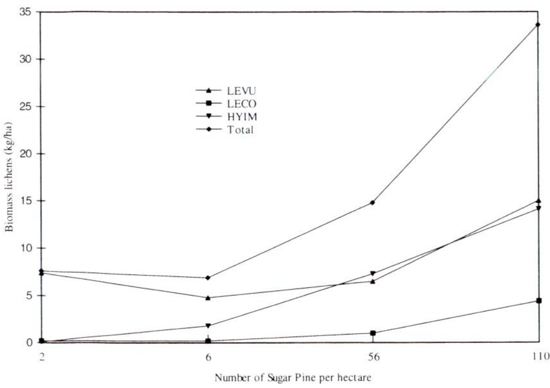

FIG. 2. Density of Sugar Pine per hectare on the four reference stands versus the standing crop of litterfall lichen biomass per hectare for total lichens, *Letharia vulpina* (LEVU), *L. columbiana* (LECO), and *H. imshaugii* (HYIM). Sugar Pine density corresponds to forest stands: 2 = Jeffrey Pine, 6 = Giant Sequoia, 56 = White Fir, 110 = Sugar Pine.

(7.6 kg/ha) stands had about one fourth that much lichen litterfall biomass as the Sugar Pine stand. In three of the four reference stands, lichen litterfall biomass was dominated by a combination of *L. vulpina* and *H. imshaugii.* In the Giant Sequoia, White Fir, and Sugar Pine stands, *L. vulpina* accounted for 44% to 70% of lichen litterfall biomass and *H. imshaugii* accounted for 25% to 49%. The Jeffrey Pine stand was unusual in that nearly all the lichen litterfall biomass (97%) was contributed by a single species, *L. vulpina.* The only other species to account for 10% or more of the lichen litterfall biomass of any stand was *L. columbiana,* which was 13% of the biomass for the Sugar Pine stand.

The ANOVA indicated significant differences between reference stands in biomass of total lichens ($P < 0.01$), *L. columbiana* ($P < 0.01$), and *H. imshaugii* ($P < 0.01$). No significant difference was found for *L. vulpina* ($P = 0.16$). Biomass of *L. columbiana* and *H. imshaugii* generally increase with increasing density of sugar pine (Fig. 2). Tree density, basal area, tree species evenness, tree species richness based on numbers, or tree species richness based on area (Table 2, 3) shows little relationship to the variation in total biomass of lichens.

DISCUSSION

Species Richness and Distribution

The lichen litter pick-up technique documented only seven species of lichens in these four forest stands. This is low species diversity, even for dry habitats. Smith (1980) found 40 species of macrolichens in the Ash Mountain to Grant Grove (Highway 198) region of Sequoia-Kings Canyon National Park and also included Cedar Grove. He sampled 13 sites using a floristic survey method that included all substrates, not just canopy lichens. The litter pick-up technique is not a 'stand-alone' method for surveys of species diversity, because species capture is low. The technique is best used in conjunction with other survey techniques that specifically search for different species of lichens (McCune and Lesica 1992; McCune 1994). However, it is a good technique for determining the relative abundance of the predominant forest canopy species. This is important for monitoring change in lichen communities.

In a study of lichens on conifers and their relation to air pollution in the Southern California mountains outside of Los Angeles, Sigal and Nash (1983) reported 16 species, the same number reported by Hasse for the same area in 1913 (in Sigal and Nash 1983). The lichen flora showed a strong relationship to air pollution: only eight of the original 16 species reported by Hasse were present in the most heavily polluted forests of the San Bernardino and San Gabriel Mountains. Sigal and Nash (1983) also rated the sensitivity of lichen species to air pollution, including several species we observed. They ranked *L. vulpina* as tolerant, *M. subolivacea* as moderately tolerant, and *B. fremontii* as very sensitive.

