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Effects of forest age versus forest structure on epiphytic lichen biomass and diversity

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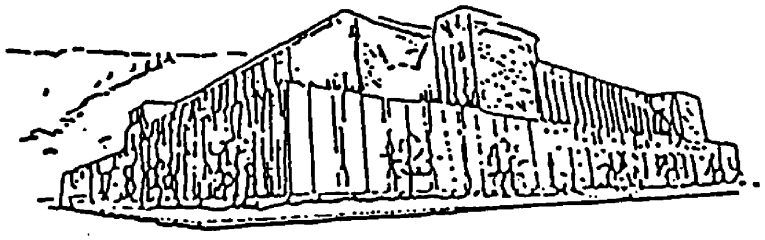

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EFFECTS OF FOREST AGE VERSUS FOREST STRUCTURE ON EPIPHYTIC LICHEN BIOMASS AND DIVERSITY

by

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B.A. The University of Montana, 1989

presented in partial fulfillment of the requirements

for the degree of

Master of Science

The University of Montana

1998

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Pipp, Andrea K., M.S. February 1998 Wildlife Biology

The Effects of Forest Age Versus Forest Structure on Epiphytic Lichen Biomass and Diversity

Director: Ragan M. Callaway RMC

Understanding the processes that affect biological diversity in old-growth forests may affect how we choose to conserve all forests. I compared forest age and forest structure as indicators of lichen biomass, richness, and community composition. This study was carried out on the Gifford Pinchot National Forest in Washington, as part of the Demonstration of Ecosystem Management Options project. Epiphytic lichens were sampled in 1995 and 1996 on 21, 13 ha forested units, ranging from 75 to 164 years old. Canopy lichen litterfall was sampled in 15, 12.6 m^2 plots per unit. Mean lichen litterfall differed significantly between years, but species composition did not. Forest structure variables were refined using principle component analysis resulting in axis 1 and 2 with a combined eigenvalue of 77.5%. These axes and forest age were then correlated with the dependant variables, lichen biomass, richness, and community composition. We used multiple regression to test the relationship of age and eight structure variables against each dependent variable, returning r^2 values between 0.46 and 0.97. In both years, and in both analyses, forest structure explained more variance in lichen biomass and richness, whereas, age explained more variance in community composition. The structural variables important for predicting lichen biomass differed from those predicting lichen richness. In mature forests, structure may be a better predictor of biological diversity than forest age.

Bryoria, an epiphytic lichen, is an important source of winter food and nesting material for *Glaucomys sabrinus.* However, the role of *Bryoria* in predicting quality habitat for *Glaucomys sabrinus* has not been investigated. I correlated the abundance of *Bryoria* with the abundance of *Glaucomys sabrinus* using simple linear regression. The abundances of *Bryoria* and *Glaucomys sabrinus* positively correlated with an r^2 of 0.54 for 1995 data and an r^2 of 0.67 for 1994-1996 data. These results support the literature that *Bryoria* may be an important component of *Glaucomys sabrinus* habitat in regions receiving a persistant snowpack.

Key Words: forest age, forest structure, epiphytic lichens, lichens, Pacific Northwest, DEMO, lichen litterfall, biological diversity, biomass, richness, community composition, Washington.

Key Phrases:

- Comparing the effects of forest age versus forest structure.
- Epiphytic lichens of northwestern forests.
- Demonstration of Ecosystem Management Options project.
- Factors affecting epiphytic lichen biomass and richness.

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THE EFFECTS OF FOREST AGE VERSUS FOREST STRUCTURE ON EPIPHYTIC LICHEN BIOMASS AND DIVERSITY

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Understanding the processes that affect biological diversity in old-growth forests may affect how we choose to conserve all forests. I compared forest age and forest structure as indicators of lichen biomass, richness, and community composition. This study was carried out on the Gifford Pinchot National Forest in Washington, as part of the Demonstration of Ecosystem Management Options project. Epiphytic lichens were sampled in 1995 and 1996 on 21, 13 ha forested units that ranged from 75 to 164 years old. Canopy lichen litterfall was sampled in 15, 12.6 m^2 plots per unit. Mean lichen litterfall differed significantly between years, but species composition did not. Forest structure variables were refined using principle component analysis. Principle components 1 and 2 explained 77.5% of the variance among units. These components and forest age were then correlated with the dependant variables, lichen biomass, richness, and community composition. We used multiple regression to test the relationship of age and eight structure variables against each dependent variable. The resulting r^2 values ranged from 0.46 to 0.97. In both years, and in both analyses, forest structure explained more variance in lichen biomass and richness, whereas, age explained more variance in community composition. The structural variables important for predicting lichen biomass differed from those predicting lichen richness. In mature forests, structure may be a better predictor of biological diversity than forest age.

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INTRODUCTION

Understanding the processes that affect biological diversity in old-growth forests may affect how we choose to conserve 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). Old-growth forests are characterized by being both old and complex in their structure. However, it is unclear whether diversity is simply a product of age or of forest characteristics that change with age. As a forest ages, developmental changes include increased variation in tree height and diameter, the creation of more snags, logs, and gaps, and the development of a heterogeneous understory (Warren 1990, Hansen et al. 1991). Thus, older forests appear to have a more spatially heterogeneous structure than young 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 forests within the same climatic zone develop structural variation over time in the same manner (Carey 1995), and large discrepancies between forest structure and forest age can occur (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 from age. Most research has compared the extremes of forest structure (managed versus natural forests) or extremes in forest ages (Mannan and Meslow 1984, Neitlich 1993, Carey 1995).

Consequently, little information is available to guide forest managers on how to assess mature forests, those between 70 and 200 years old, as potential repositories of biological diversity. Stands of these ages represent a significant amount of northwestern forests (Hansen et al. 1991). Further, research and conservation that focuses from old-growth forests to natural forests of all ages is needed to study whether old-growth forests actually differ in forest structure and species composition from younger natural forests (Hansen et al. 1991).

Epiphytic lichen communities provide a good study system for comparing the relative effects of forest structure versus forest age. Epiphytic lichens are diverse; their richness may be greater or equal to that of vascular plants at most sites (Pharo and Beattie 1997). Lichens provide food 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 (Nash 1996). Epiphytic lichens are also used to actively monitor air quality and serve as in indicator of forest health (McCune et al. 1997).

Here I compare the importance of forest age versus forest structure for predicting lichen biomass, lichen richness, and lichen community composition in fire regenerated, mature stands (70-200 years old) of the Pacific Northwest. My hypothesis is that epiphytic lichen biomass and species diversity should be more highly correlated with

forest structure than with forest age within mature forests. As forests age, their structural development varies, and forests that develop a complex forest structure should have greater epiphytic lichen biomass and diversity than forests with a simple structure. I tested this hypothesis using the lichen litterfall technique to quantify canopy lichens in naturally regenerated forests that ranged from 75 to 165 years old.

STUDY AREA

Forest structure data and lichen biomass were collected 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. units) is 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 and regenerated from fire. The Butte block is approximately 75 years old and receives about 178-203 cm of precipitation annually (Brockway et al. 1983). The Paradise Hills block ranges from approximately 122 to 150 years old and receives an estimated 254-305 cm of precipitation annually (Brockway et al. 1983). The Little White Salmon block ranges from approximately 125 to 164 years old and receives about 165 cm of precipitation annually (Brockway et al. 1983).

Young and old study units were not intermixed among blocks; thus, a high degree of spatial autocorrelation exists within the blocks of this experimental design. To reduce this effect and to acheive adequate replication, we included additional units for the study in 1996, so that some young and old forested units were sampled within the same block (Figure 1). Criteria for additional units were: (1) forests had to be dominated by *Pseudotsuga menziesii*, (2) be fire regenerated, (3) be at least 13 hectares in size, (4) be near DEMO units, and (5) the older additional units needed to be between 120 and 170 years old, and the younger additional units approximately 75 years old. Two younger units were found within the older Paradise 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 DEMO unit. Units were buffered by at least 40 meters along all edges to minimize edge effects and to provide an effective grid size for estimating the density of flying squirrels (Anonymous 1996b). Vegetation was intensively measured on a minimum of 32 alternate sampling points in each DEMO unit (Anonymous 1996a). The three additional units contained 36, 42, and 64 temporary sampling points. In each additional unit, overstory vegetation was sampled at 15 randomly selected sampling points using DEMO protocols for measuring vegetation (Anonymous 1996a).

Vegetation plots were centered on sampling points. Canopy cover was measured at plot centers and six meters from each plot center in each cardinal direction, using a spherical densiometer. In the additional units, canopy cover was measured two meters from plot center in each cardinal direction. 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). A sub-sample of 40 tree diameters per species was selected to measure their heights. Tree heights were measured using a laser (DEMO units) or clinometer and meter tape (additional units). For species with fewer than 40 individuals, each tree's height was measured. Trees with dead, broken, or forked tops or damaged trunks were excluded from height measurements. 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.

Modal forest age data was obtained for each DEMO unit from the Gifford Pinchot National Forest. On each additional unit, forest age was determined by coring randomly selected trees within the most common diameter class of those comprising the canopy.

Lichen Litterfall Sampling

Lichen biomass was collected using the lichen litterfall pickup method (McCune 1994), which estimates the biomass and species composition in the canopy by sampling

the lichen litter on the ground. In late October of 1995, lichen litterfall was sampled on all 18 DEMO units. In early 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, avoiding large pulses in litterfall associated with major storms (McCune 1994). Lichen litterfall also decomposes quickly in these forests and most of the winter litter should disappear within six months (McCune and Daly 1994). Lichen sampling was completed in seven days and no significant weather events occurred during sampling in either year.

In each unit, lichen litterfall was collected near 15 randomly picked sampling points. Each lichen plot is circular with a 2 meter radius and an area of 12.5 m^2. In each DEMO unit the lichen plot was placed such that it did not interfere with permanent vegetation sampling plots nor bisect pathways created by the field crews. Standing with the permanent sampling point at your back, lichen plots were located by travelling 10 m distant from the grid point along an azimuth unique to the unit (Appendix E, Tables E1-E2). Plot centers were then located perpendicular to this azimuth another three meters left (1995) or three meters right (1996) (Appendix E, Figure E1). Thus, the 1995 and 1996 lichen plot perimeters are about two meters apart. In the additional units, lichen plots were centered on the temporary sampling points.

All lichens collected in each plot were cleaned and sorted to species, except *Bryoria*, *Hypogymnia*, and Usnea were identified only to genus. I used Goward et al. (1994) and McCune and Goward (1995) as the basis for identification. 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, my sampling focused on intensively sampling 21 very large, homogenous units, rather than many, small areas. Lichen genera were also classified according to their functional group (McCune 1994). The cyanolichen functional group consists of all macrolichens with cyanobacteria as their photobiont; these genera fix nitrogen and are sensitive to air pollution (McCune 1994). The alectorioid functional group consists of pendant lichens which are known to serve as food sources for voles, flying squirrels, and deer (McCune 1994). The miscellaneous functional group consists of the remainder of macrolichen species, which do not fix nitrogen, are not known to be forage for mammals, and vary in their sensitivity to air pollution (McCune 1994). Species identifications were verified by Dr. Roger Rosentreter and voucher specimens were deposited in the University of Montana herbarium.

Data Analysis - Dependent variables

Three dependent variables, 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 derived using detrended correspondence analysis (DCA) (Hill 1979), which ordinates samples (study units) based on their similarity and dissimilarity in lichen species abundances (program PC-ORD, McCune 1993). Lichen community composition (or DCA axis 1) was then correlated with forest age and forest structure. Correlations and multiple regressions were conducted for each year, separately.

Data Analysis - Forest Structure

Because forest structure is ambiguous and three dimensional in nature, quantifying structure is difficult. My goal was to develop an index of forest structure that took into account its multi-dimensional nature. Thus, to develop a simple, composite structural variable for each unit, I created a samples by structure variables matrix that was analyzed using principal components analysis (PCA). The matrix consisted of 21 sample units and eight structure variables: the coefficient of variation in tree density, diameter, and height; Simpson's index of tree diversity; percent of canopy openness; a snag index; number of snags per hectare; and percent of hardwoods. A subjective index of snag quality was developed to estimate the quality of snags available in each unit for lichen habitat that incorporated the size and decay status of snags. The snag index was calculated as:

Snag Index = mean diameter x mean height class / mean decay class

I chose these eight structure variables because they have been shown to affect epiphytic lichens. Tree height affects vertical stratification in species composition (McCune 1993) and the size and variation in tree diameter and density can affect lichen abundance and diversity (Neitlich 1993). Lichen biomass may be greater in stands with large trees left from a previous cohort (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 slows down wind dispersed lichen species (Neitlich 1993). The mixture of tree

species and the ratio of deciduous to hardwood trees can also affect lichen diversity since some species prefer certain substrates. Neitlich and McCune (1996) found that lichen diversity increased within breaks in the coniferous canopy that were filled by hardwood trees and shrubs. The effects of snags on lichens have not been quantified, but they are thought to be good habitat for epiphytic lichens (Rosetreter 1995). Hard and tall snags are assumed to provide better habitat for 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 not suitable for slow growing lichens.

In the samples by structure variables matrix, I chose to emphasize the heterogeneity of the habitat in each study unit. Each structure variable was scaled using 1.0 as the minimum value. 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, I ordered variables in the matrix, such that small values represented a simple structure and larger values represented increasingly complex structure. I based structural complexity largely on variation in stand characteristics. Hansen et al. (1991) found that the density of large trees and the standard deviation in tree diameter increased with forest age. Thus, in my matrix, higher values of the coefficient of variation in tree height, density, and diameter represent increasingly greater structural complexity. Hansen et al. (1991) also found that the density of tall and large diameter snags increased with age classes. Snags are evidence of the structural legacy from a pre-disturbance condition and snags promote biological diveristy (Hansen et al. 1991); thus, I assumed that a complex forest would

have more snags per hectare than a simple structure. Zenner (Oregon State University, personal communication) found that intermediate levels of residual trees (trees left from a previous cohort) and intermediate mixtures of tree species was positively associated with structural complexity. Hardwood trees do not dominate the coniferous forests of the Pacific Northwest, but do add heterogeneity within these forests; thus, the variable, percent of hardwoods, increased with structural complexity. The percentage of forest occupied by gaps has been found to be higher in mature forests (80-200 years old) and lower in forests over 200 years old (Hansen et al. 1991). Thus, canopy openness should increase as young, dense forests become mature and gaps develop creating more patchiness in canopy cover.

