

**Lichen Abundance and Biodiversity Along a
Chronosequence from Young Managed Stands to
Ancient Forest**

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We, the members of Peter Nathan Neitlich's graduate committee, assert by our signatures that he has satisfied the requirements for graduation from the University of Vermont's Field Naturalist Program (Department of Botany). We recommend to the Graduate College of the University of Vermont that he be awarded the degree of Master of Science.

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ABSTRACT

Epiphytic lichens constitute a great portion of the vegetational biodiversity of Pacific Northwestern forests. The ecological importance of lichens in late-successional forests is increasingly appreciated, but little is known about the effect of forest management (e.g., conversion of old growth to young rotational stands) on lichen populations. This study compared the species richness and biomass of epiphytic macrolichens in four forest age classes (40, 70, 140 and 510 years after stand replacing disturbance) in the *Tsuga heterophylla*-*Pseudotsuga menziesii* zone of the western Cascades in Oregon. Litterfall plots were used to achieve a broader ecological comparison than has been possible by directly sampling individual trees.

Equal areas of each age class were sampled. Mature and old growth (140 and 510 year old) forests had 40 percent more lichen species than young and rotation-aged (40 and 70 year old) forests ($p=0.03$). Several lichen species were found only in old growth, and many others were restricted to forests at least 140 years old. Old growth forests contained 66% of the pooled biomass of all four age classes; the sum of the lichen biomass in old growth and mature stands totaled approximately 90% of the pooled biomass of all age classes. Lichen biomass of old growth stands (4.7 t/ha) was approximately 30 times that of young stands (0.2 t/ha), 6 times that of rotation-age stands (0.7 t/ha) and 3 times that of mature stands (1.5 t/ha; $0.04 > p > 0.001$). A list of old growth-associated species is proposed based on biomass and species presence data.

Conversion of old growth forests to young managed stands in the western Cascades has ripple effects in the ecosystem including 30 to 145 fold reductions in fixed nitrogen contributed by lichens, four fold reductions in lichen-associated canopy

arthropod abundance, and decreases in the availability of traditionally used forage and nesting materials among birds, small mammals and ungulates.

Key words: lichens, ecology, forest management, conservation biology, arthropods.

INTRODUCTION

Lichens play myriad and conspicuous roles in the ecology of Pacific Northwestern forests. In addition to the great biodiversity they represent (Pike et al. 1975), lichens make a sizable contribution to the forest nitrogen budget (Pike 1978), provide critical winter forage for ungulates and rodents (Richardson and Young 1977), serve as a major food base for many invertebrates (Gerson and Seaward 1977; Lawrey 1984), and provide species-specific nesting material for many birds and mammals (Sharnoff 1992). Extrapolating from studies of lichen decline elsewhere (e.g., Rose 1992; Goward 1992; Lesica et al. 1991), many ecologists feared that conversion of large tracts of late successional forest to young managed stands would eliminate the conditions supporting a rich and abundant lichen flora in the Pacific Northwest. Removal of primary lichen habitat would eliminate not only many lichen taxa, but presumably their ecological roles as well (Seaward 1988; Longton 1992).

The diversity of epiphytic lichens in old growth forests has stimulated considerable research (e.g., Howe 1978; Pike et al. 1975; Hoffman and Kazmierski 1969). Unfortunately, we possess few data on the lichen communities of younger stands or the manner in which they develop as the forest ages. As our society grapples with the consequences of habitat loss and pressure on existing natural populations, such data are acutely needed (FEMAT 1993). This paper seeks to describe the relationship between forest age and the abundance and diversity of lichens in one region, and in doing so, to invite more rigorous assessment of the conservation needs of lichens with respect to forest management. I hope, moreover, that documenting these patterns will facilitate research into age-related processes directly influencing lichen abundance and diversity.

METHODS

Study Area

Study stands were located in and around the lower elevations (≤ 1000 m above sea level) of the H. J. Andrews Experimental Forest and Hagan Block Research Natural Area (Fig. 1) near the town Blue River, Oregon ($44^{\circ}15'$ N, $122^{\circ}10'$ W). The moist, coniferous forests of this region lie on the steep ridges and abundant drainages of the western Cascade foothills. Soils are typically shallow and of pyroclastic origin; the highest ridges usually crest in basaltic outcrops derived from Pliocene volcanism (about 20 million y.b.p.) A mean annual rainfall of 2400 mm, moderate mean January temperatures $> -1.5^{\circ}$ C, and year-round fluvial processes foster high ambient moisture over most of the landscape. Steep ridges, which cover much of the terrain, funnel cold air and fog from higher elevations into riparian lowlands, which stay cool and humid for much of the year. Slightly drier than the coastal rainforests whose canopies are dominated by mosses, ancient forests here host a prolific array of epiphytic lichens.

Lichens were sampled in the western hemlock (*Tsuga heterophylla*)-Douglas-fir (*Pseudotsuga menziesii*) zone (Dyrness et al. 1974), which covers the western Cascades foothills below 1200 m. To minimize noise from environmental gradients other than stand age, I clustered sample areas toward the middle of the temperature and moisture gradients of this zone. My sampling fell within the four plant communities toward the center of the zone (Fig. 2, Table 1).