Smith (1980) has given species accounts of all 40 species he observed in Sequoia/Kings Canyon National Park, including the six species observed in this study. According to Smith, *Bryoria fremontii* is uncommon, and was only collected once from the bark and branches of *Pinus murrayana* (Sierra lodgepole pine, *P. contorta* subsp. *murrayana* (Balfour) Engelmann (Pinaceae)) in the Stony Creek area. We found *B. fremontii* in the Jeffrey Pine, Giant Sequoia, and Sugar Pine reference stands. *Hypogymnia imshaugii* was uncommon and was collected on *A. concolor* in the Crystal Cave Junction area. Smith found *H. enteromorpha* (Ach.) Nyl. (Parmeliaceae) to be common and sometimes very abundant in all areas above 450 m. This in contrast to our finding of *H. imshaugii* in all four sites, and a lack of collections for *H. enteromorpha.* Hale and Cole (1988) note that in the past, virtually all fertile Hypogymnias in California were called *H. enteromorpha,* but that this name is now limited to populations along the coast that are characterized by grossly inflated branches, and that this species does not occur in the Sierra Nevada. Hale and Cole (1988) also indicate that *H. imshaugii* is very common in Sequoia National Park.

Smith considers *Letharia columbiana* and *L. vulpina* to be two of the most common and abundant lichens in the park between 1200 m to 2700 m elevation. He found them growing on numerous tree species all through the study region. We also found these two lichens to be abundant. Interestingly, *L. vulpina* was the more abundant of the two species with 3 to 10 times the biomass of *L. columbiana* in the reference stands. Smith found *Melanelia subo-*

livacea (called *Parmelia subolivacea* Nyl.) abundant in all 13 study sites and in some trees the upper branches were completely covered by the lichen. It was present on a wide variety of conifers and hardwoods. *Parmelia exasperata* De Not. was described as commonly found on *Quercus,* widespread in the Ash Mountain area, Potwisha, Buckey Flats and Deer Ridge. This may be what we identified as *M. exasperatula.* We found these two species were present only in litterfall of the Giant Sequoia reference stand.

Abundance

Letharia vulpina was the dominant lichen in three of these forest stands, and was generally equally distributed throughout the four forest stands. *L. columbiana* and *H. imshaugii* were not equally distributed and showed strong patterns of increase with increasing sugar pine and white fir. The extreme xeric conditions of the Jeffery Pine stand may have a negative influence on *L. columbiana* and *H. imshaugii.*

McCune (1994) has investigated canopy litterfall relationships in the Pacific Northwest of North America. He found that the ratio 1:100 (litter : canopy lichens) was fairly consistent in Douglas-fir forests for late summer standing crop of lichen litter. Thus about 100 times the amount of lichen found on the forest floor in late summer will be in the canopy. This relationship has not been tested for forests of the Sierra Nevada. However if it is valid for the Sierra Nevada, the canopy biomass of macrolichens in the four reference stands would range from 0.7 Mg/ha in the Giant Sequoia stand to 3.4 Mg/ha in the Sugar Pine stand, with intermediate values for the Jeffrey Pine and White Fir stands (0.8 Mg/ha and 1.5 Mg/ha, respectively). These numbers are surprisingly large, perhaps in part because litter was collected in June rather than late summer. Typically a large pulse of lichen litter from winter storms will gradually disappear over the next 6–12 months depending on the species (McCune and Daley 1994). Another possibility is that the mildly toxic *Letharia* spp are resistant to herbivory, resulting in greater persistence on the forest floor.

Some of the most productive old-growth Douglas-fir stands in the Pacific Northwest have 1.3 to 1.9 Mg/ha of macrolichens in the canopy (McCune 1993; McCune et al. 1997). Boucher and Nash (1990) estimated 0.75 Mg/ha macrolichens for canopies of Blue Oak in California (36°N Latitude) while Turner and Singer (1976) estimated 1.9 Mg/ha for a Pacific Silver Fir stand in the western Cascades of Washington. For further information on the biomass of epiphytes see Boucher and Stone (1992) and Rhoades (1995). The relationship of lichen litter biomass to lichen biomass in the canopies of Sierra Nevadan forests is a key area for future research.

