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REMNANT TREES AND CANOPY LICHEN COMMUNITIES IN WESTERN OREGON: A RETROSPECTIVE APPROACH

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Abstract. The ''New Forestry'' practice of green-tree retention is becoming an important management tool for publicly owned lands, yet few data exist to demonstrate that this tool can succeed at enhancing biodiversity. We addressed this issue by using a retrospective approach to compare canopy lichen litter in adjacent, paired stands of rotation age (55–120 yr): one with and one without old-growth (>300 yr) remnant trees. We sampled three functional groups of lichens in 17 stands in western Oregon: alectorioid lichens, cyanolichens, and green-algal foliose lichens. Thirteen stands were low elevation (520–850 m) and four were mid-elevation (1220–1340 m). Biomass of cyanolichen and green-algal foliose lichen litter was greater in low-elevation sites, whereas alectorioid lichen litter biomass was greater in mid-elevation sites. Cyanolichens were absent from all mid-elevation sites. Biomass of alectorioid lichen and cyanolichen litter was greater in low-elevation sites with remnant trees than in those without remnant trees by 86% and 233%, respectively. The biomass of green-algal foliose lichen litter was 80% greater in mid-elevation sites without remnant trees than in those with remnant trees. Total lichen litter biomass was slightly, but not significantly, greater in stands with remnant trees at both low elevations (by 23%; ~370 kg/ha standing biomass in remnant stands) and mid elevations (by 12%; ~470 kg/ha standing biomass). Cyanolichen litter biomass was positively related to the number of remnant trees present; alectorioid and green-algal lichen litter biomass were negatively correlated with the density of trees in the regeneration cohort. Because retaining live remnant trees will differentially affect these three functional groups of macrolichens, managers must be clear as to their objectives before using green-tree retention as a tool to enhance biodiversity.

Key words: alectorioid lichens; Cascade Range; cyanolichen; epiphyte; green-algal foliose lichens; green-tree retention; lichen; new forestry; Oregon.

INTRODUCTION

Public lands managers face the challenge of preserving, and even enhancing, biodiversity in concert with continued timber production. Among other ''New Forestry'' (Franklin et al. 1985) alternative forest management practices, ''green-tree retention'' has been proposed to promote late-successional characteristics in managed forests. Public forest managers in the Pacific Northwest are now mandated (R.O.D. 1994) to leave 15% of the large living trees in future harvest units. However, few data exist to indicate actual effects of green-tree retention.

The current study was part of an interdisciplinary project aimed at evaluating the potential impacts of remnant trees, as analogues of green-retention trees, on understory herbs and shrubs (e.g., Traut 1995), the regeneration cohort (e.g., Zenner and Acker 1997), and canopy lichen communities. Because experiments on 80-yr rotations will be slow to yield results, we studied the historical impacts of natural remnant trees on canopy lichen communities. This retrospective approach enabled us to evaluate the likely impacts of leaving large remnant trees through one cutting cycle, without having to wait for the green-tree retention cuts of today to reach rotation age. Burns resulting in partial survival of canopy trees were common in the central western Cascades, as indicated by fire history studies (Stewart 1986, Morrison and Swanson 1990) and the abundance of forests composed of multiple age classes of trees.

We studied an analogous ''natural'' experiment: pairs of naturally regenerated stands, one stand with large remnant trees from a previous cohort (approximating green-retention trees) and an adjacent stand without these remnant trees. Rotation-aged forests (55–120 yr since major disturbance by fire) were chosen to provide estimates of lichen litter biomass in stands of an age comparable to the projected age of future harvest units. One member of each pair approximated a forest that would regenerate following clear-cutting and burning. The other member of each pair approximated a forest that would regenerate after a green-tree retention cut and slash burn.

We studied epiphytic lichens because of their importance in the coniferous forests of the Pacific Northwest and their strong associations with forests of dif-

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TABLE 1. Means and ranges for stand characteristics of 13 low-elevation and four mid-elevation remnant and nonremnant stands in western Oregon.

