

Effects of Forest Age and Forest Structure on Epiphytic Lichen Biomass and Diversity in a Douglas-fir Forest

Abstract

Epiphytic lichens contribute to the biological diversity of old forests, but little is known about the changes that occur in lichen communities as forests age and become structurally more complex. We compared forest age and forest structure as indicators of lichen biomass, richness, and community on the Gifford Pinchot National Forest in Washington. Epiphytic lichens were sampled in 1995 and 1996 on 21, 13 ha forested units, ranging from 75 to 165 years old. Canopy lichen litterfall was sampled in 15, 12.5 m² plots per unit. Mean lichen litterfall biomass differed significantly between years, but species composition did not. Forest structure variables were refined using principal component analysis resulting in the first two principal components accounting for 75.5% of the variation in the samples-by-structural-variables matrix. Principal components 1 and 2 represented structure and were compared to forest age by correlating each with lichen biomass, richness, and community composition. Multiple regression was also used to test the relationship of age and eight structural variables against lichen biomass, richness, and community composition. In both years, and in both analyses, forest structure explained more variance in lichen biomass and richness than forest age, whereas age explained more variance in lichen community composition. The structural variables that were important for predicting lichen biomass differed from those predicting lichen richness. In mature forests, structure may be a better predictor of lichen biomass and diversity than forest age. Techniques that emphasize structure have the potential to help forest managers assess mature stands for their biological value.

Introduction

Understanding the processes that contribute to the accumulation of biological diversity in old-growth forests may affect how we choose to manage all forests. Old-growth forests are biologically diverse and support higher numbers of amphibians, reptiles, wintering birds, small mammals, macrolichens, and vascular plants than young forests (Hansen et al. 1991, Goward 1994, Carey and Johnson 1995).

However, it is unclear whether biological diversity is a product of age or of the structural characteristics that change with age. Old-growth Douglas-fir (*Pseudotsuga menziesii*) forests are characterized by being both old and complex in their structure. As a Douglas-fir forest ages, developmental changes include increased variation in tree height and diameter and the creation of snags, logs, canopy gaps, and a heterogeneous understory (Warren 1990, Hansen et al. 1991). Thus, older forests have a more spatially heterogeneous structure than younger forests, which creates more microhabitats with the potential to support a greater array of plants and animals, particularly those with specialized niches (Kuuluvainen et al. 1996). However, not all for-

ests within the same climatic zone develop structural variation over time in the same manner (Carey 1995); thus, the structural appearance of a forest does not always reflect its true age (Carey 1995, Latham 1996). Forest structure is not only a product of age but also a product of site conditions, weather patterns, disturbance regimes, species composition, and other factors (Warren 1990).

Few studies have tried to separate the effects of forest structure and age on species abundance and diversity. Most research has compared the extremes of forest structure (i.e., managed versus natural forests) or the extremes in forest ages (Mannan and Meslow 1984, Neitlich 1993, Carey 1995). Consequently, little information is available to guide forest managers in assessing maturing natural forests, those between 70 and 200 years old, as potential repositories of biological diversity. Stands of these ages represent a substantial portion of forests in the Pacific Northwest (Hansen et al. 1991).

Epiphytic lichen communities provide a good study system for comparing the relative effects of forest structure and forest age on species diversity and abundance. Epiphytic lichen communities are diverse; their richness may be greater or equal to

that of vascular plants (Pharo and Beattie 1997). Lichens provide food and shelter for flying squirrels, deer, caribou, and invertebrates (Edwards et al. 1960, Rundel 1978, Robbins 1987, Waters and Zabel 1995, Rosentreter et al. 1997). Within forests, lichens play an integral role in nutrient cycling (Pike 1978, Callaway and Nadkarni 1991, Knops et al. 1996). This role is especially significant in the Pacific Northwest where high lichen biomass, including cyanolichens, and rapid litterfall decay provides an input of nitrogen and other minerals into the ecosystem (Pike 1978, McCune 1994). Epiphytic lichens are also actively used to monitor air quality and serve as indicators of forest health (McCune et al. 1997). Here we compare the relative importance of forest age and forest structure for predicting lichen biomass, lichen richness, and lichen community composition in mature Douglas-fir stands (75-165 years old) that have naturally regenerated after fire in the Pacific Northwest.

Study Area

Forest structure and lichen biomass were measured on the Gifford Pinchot National Forest in Washington using study sites established for the Demonstration of Ecosystem Management Options (DEMO) study sponsored by the United States Forest Service and Washington State Lands (Anonymous 1996a). This study is part of an interdisciplinary, multi-agency project to evaluate impacts of different harvest treatments on the flora and fauna of Washington and Oregon. Some of the terminology used here (e.g. 13 ha study units) are for the purpose of consistency with other DEMO publications.

Three forested regions (hereafter, called blocks) were chosen on the Gifford Pinchot National Forest (Figure 1). Each block consists of six forested units and each unit is about 13 hectares in size. Study units at the Butte block are approximately 75 years old and receive between 178 to 203 cm of precipitation annually (Brockway et al. 1983). Study units at the Paradise Hills block range from approximately 122 to 150 years old and receive between 254 to 305 cm of precipitation annually (Brockway et al. 1983). Study units at the Little White Salmon block range from approximately 125 to 165 years old and receive an average of 165 cm of precipitation annually (Brockway et al. 1983). Study units tended to be more similar