Except where noted in Table 2, plant associations were characterized by dominant overstory Douglas-fir (*Pseudotsuga menziesii*), co-dominant or, more commonly,

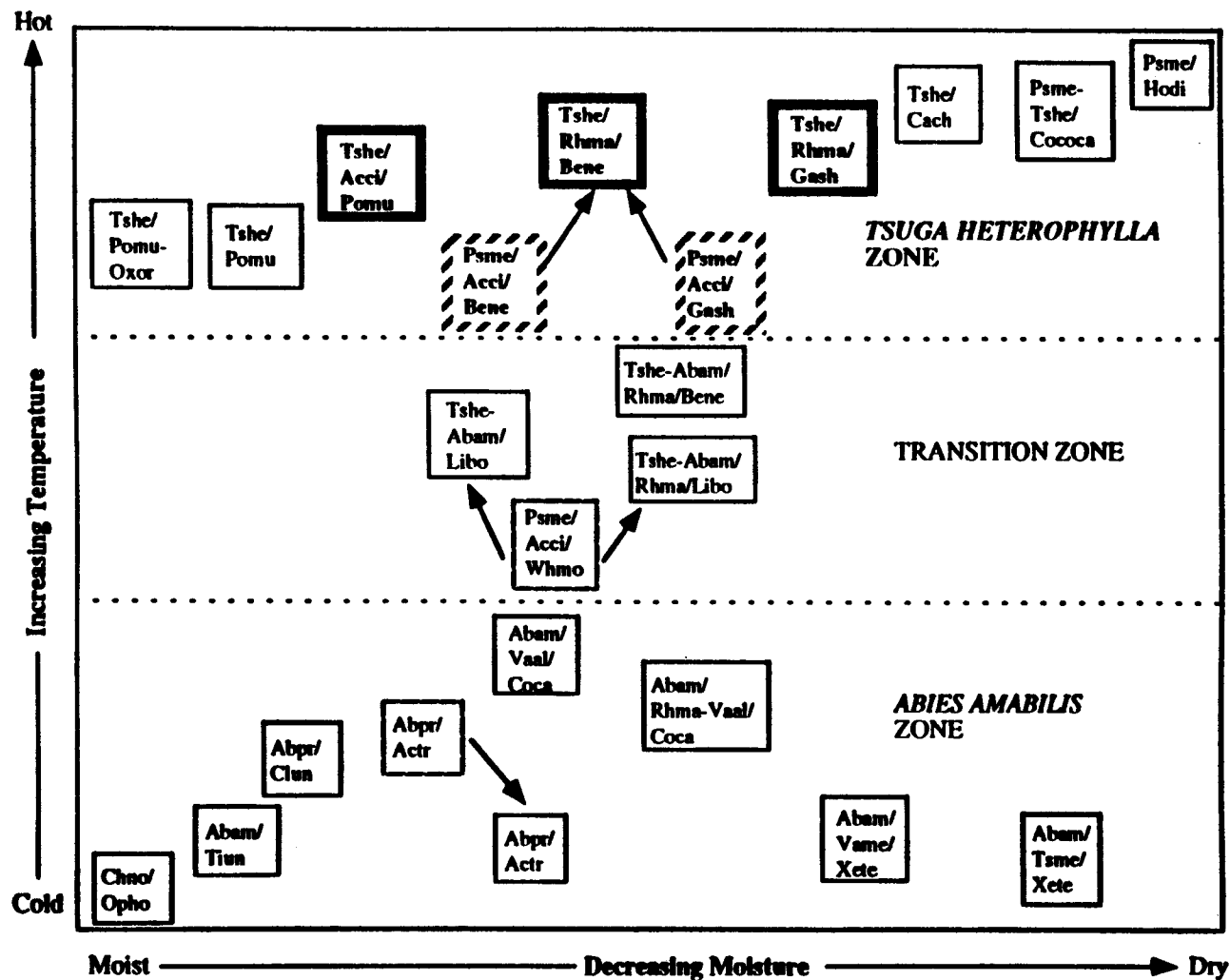


FIGURE 2. Hypothesized relationships between forest communities and environment in central western Cascades based on vegetation ordination (Dyrness et al., 1974: Fig. 5). Communities considered seral have dashed borders. Study stands were located in the *Tsuga heterophylla* zone; communities in bold are those in the study stands. Abbreviations for communities are identified in Table 1.

Table 1. Plant Communities of Fig. 2. Communities in boldface are those in study area. After Dyrness et al. (1974).