Stand characteristic	Dual-aged stands with remnant trees (remnant)	Single-aged stands without remnant trees (nonremnant)
A) Low-elevation stands (520–850 m)		
Age (yr)	88 (65–120)	85 (65–125)
Remnant density (no. trees/ha)	21 (3–57)	0
Regeneration cohort density (no. trees/ha)	810 (460–1480)	920 (440–1920)
Basal area, BA† (m^2/ha)	73 (65–89)	68 (56–86)
BA in *Tsuga heterophylla*† (%)	21 (0–65)	13 (0–61)
BA in *Pseudotsuga menziesii*† (%)	77 (23–100)	83 (39–100)
B) Mid-elevation stands (1220–1340) m		
Age (yr)	125 (80–230)	123 (70–235)
Remnant density (no. trees/ha)	36 (17–73)	0
Regeneration cohort density (no. trees/ha)	1515 (700–2520)	2580 (780–4680)
Basal area† (m^2/ha)	80 (65–87)	70 (46–88)
BA in *Tsuga heterophylla*† (%)	18 (0–63)	8 (0–30)
BA in *Pseudotsuga menziesii*† (%)	22 (0–84.5)	53 (0–96)

† Indicates regeneration cohort only.

ferent age classes. Alectorioid lichens provide food and habitat for wildlife (Maser et al. 1985, Rominger and Oldemeyer 1989, Servheen and Lyon 1989, Sharnoff 1994), whereas cyanolichens fix nitrogen (Pike et al. 1972, Pike 1978, Knops et al. 1991). Arthropods and birds utilize epiphytic lichens (Gersun and Seaward 1977, Schowalter 1988, 1995, Lattin 1993), and their diversity and abundance have been linked to epiphyte diversity (Pettersson et al. 1995). Old-growth forests are particularly rich in epiphytes, with more than twice the biomass of epiphytes in even-aged, rotation-aged (70–95 yr-old) stands (Lesica et al. 1991, McCune 1993). In addition, the proportion of cyanolichens and alectorioid lichens, relative to green-algal foliose lichens, is greater in old-growth stands than in 40-, 70-, and even 140-yr-old Douglas-fir and western hemlock stands (Neitlich 1993).

Green-tree retention is thought to promote lichen community development in two ways. First, retaining large, live trees retains the epiphytic lichens in those trees. Second, these legacy populations are a source for propagules that can become established in the regeneration cohort. Lichens are, to some unknown extent, dispersal limited (Armstrong 1987, 1990, Stevenson and Enns 1992). If dispersal is strongly limiting, forests regenerating after green-tree retention cuts would be expected to have a greater lichen biomass than clearcuts, due to the proximity of lichen propagule sources. If, however, substrate and/or microclimate are more critical than dispersal for determining the establishment and growth of epiphyte communities, only minor differences between green-tree retention cuts and clearcuts would be expected. We hypothesized that stands regenerating after green-tree retention cuts would have a greater biomass of lichens associated with old growth (e.g., *Alectoria sarmentosa* and the cyanolichen *Lobaria oregana*) than stands without retained trees.

METHODS AND MATERIALS

Sites

Aerial photographs of the Willamette National Forest, in the western Cascade Mountains of Oregon, USA, were examined to locate relatively homogeneous stands with some remnant trees that were >20 m from a clearcut edge and were of sufficient size to accommodate two paired plots (~1–2 ha). One plot of each pair had live remnant trees over a regeneration cohort (the ''remnant'' plots) and the other plot had only the regeneration cohort (the ''nonremnant'' plots). Nonremnant plots had dominant and codominant trees that differed in age by <20 yr, on average (Zenner and Acker 1997), whereas remnant plots were dual aged, with live ≥300-yr-old remnant trees at densities of 3–57 trees/ha over the regeneration cohort. The adjacent paired plots were 5–50 m apart on the same slope and were of comparable age, all stands having burned between 55 and 120-yr ago (Table 1). Thirteen of the sites were ''low elevation'' (520–855 m), located in the *Tsuga heterophylla* (western hemlock) zone (Franklin and Dyrness 1973). *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) and *Tsuga heterophylla* (Raf.) Sarg. dominated these sites, and *Thuja plicata* Donn. (western red cedar) and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) were often present in the understory. Four of the sites were considered ''mid elevation'' (1220–1340 m), located in the *Abies amabilis* zone, with *Abies amabilis* the dominant species.