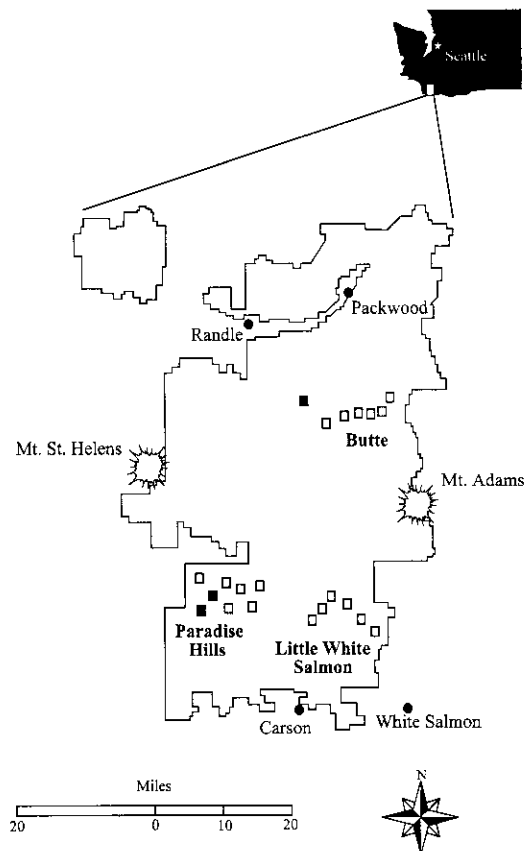


Figure 1. Gifford Pinchot National Forest, Washington. 21 study units: 18 DEMO units (□) and 3 additional units (■). Study units are not to scale.

to each other within blocks than among blocks (Table 1).

Young (Butte) and old (Paradise Hills, Little White Salmon) study units were not intermixed among blocks; thus, a high degree of spatial autocorrelation exists within the blocks of this experimental design (Table 1). To reduce this effect and to achieve better replication, we included additional units in the 1996 sampling so that some young and old forested units were sampled within some of the same blocks (Figure 1). Criteria for additional units were that forested stands had to (1) be dominated by *Pseudotsuga menziesii*, (2) be fire-regenerated, (3) contain no or little previous logging, (4) be at least 13 hectares in size, (5) be near DEMO units, (6) be between 120 and 170 years old to be considered older, and (7) be about 75 years old to be considered younger. Two younger units were found within the older Para-

TABLE 1. Environmental variables associated with each DEMO and additional unit (A1, A2, A3). LWS = Little White Salmon, PH = Paradise Hills.

Block	Unit	Forest Age (yrs.)	Mean Aspect	Elevational Range (m)	Mean Slope (%)
Butte	1	75	SE	963-1158	52
	2	75	SSE	988-1146	36
	3	75	E	1134-1280	42
	4	75	SE	1012-1134	40
	5	75	SE	1000-1207	47
	6	75	SE	975-1158	53
	A3	156	SW	1085-1207	46
LWS	1	157	W	841-1000	44
	2	148	N	805-988	65
	3	150	NW	829-975	43
	4	150	ENE	841-1012	52
	5	165	NW	902-1012	40
	6	125	NE	805-939	45
PH	1	128	ESE	878-920	13
	2	146	SSW	902-963	33
	3	128	N	927-969	09
	4	122	E	969-1000	18
	5	149	W	890-951	20
	6	150	SE	975-1024	11
	A1	82	W	939-1024	27
	A2	90	NE	988-1036	24

dise Hills block and one older unit was found near the younger Butte block. No suitable younger units were found near the Little White Salmon block.

Methods

Overstory Vegetation Sampling

A grid system of 63 or 64 permanent sampling points, spaced 40 meters apart, was laid out within each 13 ha DEMO unit. Most study units were buffered on all edges by at least 40 meters to minimize edge effects (Anonymous 1996b). Within each DEMO unit, at least 32 (of the 63 or 64) alternately spaced sampling points were selected to intensively measure the vegetation (Anonymous 1996a). In the three additional units, a grid system of 36, 42, and 64 temporary sampling points was established, of which 15 sampling points were randomly selected to intensively measure the vegetation.

All vegetation plots were centered on sampling points (hereafter, referred to as plot center). In each DEMO unit, canopy cover was measured at plot center and six meters from plot center in each cardinal direction, using a spherical densiometer. In the additional units, canopy cover was mea-

sured two meters from plot center in each cardinal direction with a spherical densiometer. The species and diameter at breast height (DBH) for trees of 5-14.9 cm DBH were recorded within a 0.01 ha plot (5.64 m radius) while all trees greater or equal to 15 cm DBH were recorded within a 0.04 ha plot (11.28 m radius). For each species, 40 trees were selected for height measurements. For species with fewer than 40 individuals, each tree's height was measured. Trees with dead, broken, or forked tops or damaged trunks were not sampled. Tree heights were measured using a laser (DEMO units) or clinometer and meter tape (additional units). Snags and stumps were measured within a 0.08 ha plot (15.96 m radius) and had to be at least 0.5 m tall and 25 cm in diameter. For each snag and stump, the species, diameter, height class, decay class, and angle from vertical lean were recorded (Anonymous 1996a). Elevation, slope, and aspect were also measured at the vegetation plot centers.

The modal forest age was determined using stand exam records for each DEMO unit from the Gifford Pinchot National Forest. On each additional unit, forest age was determined by coring randomly selected mature trees within the most common diameter class of those comprising the canopy.

Lichen Litterfall Sampling

Lichen biomass was sampled using the litterfall method developed by McCune (1994), which estimates the biomass and species composition in the canopy by sampling the lichen litter on the ground. In October of 1995, lichen litterfall was sampled on all 18 DEMO units. In October of 1996, lichen litterfall was re-sampled on nine DEMO units (three from each block) and on three additional units. Collecting lichens in the late summer or fall is preferred because weather patterns tend to be more calm; thus, large pulses in litterfall associated with major storms are avoided (McCune 1994). Lichen litterfall also decomposes quickly in these forests and most of the winter litter disappears within six months (McCune and Daly 1994). Lichen sampling was completed in seven days and no significant weather events occurred.

In each unit, lichen litterfall was collected near 15 random sampling points. Each lichen plot was circular with a 2 meter radius and an area of 12.5 m². In units with two years of sampling, the 1995

and 1996 lichen plot perimeters were about two meters apart.

All macrolichens collected in each plot were cleaned and sorted according to species and *Bryoria*, *Hypogymnia*, and *Usnea* only according to genus (Goward et al. 1994, McCune and Goward 1995). Each species was dried at 60°C for 24 hours and then weighed to the nearest mg. Mass for each species, in each of the 15 sample plots, was pooled at the unit level and converted to kilograms per hectare per year. Thus, our study focused on intensively sampling 21 very large (13 ha), homogenous units, rather than many small areas.