This matrix was analyzed using principal components analysis (PCA) (SPSS, version 6.1, 1994). The first and second principal components were then regressed with lichen biomass, lichen richness, and lichen community composition. Forest age was also regressed against these dependent lichen variables. Because the risk of a type-1 error increases when conducting many significance tests that address a common null hypothesis, alpha levels were adjusted using the sequential Bonferroni test (Rice 1988).

Backward stepwise multiple regression was used as a second approach to examine the relationship between the dependent variables, lichen biomass, richness, and community composition and the nine independent variables (age and structure variables combined) for 1995 and 1996 (SPSS, release 6.1, 1994). 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 of snag index was used in the lichen richness regression, and the square of snag number was used in the lichen community composition regression.

The principal components analysis was used to create an index of structural complexity that combined structural variables which interact in nature. This approach was an attempt to examine structure in its natural, multi-dimensional state. Age was not incorporated within PCA in order to test whether time or forest characteristics that may change with time contribute to lichen biomass, richness, and community composition. The multiple regression technique was used to compare age and each structure variable independently, in order to evaluate what attributes of a mature forest contribute to predicting lichen biomass, richness, and community composition.

RESULTS

Comparison of the nine units sampled in 1995 and 1996, showed that mean epiphytic lichen biomass was significantly higher in 1996 (13.8 kg/ha ± 2.6 S.E. in 1995, 20.3 kg/ha ± 4.7 S.E. in 1996; paired t = -2.629, df = 8; P = .030). Although total lichen biomass differed between years, species composition and relative proportions were similar between years (Figure 2).

Principal components analysis (PCA) ordination accounted for 75.5% of the variation in the forest structure variables by sample units matrix, with principle components 1 and 2 representing, 42.5% and 33.0%, respectively. Coefficient of variation in tree height, c.v. in tree density, percent of canopy openness, and percent of hardwoods were the dominant variables in principle 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 principle component 2 (PC 2) (Table 1). Princple 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.

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 ($r^2 = 0.34$, P = 0.155) than forest age ($r^2 = 0.22$, P = 0.394) in 1995, and in 1996 ($r^2_{structure} = 0.63$, P = 0.031 versus $r^2_{age} = 0.17$, 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 these 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 comprise PC 1 (c.v. tree density, c.v. tree height, percent canopy openness, and percent hardwoods) were highly significant in explaining epiphytic lichen biomass. Based on regressions with PC 2, c.v. tree diameter, tree diversity, snag number, and snag index correlated poorly with epiphytic lichen biomass.

Multiple regression found that 78% of the variance in 1995 lichen biomass was explained by percent of canopy openness, forest age, coefficient of variation in tree height, and percent of hardwoods while 96% of the variance in 1996 lichen was attributed to c.v. in tree diameter, percent of canopy openness, forest age, and percent of hardwoods (in order of importance) (Table 2). Multiple regression supported the correlations of biomass with age, PC 1, and PC 2.

Lichen Richness

Epiphytic lichen richness increased linearly with increasing forest structure (PC 1) complexity and forest age in both years. However, PC 1 of forest structure explained more variation in lichen richness than forest age in 1995 ($r^2_{structure} = 0.53$, $P = 0.017$ versus $r^2_{age} = 0.06$, $P = 0.794$), and in 1996 ($r^2_{structure} = 0.19$, $P = 0.754$ versus $r^2_{age} < 0.01$, $P = 0.996$) (Figure 4). Lichen richness did not correlate with PC 2 of forest structure in 1995

($r^2 < 0.01$, $P = 0.996$), but 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 than 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 was attributed to snag index and percent of hardwoods (in order of importance) (Table 3). These results support the multivariate analyses in that structural variables predict lichen richness better than age.

Lichen biomass and richness were significantly correlated in 1995 ($r^2 = 0.29$, $P = 0.022$) and in 1996 ($r^2 = 0.34$, $P = 0.046$). However, higher richness in 1996 was a result of finding very small amounts of a few uncommon species (<0.5% of total biomass) rather than large-scale changes in dominant species.

Lichen Community Composition

To describe lichen community composition, a matrix of study units by lichen species abundances was analyzed using detrended correspondence analysis (DCA). DCA ordinates study units based on their similarity and dissimilarity in lichen species abundances. 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). PC 2 of forest structure was not significantly related to lichen composition in 1995 ($r^2 = -0.24$, $P = 0.394$), nor in 1996 ($r^2 = 0.17$, $P = 0.754$). The distribution of study units along the DCA ordination axis 1 was correlated with their geographic location in 1995 (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 structure, both variables are confounded to the same degree.

The 1995 multiple regression model attributed 97% of the variance to forest age, c.v. in tree density, c.v. in tree height, and tree diversity (in order of importance) (Table 4). The 1996 model attributed 82% of the variance to snag number, c.v. tree density, and percent of canopy openness (in order of importance) (Table 4). Therefore, forest age was important in 1995, but its effect diminished in 1996 where old and young stands were sampled within the same block.

Responses by Functional Groups and Species

In both years, all units contained the alectorioid and miscellaneous functional groups; however, cyanolichens were found in only one unit per year (see methods for definitions). The alectorioid functional group did not correlate with either forest age or structure in 1995 or 1996 (Table 5). Forest structure explained more variation in biomass of the miscellaneous functional group and was highly significant in 1995 ($r^2 = 0.41$, $P = 0.004$)

and 1996 ($r^2 = 0.52$, $P = 0.008$) (Table 5).

Seven common species were correlated with forest age and structure to assess the responses of individual species (Table 5). *Hypogymnia* biomass was the only lichen to correlate significantly with forest age in both 1995 and 1996 and to also correlate poorly with forest structure. Further, the relationship of *Hypogymnia* to both forest age and structure was negative. *Alectoria sarmentosa*, *Cetraria platyphylla*, *Platismatia glauca*, *P. stenophylla*, and *Usnea* had a direct linear increase in biomass with forest age and forest structure. *Cetraria platyphylla*, *Platismatia stenophylla*, and *Usnea*, significantly correlated more strongly with forest structure in both years than with forest age. However, *Platismatia stenophylla* also correlated significantly with forest age in 1995. *Platismatia glauca* correlated more strongly with forest structure in both years, but it was only significant in 1996. *Alectoria sarmentosa* and *Bryoria* were the only common lichen species for which there were inconsistent correlations between years and forest parameters. *Bryoria* was far more abundant in the young Butte units than in the older Paradise Hills and Little White Salmon units in 1995. The 1996 sampling design demonstrated that *Bryoria* was more abundant at the young and old Butte units, but less abundant in the young and old Paradise Hills units and in the old Little White Salmon units. Therefore, it is hard to separate geographical effects from the effects of forest age and structure on *Bryoria*'s abundance.

DISCUSSION

My results suggest that predictions of epiphytic lichen biomass and species richness in mature forests are much improved by incorporating attributes of structure, rather than relying strictly 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." My results also correspond with those from young, managed stands, in which epiphytic lichen abundance and diversity were linked to the structural diversity of young coniferous forests (Neitlich and McCune 1997).

Forest age does play a role in the development of a forest and often may correlate with structural development. Epiphytic lichen communities may be slow to establish and some cyanolichens may be slow dispersers; thus, forests that persist through time should accumulate lichen biomass as well as species diversity (Sillett and Neitlich 1996). My results indicate that time is needed for lichen biomass to accumlate; however, age did not correlate with lichen richness. As previously mentioned structural complexity may not build over time. Carey (1995) also found that attributes of forest structure (snag abundance and ericaceous shrubs) can function independently of forest age. One stand of 57 years old, surpassed all other young stands in structurally complexity, and even surpassed shrub cover in the old stands (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 age.

Forests similar in age can develop substantially different structures. Environmental and biotic factors can interact with forest age causing structural development to accelerate, stagnate, or cycle (Latham 1996). However, few studies have attempted to separate the effects of forest age and forest structure on plant and animal species. Halpern and Spies (1995) studied plant diversity along a chronosequence of natural forests and in 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 for 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.

Forest structure is an elusive concept, but the eight structural variables used here are likely to represent characteristics of forests that are meaningful to lichens. Tree diversity reflected the floristic component of forest structure, light is a resource for plants, and the other six variables quantified the vertical and horizontal variation in each forest. The multivariate and multiple regression approaches used to compare the importance of forest age and structure for predicting lichen biomass were highly complimentary. Five variables contributed the most to predicting lichen biomass. In order of importance, these were: (1) greater canopy openness, (2) higher percentage of hardwoods, (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. These five variables also comprised PC 1 of forest structure. Structure variables of PC 2, tree diversity, snag number, and snag index, were not useful in predicting lichen biomass.

Tree height, tree diameter, light penetration, and hardwoods have been shown to influence lichen biomass in other research (Neitlich 1993, Halpern and Spies 1995, McCune et al. 1997, Peck and McCune 1997). High coefficients of variation in tree height and diameter indicate the presence of very tall and large trees. In Oregon, McCune (1993) found higher epiphytic lichen biomass on larger trees within a stand. Furthermore, the distribution of functional groups changed along a tree's vertical profile and followed the sequence, from top to bottom: miscellaneous, alectoriod, cyanolichen, and bryophytes (McCune 1993). McCune et al. (1997) also found the alectorioid functional group increased in percent cover with tree height and tended to dominate the canopy top. In contrast, cyanolichens dominated the light transition zone, that area marked by an abrupt change from bright light to dark (McCune et al. 1997). Both alectorioid and cyanolichen functional groups have been found to be more abundant in stands that retain remnant trees from a previous cohort (Peck and McCune 1997). Halpern and Spies (1995) suggested that increased vertical diversity and complexity of forest canopies with age could be the mechanism for a higher diversity of lichen species, particularly *Lobaria* spp., and vascular plants. In this study, the coefficient of variation in tree diameters may not have as consistently contributed to biomass as found in other studies because we focused on canopy lichens rather than species confined to tree trunks. Vertical variation in the canopy may be more highly correlated with lichen biomass and diversity (McCune 1993).

Hardwoods can enhance lichen biomass by increasing the light and moisture reaching neighboring trees and by providing a less acidic bark substrate (Neitlich 1993).

Forest structure (PC 1) explained more variation in lichen richness than forest age; however, the structural attributes that contributed to 1995 richness (c.v. tree density) differed from those explaining 1996 richness (snag index and percent of hardwoods). Study units with the highest richness in 1995 did not have the highest richness in 1996 due to an increase in the number of lichen species (of very low biomass) collected in the Butte units in 1996 relative to the other units. Pairwise correlations (Appendix D, Table D2) between richness and each structure variable demonstrated that c.v. tree height, c.v. tree density, percent of canopy openness, and percent of hardwoods were significant in explaining 1995 lichen richness, but no structural variables were significantly correlated with 1996 richness. Thus, the multivariate (PC 1) approach found a stronger, more consistent relationship between the composite structural variable and lichen richness rather than between age and lichen richness or any individual structure variable.

Variation in tree density, light penetration, hardwoods, and snags have been shown to influence lichen richness in other research (Neitlich 1993). Neitlich (1993) hypothesized that high branch density may block the movement of wind-dispersed lichen propagules and reduce light penetration, adversely affecting lichen establishment and growth. Thus, as forest density becomes more variable, light penetration increases in places, creating suitable habitat for other lichen species. In coniferous dominated forests, hardwoods can increase species diversity because some lichen species appear to prefer the less acidic bark of a deciduous tree, and hardwoods increase moisture availability and

light for surrounding trees in the winter and spring (Neitlich 1993). My snag index measured snag quality (hard versus decayed and tall versus short), which could affect species diversity since snags are legacies of pre-disturbance conditions, providing a source of propagules and a suitable substrate. For example, *Letharia vulpina* appears to be particularly common on hard snags lacking bark (A. Pipp, personal observation).

Even though the lichen species in this study have wide distributions (McCune and Goward 1995), DCA ordinations demonstrated a strong correlation between region (block) and lichen community composition. The stronger relationship between forest age and lichen community composition may have been an artifact of geographic location, because forest age was more highly associated with geography than was forest structure. In contrast to the 1995 multiple regression model, forest age did not contribute to the 1996 regression which paired young and old units within the same block.

The Demonstration of Ecosystem Management Options project was designed to examine large-scale forest patterns. In keeping with this purpose, this study compared the relationship of forest age versus structure over a large geographical region, the Gifford Pinchot National Forest, using exceptionally large study units. Given this study design, my sample size was low for conducting regression analysis; however, each study unit was much larger than is typically used for vegetation studies (most units covered 13 ha) and each unit was intensively sampled for vegetation and for lichens.

The lichen litterfall pick-up method was designed for large-scale surveys of lichen biomass where large differences in epiphytic biomass are expected (McCune 1994). This method has been used throughout the Pacific Northwest (Peck and McCune 1997);

however, data on yearly variation in lichen litterfall is still lacking. My data demonstrates that lichen litterfall may differ between consecutive years; however, species composition and their relative abundance in the litterfall was enough to support the use of this method in studies comparing relative differences in species abundances and diversity. Storms may vary among years resulting in annual variation in the absolute quantity of lichen litterfall. Although not quantified, the difference in lichen litterfall between years may have been due to more turbulent weather patterns in 1996. Effective sampling of lichens using the litterfall technique requires collecting data in more than one year to determine trends and averages (McCune 1994).

The low occurrence of cyanolichens was surprising, but reflected my field observations. The rarity of *Lobaria pulmonaria* and *L. oregana* in this study corresponds with current ecological knowledge. Both species are regarded as indicators of old growth (Shirazi et al. 1996) and, in this study, both were found in only older units of 157 (Little White Salmon) and 150 (Paradise Hills) years old, respectively. My study units do not represent productive cyanolichen habitat because they are upland forests at mid-elevation rather than low elevation sites near large streams (Sillett and Neitlich 1996).