PLANT COMMUNITY NAME	ABBREVIATION
<i>Tsuga heterophylla</i> Zone	
<i>Pseudotsuga menziesii</i> / <i>Holodiscus discolor</i>	Psme/Hodi
<i>Pseudotsuga menziesii</i> - <i>Tsuga heterophylla</i> / <i>Corylus cornuta</i>	Psme-Tshe/Coco
<i>Tsuga heterophylla</i> / <i>Rhododendron macrophyllum</i> / <i>Gaultheria shallon</i>	Tshe/Rhma/Gash
<i>Pseudotsuga menziesii</i> / <i>Acer circinatum</i> / <i>Gaultheria shallon</i>	Psme/Acci/Gash
<i>Tsuga heterophylla</i> / <i>Rhododendron macrophyllum</i> / <i>Berberis nervosa</i>	Tshe/Rhma/Bene
<i>Pseudotsuga menziesii</i> / <i>Acer circinatum</i> / <i>Berberis nervosa</i>	Psme/Acci/Bene
<i>Tsuga heterophylla</i> / <i>Acer circinatum</i> / <i>Polystichum munitum</i>	Tshe/Acci/Pomu
<i>Tsuga heterophylla</i> / <i>Polystichum munitum</i>	Tshe/Pomu
<i>Tsuga heterophylla</i> / <i>Polystichum munitum</i> / <i>Oxalis oregana</i>	Tshe/Pomu/Oxor
Transition Zone	
<i>Tsuga heterophylla</i> - <i>Abies amabilis</i> / <i>Rhododendron macrophyllum</i> / <i>Berberis nervosa</i>	Tshe-Abam/Rhma/Bene
<i>Tsuga heterophylla</i> - <i>Abies amabilis</i> / <i>Rhododendron macrophyllum</i> / <i>Linnaea</i>	Tshe-Abam/Rhma/Libo
<i>Tsuga heterophylla</i> - <i>Abies amabilis</i> / <i>Linnaea borealis</i>	Tshe-Abam/Libo
<i>Pseudotsuga menziesii</i> / <i>Acer circinatum</i> / <i>Whipplea modesta</i>	Psme/Acci/Whmo
<i>Abies amabilis</i> Zone	
<i>Abies amabilis</i> - <i>Tsuga mertensiana</i> / <i>Xerophyllum tenax</i>	Abam-Tsme/Xete
<i>Abies amabilis</i> / <i>Vaccinium membranaceum</i> / <i>Xerophyllum tenax</i>	Abam/Vame/Xete
<i>Abies amabilis</i> / <i>Rhododendron macrophyllum</i> - <i>Vaccinium alaskense</i> / <i>Cornus canadensis</i>	Abam/Rhma-Vaal/ Coca
<i>Abies amabilis</i> / <i>Vaccinium alaskense</i> / <i>Cornus canadensis</i>	Abam/Vaal/Coca
<i>Abies procera</i> / <i>Achlys triphylla</i>	Abpr/Actr
<i>Abies amabilis</i> / <i>Achlys triphylla</i>	Abam/Actr
<i>Abies procera</i> / <i>Clintonia uniflora</i>	Abpr/Clun
<i>Abies amabilis</i> / <i>Tiarella unifoliata</i>	Abam/Tiun
<i>Chamaecyparis nootkatensis</i> / <i>Oplopanax horridum</i>	Chno/Opho

Table 2. Study stands, in vicinity of H. J. Andrews Experimental Forest, Willamette National Forest, western Cascades, Oregon. Sites are mapped in Fig. 1.

Stand Number	Forest Age (yrs)	Location*	Elevation (m)	Aspect	Riparian: Yes or No; Vertical Distance (m) †	Dominant Tree Species ‡	Moisture Regime	Notes on Stand Structure	Date(s) Sampled
510									
1		N of RS 5 (HJA).	640 - 700	N	Y: 10-50m	Psme, Tshe	Extremely mesic	Size class extremely large.	6/3-8/93
2		Mack Creek upland (HJA)	670 - 825	N	Y:20-100m	Psme, Thpl, Tshe	Extremely mesic/riparian		6/22-3/93
3		E of L 114 (HJA)	850 - 915	NNW	N	Psme, Tshe	Xeric upland	Extensive wind damage.	6/26-7/93
140									
4		Hagan Block: End of J FS 090 (HB)	610 - 685	N	Y: 10-70m	Psme, Acma, Tshe,	Extremely mesic/riparian	Thinned upslope of sampling.	6/15, 6/16/93
5		Blue River Basin (BRRD)	730 - 825	N	Y: 10-60m	Psme, Tshe, Acma, Thpl	Extremely mesic/riparian		7/13/93
6		SW of L304 (HJA)	850 - 915	NNW	Y:30-100m	Tshe	Mesic	Size class relatively small for age class.	8/3/93
70									
7		End of 611 (BRRD)	610 - 730	NW	Y: 150m	Psme	Moderately xeric	Thinned close to sampling.	7/26/93
8		Jct 610/611 (BRRD)	790 - 915	NW	N	Psme	Moderate	Thinned close to sampling.	7/28/93
9		Tidbits Creek (BRRD)	700 - 790	N	Y:100-150m	Tshe, Psme	Moderate	Size class small due to species and steep slope.	8/5/93
40									
10		L102 (HJA)	640 - 700	N	Y: 0-50m	Psme, Tshe	Extremely mesic		6/12/93
11		L109 (HJA)	700 - 825	N	Y:40-150	Psme	Mesic	Size class small due to steep	7/6-7/93
12		L202 (HJA)	825 - 915	N	N	Psme, Acma	Moderately xeric		7/15/93