Data Analysis

Dependent Variables

Three dependent variables (i.e., lichen biomass, lichen richness, and lichen community composition) were used to compare forest age to forest structure. Lichen richness was calculated as the number of lichen species sampled per unit per year. Lichen community composition was analyzed using detrended correspondence analysis (DCA) (Hill 1979), which ordines samples (study units) based on their similarity and dissimilarity in lichen species abundances (program PC-ORD, McCune and Medford 1997). Lichen community composition (or DCA axis 1) was then correlated with forest age and forest structure. Correlations and multiple regressions were conducted separately for each year.

Forest Structure and PCA

Because forest structure is ambiguous and three dimensional in nature, quantifying structure is difficult. Our goal was to develop an index of forest structure that took into account its multi-dimensional nature. Age was excluded in order to test whether time or forest characteristics that may change with time contribute to the three dependent variables. To develop a simple, composite structural variable for each unit, we created a samples-by-structural-variables matrix that was analyzed using principal components analysis (PCA). The matrix consisted of 21 sample units and eight structural variables: the coefficients of variation in tree density, diameter, and height; Simpson's index of tree diversity; percent canopy openness; a snag index; number of snags per hect-

are; and percent of hardwood tree density. The snag index was calculated as:

$$\text{Snag Index} = \frac{\text{mean diameter} \times \text{mean height class}}{\text{mean decay class}}$$

The first and second principal components were then regressed with lichen biomass, lichen richness, and lichen community composition. Because the risk of a type-I error increases when conducting many significance tests that address a common null hypothesis, alpha levels were adjusted using the sequential Bonferroni test (Rice 1988).

We chose these eight structure variables because they have been shown to affect epiphytic lichens. Tree height affects vertical stratification in lichen species composition (McCune 1993). The size and variation in tree diameter and density can affect lichen abundance and diversity (Neitlich 1993), such that stands with large trees left from a previous cohort may have greater lichen biomass (Peck and McCune 1997). Lichen biomass has been negatively correlated with increasing percent of canopy closure and with increasing stand density, presumably because low light levels retard lichen growth and high tree density retards colonization of wind-dispersed lichen species (Neitlich 1993). The composition of tree species and the ratio of deciduous to coniferous trees can also affect lichen diversity since some species prefer certain substrates. Higher lichen diversity was found in coniferous canopies broken up by hardwood trees and shrubs (Neitlich and McCune 1997). Snags are thought to provide good habitat for epiphytic lichens (Rosentreter 1995). Hard and tall snags are assumed to provide better habitat for most epiphytic lichens because hard snags offer a sturdy substrate and tall snags may provide more surface area with high light conditions. Soft snags provide a crumbly substrate, which may be difficult for lichens to colonize.

In the samples-by-structural-variables matrix, we chose to emphasize the heterogeneity of the habitat in each study unit. For each structural variable, the lowest number was set equal to one and all other numbers represent the order of magnitude higher than 1.0. This was done so that the measurement unit of a particular variable would not disproportionately bias the ordination. To test whether complex structure yielded greater lichen biomass and species diversity than simple structure, we ordered variables in the matrix, such that

small values represented a simple structure and larger values represented increasingly complex structure. We based structural complexity largely on variation in stand characteristics. The density of large trees and the standard deviation in tree diameter has been shown to increase with forest age (Hansen et al. 1991). Thus, in our matrix, higher values of the coefficient of variation in tree height, density, and diameter represent increasingly greater structural complexity. Snags are evidence of the structural legacy from a pre-disturbance condition and snags promote biological diversity (Hansen et al. 1991); thus, we assumed that a complex structured forest would have more snags per hectare than a simple structured forest. Zenner (2000) found that intermediate numbers of residual trees (those surviving a disturbance) and intermediate mixtures of tree species were positively associated with structural complexity. Hardwood trees do not dominate the coniferous forests of the Pacific Northwest, but they do add heterogeneity within these forests; thus, hardwood tree density should increase with structural complexity. As a young, dense forest grows, gaps develop in the canopy due to disease, fire, and other causes. Thus, a more complex forest structure should have a larger percent of canopy openness, as well as canopy patchiness.

Multiple Regression

Backward stepwise multiple regression was used to compare age and each structural variable independently, in order to evaluate what attributes of a mature forest contribute to predicting lichen biomass, richness, and community composition (SPSS, release 6.1, 1994). Data sets for 1995 and 1996 were analyzed separately. Problems with multiple regression include curvilinearity, heteroscedasticity, non-normality, and outliers, which can be assessed using plots of residual versus predicted values (Hamilton 1992). Each dependent variable model was assessed for potential problems, and to obtain a more normal distribution of the residuals, the square-root of age was used in the lichen biomass regression, the log base 10 of snag index was used in the lichen richness regression, and the square of snag number was used in the lichen community composition regression.

Results

Comparison of the nine units that were sampled in both 1995 and 1996, showed that mean epi-

phytic lichen biomass was significantly higher in 1996 ($13.8 \text{ kg/ha} \pm 2.6 \text{ S.E.}$ in 1995, $20.3 \text{ kg/ha} \pm 4.7 \text{ S.E.}$ in 1996; paired $t = -2.629$, $df = 8$; $P = .030$). In addition, lichen richness in 1995 was equal to or lower than lichen richness in 1996 for all units. We found lichen biomass and richness were significantly correlated in 1995 ($r^2 = 0.29$, $P = 0.022$) and 1996 ($r^2 = 0.34$, $P = 0.046$) implying that greater biomass can result in higher richness. However, the higher richness in 1996 was a result of finding minute quantities of a few uncommon species (<0.5% of total biomass) rather than large-scale changes in dominant species (Figure 2).