Factors Influencing Lichen Abundance

Lichen species composition and abundance in forest canopies is influenced by a multitude of factors. Among other things, this includes tree species, bark texture/chemistry, stand age, ecological continuity of the forest (Bates and Farmer 1992), tree density, forest structure, disturbance history, air pollution, climatic conditions, and forest management practices (Hale 1974; McCune 1993; Rhoades 1995). Within the southern Sierran mixed-conifer forests that we sampled, the most obvious influences on lichen species composition and abundance include tree species composition, stand density, and forest stand structure. It should be stressed that the generality of our interpretation is limited by the small sample size and no replication of stand types.

Differences in tree density did not directly correspond to differences in lichen biomass as stands with similar tree density differed in lichen biomass by a factor of 2 (Sugar Pine and White Fir) and stands with similar lichen biomass differed in tree density by 50% (Giant Sequoia and Jeffrey Pine). Tree species composition may explain some of these differences. Though they were similar in density, the Sugar Pine and White Fir stands were very different in stand structure and species composition. The White Fir stand was uniform in stand structure creating more evenly shaded tree boles, and had over twice as many incense cedar (78/ha in the Sugar Pine to 177/ha in the White Fir stand). Incense Cedar has exfoliating bark that sheds lichens. The Sugar Pine stand was more open with twice the number of sugar pine trees (110/ha in sugar pine to 56/ha in the fir stand) and a complement of dominant and codominant trees in the overstory, which provides for more sunlight on tree boles and branches. Thus, the Sugar Pine stand may have had an optimal combination of tree species composition and stand structure to provide for abundant lichen biomass.

Giant Sequoia represented 74% of the basal area and 80% of the stand wood volume in the Giant Sequoia stand although accounting for only 7% of the stems. Giant sequoia also has exfoliating bark, hence the lichens are rare on the tree bole, and only abundant on dead wood and cones (Steve Sillett and Joel Clement, personal communication). This might explain why the Giant Sequoia and Jeffrey Pine stands were similar in lichen litterfall biomass even though the sequoia stand had 50% more trees. The Jeffrey Pine stand approached a woodland setting, with widely scattered trees, among outcrops of rock. *Letharia vulpina* was the dominant lichen in this forest, perhaps showing a tolerance for xeric conditions and compatibility for Jeffery pine bark texture and chemistry.

The physical settings of the forest plots, such as aspect and proximity to streams, may also play a role in lichen abundance. The Giant Sequoia stand had a stream running through it, the White Fir stand and Sugar Pine stands were adjacent a stream, and the Jeffrey Pine stand was not influenced by a stream. A xeric to mesic environmental gradient was not measured in a systematic and replicated way in this study, and therefore conclusions regarding the overall effect of tree species composition as the major influencing factor associated with lichen abundance should be taken as a hypothesis needing further study.

Conclusions

We observed low species diversity of canopy lichens in the mixed-conifer forests of the southern Sierra Nevada Mountains, yet an unusually high stand biomass of lichen litterfall. The Sugar Pine stand would be one of the highest biomass estimates for lichens in North America if the 1:100 ratio of litterfall to canopy lichen biomass for Northwestern forests (McCune 1994) holds true in Sierran forests. The early summer sample period and possibility of longer persistence on the forest floor by *Letharia* spp. may explain these higher numbers. Tree species composition (especially abundance of sugar pine), and canopy openness/vertical structure appear to play a role in the abundance of canopy macrolichens, although the lack of replication within stand types and along the environmental moisture gradient preclude a definitive analysis. Characteristics of forest stands are controlled by a complex of factors, but in the future, anthropogenic influences such as fire suppression and controlled burning, air pollution, and climate change may become very important in determining lichen abundance. Long-term monitoring of lichens is important for understanding their role in the dynamics of ecosystems and how they will respond to anthropogenic influences.

Acknowledgments

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