† Riparian stands are those within 150 m vertical distance of a year round stream (Howe 1978)

‡ Dominant trees (those visually assessed to constitute > 15% of stems over 10 cm dbh in stand):

Psme (*Pseudotsuga menziesii*) - Douglas fir

Tshe (*Tsuga heterophylla*) - Western hemlock

Thpl (*Thuja plicata*) - Western red cedar

Acma (*Acer macrophyllum*) - Big leaf maple

* Locations: (HJA) H. J. Andrews Experimental Forest, Willamette National Forest, near Blue River, western Cascades, OR; (BRRD) Blue River Ranger District, Willamette National Forest, OR; (HB) Hagan Block Research Natural Area, Finn Rock, OR.

subcanopy western hemlock (*Tsuga heterophylla*), scattered co-dominant western red cedar (*Thuja plicata*) and understory Pacific yew (*Taxus brevifolia*). Rare in old growth stands, big leaf maple (*Acer macrophyllum*) was often present in moderate densities in stands up to 140 years old, where it hosted a rich community of epiphytes. A tall shrub layer included rhododendron (*Rhododendron macrophyllum*), and/or vine maple (*Acer circinatum*), which was most dominant in gaps and younger stands. Except in the youngest stands, low shrubs and herbs covered much of the ground. Most common among these were Oregon grape (*Berberis nervosa*), huckleberries (*Vaccinium* spp.), sword fern (*Polystichum munitum*), and twinflower (*Linnea borealis*). A moss mat, which grew increasingly robust with age, was dominated by *Eurhynchium oreganum*.

Forty and 70 year old seral stands were dominated by a dense canopy of regenerating Douglas-fir (or occasionally western hemlock) and tall shrubs (Fig. 2). In the open understory, low shrubs and herbs tended to be more sparse. Understory herbs and shrubs appeared to reach their peak of dominance in mature stands (140 years old). As the forest aged to old growth, these understory vascular plants ceded somewhat to mosses, which covered the ground and abundant decaying logs in this more heterogeneous plant association.

Study Sites

Lichens were studied in forested stands originating after stand-replacing fires 510, 140, 70 years ago (Teensma 1987) or after clearcuts 40 years ago. Howe (1978) found that northern aspects in old growth reference stands at the H. J. Andrews had greater lichen biomass than southern exposures, and that cyanolichen abundance was greatly limited beyond 150 m vertical distance above streams. In this study I sought to observe

how the lichens of different forest age classes compared under optimal conditions and, therefore, chose northern aspects within riparian environments. I hypothesized that sub-optimal conditions might mask differences in abundance and biomass among the younger age classes. To focus primary attention on differences among age classes, I tried to maintain as many other environmental variables as possible constant.

Three study stands were chosen to represent each age class. Stands were chosen according to the following criteria:

1. Elevations ranged from 610 m to 915 m above sea level (2000 to 3000 ft).
Stands were chosen to avoid elevational overlap such that each site covered about one-third of the 305 m.
2. Site aspect ranged from N (0°) to NW (315°).
3. The highest site in each age class was, because of sharp local topography, higher than 150 m vertical distance above the closest stream. The lower two sites were placed within 150 m vertical distance above a stream. (Because of a shortage of 140 year old sites that met these criteria, all three of the sites in this age class fell within 150 vertical m of a stream.)
4. Stands were located in or as close as possible to the H. J. Andrews Experimental Forest (Fig. 1, Table 2).
5. Stands presumably resulted from catastrophic disturbance which left no remnant vegetation from an older period (Teensma 1987). Stands which had sub-catastrophic disturbances after the initial year of establishment were avoided.
6. Chen and Franklin (1992) found that edge influence on such biological variables as canopy cover, tree density and seedling regeneration extended up to 80 m into old

growth Douglas-fir forests. Edge effects for most variables extended only 60 m--approximately one old growth tree length. Using these criteria, I chose stands which had a minimum of two hectares located 120 m (two tree lengths) or more from other age classes or remnant trees. Eleven of the twelve stands had between 15 and several thousand hectares greater than 120 m from other age classes or remnant trees.

Field methods

Biomass

Ten 2 m radius circular plots were chosen at random within each site. All lichen litterfall within each plot was gathered according to the protocol of McCune (1993a): Lichens were cleaned of debris, and sorted into bags according to three functional groups--"cyanolichens", "Alectorioid" lichens, and "other" lichens. "Cyanolichens" were defined as those macrolichens employing cyanobacteria as primary or secondary photobionts (mainly *Lobaria*, *Nephroma*, *Pseudocyphellaria*, *Sticta*, and *Peltigera* in the western Cascades.) "Alectorioid" lichens were defined as pendulous or tufted fruticose lichens in the genera *Alectoria*, *Bryoria*, and *Usnea*. "Other" lichens included all remaining lichens.