Principal components analysis (PCA) ordination showed that principal components 1 and 2 accounted for 75.5% of the variation found within the unit sample-by-structure-variables matrix. Specifically, principal component 1 accounted for 42.5% and principal component 2 accounted for

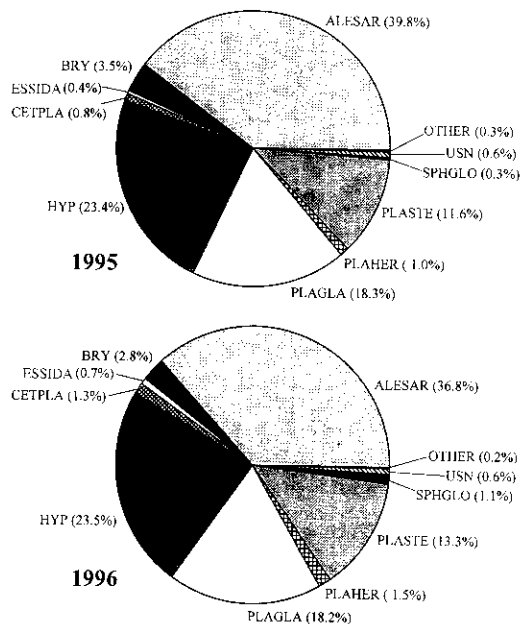


Figure 2. Species composition of total lichen litterfall biomass in 1995 and 1996. ALESAR = *Alectoria sarmentosa*, BRY = *Bryoria*, ESSIDA = *Exsingeriana idahoensis*, CETPLA = *Cetraria platyphylla*, HYP = *Hypogymnia*, PLAGLA = *Platismatia glauca*, PLAHER = *Platismatia herrei*, PLASTE = *Platismatia stenophylla*, SPHGLO = *Sphaerophorus globosus*, USN = *Usnea*, OTHER = species with less than 0.1% biomass.

33.0%. The other six principal components accounted for the remaining 24.5% of the variation in the matrix and each had eigenvalues less than 1.0. Coefficient of variation (c.v.) in tree height, c.v. in tree density, percent of canopy openness, and percent of hardwoods were the dominant variables in principal component 1 (PC 1) while c.v. in tree diameter, Simpson's index of tree diversity, number of snags per hectare, and snag index dominated principal component 2 (PC 2) (Table 2). Principal component 1 of forest structure ranged from simple to complex with all Little White Salmon units falling on the complex end, and Butte and Paradise Hills units intermixed towards the simple end of the gradient.

TABLE 2. Coefficients of determination (r^2) for structure variables regressed against forest age. Factor loadings of each structure variable on principal components 1 and 2 are also shown. CVDBH, CVHT, and CVTREE = coefficient of variation in tree diameter, height, and density; DIVERSITY = Simpson's index of tree diversity; LIGHT = percent canopy openness; SNAG NO = snag number per hectare; SNAG INDEX = snag index; WOOD = percent hardwoods.

Structure Variables	AGE	PC 1	PC 2
LIGHT	0.05	0.91**	-0.13
CVHT	0.08	0.80**	-0.01
CVTREE	0.22*	0.81**	-0.15
WOOD	0.12	0.87**	0.25
CVDBH	0.16	0.53*	0.75**
DIVERSITY	0.10	-0.12	0.91**
SNAG NO	0.06	-0.46	0.62
SNAG INDEX	-0.26*	-0.02	-0.87**

* Significant at the 0.05 level.

** Significant at the 0.01 level.

Lichen Biomass

In 1995 and 1996, epiphytic lichen biomass increased linearly with increasing forest age and with PC 1 of forest structure (Figure 3). However, PC 1 of forest structure explained more variation in lichen biomass than did forest age in 1995 ($r^2_{\text{structure}} = 0.34$, $P = 0.155$ versus $r^2_{\text{age}} = 0.22$, $P = 0.394$) and in 1996 ($r^2_{\text{structure}} = 0.63$, $P = 0.031$ versus $r^2_{\text{age}} = 0.17$, $P = 0.754$) (Figure 3). Lichen biomass did not correlate with PC 2 of forest structure in 1995 ($r^2 < -0.01$, $P = 0.996$) or in 1996 ($r^2 = -0.15$, $P = 0.754$). Based on the corrected P -values, using the sequential Bonferroni test, only the relationship between 1996 lichen biomass and

PC 1 of forest structure was statistically significant. These regressions indicate that the four attributes of forest structure that are the primary correlates with PC 1 (c.v. tree in density, c.v. tree in height, percent canopy openness, and percent hardwoods) were significant in explaining epiphytic lichen biomass. Based on regressions with PC 2, c.v. in tree diameter, tree diversity, snag number, and snag index correlated poorly with epiphytic lichen biomass.

Multiple regression showed that 78% of the variance in 1995 lichen biomass was explained by percent canopy openness, forest age, c.v. in tree height, and percent hardwoods, while 96% of the variance in 1996 lichen biomass was attributed to c.v. in tree diameter, percent canopy openness, forest age, and percent hardwoods (in order of importance) (Table 3). Thus, multiple regression analysis supported the simple correlations in that structural components of forest were better correlates with lichen biomass than forest age.

Lichen Richness

Epiphytic lichen richness increased linearly with increasing forest structure (PC 1) complexity in both years; whereas, the relationship between lichen richness and forest age resulted in nearly a flat slope (Figure 4). Principal component 1 of forest structure explained more variation in lichen richness than forest age in 1995 ($r^2_{\text{structure}} = 0.53$, $P = 0.017$ versus $r^2_{\text{age}} = 0.06$, $P = 0.794$) and in 1996 ($r^2_{\text{structure}} = 0.19$, $P = 0.754$ versus $r^2_{\text{age}} < 0.01$, $P = 0.996$) (Figure 4). Lichen richness did not correlate with PC 2 of forest structure in 1995 ($r^2 < 0.01$, $P = 0.996$), but it did correlate in 1996 ($r^2 = 0.35$, $P = 0.394$). Based on the corrected P -values, using the sequential Bonferroni test, only the relationship between 1995 lichen biomass and PC 1 of forest structure was significant.