We sampled each plot with a 12.6 m radius ''detection plot'' nested within a ''megaplot'' of 30.9 m radius (Fig. 1). Nesting the detection plot allowed for a buffer zone (18.3 m) where remnant density was similar within and around the sampling area. Site and stand characteristics were recorded for each remnant and nonremnant plot. Paired plots were placed to keep elevation, slope, azimuth, and topographic position as sim-

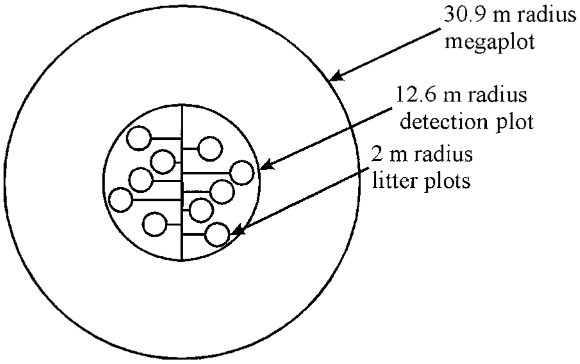

FIG. 1. Sampling schematic, showing the lichen litter plots within the detection plot portion of the megaplot.

ilar as possible within the same site. Azimuth was adjusted to a more biologically meaningful scale, with north and south at the poles (0° = north; 180° = south; 90° = east and west). Because cyanolichen abundance may vary with distance from water (Howe 1978), horizontal and vertical distances from the nearest perennial stream or standing body of water were also recorded. Basal areas of conifers and hardwoods were measured in the detection plot, and stand ages were determined from increment cores from dominant trees in the detection plot (Zenner and Acker 1997). The total number of live remnants was also recorded.

Because most macrolichen species rely on wind dispersal of relatively large propagules, the effectiveness of dispersal is uncertain (e.g., Sillett and Neitlich 1996). To evaluate the potential influence of nearby forests as propagule sources, we created forest "context" variables. These variables were created by examining recent (1989) aerial photographs of each stand and assigning percent cover to four categories of forest in 3.14-ha, 31.4-ha, and 314-ha concentric circles centered on our plots: young (0–100 yr), mature (100–250 yr), old (>250 yr), and other (e.g., water, rock outcrops). These "current" context variables index the current availability of propagule sources from older forests, which support high lichen biomass and, subsequently, large numbers of lichen propagules. We also obtained older (1946 or 1949) aerial photographs of our stands and repeated these estimates. Due to the lower quality of the older photographs, we assigned percent cover only to three categories: young (0–100 yr), old (>100 yr), and other. These "historic" context variables index the availability of propagule sources from the surrounding landscape during the first ~40 yr of stand (and lichen community) development.

Litterfall collection

Accurate estimates of epiphytic lichen biomass are difficult to obtain without extensive direct sampling in the canopy. Such sampling is costly and time consuming. McCune (1994), however, found a strong relationship between late-summer lichen litter in western Cascade forests in Oregon and the standing canopy lichen biomass, in an approximate ratio of 1:100 ($\sqrt{\text{litter}} = 0.1 \times \sqrt{\text{biomass}}$; $r^2 = 0.87$, $n = 18$). This model was based on direct sampling of epiphytes on felled trees in stands in which epiphyte litter had previously been collected. These stands were similar in elevation and species composition to those reported here. Epiphytic litter is sampled in late summer to avoid the large and variable pulses of litterfall that have been recorded in winter months for some forests (Stevenson and Rochelle 1984, Esseen 1985). Because lichen litter disappears rapidly in these forests (McCune and Daly 1994), and most lichen litter falls in the winter, a single summertime sample cannot be used directly as an estimate of the annual rate of litterfall. Data from this method, subsequently, are not an estimation of annual litterfall, but are used to indicate lichen biomass in the canopy.