My results indicate that lichen species differ in their response to forest age and structure in terms of biomass. For example, *Hypogymnia* decreased in biomass with increasing age. Lesica et al. (1991) found that four species, *Hypogymnia tubulosa*, *H. metaphysodes*, *H. physodes*, and *H. imshaugii,* were more abundant in a 70 year old, second-growth forest than in old growth. The latter two species were significant in abundance. Lesica et al. (1991) also showed that the second-growth forest was more

homogenous in structure than the old-growth forest. The green-algae foliose functional group comprised mostly of *Hypogymnia* and *Platismatia* has been positively correlated with the basal area of the regeneration tree cohort in stands containing remnant trees (Peck and McCune 1997). In my study, *Hypogymnia* dominated 70-90 year old stands which contained the highest tree density, but also contained some remnant trees. McCune (1993, 1997) found that the genus, *Platismatia*, dominated the entire canopy in young forests, but occupied only the upper canopy of older trees. This suggests that structure may be influencing the abundance and spatial distribution of *Platismatia*. In this study, *Platismatia* was ubiquously common, but was more abundant in forests with more structural complexity. Lesica et al. (1991) also found significantly higher abundances of *Platismatia glauca* in old growth than in the 70 year old, second-growth forest. Peck and McCune (1997) suggest that *Hypogymnia* and *Platismatia* may be more effective at dispersing and colonizing than species of the alectorioid and cyanolichen functional groups.

Usnea abundance correlated significantly with forest structure (PC 1), but not with forest age. The different growth forms of *Usnea,* tufted versus pendant, have been hypothesized to reflect their preferred ecological habitat. For example, *Usnea filipendula* is slender and pendant and prefers dense forests while *Usnea hirta* is tufted and prefers more open stands (Hyvärinen et al. 1992). *Usnea longissima*, a vagrant, epiphytic lichen (lives unattached on branches), is hypothesized to grow better in open forests with enough light penetration to prevent the abscision of lower branches (Gauslaa 1997). *Usnea* species in this study were short and pendant or tufted and their biomass correlated

strongly with increasing light penetration ($r^2_{1995} = 0.36$, P = 0.008 and $r^2_{1996} = 0.31$, P = 0.60) and increasing patchiness in tree density ($r^2_{1995} = 0.49$, P = 0.001 and $r^2_{1996} = 0.51$, P = 0.009).

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). This literature demonstrates 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 harvested 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 are often underestimated in their potential to harbor biological diversity (Hansen et al. 1991). If we are to maintain flora and fauna diversity at large, regional scales, then mature forests must now be managed to balance resource use and biological diversity.

This study supports the concept that the structural complexity of the vegetation enhances species diversity (see Kuuluvainen et al. 1996). Others have suggested that mature forests can be managed to promote structural complexity. Halpern and Spies (1995) argue that the complexity of forest structure creates a shifting mosaic of resources and environments that potenially support a greater diversity of species. Bailey and

Tappeiner (in press) 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 multi-aged 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.

Lichens may serve as indicators for other taxa. Epiphytic lichens are used by a variety of canopy invertebrates as food and shelter, and the physical structure of this habitat 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. 1997). Declines in many non-migratory birds, that rely on these invertebrates, may be a result of degraded feeding habitat (Pettersson et al. 1997). In addition, the diversity and abundance of old growth-dependent macrolichens may be a better indicator of how long a forest has developed without disturbance (forest continuity) than forest age (Goward 1994).

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 biological diversity (Kuuluvainen et al. 1996). My data indicates 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). This study supports the conclusions of other research that suggests promoting hardwoods, retaining snags, and retaining remnant (large or old) trees during harvesting can increase structural complexity

and create a mosaic of light conditions, tree densities, multi-canopy layering, and maintain higher lichen biomass and diversity (Halpern and Spies 1995, Rosentreter 1995, Neitlich and McCune 1997, Peck and McCune 1997).

Conclusion

For unmanaged stands that vary in age by approximately 100 years, forest structure predicted lichen biomass and diversity more accurately than forest age. Approaches that emphasize structure have the potential to help forest managers assess stands for their biological value. My results suggest that if complex forest structures are retained and managed for, lichen abundance and richness would be enhanced. Enhancing structural complexity in forests may include, maintaining gaps, high proportions of hardwoods, and a variety of tree heights, diameters, and densities. However, not all plant, animal, and lichen species may benefit from structural complexity (Peck and McCune 1997); thus, it is important that a mosaic of different structures be maintained within forests of the Pacific Northwest, in order to maintain a wider array of habitats for a greater number of species.

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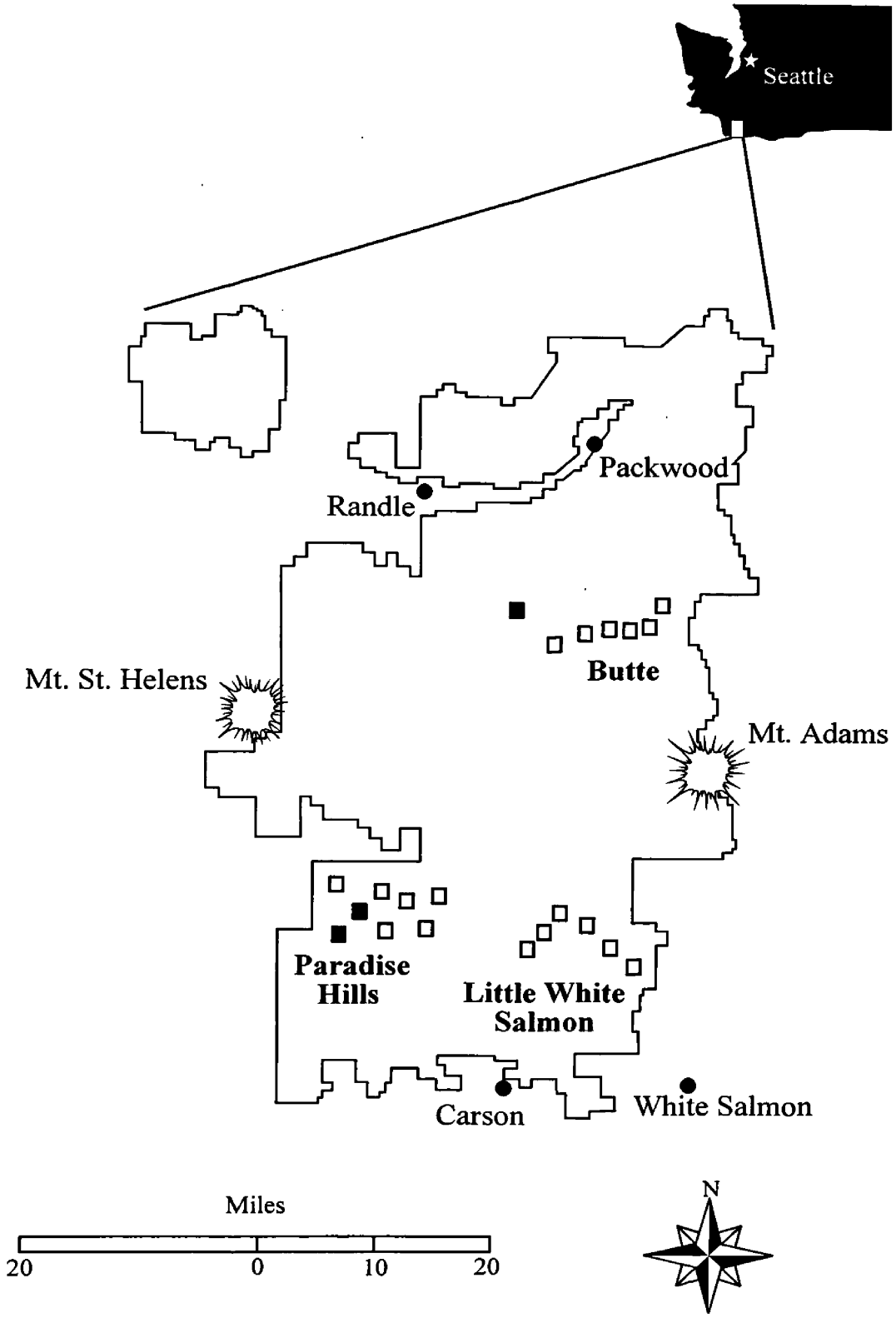

Fig. 1. Gifford Pinchot National Forest, Washington.
21 study sites: 3 Additional Units (■) and 18 DEMO Units (□).
Study sites are not to scale, but show relative location.

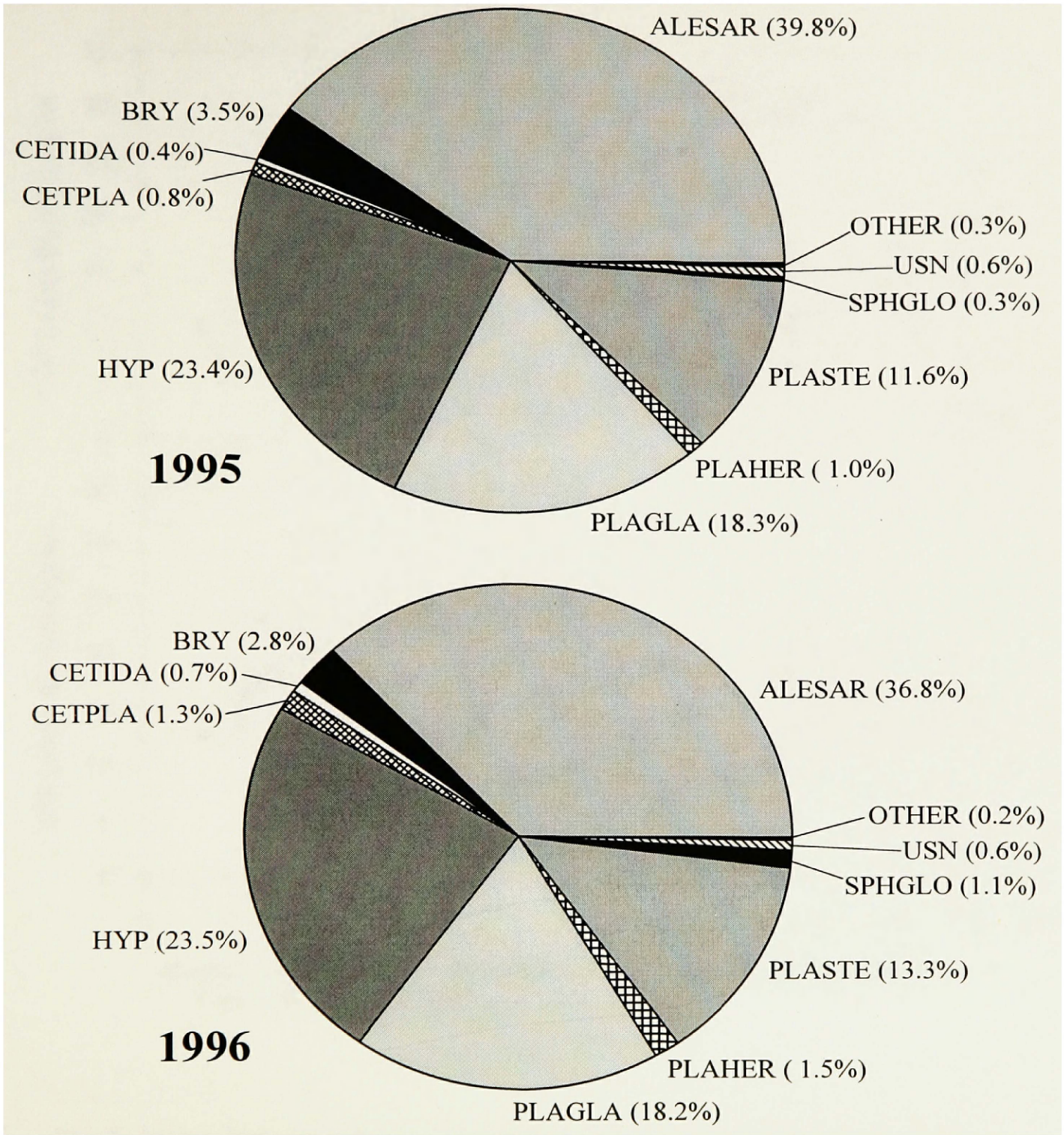

Fig. 2. Species composition of total lichen litterfall biomass in 1995 and 1996. Species codes are defined in Appendix A, Table A1. OTHER denotes species with < 0.1% biomass.