The variables that were significant in the multiple regressions for lichen richness were different from those in the multiple regressions for lichen biomass. In 1995, 46% of the variance in lichen richness was attributed to the c.v. in tree density, while in 1996, 62% of the variance in lichen richness was attributed to snag index and percent hardwoods (in order of importance) (Table 4). These results support the multivariate analyses in that structural variables predict lichen richness better than age.

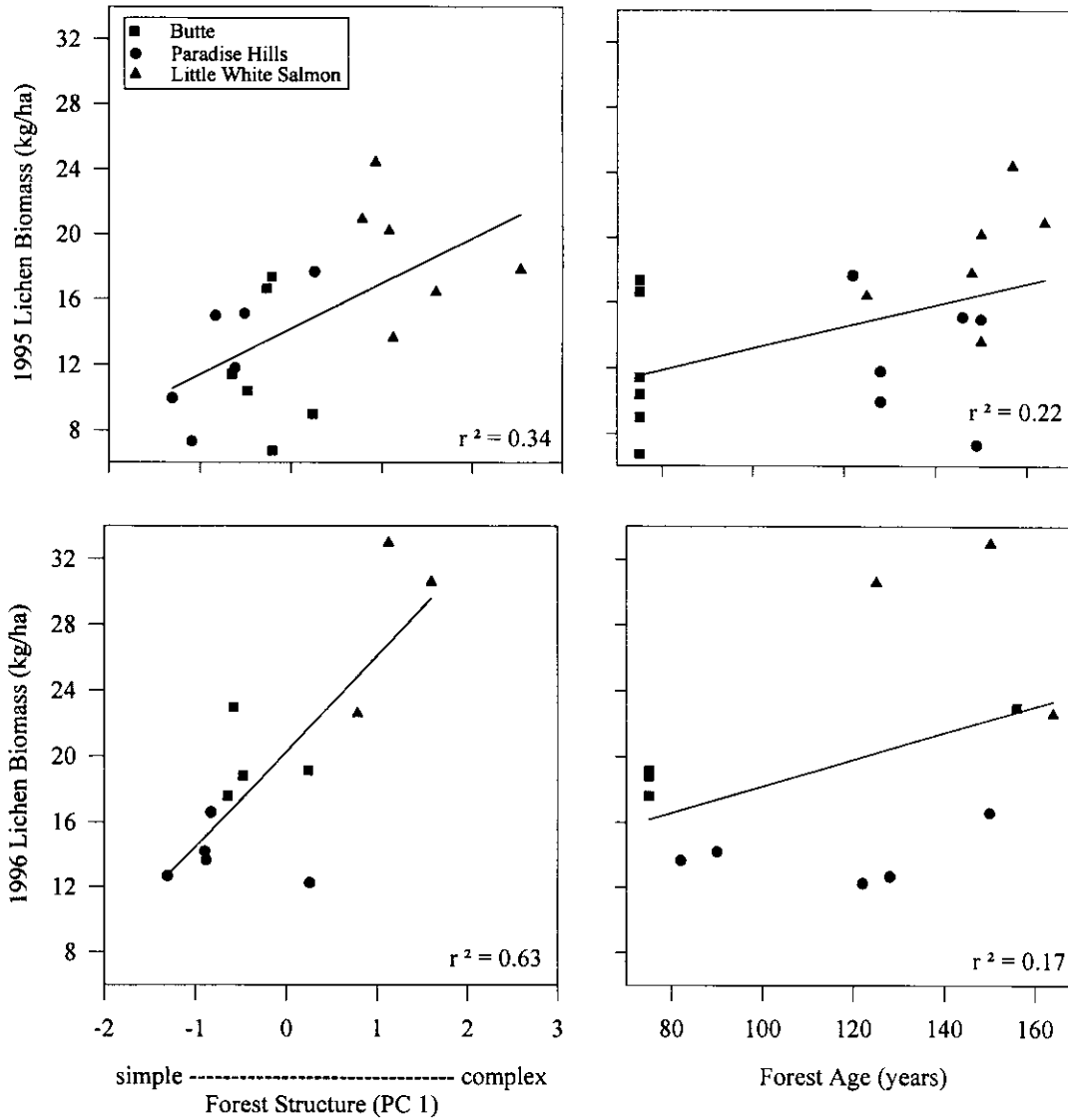


Figure 3. Lichen biomass regressed against forest structure (PC 1) and forest age for 1995 and 1996.

TABLE 3. Coefficients for lichen biomass regressed against structure and age variables in 1995 and 1996 using backward multiple regressions. SQAGE = square-root of forest age; CVDBH, CVHT, CVTREE = coefficient of variation in tree diameter, height, and density; DIV = Simpson's index of tree diversity; LIGHT = percent canopy openness; SNAG NO = number of snags per ha; SNAG INDX = snag index; WOOD = percent hardwoods.

Dependent Variable	SQ AGE	CV DBH	CV HT	CV TREE	DIV	LIGHT	SNAG NO	SNAG INDX	WOOD	constant	F value	R ²	N
Lichen Biomass—1995	1.32**	—	-0.14	—	—	0.56**	—	—	-0.21	-5.38	11.80**	0.78	18
Lichen Biomass—1996	1.67**	-0.71**	—	—	—	0.66**	—	—	0.63**	18.23	37.04**	0.96	12

* Significant at the 0.05 level.