This method has since been used extensively (Neitlich 1993, Sillett and Goslin 1995; A. Pipp, *personal communication*), such that our biomass estimates will be able to be directly compared to other studies. We chose to estimate epiphyte biomass from collections of epiphyte litter from the forest floor, because of the impracticality of extensive direct sampling of canopy epiphytes, the existence of an established method for estimating canopy biomass from litterfall samples, and because the objective of this study was to compare paired remnant and nonremnant plots, rather than to estimate annual litterfall. Because of the paired design, and because both pairs were sampled at the same time, we were able to presume that litterfall in the plots of each pair were subject to roughly the same influences from wind, herbivory, decomposition, and other factors.

We sampled litter in the detection plot (Fig. 1) within each paired plot. A transect was laid on the contour through the center of the detection plot. From this transect, 10 perpendicular transects were laid across the contour at random intervals, and one 2 m radius litter plot was sampled on each of these perpendicular transects. Litter plots were placed so as not to overlap with previously sampled litter plots.

Epiphytic macrolichen litter (all non-necrotic loose litter and any litter present on downed branches <10 cm in diameter) was collected in paper bags, air dried, and stored at room temperature. In the lab, samples were dried at 60°C for 24 h and were weighed to the nearest milligram. Litterfall from each plot was processed separately, according to McCune (1994). Lichen litterfall was sorted into the three functional groups of McCune (1993): alectorioid lichens, cyanolichens, and all remaining lichens, which are mostly green-algal foliose species. The alectorioid lichens were composed of *Alectoria sarmentosa*, species in the *Usnea filipendula* group, and several species of *Bryoria* (*B. capillaris, B. friabilis, B. fuscescens, B. oregana, B. pseudofuscescens*). The cyanolichens consisted primarily of *Lobaria oregana*, with small amounts of *Nephroma*, *Pseudocyphellaria*, and *Sticta* species. The green-algal foliose lichens were primarily *Hypogymnia apinnata, H. enteromorpha, H. imshaugii, H. inactiva, Platismatia glauca, P. herrei, P. stenophylla,* and *Sphaerophorus globosus.* Nomenclature of lichens follows Egan (1987).

Litter biomass (in grams per square meter) was converted to standing epiphyte biomass (in kilograms per hectare), based on McCune's (1994) estimation of a 1:100 relationship between lichen litter and standing biomass. Biomass for each functional group was extrapolated to the stand level separately.

Statistical analysis

The alectorioid lichen and cyanolichen data were square-root transformed prior to correlative and comparative analyses to reduce skewness. A log transformation was used to improve the normality of the green-algal foliose lichen data. An arcsine square-root transformation was used for proportions (the current and historic context variables).

Low- and mid-elevation sites, and remnant and nonremnant plots, were compared on the basis of litter biomass for each functional group using *t* tests (paired for the remnant–nonremnant comparison). Due to a significant difference in biomass between the low- and mid-elevation sites for all three functional groups, and the low sample size of mid-elevation sites ($n = 4$), we report biomass for each elevation group separately (Table 1) and consider only the low-elevation sites in analyzing the influence of remnant trees. Pearson correlation coefficients were calculated to assess the relationships between stand and site characteristics and lichen litter biomass (in grams per square meter) for low-elevation sites. We believe that correlation coefficients appropriately represent the limited inference of a retrospective study.

RESULTS

Biomass of epiphytic lichen litterfall differed between low- and mid-elevation stands as well as between remnant and nonremnant plots for low-elevation stands. Alectorioid lichens were most abundant in mid-elevation stands, whereas cyanolichens and green-algal foliose lichens were most abundant in low-elevation stands. Alectorioid lichens and cyanolichens were most abundant in remnant plots, whereas green-algal foliose lichens were most abundant in nonremnant plots.

The mean biomass of alectorioid lichen litter was 0.66 g/m^2 higher in the mid-elevation sites than in the low-elevation sites (df = 16, $P < 0.001$). The mean biomass of cyanolichen litter and of green-algal foliose lichen litter was 0.05 g/m^2 (df = 16, $P = 0.01$) and 0.29 g/m^2 (df = 16, $P = 0.03$) higher in the low-elevation sites than in the mid-elevation sites, respectively. Cyanolichens were absent in all mid-elevation sites and some low-elevation sites. Results of subsequent analyses apply only to the low-elevation sites.