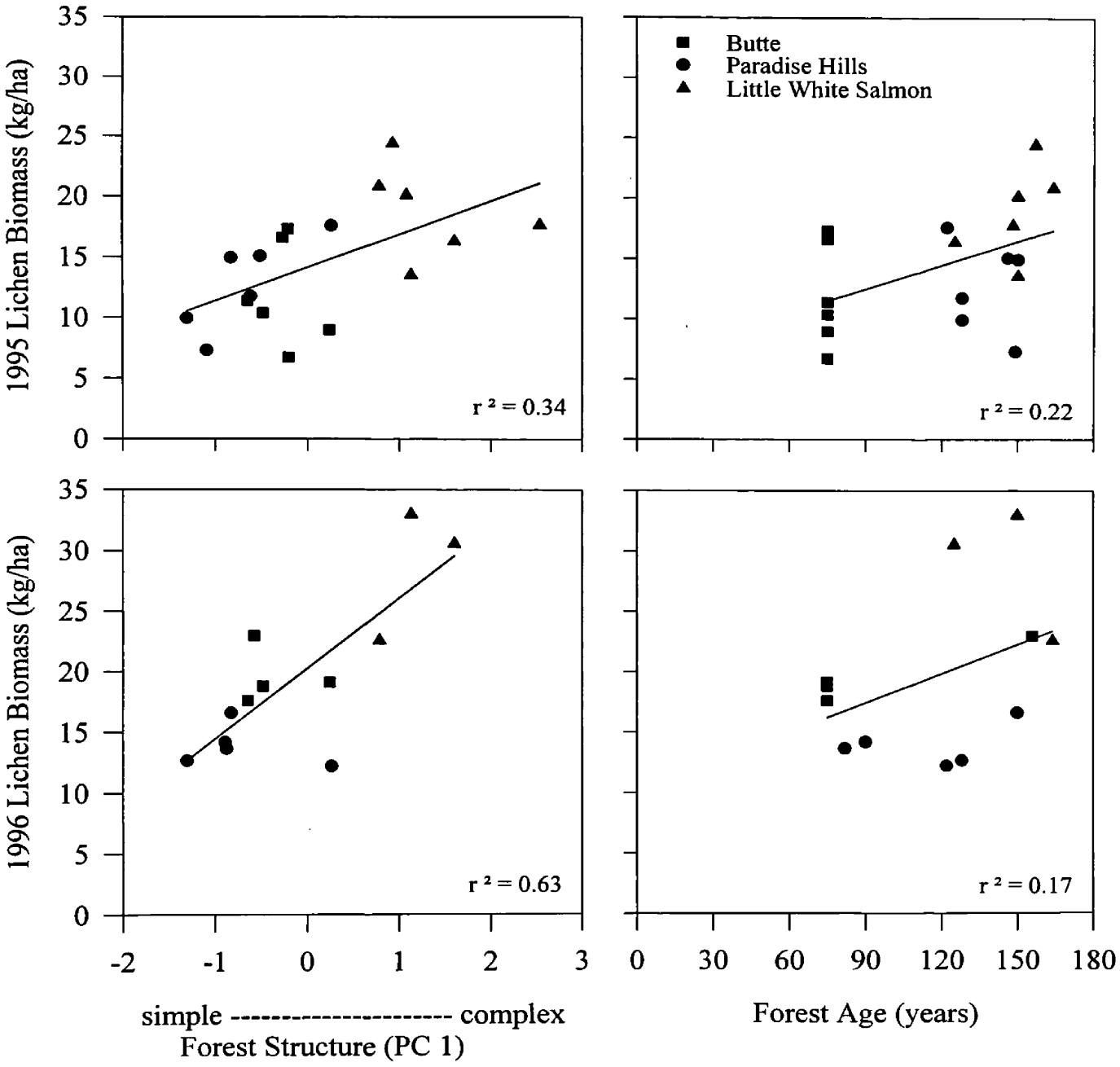

Fig. 3. Lichen biomass regressed against forest structure (PC 1) and forest age for 1995 and 1996.

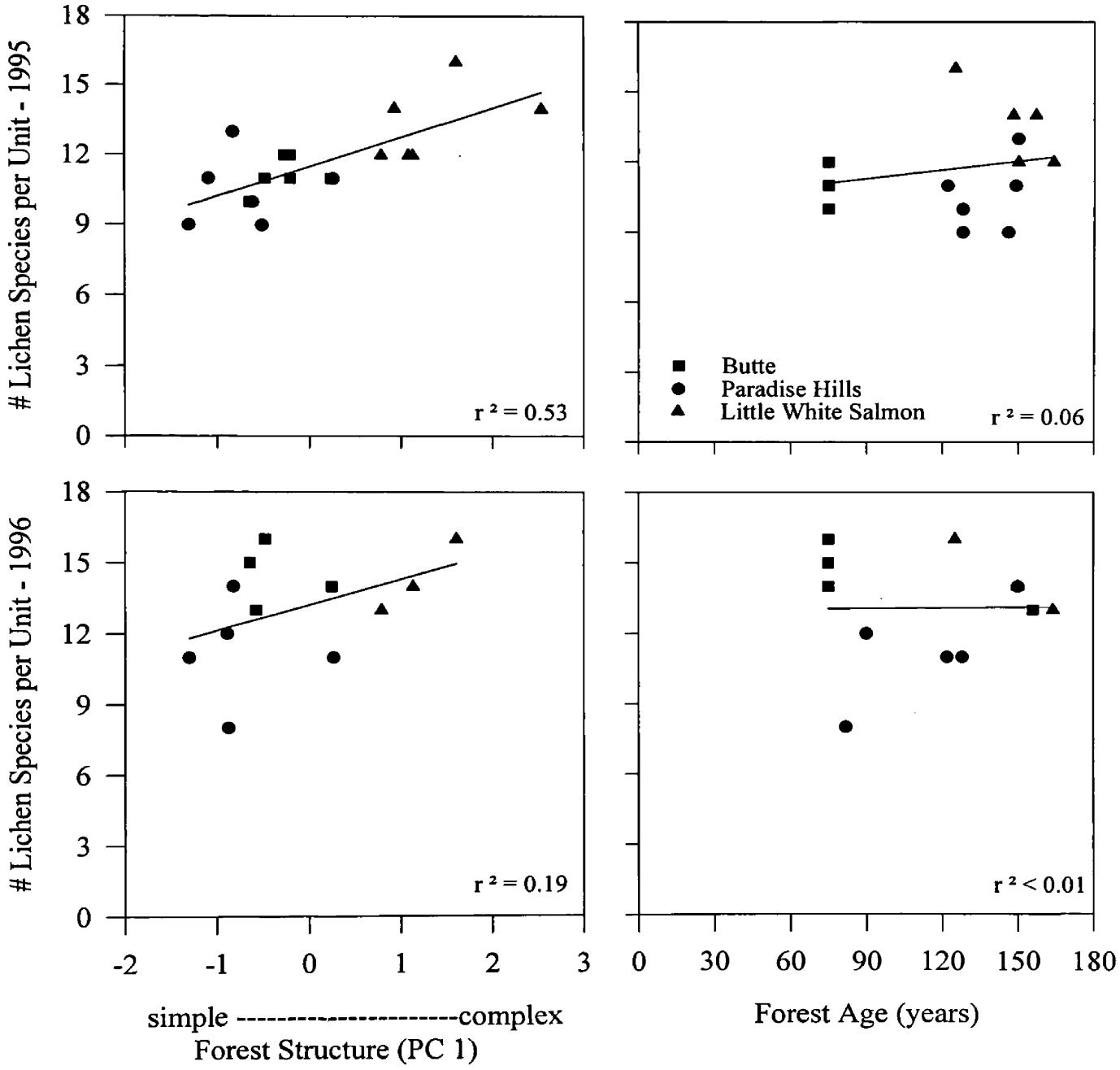

Fig. 4. Lichen richness per unit regressed against forest structure (PC 1) and forest age for 1995 and 1996.

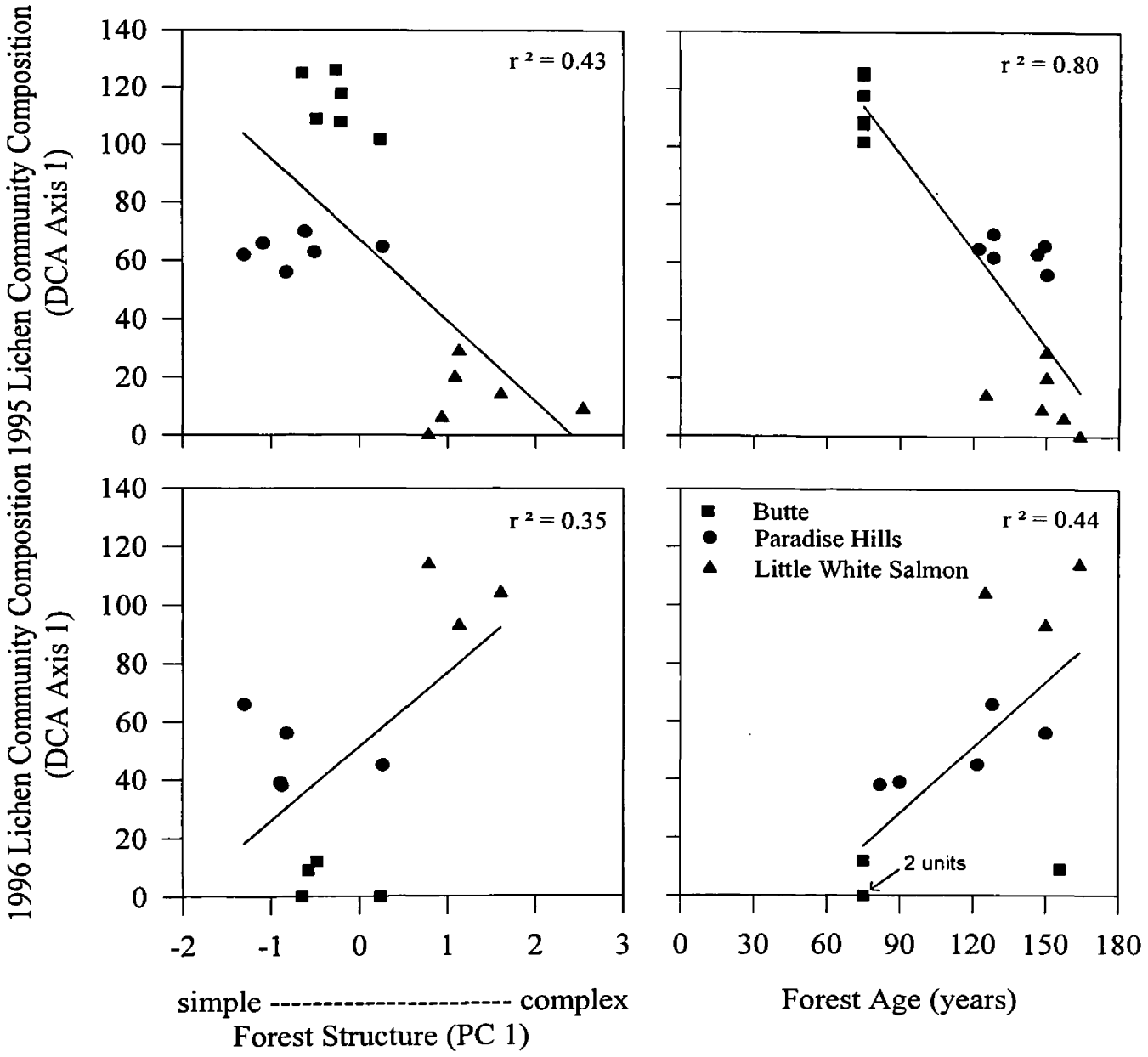

Fig. 5. Lichen community composition regressed against forest structure (PC 1) and forest age for 1995 and 1996.

Table 1. Coefficients of determination (r^2) for structure variables regressed against forest age. Factor loadings of each structure variable for principal components1 and 2. CVDBH, CVHT, and CVTREE = coefficient of variation in tree diameter, height, and density; DIVERSITY = Simpson's index of tree diversity; LIGHT = percent of canopy openness; SNAG NO = snag number per hectare; SNAG INDEX = snag index; WOOD = percent of hardwoods.

Structure Variables	AGE	PC 1	PC 2
LIGHT	0.05	0.84**	- 0.01
CVHT	0.08	0.65**	<-0.01
CVTREE	0.22*	0.66**	- 0.02
WOOD	0.12	0.74**	0.08
CVDBH	0.16	0.25*	0.59**
DIVERSITY	0.10	- 0.02	0.82**
SNAG NO	0.06	- 0.23*	0.37**
SNAG INDEX	-0.26*	<- 0.01	- 0.76**

* Significant at the 0.05 level.
** Significant at the 0.01 level.

Table 2. Coefficients for lichen biomass regressed against structure and age variables in 1995 and 1996 using backward multiple regressions. AGESQ = square-root of age; CVDBH, CVHT, CVTREE = coefficient of variation in tree diameter, height, and density; DIV = Simpson's index of tree diversity; LIGHT = pecent of canopy openness; SNAG NO = number of snags per ha; SNAG INDX = snag index; WOOD = percent of hardwoods.

Dependent Variable	AGE SQ	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.

Table 3. 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 of canopy openness; SNAG NO = number of snags per ha; LSNAG INDX = snag index logged; WOOD = percent of hardwoods.

Dependent Variable	AGE	CV DBH	CV HT	CV TREE	DIV	LIGHT	SNAG NO	LSNAG INDX	WOOD	constant	F value	R^2	N
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.

Table 4. 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 of canopy openness; SNAG NO 2 = square of snag number; SNAG INDX = snag index; WOOD = percent of hardwoods.

Dependent Variable	AGE	CV DBH	CV HT	CV TREE	DIV	LIGHT	SNAG NO 2	SNAG INDX	WOOD	constant	F value	R^2	N
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.

Table 5. Coefficients of determination (r^2) for biomass of functional groups (FG) and species correlated against forest age and structure (PC 1). Refer to Appendix A, Table A1 for species codes.

	AGE		STRUCTURE	
SPECIES / FG	**1995**	**1996**	**1995**	**1996**
Alectoriod FG	0.06	0.12	<0.01	0.22
Misc. FG	0.16	0.10	0.41**	0.52**
ALESAR	0.14	0.16	<0.01	0.26
BRY	-0.65*	-0.02	-0.06	<-0.01
CETPLA	0.10	0.21	0.23*	0.34*
HYP	-0.44**	-0.35*	-0.04	-0.05
PLAGLA	0.42**	0.11	0.51**	0.38*
PLASTE	0.43**	0.32	0.46**	0.62**
USN	0.16	0.09	0.50**	0.56**

* Significant at the 0.05 level.
** Significant at the 0.01 level.

APPENDIX A

SPECIES CODES

Table A1. Lichen species codes.

SPECIES CODE	SPECIES NAME
ALESAR[1]	*Alectoria sarmentosa*
BRY[1]	*Bryoria* species
CETCAN[2]	*Cetraria canadensis*
CETCHL[2]	*Cetraria chlorophylla*
CETIDA[2]	*Cetraria idahoensis*
CETMER[2]	*Cetraria merrillii*
CETORB[2]	*Cetraria orbata*
CETPAL[2]	*Cetraria pallidula*
CETPLA[2]	*Cetraria platyphylla*
EVEPRU[2]	*Evernia prunastri*
HYP[2]	*Hypogymnia* species
LETVUL[2]	*Letharia vulpina*
LOBORE[3]	*Lobaria oregana*
LOBPUL[3]	*Lobaria pulmonaria*
MELEXA[2]	*Melanelia exasperatula*
PARHYG[2]	*Parmelia hygrophila*
PARSUL[2]	*Parmelia sulcata*
PLAGLA[2]	*Platismatia glauca*
PLAHER[2]	*Platismatia herrei*
PLASTE[2]	*Platismatia stenophylla*
RAMFAR[1]	*Ramalina farinacea*
SPHGLO[2]	*Sphaerophorus globosus*
USN[1]	*Usnea* species

[1] alectorioid functional group.
[2] miscellaneous functional group.
[3] cyanolichen functional group.