** Significant at the 0.01 level.

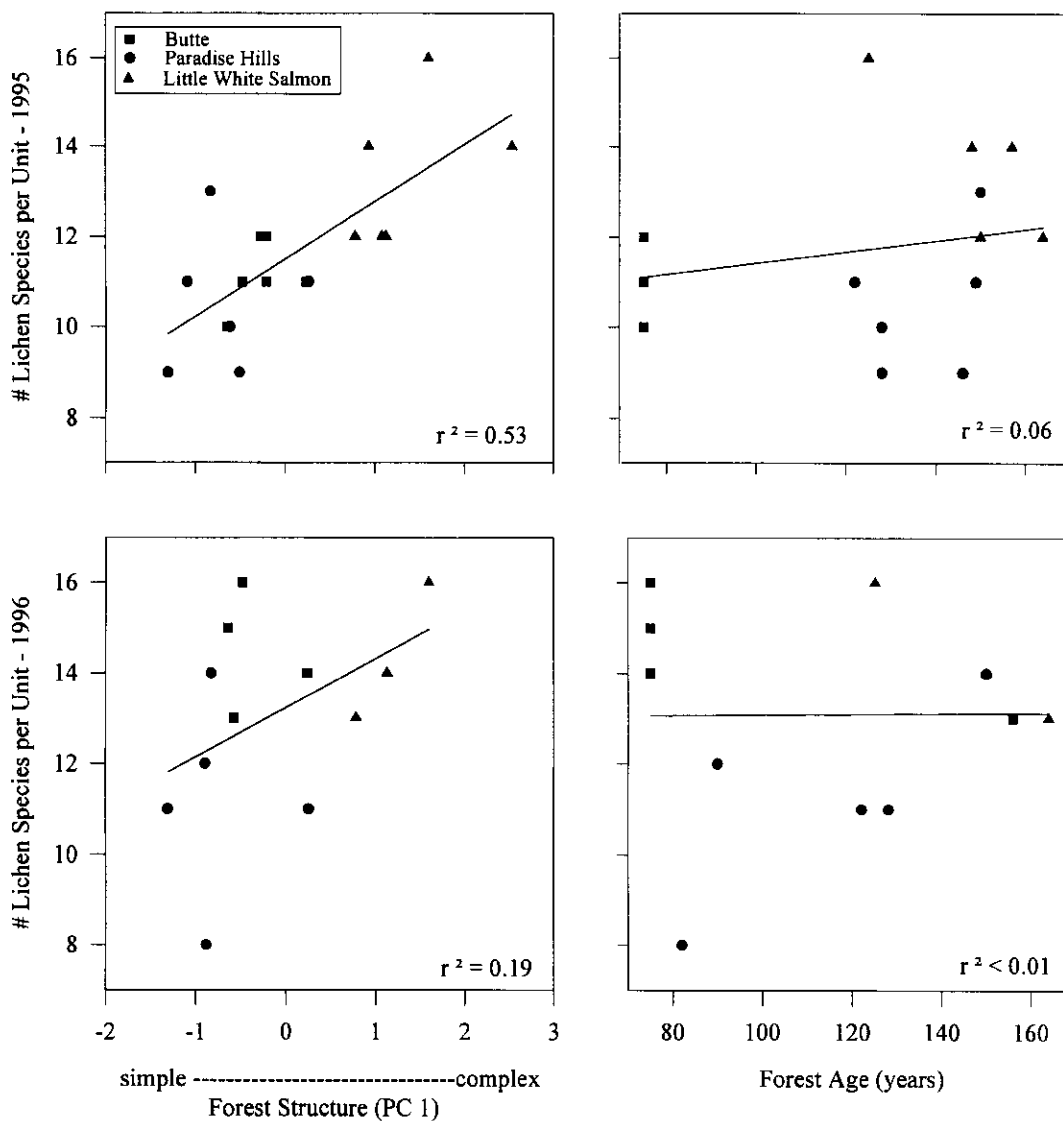


Figure 4. Lichen richness regressed against forest structure (PC 1) and forest age for 1995 and 1996.

TABLE 4. Coefficients for lichen richness regressed against structure and age variables in 1995 and 1996 using backward multiple regressions. AGE = forest age; CVDBH, CVHT, CVTREE = coefficient of variation in tree diameter, height, and density; DIV = Simpson's index of tree diversity; LIGHT = percent canopy openness; SNAG NO = number of snags per ha; LSNAG INDX = log 10 of snag index; WOOD = percent hardwoods.

Dependent Variable	CV		CV	CV	DIV	LIGHT	SNAG LSNAG			constant	F value	R ²	N
	AGE	DBH	HT	TREE			NO	INDX	WOOD				
Lichen Richness—1995	—	—	—	0.07**	—	—	—	—	—	9.03**	13.70**	0.46	18
Lichen Richness—1996	—	—	—	—	—	—	—	9.76**	0.23*	-3.29	7.38*	0.62	12

* Significant at the 0.05 level.

** Significant at the 0.01 level.

Lichen Community Composition

Forest age explained more variation in lichen community composition and was significant (based on the corrected P -values using the sequential Bonferroni test) in 1995 ($r^2 = 0.80$, $P < 0.017$), but not significant in 1996 ($r^2 = 0.44$, $P = 0.220$) (Figure 5). Although PC 1 of forest structure explained less variation in lichen community composition, the correlation was significant (based

on the corrected P -values using the sequential Bonferroni test) in 1995 ($r^2 = 0.43$, $P = 0.044$) but not significant in 1996 ($r^2 = 0.35$, $P = 0.394$) (Figure 5). Principal component 2 of forest structure was not significantly related to lichen composition in 1995 ($r^2 = -0.24$, $P = 0.394$) or in 1996 ($r^2 = 0.17$, $P = 0.754$). The distribution of study units along the DCA ordination axis 1 was highly correlated with their geographic locations in 1995