Lichenologists have been traditionally limited in their ability to undertake large scale ecological studies by the time required to rig and sample individual trees. In attempting to design a method to quantify standing lichen biomass without having to climb (and pillage the epiphytes of) hundreds of trees, McCune (1993a) studied the relationship between lichen litterfall and standing crop. His litterfall pickup methodology was designed to capture the steady rain of lichens falling freely from the canopy or attached to small

branches. He reports that the correlation between litterfall and standing biomass was highest ($r^2 = 0.87$) when he discounted decomposing lichens and large, anomalous clusters of lichens attached to large limbs. As the latter occur only rarely in litterfall plots, he reasoned, collecting such clusters would have generated unnecessary statistical noise.

Employing McCune's guidelines, lichens were left uncollected if :

- 1) they were attached to woody debris with a basal diameter greater than 10 cm.
- 2) they were incorporated into the forest floor by fungal hyphae or were mostly buried in decomposing litter.
- 3) they were suspended in the understory higher than 2 m
- 4) they had re-established and taken up new residence
- 5) they normally grew terrestrially, e.g., *Peltigera* spp., and *Cladonia* spp., and represented direct, rather than litterfall, biomass samples.

Species capture

Direct observation of the canopy by climbing suggested that biomass sampling plots detected the lichen species that constituted the vast majority of lichen biomass in the forest, but did not adequately detect rare lichens. In characterizing the species composition of stands for forest health/air quality monitoring, McCune and Dey (1992) found that most lichen species in a stand may be found within a 36.56 m (120 ft) radius sample plot (0.42 ha). Adapting this methodology, lichen species not already encountered in the biomass sample plots were collected from within a circle of 11.56 m radius around plot center. The ten combined species plots were equal in area to one 36.56 m circle.

Species collections were limited to epiphytic macrolichens. Terrestrial lichens, though important in the ecosystem, were avoided for two reasons. First, McCune's litterfall ratio did not adequately quantify their biomass or their biomass importance relative to other lichens; and second, neither litterfall plots nor species capture plots adequately sampled them, as they often grow on patchily distributed mineral soil, rocks, or coarse woody debris. Crustose lichens were avoided for the same reasons. Epiphytic macrolichens were defined as those growing higher than 2 m above the ground in order to exclude species found equally on tree bases and coarse woody debris or soil (e.g., *Cladonia* spp. and *Peltigera* spp.)

Measurements of stand structure

Tree height, crown radius, and first branch height of the closest tree to plot center were measured in each plot. The number of trees with a diameter at breast height (dbh) greater than 10 cm within an 8.9 m radius (250 m²) were counted. Percent canopy closure was assessed visually from plot center. Crown volume was calculated by treating the crown as an idealized cone with the formula

$$\text{Volume} = 1/3 \pi r^2 h,$$

where h is the height from the first branch to the treetop, and r is the crown radius.

Lab Analysis

Lichens were oven dried at 60° C for 24 hr according to the methodology of McCune (1993a). Functional group bags from each plot were then weighed to the nearest 0.01 g. Species biomass was assessed visually as a percent of the functional

group biomass in each bag. Lichens were identified to the most specific taxonomic level possible, using Goward et al. (1992), Brodo and Hawksworth (1977), Hale (1979) and herbarium specimens at Oregon State University (OSC). Nomenclature follows Egan (1987). Identifications were verified by Dr. Bruce McCune.

Data Analysis

Data were analyzed using descriptive statistics, ANOVA, and regression. Raw biomass values were converted to estimated standing biomass according to McCune's (1993b) conclusion that lichen litterfall in western Cascade forests of Oregon and Washington relates to standing biomass in a ratio of 1:100 ($\text{sqrt litterfall} = 0.1 \text{ sqrt biomass}$; $r^2 = 0.87$, $n=18$.) Data were also analyzed using Bray-Curtis multivariate ordination (Gauch 1982). Ordination was based on the 37 most abundant species in biomass plots. Ordination displayed two dimensionally the results of the three dimensional Euclidean distances between each species' biomass in 120 biomass plots.

RESULTS and DISCUSSION

Effect of Stand Age on Lichen Species Composition

A total of 59 epiphytic macrolichen species were found in the four age classes (Fig. 3, Table 3). The maximum species richness (52 species, 90% of the total) occurred in old growth (510 year-old age class) while the minimum (34 species, 58% of the total) occurred in the 70 year-old age class. Old growth displayed 60% greater mean species richness per stand than 70 or 40 year-old stands. Examination of means and totals revealed a significant difference in species richness between the two older stands compared to the two younger stands ($p=0.03$ for means), but little difference between stands of 510 versus 140 years, or between stands of 70 versus 40 years. (See Appendix 1a and b for statistical analyses.)