TABLE 2. Mean biomass of epiphytic lichen litter (g/m^2) in nonremnant and remnant stands in western Oregon. The standard deviation is given in parentheses. For low-elevation stands, $n = 13$; for mid-elevation stands, $n = 4$.

Litter component	Dual-aged stands with remnant trees (remnant)	Single-aged stands without remnant trees (nonremnant)
A) Low-elevation stands (520–850 m)		
Alectorioid lichens	0.39 (0.25)	0.21 (0.13)
Cyanolichens	0.07 (0.09)	0.03 (0.04)
Green-algal foliose lichens	0.64 (0.38)	0.66 (0.41)
Total lichen biomass	0.37 (0.36)	0.30 (0.37)
B) Mid-elevation stands (1220–1340 m)		
Alectorioid lichens	1.16 (0.76)	0.77 (0.44)
Cyanolichens	0 (0)	0 (0)
Green-algal foliose lichens	0.26 (0.21)	0.47 (0.42)
Total lichen biomass	0.47 (0.67)	0.42 (0.47)

Total lichen biomass was not significantly greater in the remnant plots than in the nonremnant plots (df = 25, $P = 0.34$; Table 2). The biomass of alectorioid lichens and cyanolichens was greater in the remnant plots (paired *t* test, df = 25, $P < 0.01$), with a mean difference in biomass between the remnant and the nonremnant plots (remnant − nonremnant) of 0.23 ± 0.03 g/m^2 (mean ± 1 SD) for alectorioid lichens and 0.08 ± 0.09 g/m^2 for cyanolichens. Green-algal foliose lichen litter biomass was greater, on average, by 1.3 ± 0.40 g/m^2 in nonremnant plots (df = 25, $P < 0.001$) than in remnant plots.

Alectorioid lichen biomass was negatively correlated with the density of the regeneration cohort in the nonremnant plots ($r = -0.56$, $P = 0.04$). Alectorioid lichen biomass was not correlated with any other stand characteristic or any of the current or historic context variables.

Cyanolichen biomass was positively correlated with the number of live remnants per hectare among the remnant plots ($r = 0.59$, $P = 0.04$). Cyanolichen biomass was positively correlated with the percentage of *Tsuga heterophylla* in the regeneration cohort among the remnant plots ($r = 0.73$, $P < 0.01$). The percentage of *Pseudotsuga menziesii* in the regeneration cohort was negatively correlated with cyanolichen biomass among remnant plots ($r = -0.70$, $P < 0.01$). Cyanolichen biomass was also negatively correlated with the adjusted aspect among remnant plots ($r = -0.58$, $P = 0.04$). Cyanolichen litter biomass was not related to the current or historic context variables, or to any stand characteristic among the nonremnant plots.

Green-algal foliose lichen biomass was positively correlated with the basal area of the regeneration cohort ($r = 0.38$, $P = 0.05$) among the remnant plots, and negatively correlated with the density of understory conifers among the remnant plots ($r = -0.68$, $P = 0.01$) and among the nonremnant plots ($r = -0.78$, *P*

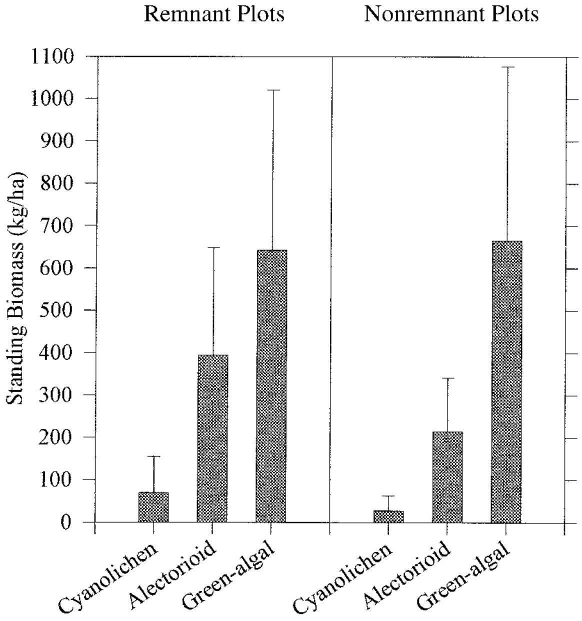

FIG. 2. Standing biomass (kg/ha) of epiphytic canopy lichens in remnant and nonremnant stands in western Oregon. Bars are means + 1 SD.