APPENDIX B

BIOMASS OF LICHEN SPECIES BY UNIT

Table B1. Biomass (kg/ha) of each species collected per unit for 1995. Biomass is written on the first line. Frequency is the number of plots per unit containing that species and is written beneath biomass. Maximum frequency per unit is 15. Blank cells indicate the species was absent. Refer to Appendix A, Table A1 for species codes.

	BUTTE						LITTLE WHITE SALMON						PARADISE HILLS					
SPECIES	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
ALESAR	7.9541 15	4.0693 15	3.4108 15	2.0104 14	4.7988 15	3.4996 15	6.5204 15	5.9472 14	5.5349 15	8.4920 15	5.2882 15	3.6420 15	4.9830 15	11.8458 14	6.8171 15	10.5727 15	4.0478 15	4.7588 15
BRY	1.1160 15	0.9511 13	0.7685 14	0.4032 14	1.7212 13	1.2350 15	0.2193 13	0.1020 13	0.2074 12	0.3155 13	0.3090 13	0.2105 11	0.1495 11	0.0855 7	0.3881 13	0.6895 14	0.1381 5	0.1907 9
CETCAN						0.0004 1												
CETCHL	0.0026 5	0.0059 7	0.0187 5	0.0083 4	0.0171 6	0.0111 5	0.0023 2	0.0060 2	0.0008 1	0.0055 3	0.0071 2	0.0073 4				0.0025 2	0.0004 1	0.0340 7
CETIDA				0.0074 2			0.2424 6	0.0658 9	0.1452 5	0.0068 2	0.2365 5	0.3100 11						
CETMER	0.0012 1				0.0005 1	.0002 1												
CETORB	0.0241 7	0.0044 4	0.0011 1	0.0126 3	0.0110 9	0.0210 7	0.0056 1	0.0064 3		0.0057 2	0.0003 1	0.0203 4				0.0022 1	0.0004 1	0.0040 2
CETPAL		0.0006 1					0.0058 2											
CETPLA	0.0904 13	0.0259 9	0.0086 7	0.0286 10	0.1502 15	0.1873 9	0.5246 12	0.0519 9	0.1677 14	0.1674 13	0.3868 13	0.3124 12	0.0061 2	0.0278 5	0.0293 7	0.0345 9	0.0031 2	0.0197 4
EVEPRU								0.0597 2	0.0031 1									
HYP	6.7220 15	3.9982 15	3.1887 15	3.5092 15	8.2990 15	5.5070 15	3.9137 15	1.9027 15	2.2495 15	2.0212 15	2.8008 15	2.8794 15	2.0111 15	1.6134 15	2.3661 15	2.6550 15	1.3667 15	4.1190 15
LETVUL			0.0008 1															

Table B1. 1995 continued.

	BUTTE						LITTLE WHITE SALMON						PARADISE HILLS					
SPECIES	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
LOBPUL							0.1612 1											
MELEXA												0.0069 1						
PARHYG												.0109 1						
PARSUL					0.0051 2		0.0015 1	0.0060 3		0.0014 3	0.0040 3	0.0244 6			0.0163 1			0.0983 2
PLAGLA	1.3188 15	1.2882 15	1.2255 15	0.7365 15	1.5416 15	0.8897 13	5.1124 15	5.3640 15	2.0842 15	4.9434 15	4.6553 15	5.4189 15	2.1130 15	1.0805 15	1.6317 15	3.0606 15	1.1692 15	4.3355 15
PLAHER	0.0080 3	0.0155 5	0.3867 4	0.0082 4	0.0658 7	0.0505 3	0.1952 6	0.2712 9	0.1398 7	0.2102 7	0.1743 7	0.1072 6	0.2808 9	0.0744 6	0.0625 4	0.0874 11	0.3585 12	0.1696 11
PLASTE	0.0180 4	0.0440 8	0.0042 1	0.0068 2	0.0265 6	0.0342 6	7.3537 15	3.7978 14	2.9527 15	3.6519 15	6.8250 15	2.9551 15	0.2886 9	0.2966 8	0.4404 13	0.4815 13	0.1370 9	1.0175 15
RAMFAR												0.0006 1						
SPHGLO	0.0914 1							0.0051 1	0.1006 2				0.1371 6	0.0757 3	0.0112 2	0.0267 5	0.0885 1	0.2136 5
USN	0.0019 2	0.0056 5	0.0002 1	0.0068 3	0.0079 4		0.1615 10	0.2080 12	0.0170 9	0.3651 12	0.2114 11	0.5078 14	0.0030 2	0.0147 2	0.0387 1	0.0377 6	0.0059 2	0.0107 3
TOTAL	17.35	10.41	9.01	6.74	16.64	11.44	24.42	17.79	13.60	20.19	20.90	16.41	9.97	15.11	11.80	17.65	7.32	14.97

Table B2. Biomass (kg/ha) of each species collected per unit for 1996. Biomass is written on the first line. Frequency is the number of plots per unit containing that species and is written beneath biomass. Maximum frequency per unit is 15. Blank cells indicate absence of species. Refer to Appendix A, Table A1 for species codes.

	BUTTE			LITTLE WHITE SALMON			PARADISE HILLS			ADDITIONAL		
SPECIES: BIO												
	2	**3**	**6**	**3**	**5**	**6**	**1**	**4**	**6**	**A1**	**A2**	**A3**
FRQ												
ALESAR	7.4958	8.0784	5.0701	14.7922	7.3501	7.1323	4.6180	7.4913	5.3335	7.4683	3.5169	11.7341
	15	15	15	15	15	15	15	15	15	15	15	15
BRY	0.7239	2.2393	0.8322	0.3006	0.1214	0.1853	0.1477	0.2440	0.2752	0.1691	0.1240	2.2146
	14	15	15	12	8	14	9	12	15	12	13	15
CETCAN	0.0001	0.0011	0.0010									
	1	1	2									
CETCHL	0.0388	0.0290	0.0225	0.0219	0.0012	0.0102	0.0016	0.0003	0.0407	0.0021	0.0029	0.0093
	13	11	11	3	2	4	1	1	11	2	3	5
CETIDA	0.0001		0.0127	0.3168	0.2758	0.6347	.0003				0.0015	0.0152
	1		3	10	5	14	1				1	2
CETMER	0.0004	0.0004										
	2	1										
CETORB	0.0173	0.0130	0.0465	0.0033	0.0092	0.0135			0.0026		0.0003	0.0207
	10	10	14	4	4	8			2		1	12
CETPAL		0.0001	0.0005									0.0006
		1	1									1
CETPLA	0.1052	0.1117	0.3861	0.6993	0.3272	0.7404	0.0027	0.1124	0.0143		0.0406	0.8625
	12	12	12	13	11	15	2	6	6		7	14
EVEPRU				0.0009		0.0003						
				1		1						

Table B2. 1996 Continued.

SPECIES: BIO FRQ	BUTTE			LITTLE WHITE SALMON			PARADISE HILLS			ADDITIONAL		
	2	3	6	3	5	6	1	4	6	A1	A2	A3
HYP	7.7128 15	6.2377 14	9.0271 15	3.9256 15	2.4685 15	4.6761 15	2.4709 15	2.1760 13	4.2942 15	3.6920 15	6.1055 15	6.2508 15
LETVUL	0.0008 12		0.0001 2			0.0001 1		0.0002 1				
LOBORE									0.0048 1			
MELEXA						0.0044 1						
PARHYG	0.0030 1					0.0010 1			0.0006 1			
PARSUL	0.0017 3	0.0052 5	0.0001 1	0.0109 2	0.0037 2	0.0333 5			0.0139 3			
PLAGLA	2.4938 15	2.0024 15	1.9880 15	3.6620 15	4.2449 15	9.7883 15	3.1558 15	1.6463 13	4.4478 15	1.7727 15	2.6062 15	1.7131 14
PLAHER	0.1682 10	0.3993 8	0.1466 9	0.4584 12	0.1156 5	0.1946 11	0.6047 11	0.1870 7	0.4704 13	0.0403 8	0.2870 12	0.1042 10
PLASTE	0.0407 7	0.0050 3	0.0740 8	8.0820 15	7.3137 15	6.5108 15	0.9327 9	0.2838 8	1.0495 13	0.4483 13	1.3782 15	0.0291 3
SPHGLO				0.5785 5	0.0268 3		0.7191 6	0.1178 4	0.6155 9		0.0498 5	0.0026 1
USN	0.0032 4	0.0126 5	0.0045 3	0.1054 9	0.3173 12	0.6541 14	0.0037 2	0.0271 4	0.0242 4	0.0491 3	0.0647 6	0.0099 2
TOTAL	18.81	19.14	17.61	32.96	22.58	30.58	12.66	12.24	16.59	13.64	14.18	22.97

APPENDIX C

ENVIRONMENTAL DESCRIPTIONS OF STUDY UNITS

Table C1. Environmental variables associated with each DEMO and additional unit.

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	164	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

APPENDIX D

UNIVARIATE REGRESSIONS OF BIOMASS AND RICHNESS AGAINST STRUCTURE

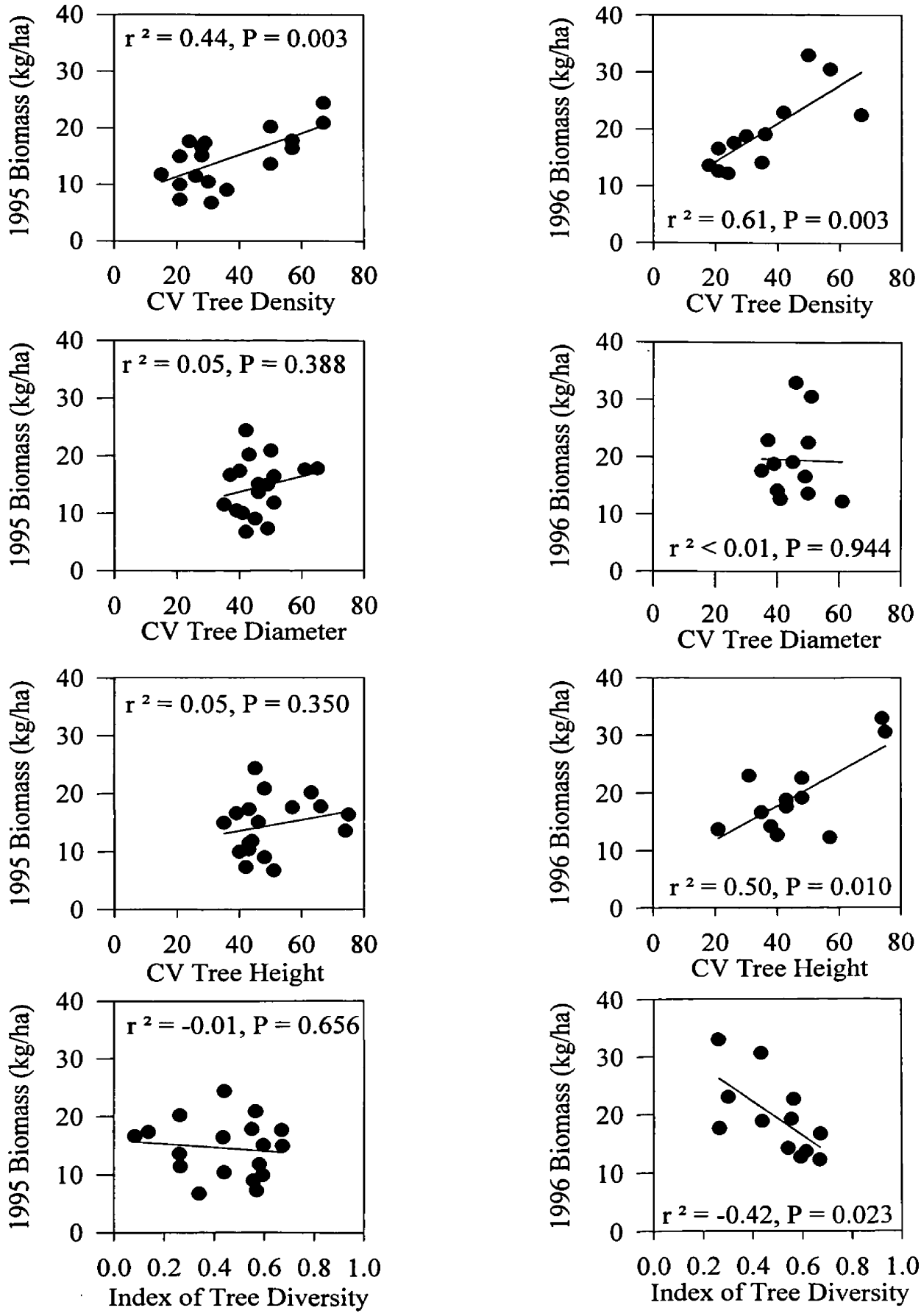

Fig. D1. 1995 and 1996 lichen biomass correlated against each structure variable.