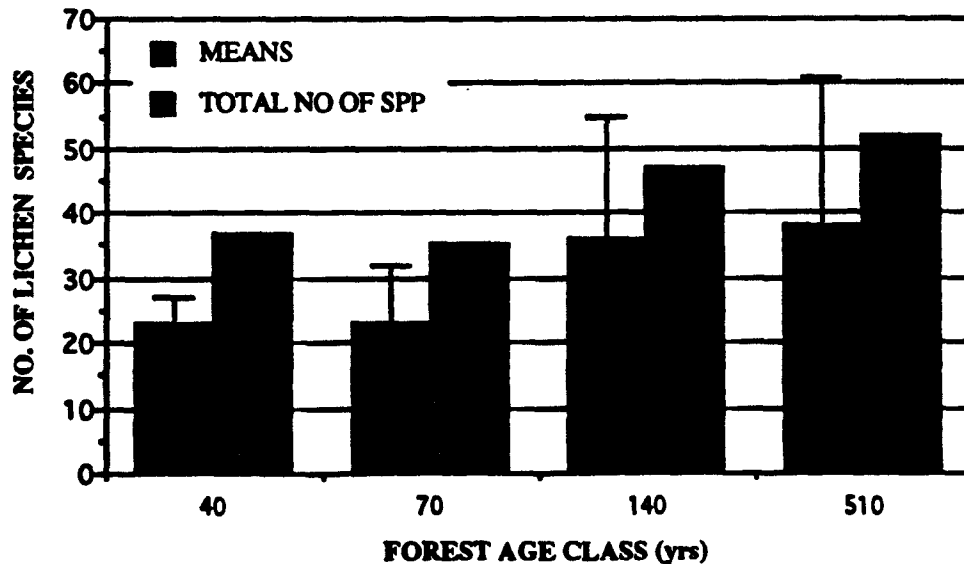


FIG. 3. The mean and total number of epiphytic macrolichen species per age class, H. J. Andrews Experimental Forest, OR. Means are derived from $n=3$ sites, each 0.42 ha. Totals are based on the sum of these three sites, or 1.26 ha. Error bars display the 95% confidence limits of the means.

Table 3. Epiphytic macrolichen species present in forest study stands of four ages. Stands were located in and around the H. J. Andrews Experimental Forest, Willamette National Forest, OR (see Figure 1 for locations).

LICHEN SPECIES	STANDS											
	Stand Age (yrs)											
	510			140			70			40		
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Alectoria sarmentosa</i>	x	x	x	x	x	x	x	x	x	x	x	x
<i>Alectoria vancouverensis</i> ◊		x					x				x	
<i>Bryoria capillaris</i>		x		x	x		x					
<i>Bryoria friabilis</i>	x	x	x	x	x	x	x	x			x	x
<i>Bryoria fuscescens</i>	x		x	x	x		x	x	x		x	x
<i>Bryoria oregana</i> ◊	x	x	x	x	x	x	x	x			x	x
<i>Bryoria pikei</i> ◊	x	x	x	x	x			x		x		
<i>Bryoria pseudofuscescens</i> ◊		x			x		x					
<i>Cavernularia hultenii</i>		x			x	x			x	x		x
<i>Cetraria canadensis</i>							x					
<i>Cetraria chlorophylla</i>	x	x	x	x	x			x	x		x	x
<i>Cetraria idahoensis</i> ◊*		x	x	x								x
<i>Cetraria orbata</i>	x	x		x	x	x	x	x				x
<i>Cetraria pallidula</i> ◊					x							x
<i>Cetraria platyphylla</i> ††	x											
<i>Cladonia coniocraea</i> ‡		x										
<i>Cladonia squamosa</i> ‡		x										
<i>Evernia prunastri</i>				x			x				x	
<i>Hypogymnia apinnata</i> ◊†	x	x		x								
<i>Hypogymnia austerodes</i> ††	x											
<i>Hypogymnia enteromorpha</i> ◊	x	x	x	x	x	x	x	x	x	x	x	x
<i>Hypogymnia imshaugii</i>	x	x	x	x	x	x	x	x	x	x	x	x
<i>Hypogymnia inactiva</i>	x	x	x	x	x	x	x	x	x	x	x	x
<i>Hypogymnia metaphysodes</i> ◊	x	x	x	x	x	x				x		
<i>Hypogymnia occidentalis</i> ◊		x		x	x	x		x				
<i>Hypogymnia oceanica</i> ◊††		x										
<i>Hypogymnia physodes</i>	x	x	x	x	x	x	x	x	x	x	x	x
<i>Hypogymnia tubulosa</i>	x	x	x	x	x	x			x	x	x	
<i>Hypotrachyna sinuosa</i>				x						x		x
<i>Lobaria oregana</i> ◊	x	x	x	x	x	x	x	x	x	x	x	x
<i>L. oregana</i> (blue green morph) ††					x							
<i>Lobaria pulmonaria</i>	x	x	x	x	x	x	x	x		x		
<i>Lobaria scrobiculata</i> *	x	x	x	x	x	x				x		
<i>Nephroma bellum</i> †	x	x	x	x	x	x						
<i>Nephroma helveticum</i> *	x	x	x	x	x	x				x		
<i>Nephroma laevigatum</i> †		x		x	x							
<i>Nephroma occultum</i> †◊		x		x								
<i>Nephroma parile</i> †		x		x	x							
<i>Nephroma resupinatum</i> †	x	x			x							
<i>Omphalina</i> sp.	x											