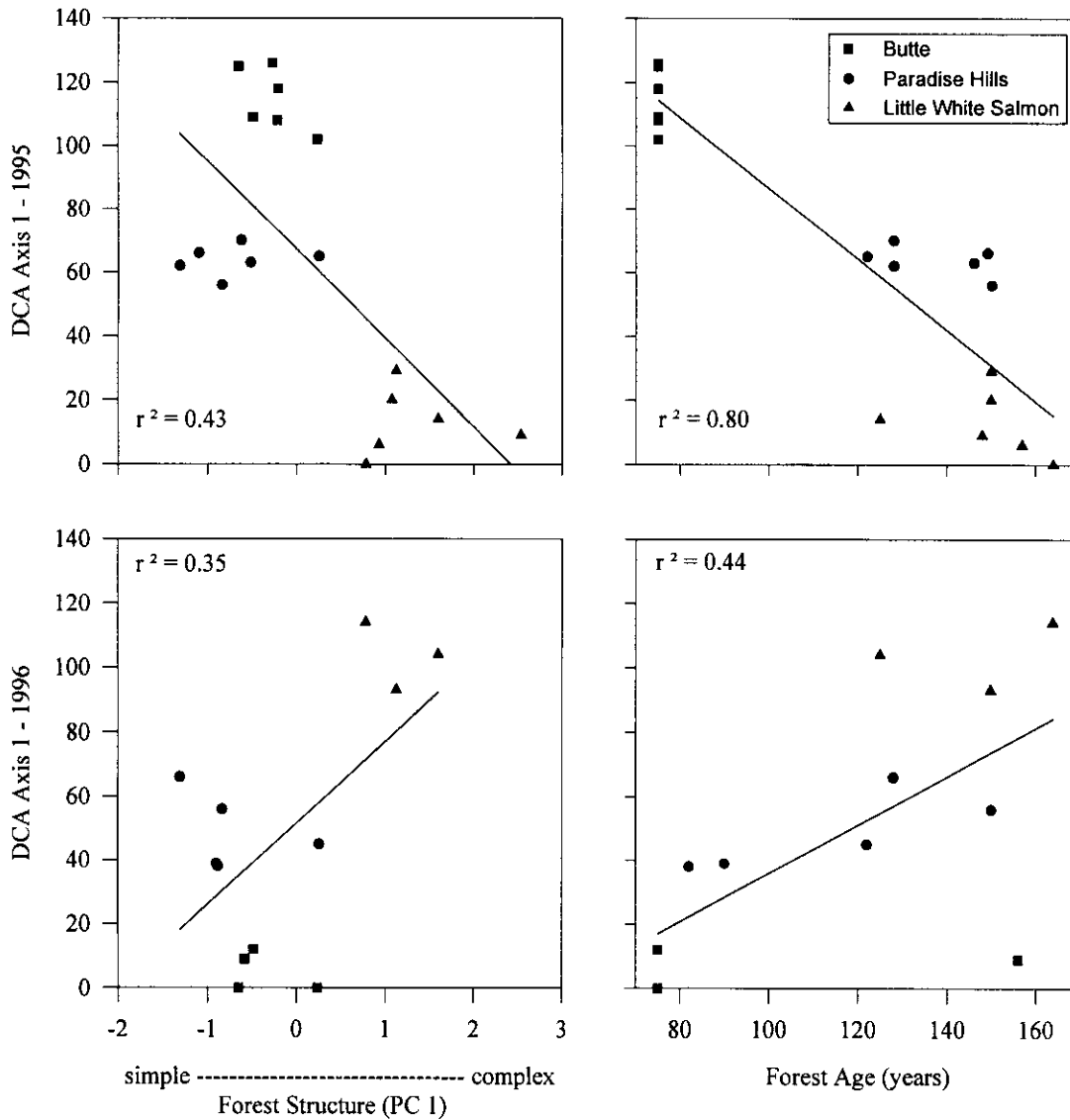


Figure 5. DCA axis 1 (lichen community composition) regressed against forest structure (PC 1) and forest age for 1995 and 1996.

Table 5. Coefficients for lichen community composition (DCA axis 1) regressed against structure and age variables in 1995 and 1996 using backward multiple regressions. AGE = forest age; CVDBH, CVHT, CVTREE = coefficient of variation in tree diameter, height, and density; DIV = Simpson's index of tree diversity; LIGHT = percent canopy openness; SNAG NO 2 = square of snag number; SNAG INDX = snag index; WOOD = percent hardwoods.

Dependent Variable	CV			DIV	LIGHT	SNAG			constant	F value	R ²	N
	AGE	DBH	HT			TREE	NO 2	INDX				
Composition—1995	-0.78**	—	-0.55*	-1.01**	-28.50	—	—	—	235.18**	94.94**	0.97	18
Composition—1996	—	—	—	1.91**	—	3.37*	130.19**	—	-317.83**	11.80**	0.82	12

* Significant at the 0.05 level.

** Significant at the 0.01 level.

(Figure 5). In 1996 sampling efforts were designed to minimize geographic effects by pairing young and old units within the same block. Although geographic location does confound the relationship between age and lichen community composition and the relationship between forest structure and lichen community composition, it does not confound the comparison of age to forest structure.

The 1995 multiple regression model attributed 97% of the variance in lichen community composition to forest age, c.v. in tree density, c.v. in tree height, and tree diversity (in order of importance) (Table 5). The 1996 model attributed 82% of the variance in lichen community composition to snag number, c.v. in tree density, and percent canopy openness (in order of importance) (Table 5). Therefore, forest age was important in 1995, but its effect diminished in 1996 where old and young stands were sampled within the same block.

Discussion

Our results suggest that predictions of epiphytic lichen biomass and species richness in mature forests are improved by incorporating attributes of structure rather than by relying solely on forest age. This supports the statement of Peck and McCune (1997) that variation in the structure of young stands has been largely neglected as a factor controlling the rate and type of epiphyte development. Our results also agree with a study of young, managed coniferous stands in which epiphytic lichen abundance and diversity was linked to their structural diversity (Neitlich and McCune 1997).

Because epiphytic lichen communities may be slow to establish and some nitrogen-fixing lichens

may be slow to disperse (Sillett et al. 2000), lichens may accumulate in biomass and numbers simply as a function of forest age (Sillett and Neitlich 1996). However, forests that are similar in age can develop substantially different structures (Latham 1996). Environmental and biotic factors interact with forest age causing structural development to accelerate, stagnate, or cycle (Latham 1996). Therefore, the diversity and abundance of old growth-dependent macrolichens may actually be an indicator of how long a forest has developed without a major disturbance (forest continuity) rather than the forest's true age (Goward 1994). Forested stands growing on similar sites (i.e., parent soil materials, topographic position) were found to have large differences in species composition and these differences were attributed to historical events (e.g. fire, timing of good seed crops with weather) (McCune and Allen 1985). In Oregon, two attributes of forest structure (i.e., number of snags, abundance of ericaceous shrubs) were found to develop independently of forest age (Carey 1995). Although forest age may be a convenient summary of aspects of forest structure, it is not a direct measure and may be misleading in describing mature, fire-regenerated forests of similar ages on similar sites.