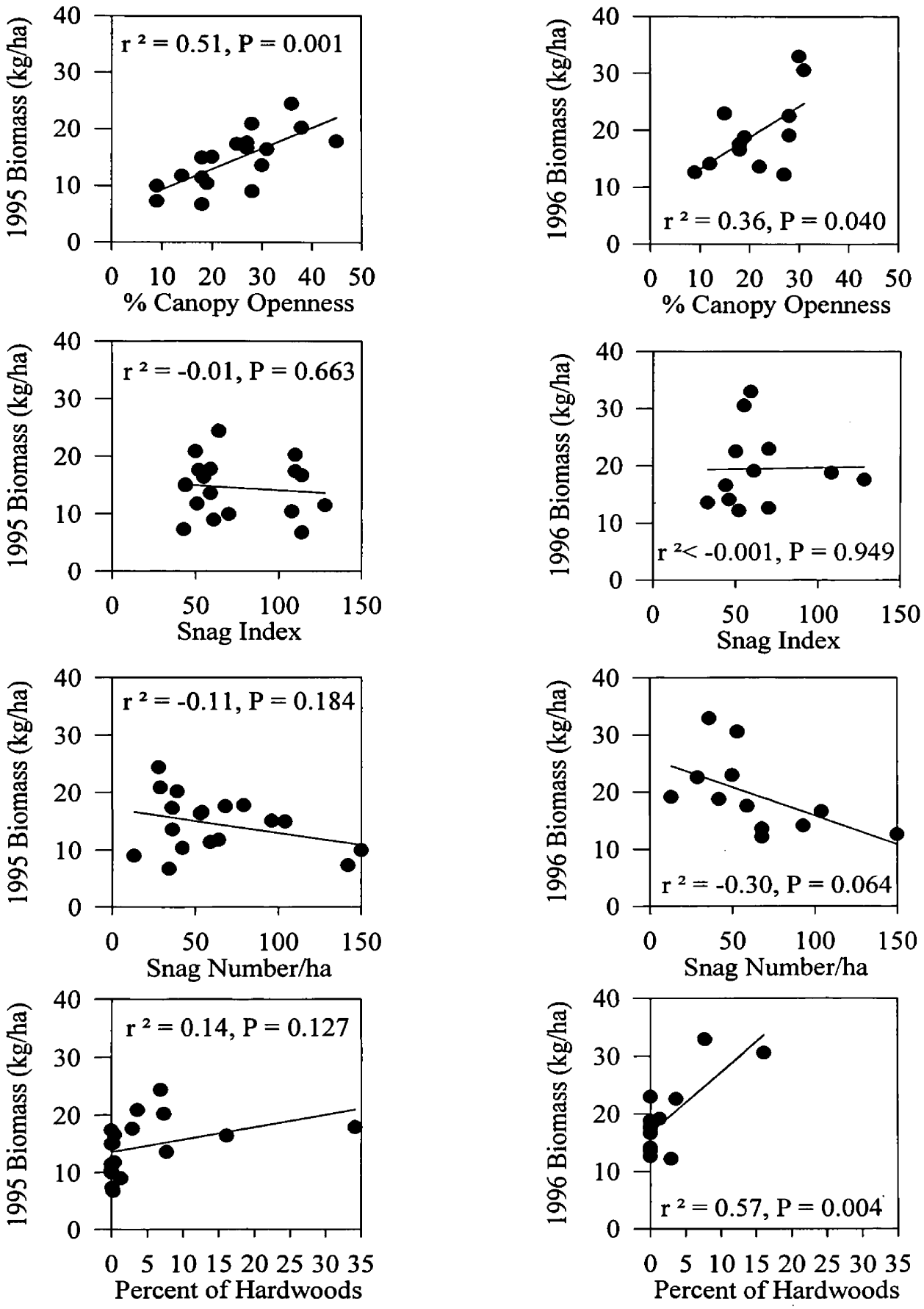

Fig. D1 (cont.). 1995 and 1996 lichen biomass correlated against each structure variable.

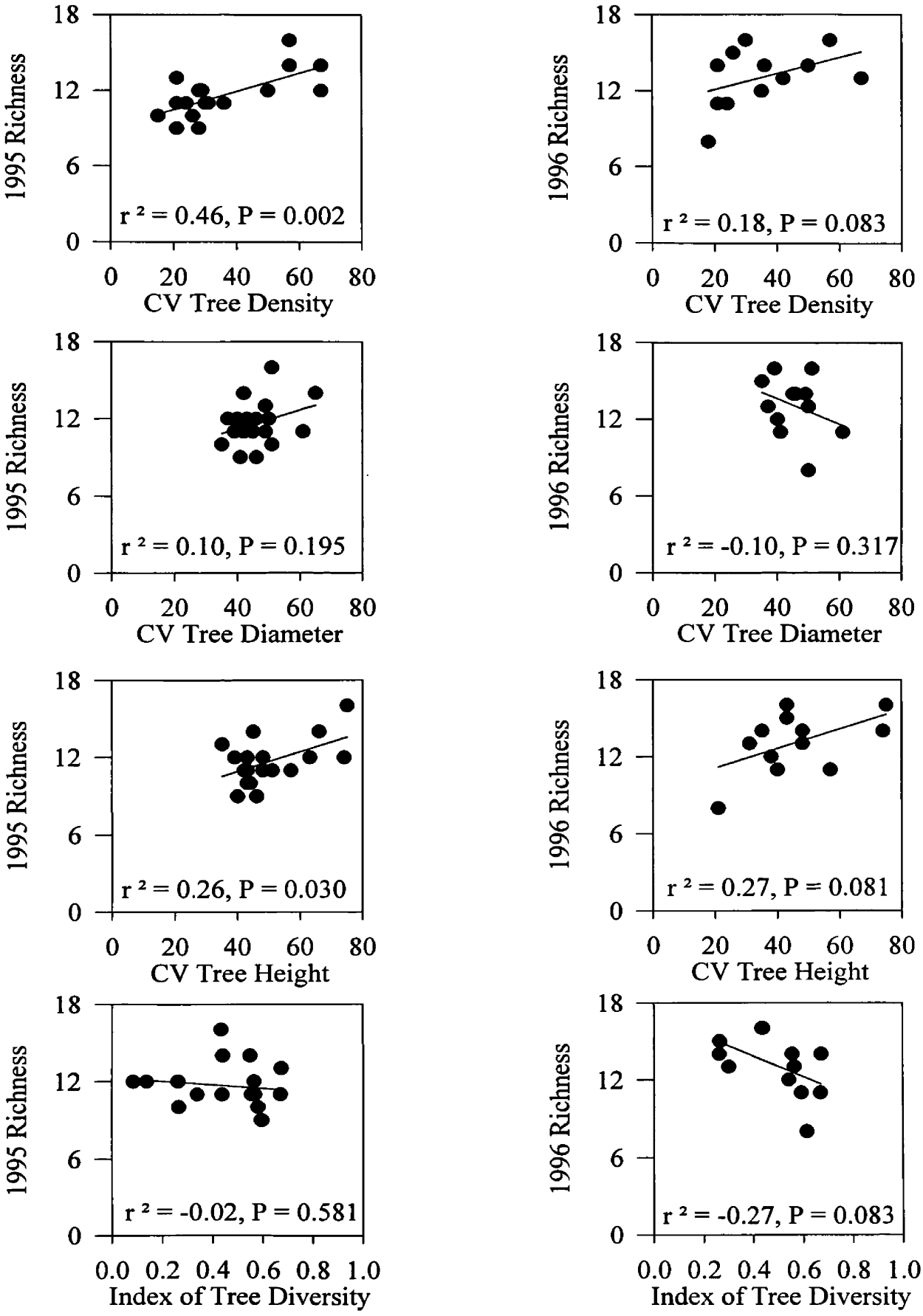

Fig. D2. 1995 and 1996 lichen richness correlated against each structure variable.

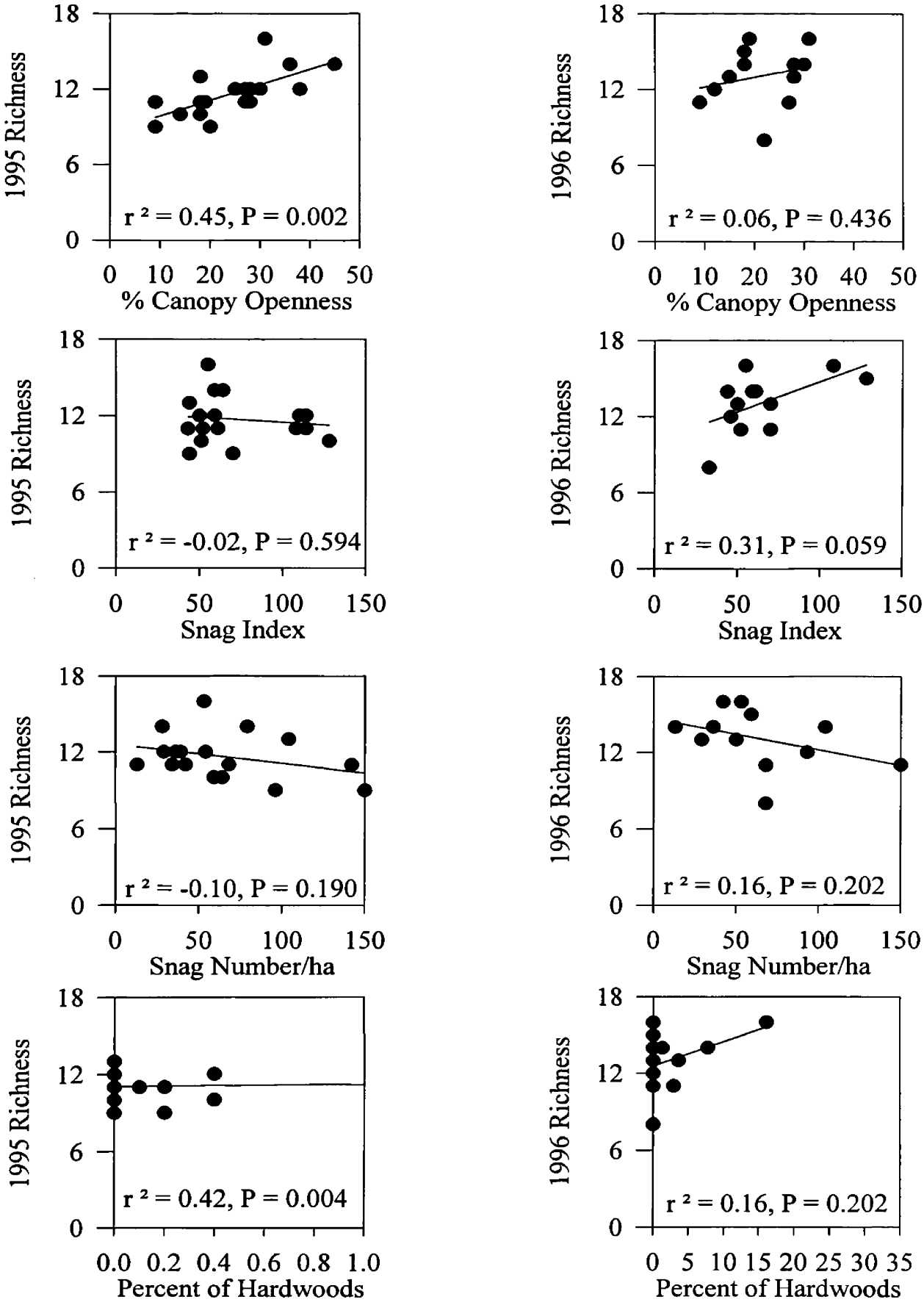

Fig. D2 (cont.). 1995 and 1996 lichen richness correlated against each structure variable.

APPENDIX E

ESTABLISHING THE LICHEN LITTERFALL PLOTS

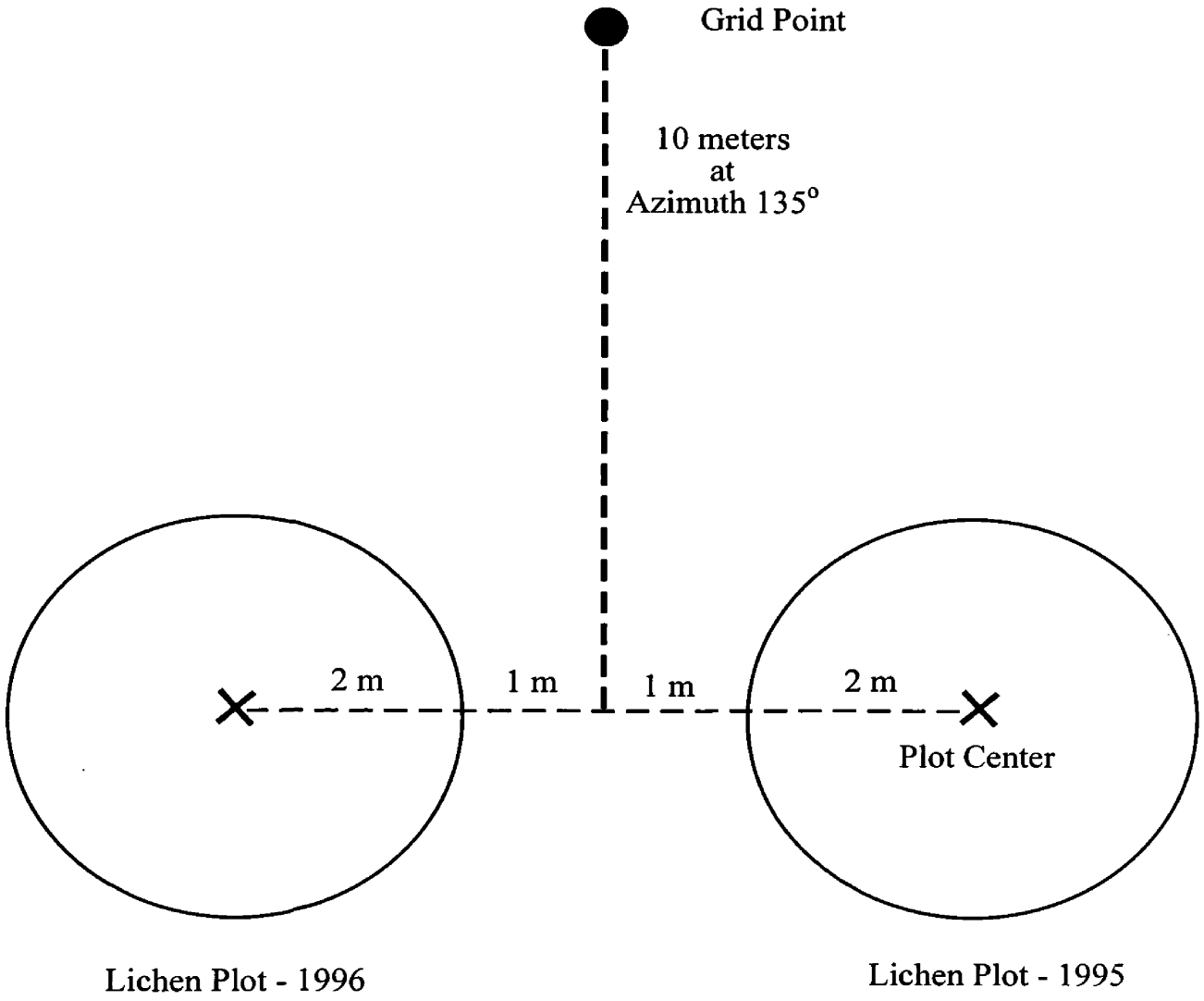

Fig. E1. Location of the lichen litterfall plot in relation to the grid (sampling) point.