Continued

TABLE 3, CONTD

LICHEN SPECIES	STANDS											
	Stand Age (yrs)											
	510			140			70			40		
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Parmelia pseudosulcata</i>	x	x	x	x	x	x	x	x			x	
<i>Parmelia saxatilis</i>		x			x	x	x					x
<i>Parmelia squarrosa</i> ††		x										
<i>Parmelia sulcata</i>	x	x	x	x	x	x	x	x	x	x	x	x
<i>Parmeliopsis hyperopta</i>	x	x	x		x	x		x	x		x	
<i>Platismatia glauca</i>	x	x	x	x	x	x	x	x	x	x	x	x
<i>Platismatia herrei</i> †	x	x	x	x	x	x	x	x	x	x	x	x
<i>Platismatia stenophylla</i> †	x	x	x	x	x	x	x	x		x	x	x
<i>Pseudocyphellaria anomala</i> †	x	x	x	x	x	x			x	x	x	x
<i>Pseudocyphellaria anthraxis</i> ††	x	x	x	x	x							
<i>Pseudocyphellaria crocata</i> *	x	x		x						x		
<i>Pseudocyphellaria rainierensis</i> ††††	x	x	x									
<i>Ramalina farinacea</i>				x	x		x					
<i>Sphaerophorus globosus</i>	x	x	x	x	x	x	x	x	x	x		
<i>Sticta beauvoisii</i> ††††		x										
<i>Sticta fuliginosa</i>		x		x	x				x	x		
<i>Sticta limbata</i>				x						x		
<i>Usnea</i> spp. pendant	x	x	x	x	x	x	x	x	x	x	x	
<i>Usnea</i> spp. tufted	x	x	x	x	x		x	x	x	x	x	x
Total for Stand	36	48	30	41	41	27	26	23	19	25	22	22
Mean for Age Class		38			36.3			22.7			23	
Total for Age Class		52			48			34			37	
Percent of Total Species in Study		88			81			58			63	

* Mostly restricted to stands of 140 years or older in this study (3)

† Restricted to stands 140 years or older in this study (8)

†† Restricted to old growth in this study (4)

††† Restricted to old growth in this study and probably restricted to old growth globally (3)

‡ Probably restricted only *epiphytically* to old growth in this study (2)

‡ "Nephroma silviae-veteris" (Goward et al. 1992).

‡ Endemic to Pacific Northwest

Nine species in the study area were restricted to old growth (Table 3), and 10 other species were restricted to forests of 140 years or older (totaling 29% of all epiphytic macrolichens). Of the former nine, probably two (*Pseudocyphellaria rainierensis* and *Sticta beauvoisii*) depend upon old growth globally (B. McCune, personal communication). The remaining seven probably occur in these old growth forests for one of three other reasons:

- 1) The moisture regime in Cascadian old growth matches their mostly coastal or boreal/montane distributions (e.g., *Hypogymnia oceanica*, *H. austerodes*).
- 2) These species are outside of their central range and microclimatic preferences (e.g. *Cetraria platyphylla*, found widely in dry forests east of the Cascade crest), but may grow in the dry microclimate of the upper canopy. Old forests are likely to accumulate a greater proportion of range anomalies than other age classes by virtue of the great time they have stood awaiting the unlikely arrival of propagules, and the greater variety of microclimates present.
- 3) Some species may occur in other forest age classes, but occur *epiphytically* only in old growth (e.g., *Cladonia* spp., which may inhabit the decomposing bark or limbs typical of live old growth or of dead wood in other age classes).

High specificity and greater species richness of lichens in old growth corroborate similar findings in other parts of the world (e.g., Rose 1976; Goward 1992), and illustrate the unique role of old growth forest in conserving such habitat-specific and dispersal-limited taxa. Difficulties in colonization even after 40 years were evident in walking the edges of post-clearcut stands in the western Cascades: while some old growth associated species such as *Lobaria oregana* established in the second growth

within 10 m of the edge, they were very sparse or more commonly lacking in the interior of these stands (Table 3). Not until the interior forest study stands had attained an age of 140 years did they begin to take on a species richness close to that of old growth stands. Not even 140 years of development permitted a full assemblage of old growth specifics, however. The occurrence of several lichens both endemic to the Pacific Northwest and specific to late successional forest deserves special note as debate over allowable cut rages over the remaining 5% of original old growth (FEMAT 1993).

One drawback of the litterfall method is that it may fail to detect rare species that may be easily located by direct access (e.g., climbing or sampling windthrows or cut trees). This is most true in old growth where the richest lichen communities are located on stout, infrequently falling mid-crown limbs (McCune 1993b). Many old growth species probably went undetected in these litterfall plots even when they were present above. While litterfall plots allow coverage of great areas, they should be regularly appended with direct access data for more accurate conservation inventories.