< 0.01). No relationship was seen between green-algal foliose lichen biomass and any current or historic context variable.

Lichen litter biomass for all functional groups, extrapolated to standing canopy biomass, is shown in Fig. 2. These values were simply converted from grams per square meter to kilograms per hectare and were then extrapolated to standing biomass by a factor of 100, based on McCune (1994).

DISCUSSION

Our data indicate that the biomass of two groups of lichens associated with old growth, cyanolichens and alectorioid lichens, was greater in stands with remnant trees than in those without. This difference may be a function of several factors. First, some of the litterfall collected in remnant tree stands undoubtedly arose from lichen populations in the remnant trees, rather than in the regeneration. Field observations, however, suggest that lichen biomass in the young cohort was high, and any litterfall in the nonremnant tree stands clearly arose from the young cohort. Second, the closer propagule sources in the remnant tree stands may have increased the rate of population development in the young cohort. Third, although stand characteristics were comparable between the remnant and nonremnant tree stands, microclimates within the stands were probably different, historically as well as currently. In particular, scattered remnant trees may have ameliorated any microclimate extremes in the early years after disturbance, and may have helped to preserve legacy populations.

The greater biomass of alectorioid lichens in remnant than in nonremnant stands was not supported by a positive correlation with the number of live remnant trees, as it was for cyanolichens. This lack of correlation may reflect the high variability in both the alectorioid lichen biomass and the number of remnant trees per stand, particularly considering our low sample size. However, alectorioid lichen biomass may be greater in remnant stands due to indirect factors associated with remnant trees, such as increased regeneration cohort density, rather than directly due to the presence of remnant trees.

We make two predictions about the probable influences of remnant trees and young stand development on epiphytic lichens (Fig. 3). We hypothesize mechanisms behind each prediction that are consistent with the observed correlation structure of our data, but that require further work for confirmation.

1) Prediction 1: Leaving remnant trees will increase alectorioid lichen and cyanolichen biomass. Mechanism (a): Directly, remnant trees may provide canopy habitat that maintains the environment necessary for the establishment and growth of *Lobaria oregana* and alectorioid lichens. Mechanism (b): Remnant trees may maintain a source of propagules, from persistent populations of species associated with old growth, which rebuild populations in the regeneration cohort at a greater rate than in stands lacking nearby propagule sources. Mechanism (c): Indirectly, remnant trees may shade regenerating stands and promote both lichens associated with old growth and *Tsuga heterophylla.*

2) Prediction 2: A dense regeneration cohort will

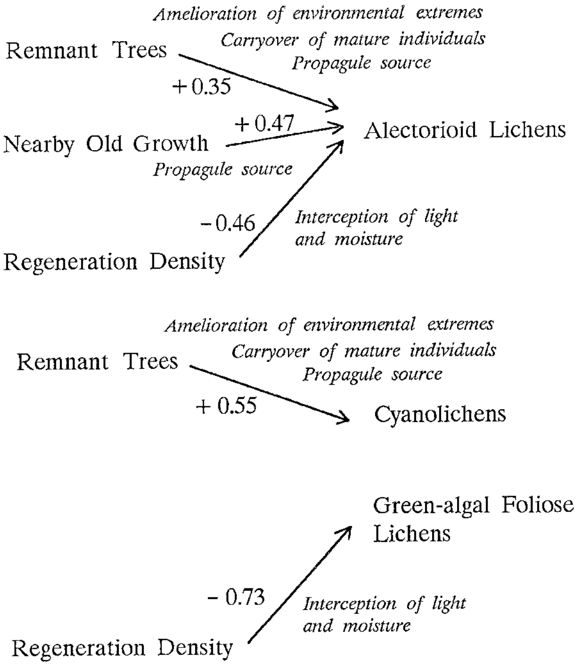

FIG. 3. Proposed hypothetical relationships between the number of remnant trees, regeneration density, and lichen biomass. Signs indicate expected direction of relationships.