Halpern and Spies (1995) studied plant diversity along a chronosequence of natural and managed forests in which forest structure complexity increased with forest age. They proposed three mechanisms that could account for the greater species diversity or the close affinity of certain plant species found within old-growth forests: changes in forest resources (a mosaic of light conditions, greater soil moisture, higher humidity); greater complexity of the vertical and horizontal components of the forest; and a high

sensitivity of associated plant species to fire disturbance, such as having slow re-establishment rates after disturbance. All of these mechanisms are likely to be correlated with structural attributes of forests.

In this study the multivariate and multiple regression approaches used to compare the importance of forest age and structure were very complementary. The variables that contributed the most to predicting lichen biomass were five structural components. In order of their importance, these were: (1) greater canopy openness, (2) higher percentage of hardwood trees, (3) higher coefficient of variation in tree height, (4) higher coefficient of variation in tree diameter, and (5) higher coefficient of variation in tree density. Although not consistent between years, three structural variables contributed the most to predicting lichen richness: (1) coefficient in tree density, (2) snag index, and (3) percent hardwoods.

Lichen biomass and richness may reflect the forest's vertical and horizontal architecture, tree and shrub species composition, and the forest's available resources. High coefficients of variation in tree height and diameter generally indicate the presence of very tall and large trees, which have been found to support higher quantities of epiphytic lichens (McCune 1993). The distribution of lichen "groups" change along a tree's vertical profile, from top to bottom: green algal foliose lichens (e.g., *Hypogymnia*, *Platismatia*), green-algal pendent lichens (e.g., *Alectoria sarmentosa*), cyanolichens (nitrogen-fixing lichens), tufted fruticose lichens (e.g., *Sphaerophorus* and *Cladonia*), and bryophytes (McCune 1993, McCune et al. 1997b). Cyanolichen species concentrate in the "light transition zone" (13 to 37 m in height), that area marked by an abrupt change from bright light to dark (McCune et al. 1997b). Green algal fruticose and cyanolichen species are more abundant in stands that retain remnant trees from a previous cohort (Peck and McCune 1997). Remnant trees may influence the forest stand in two ways: (1) They may maintain a persistent source of lichen propagules. Recent studies demonstrate that the old-growth-associated cyanolichen, *Lobaria oregana*, is capable of growing on both young and old trees, but disperses itself poorly (Sillett et al. 2000). Thus, large trees containing *Lobaria oregana* facilitate its colonization by inoculating surrounding trees (Sillett et al. 2000); (2) Dense stands of trees may suppress

lichen establishment (Peck and McCune 1997). High branch density may block the movement of wind-dispersed lichen propagules and reduce light penetration, adversely affecting lichen establishment and growth of certain species (Neitlich 1993). Thus, as forest density becomes more variable, light penetration increases, and suitable habitat is created for other lichen species. Hardwood trees, especially within coniferous dominated forests, increase species diversity because some lichen species appear to prefer their less acidic bark (Neitlich 1993). Deciduous trees also increase lichen biomass by allowing precipitation and light to reach surrounding trees and shrubs during the winter and spring (Neitlich 1993).

High lichen diversity and abundance can have positive effects on other forest species. Epiphytic lichens provide food and shelter to a variety of canopy invertebrates; this physical structure created by lichens can influence spider communities (Uetz 1991). In northern Sweden, lichen abundance has been strongly correlated with the number and mass of invertebrates (Pettersson et al. 1995). Declines in many non-migratory birds, that rely on these invertebrates, may be a result of degraded (lichen) feeding habitat (Pettersson et al. 1995). The epiphytic lichen, *Bryoria*, provides important winter food for deer, flying squirrels, and caribou (Edwards et al. 1960, Rosentreter et al. 1997, Ward 1999).

Implications for Forest Management

Many studies have compared the flora and fauna of old-growth stands to that of naturally young stands and various degrees of managed stands (Mannan and Meslow 1984, Hejl and Wood 1991, Lesica et al. 1991, Hyvärinen et al. 1992, Neitlich 1993, Halpern and Spies 1995). These studies demonstrate that old-growth forests contain important components of biological diversity and therefore serve as a standard of comparison for other forests. As old-growth forests are logged or set aside as reserves, young and mature forests (70-200 years old) will supply an even greater portion of our timber needs (Hansen et al. 1991). Yet this age group, which covers a large proportion of our national forests, is often underestimated in its potential to harbor biological diversity (Hansen et al. 1991). If we are to maintain flora and fauna diversity at regional scales, mature forests must be managed to balance resource use and biological diversity.

Inventories of the complete biodiversity in forests are expensive and exceedingly difficult; however, relatively simple measurements of forest structure may serve as a good surrogate for the direct measurements of biological diversity (Kuuluvainen et al. 1996). Our data indicate that attributes of forest structure may serve as an assessment tool in middle-aged forests, as has been shown for old-growth forests (Warren 1990). Bailey and Tappeiner (1998) suggest that to achieve old growth characteristics in younger stands, the spatial arrangement and heterogeneity of stand structure must be managed and can be accomplished through altering the uniformity of thinning. O'Hara (1996) has showed that multiaged stands (structurally complex) can supply continuous wood production, as well as provide habitat for many species and aesthetic quality, if sustainable age/size class distributions are maintained. Our study supports the conclusions of other research, suggesting that retaining hardwoods, snags, and remnant (large or old) trees during logging would promote structural complexity and create a mosaic of light conditions, tree densities, and multi-canopy layering

(Halpern and Spies 1995, Rosentreter 1995, Neitlich and McCune 1997, Peck and McCune 1997). This would help maintain lichen biomass and diversity.

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