Table E1. Grid points sampled for lichen litterfall in 1995 and 1996.

Block	Grid Points Used At Each Unit					
Butte	**1**	**2**	**3**	**4**	**5**	**6**
	A1	A2	A4	A1	A3	A9
	B6	A7	B7	A6	A7	B6
	B7	B1	C6	B1	B1	B7
	C4	B4	C8	B2	B3	B9
	C6	B7	C9	B6	B6	C7
	D2	C2	D2	C6	C4	C8
	D5	C4	E3	D1	D3	D1
	E1	D4	F2	D9	D6	D6
	E3	F3	F3	E2	E2	D8
	E7	F4	F4	E8	E7	E8
	F6	G2	F7	F1	F2	F4
	G2	G7	G2	F3	F7	G2
	G4	H3	G7	F9	G3	G5
	G7	H5	G8	G3	G6	G8
	H1	I7	G9	G7	H4	G9

LWS	**1**	**2**	**3**	**4**	**5**	**6**
	A2	A3	A5	B2	A1	A3
	A6	A4	A6	B4	A6	A5
	A7	A6	B6	C1	B1	A9
	B5	B1	D1	C5	B2	B3
	B7	B2	D2	C7	B6	B4
	C3	B7	D7	D3	B8	C1
	D1	C3	D8	D6	C4	C7
	E3	D5	E3	E2	C8	D3
	E4	E1	E6	E5	D8	D4
	G2	E3	F5	F3	E9	D6
	G3	F6	F7	F7	F1	E6
	I1	G2	G4	G4	F7	F9
	I2	H2	H2	H5	F9	G2
	I3	H5	H3	H6	G9	G3
	I6	I2	H7	I6	E4	G4

Table E1 (cont.). Grid points sampled for lichen litterfall in 1995 and 1996.

Block	Grid Points Used At Each Unit					
PH	**1**	**2**	**3**	**4**	**5**	**6**
	A7	A5	A3	A2	A1	A2
	B5	A6	A5	C3	A3	A5
	B7	B2	B2	C4	C1	A6
	C2	B6	B8	C7	C2	B1
	C5	B8	B9	D6	C4	C2
	D4	B9	C6	D7	E3	C3
	D6	C3	D2	E2	F4	C8
	D7	C5	D4	E5	G2	D3
	E1	D7	E1	E8	G6	D5
	E2	D9	E9	F5	H3	D6
	E8	E1	G1	F8	H4	F1
	F7	E9	G4	G2	H5	F3
	G1	F3	G6	G3	I3	F9
	G4	F6	G8	G6	I4	G4
	H7	G2	G9	H3	I5	G6

Table E2. Azimuth from grid point used to locate the lichen litterfall plot.

Block	1	2	3	4	5	6
Butte	135°	135°	90°	135°	135°	145°
LWS	320°	10°	314°	36°	326°	9°
PH	40°	180°	155°	79°	352°	78°

CHAPTER II

DOES *GLAUCOMYS SABRINUS* TAKE A "LICHEN" TO *BRYORIA*?

Pipp, Andrea K., M.S. February 1998 Wildlife Biology

Director: Ragan M. Callaway

Does Glaucomys *sabrinus* take a "lichen" to *Bryoria*?

Abstract. *Bryoria*, an epiphytic lichen, is an important source of winter food and nesting material for *Glaucomys sabrinus*. However, the role of *Bryoria* in predicting quality habitat for *Glaucomys sabrinus* has not been investigated. I correlated the abundance of *Bryoria* with the abundance of *Glaucomys sabrinus* using simple linear regression. The abundances of *Bryoria* and *Glaucomys sabrinus* positively correlated with an r^2 of 0.54 for 1995 data and an r^2 of 0.67 for 1994-1996 data. These results support the literature that *Bryoria* is an important component of *Glaucomys sabrinus* habitat in geographic regions receiving a persistant winter snowpack.

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INTRODUCTION

The northern flying squirrel, *Glaucomys sabrinus*, has a broad distribution (Maser et al. 1985) in the USA and the factors that control their distribution are still being debated. Flying squirrel densities may be limited by the availability of den cavities (Carey 1991, Carey et al. 1992). Studies conducted in western Oregon and Washington suggest that the percent cover of ericaceous shrubs, the number of snags per hectare, and the origin of the stand (wind/fire versus clearcut) produced good predictive power for predicting the number of flying squirrels (Carey 1995). However, in northern California, a higher correlation between mean flying squirrel density and the sporocarps of hypogeous fungi led Waters and Zabel (1995) to suggest that flying squirrel densities may be limited by hypogeous fungi rather than cavities or understory plant cover.

The northern flying squirrel is mycophagous, relying on lichens, epigeous fungi, and hypogeous fungi for their food source (Carey 1995). Comparative studies of the summer and winter diets of flying squirrels show that epiphytic lichens are consumed more in the winter than in the summer while sporocarps of hypogeous fungi are consumed more in the summer (Maser 1985, Hall 1991, Rosentreter et al. 1997). Epiphytic lichens may be particularly important to their winter diet in portions of their range where a persistent snowpack develops. Further, studies have shown that the most common lichen consumed are species of the genus, *Bryoria* (Maser et al. 1978, Maser et al. 1985, Rosentreter et al. 1997, Zabel and Waters 1997). In addition, lichens are often used as nesting material and *Bryoria* is the commonly used lichen (Maser et al. 1985, Hayward and Rosentreter 1994). However, there have been no studies correlating the

abundances of *Bryoria* and flying squirrels in mature forests that maintain a winter snowpack.

STUDY AREA

An opportunity to study the relationship between *Bryoria* and *Glaucomys sabrinus* came about through the multi-agency project, The Demonstration of Ecosystem Management Options (DEMO), which will evaluate the impacts of different harvest treatments on the flora and fauna of forests in Oregon and Washington (Anonymous 1996a). Baseline data on epiphytic lichens and small mammals were collected, prior to harvesting, on the Gifford Pinchot National Forest in Washington using DEMO study sites. The terminology used will be consistent 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 that have re-generated from fire and are each 13 hectares in size. Each unit consists of either a 7x9 or 8x8 grid with 63 or 64 sampling points separated by 40 meters. Each unit is buffered on all sides by at least 40 meters to minimize the effects of forest edges and to provide an effective grid size for estimating the density of flying squirrels (Anonymous 1996b). The Butte block is approximately 75 years old and receives about 178-203 cm of precipitation annually (Brockway et al. 1983). The Paradise Hills block ranges from approximately 122 to 150 years old and receives an estimated 254-305 cm of precipitation annually (Brockway et al. 1983). The Little White Salmon block ranges from approximately 125 to 164 years old and receives about 165 cm of precipitation annually (Brockway et al. 1983).

METHODS

Lichen Litterfall Sampling

Lichen biomass was collected using the lichen litterfall pickup method (McCune 1994), which estimates the biomass and species composition in the canopy by sampling the lichen litter on the ground. In late October of 1995, lichen litterfall was sampled on all 18 DEMO units. In early October of 1996, lichen litterfall was re-sampled on nine of these units. Collecting lichens in the fall is preferred because weather patterns tend to be more, thus, avoiding large pulses in litterfall associated with major storms (McCune 1994). Lichen sampling was completed in seven days and no significant weather events occurred during sampling in either year.

In each unit, lichen litterfall was collected near 15 randomly picked sampling points. Each lichen plot is circular with a radius of 2 m and an area of 12.5 m^2. For units with two years of sampling, lichen plot perimeters were approximately two meters apart. All epiphytic lichens that had blown down from the canopy or were attached to fallen branches were collected according to guidelines developed by McCune (1994).

In the lab, each lichen plot was cleaned and sorted to species, except *Bryoria*, *Hypogymnia*, and *Usnea* were identified only to the genus level. I used Goward et al. (1994) and McCune and Goward (1995) to identify species. 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 plots was pooled at the unit level and converted to kilograms per hectare per year.

Glaucomys sabrinus Trapping

Arboreal and small terrestrial mammals were trapped on all DEMO units from 1994 to 1996 (Anonymous 1996a). Northern Flying squirrels (*Glaucomys sabrinus*) were live-trapped in the fall using one Tomahawk 201 trap at each sampling point (63 or 64 traps/unit). Placement of the trap on the ground or on the tree was alternated at sampling points. Traps were baited, covered, and contained an insulated nest cup to reduce the risk of death due to hypothermia. In 1994, flying squirrels were trapped for a total of eight nights over a two week period in all units, except Little White Salmon unit two was not trapped. In 1995, flying squirrels were trapped for 16 nights over a five week period at the Butte units and for eight nights at the Little White Salmon and Paradise Hills units over a two week period. However, unit two in each block was not trapped for flying squirrels. Due to very low abundances in the Little White Salmon and Paradise Hills blocks during 1994 and 1995, only the Butte block was trapped in 1996. Trapping at all Butte units occurred for a total of 16 nights over a five week period in 1996.

Statistical Analysis

Simple linear regression was used to correlate flying squirrel abundance with *Bryoria* abundance for 1995 (Norusis, SPSS, version 6.1). Prior to this, the number of individual flying squirrels caught per unit was converted to trapping effort per 100 trapnights for each unit, using the equation:

$$\#\text{ of different flying squirrels caught} \div \left[\frac{\text{number of traps X number of nights}}{\text{100 trapnights}}\right]$$

This was done to make comparisons between units and between years possible. Simple linear regression was also used to correlate *Bryoria* biomass with flying squirrel abundances over the course of the study. To do this, *Bryoria*'s biomass was averaged over two years and the trapping effort per 100 trapnights was averaged over three years.

RESULTS

Bryoria

Comparison of the nine units sampled in 1995 and 1996, showed that epiphytic lichen biomass was significantly higher in 1996 (13.8 kg/ha ± 2.6 S.E. in 1995, 20.3 kg/ha ± 4.7 S.E. in 1996; paired $t = -2.629$, $df = 8$; $P = .030$). Although lichen biomass differed between years, species composition and their relative abundances in each unit was proportionately similar between years.

In 1995, the biomass and number of plots containing *Bryoria* differed among the three blocks (Table 1). Within the Butte block, *Bryoria* averaged 1.0 kg/ha and ranged from 0.40 to 1.72 kg/ha. *Bryoria* also occurred in 87% to 100% of the 15 plots in each unit. Within the Little White Salmon block, *Bryoria* averaged 0.23 kg/ha and ranged from 0.10 to 0.32 kg/ha. *Bryoria* occurred in 73% to 87% of the 15 plots in each unit. Within the Paradise Hills block, *Bryoria* averaged 0.31 kg/ha and ranged from 0.09 to 0.69 kg/ha. *Bryoria* occurred in 33% to 93% of the 15 plots per unit.

Bryoria showed a similar trend to the 1995 data in 1996 (Table 1). Within the Butte block, *Bryoria* averaged 1.3 kg/ha, ranging from 0.72 to 2.24 kg/ha. *Bryoria* was found in 93% to 100% of the 15 plots in each unit. In the Little White Salmon block,

Bryoria averaged 0.20 kg/ha, ranging from 0.10 to 0.30 kg/ha, and occurring in 53% to 93% of the 15 plots in each unit. In the Paradise Hills block, *Bryoria* averaged 0.31 kg/ha, ranging from 0.10 to 0.20 kg/ha, and occurring in 60% to 100% of the 15 plots in each unit.

Glaucomys sabrinus

From 1994 to 1996, flying squirrels were captured in all Butte units sampled (Table 1). In 1994 and 1995, flying squirrels were captured in two and four units of Little White Salmon and in two and one unit(s) of Paradise Hills, respectively (Table 1). In 1994, flying squirrel abundances were highest within the Butte block, lower within the Paradise Hills block, and least within the Little White Salmon block. In 1995, the Butte block still contained the highest flying squirrel abundances, but Paradise Hills and Little White Salmon reversed their trend from 1994.

In 1995, the correlation of *Bryoria* biomass against the number of flying squirrels captured per 100 trapnights was positive ($r^2 = 0.54$, $P = 0.002$, $n = 15$ units) (Figure 2). The correlation between mean *Bryoria* biomass (1995-1996) and the mean number of flying squirrels caught per 100 trapnights (1994-1996) also produced a positive, linear relationship ($r^2 = 0.67$, $P = 0.007$, $n = 9$ units) (Figure 3).

DISCUSSION

My results suggest that *Bryoria*, an epiphytic lichen, may influence flying squirrel populations as evidenced by the parallels in flying squirrel abundances of 1994, 1995, and 1996 with *Bryoria* abundances of 1995 and 1996. It has been well documented that *Bryoria* provides food as well as nesting material for the northern flying squirrel (McKeerver 1960, Maser et al. 1985, Hall 1991, Hayward and Rosentreter 1997, Rosentreter et al. 1997, Zabel and Waters 1997). In northeastern Oregon, flying squirrel stomachs contained only three percent of hypogeous fungi from December - April, but from May to October, the percent of hypogeous fungi rose from 13% to 56%, respectively (Maser et al. 1995). In contrast lichen species comprised 93% of the contents from December - April, and from May to October, the percentage declined from 68% to eight percent, respectively (Maser et al. 1985). *Bryoria fremontii* was the dominant lichen eaten as well as the only lichen used for nesting material (Maser et al. 1985). In central Idaho, 86% percent of winter scats and 25% of summer scats contained lichens (Rosentreter et al. 1997). Winter scats consisted primarily of lichens, but also had significant amounts of hypogeous fungi (Boletoid genera, Coreinaroid genera, and *Gautieria*) while summer scat consisted of a wide variety of hypogeous fungi and small amounts of lichens (Rosentreter et al. 1997). Flying squirrels have been observed to cache *Gautieria* in the trees during the summer, thus, possibly creating a winter food supply (Rosentreter et al. 1997). In California, fecal and stomach samples of flying squirrels revealed that epiphytic lichens were predominantly consumed during the snow-covered season with a greater diversity of hypogeous fungi being consumed during the

snow-free season (Hall 1991). In central Idaho and western Montana, flying squirrels nesting in Boreal owl nest boxes, constructed their nests almost completely of epiphytic lichen species, using predominantly *Bryoria fremontii*, *B. fuscescens*, and *B. pseudofuscescens* (Hayward and Rosentreter 1994). Proper nesting material for flying squirrels is important, as it may reduce thermal energy expenditures during the winter and/or act as food caches (Hayward and Rosentreter 1994). Although low in proteins, *Bryoria* does provide some carbohydrates and depending upon the species contains few to no secondary chemical acids evident in other lichen species (Hayward and Rosentreter 1994). These studies led to the hypothesis that *Bryoria* is an important winter food for flying squirrels, especially for populations living in areas with persistent snowpacks (Rosentreter et al. 1997).