reduce alectorioid and green-algal foliose lichen biomass. Mechanism: Lichen growth and establishment may have been suppressed in dense stands, due to decreased light and moisture penetration through the canopy.

In our study, as levels of green-tree retention increased in our stands, the basal area of *T. heterophylla* tended to increase slightly, whereas that of *Pseudotsuga menziesii* decreased (Zenner and Acker 1997). Differences in understory vascular plants in these stands (Traut 1994) suggest that factors such as light interception, throughfall, and other microclimatic conditions differed between the remnant and nonremnant tree stands. Some of these differences may be mediated by the larger proportion of *Tsuga* in the remnant tree stands, facilitating survival of residual canopy lichen communities. The effectiveness of remnant trees in rebuilding epiphyte populations depends on the survival of the trees and their epiphytes after the canopy is opened. There is considerable concern that remnant trees will blow down soon after their neighbors are harvested, but it appears that, in the Pacific Northwest, at least some remnant trees persist for a long time (Spies and Franklin 1988, Agee 1991). Survival of the epiphytes in isolated trees has not been studied directly in the Pacific Northwest, but results from the tropics suggest that the distribution and abundance of nonvascular epiphytes will change, but that species associated with old growth may persist (Sillett et al. 1995). Variation in the structure of young stands has been largely neglected as a factor controlling the rate and type of epiphyte development. However, diversity and abundance of epiphytic lichens are linked to the structural diversity of young conifer stands, particularly to the presence of canopy gaps filled with hardwood trees and shrubs (Neitlich and McCune 1997). In Montana, stands partially opened by disease or fire often host richer epiphyte communities (McCune and Antos 1981).

None of our landscape context variables, current or historic, was strongly related to current biomass of epiphytic macrolichens. Observations that the landscape context is important for rebuilding epiphyte species are primarily anecdotal. Many observers have noted that cyanolichens are more abundant in the edges of young stands that adjoin old forests than in the interior of large, young stands. Sampling lichen litter fragments on a transect from an old forest into a clearcut revealed an exponential decline in the biomass of fragments, moving away from the forest edge (0–50 m from the edge; B. McCune, *unpublished data*). Based upon Stevenson's (1978) report of a similar pattern with *Alectoria* and *Bryoria* fragments, Esseen et al. (1996) proposed that, due to the large size of their fragments, alectorioid lichens disperse shorter distances than species that rely on soredia or other, smaller propagules. Our failure to detect an influence on canopy lichen biomass by the current or historic landscape context around out plots suggests that either microclimate or substrate conditions in green-tree retention stands are not suitable for the establishment and growth of these epiphytes, or that lichen dispersal is far more limited than we had believed, such that dispersal over distances >35 m is ineffective.

CONCLUSIONS

This study addressed the need to quantify the influence of green-tree retention, via comparisons of stands with and without analogous remnant trees, on canopy lichen communities. Our results indicate that, in lower elevation stands, dispersal is potentially limiting for alectorioid lichens and cyanolichens, but not for the dominant green-algal foliose lichens. If we assume that epiphytes respond similarly to green-tree retention cuts and to fires that result in scattered remnant trees, then our retrospective study leads to the following predictions: (1) Alectorioid lichens and cyanolichen species, such as *Lobaria oregana*, that are associated with old growth will be favored by leaving 3–24 dominant and codominant green trees, rather than clear-cutting; (2) Populations of green-algal foliose species, particularly in the genera *Hypogymnia* and *Platismatia*, may be relatively resilient to both clearcuts and green-tree retention cuts. These species may be more effective at dispersal and colonization than are alectorioid lichens and cyanolichens.

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