In this study, flying squirrel abundances were consistently higher at the young Butte units (75 years old) and very low to absent at the older Paradise Hills and Little White Salmon units (122 to 165 years old). All 18 forested units have regenerated from fire and vary greatly in their forest structure; many of the Butte units are structurally more complex than some of the Paradise Hills units in that they have more canopy openness, greater variation in tree density (patchiness), and contain remnant snags and trees (Pipp unpublished thesis). In addition, all 18 units have a persistent winter snowpack (J. White, personal communication).

The apparent contrast between flying squirrel abundances and forest habitat in this study may reflect local differences in climate and forest type. The northern flying squirrel consumes fungi througout its range; however, the type and amount of fungi may vary

with regional changes in climate and floristics (Carey 1995). In the Pacific Northwest, there is a general shift from an abundance of western hemlock (*Tsuga heterophylla*), pacific silver fir (*Abies amabilis*), and western red cedar (*Thuja plicata*) in the north to an abundance of Douglas-fir (*Pseudotsuga menziesii*) in the south; an increase in humus, litter, and coarse woody debris from north to south; and a shift in the prevalence of deciduous shrubs and lichens in the north to a prevalence of evergreen shrubs and broad-leaved evergreen trees in the south (Carey 1995). These changes could account for the seemingly lower abundance and diversity of hypogeous fungi in the north and higher abundance and diversity of hypogeous fungi found in the south (Carey 1995). Consequently, the species diversity, abundance, and seasonal variation in sporocarp production which differs between north and south regions may determine what type of food is available for flying squirrels over time (Carey 1995).

While this study provides evidence that *Bryoria* is an important component of flying squirrel habitat, it is not the only component determining quality habitat for northern flying squirrels. Other forest attributes that affect the availability of denning sites and hypogeous fungi as well as population dynamics may greatly influence flying squirrel abundances in the Pacific Northwest. Flying squirrel populations have been found to be higher in old-growth forests than in managed or young, unmanaged forests (Carey 1995, Waters and Zabel 1995). In contrast, Rosenberg and Anthony (1992) found no statistical difference in flying squirrel abundances between unmanaged old-growth and unmanaged young, second-growth forests. However, their second-growth forests contained remnant old growth components such as, large snags, large woody debris, and

large live trees (Rosenberg and Anthony 1992). Carey (1991, 1995) suggested that cavities and snags may limit flying squirrel densities. Flying squirrels use many different denning sites throughout the year for protection from predators, shelter from the environment, and to raise young; however, flying squirrels are generalists, using cavities in live and dead trees, crevices in large stumps, hollows of fallen branches, and external nests in trees infected with witch's broom rust, stick nests, moss nests, and lichen and twig nests (Rosenberg and Anthony 1992; Carey 1995). As previously shown hypogeous fungi are an important component of the summer diet for flying squirrels throughout their range. More quantitative data is required to fully understand the interaction between *Bryoria* and flying squirrel populations. On-going research at the Gifford Pinchot National Forest on hypogeous fungi, vegetation, and small mammals should also include experiments with *Bryoria* and would provide further insight into habitat variables important to maintain flying squirrel populations.

In regions that maintain a persistant winter snowpack, the biomass of *Bryoria* may limit the distribution and abundance of flying squirrels. *Bryoria* should be maintained and encouraged in forests where appropriate to promote flying squirrels populations that will help disperse and maintain fungal populations, both hypogeous fungi and epiphytic lichens.

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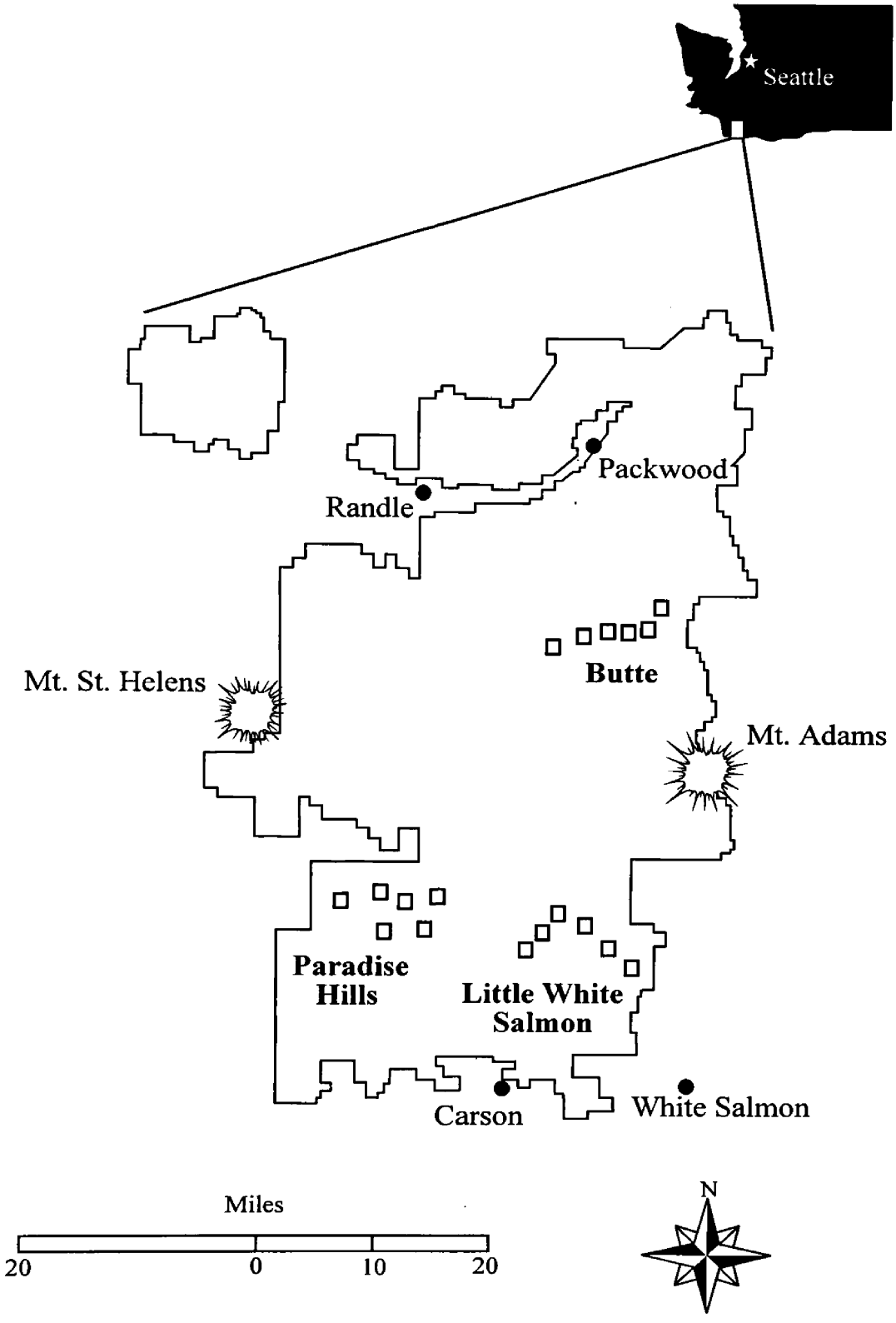

Fig. 1. Gifford Pinchot National Forest, Washington. 18 DEMO (□) study units. Study units are not to scale, but show relative location.

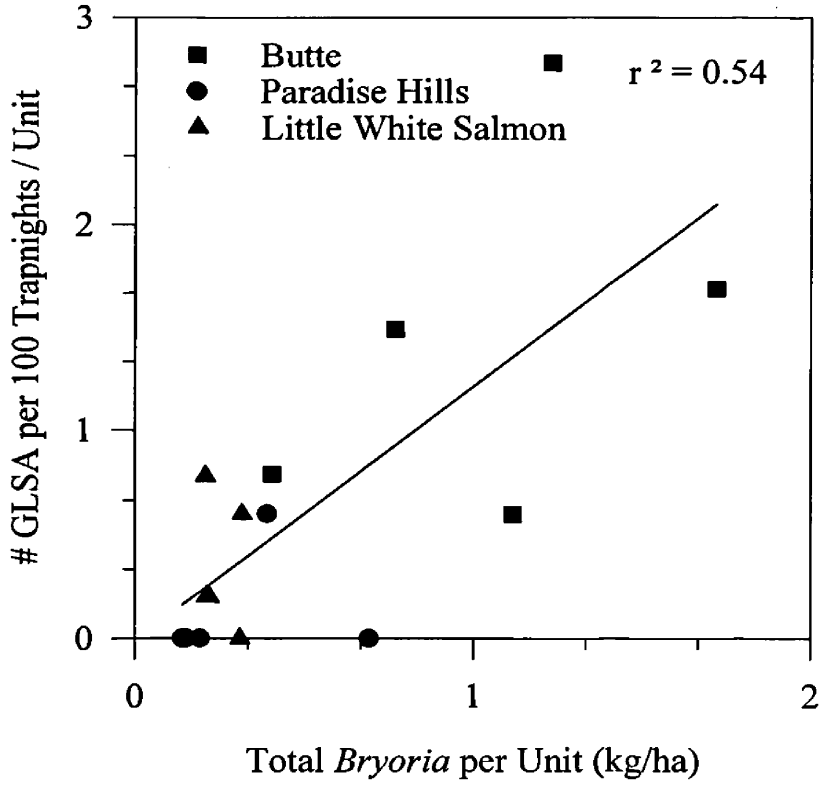

Fig. 2. Number of *Glaucomys sabrinus* (GLSA) per 100 trapnights per unit in 1995 regressed against biomass of *Bryoria* in 1995.

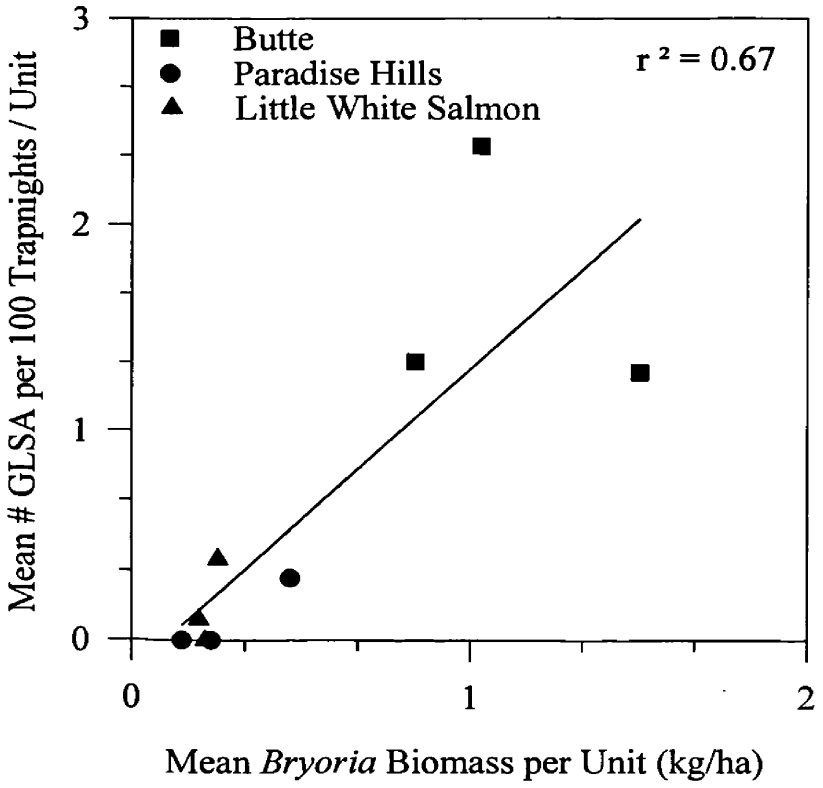

Fig. 3. Mean number of *Glaucomys sabrinus* (GLSA) per 100 trapnights per unit regressed against the mean biomass of *Bryoria* covering 1994 to 1996.

Table 1. Biomass of *Bryoria* per study unit in kg/ha for 1995 and 1996. The number of plots containing *Bryoria* is written in parenthesis. Maximum frequency is 15 plots per unit. The number of *Glaucomys sabrinus* (GLSA) per 100 trapnights per unit for 1994-1996. Blank cells represent no data collected.

Block	Unit	*Bryoria* 1995	*Bryoria* 1996	GLSA 1994	GLSA 1995	GLSA 1996
Butte	**1**	1.12 (15)		0.40	0.60	1.69
	2	0.95 (13)	0.72 (14)	0.60		2.08
	3	0.77 (14)	2.24 (15)	0.40	1.49	1.98
	4	0.40 (14)		0.99	0.79	1.39
	5	1.72 (13)		0.99	1.69	2.38
	6	1.24 (15)	0.83 (15)	1.39	2.78	2.98
LWS	**1**	0.22 (13)		0.60	0.20	
	2	0.10 (13)				
	3	0.21 (12)	0.30 (12)	0	0.78	
	4	0.32 (13)		0.20	0.60	
	5	0.31 (13)	0.12 (8)	0	0	
	6	0.21 (11)	0.19 (14)	0	0.20	
PH	**1**	0.15 (11)	0.15 (15)	0	0	
	2	0.09 (7)		0		
	3	0.39 (13)		0.40	0.60	
	4	0.39 (14)	0.24 (12)	0.59	0	
	5	0.69 (5)		0	0	
	6	0.14 (9)	0.28 (15)	0	0	