The microclimate and plant associations in young stands allowed for colonization of epiphytes rarely found in the western Cascades. The lichens of young stands consisted overwhelmingly of those in the "other" functional group. These lichens are most abundant in the relatively dry moisture regime of the upper crown of older trees and in the drier climate of forests east of the Cascade crest. Given a microclimate drier than in other age classes, young stands hosted abundant crustose lichens (e.g. *Pertusaria* spp.) and certain dry climate range extensions such as *Cetraria canadensis*. These may be present in older forests, but were not detected by litterfall examination. The abundant hardwoods in young stands also boosted diversity somewhat, hosting such species as

Evernia prunastri and *Ramalina farinacea*, which grow commonly on hardwoods in the Willamette Valley. These species were rare or absent in the hardwood-poor plant associations in old growth forests.

Effect of Stand Age on Lichen Abundance

Species presence data provide essential information about age class specificity and rare species, but tell us little about the strength of age class affinities among more widely distributed lichens. Uncoupled from abundance data, species presence data fail to distinguish between a thriving population and an isolated fleck barely surviving outside its optimal habitat. Species presence data thus equates the several tons per hectare of *Lobaria oregana* in old growth forests with the few kilograms per hectare present in young forests. By contrast, analysis of lichen biomass distribution reveals an overwhelming affinity of most of the species in this study for old growth.

Epiphytic macrolichen biomass changed dramatically over a 500 year course of forest succession (Fig. 4). The total biomass in 510 year old forest is approximately 30

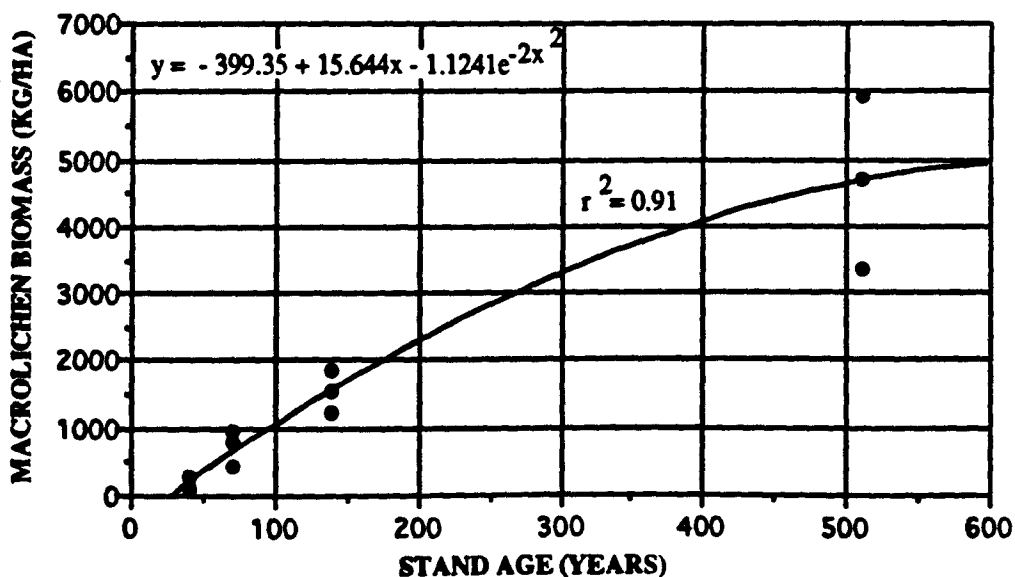


FIG. 4. Epiphytic macrolichen biomass as a function of forest age in 12 sites, H. J. Andrews Experimental Forest, Willamette National Forest, western Cascades, OR; n=12 stands.

times that of 40 year old forest, 6 times that of rotation age forests (70 years old), and 3 times that of mature forest (140 years old; Table 4). Regressed with a second order polynomial which levels off with increasing age as intuitively expected, biomass was strongly correlated to forest age ($r^2=0.91$). (Linear regression yielded an r^2 of 0.89. Appendices 2 and 3 present statistical summaries of biomass data.) The difference between mean biomass of at least one age class versus all others was highly significant in ANOVA ($p=0.0001$ for untransformed data). The high biomass in old growth increased the variance of this age class dramatically relative to other age classes, thus requiring data transformation to normalize residuals (Appendices 2a and b.) Square root transformed data yielded the most normal residual pattern and revealed significant differences between the mean biomass of each age class relative to others ($0.04 > p > 0.0001$).

Based on equal sample areas for each age class, eight species showed greater than 75% of their pooled biomass from all age classes in old growth; twenty species showed greater than 50% of their biomass in old growth (Table 5). Approximately 90% of all species found in biomass plots had more biomass in forests of 140 years old or older than in younger stands. This nearly universal affinity of macrolichen biomass to older forests suggests a far more sweeping conclusion than indicated by simple species presence data. The strong clustering of biomass plots according to age class in Bray-Curtis ordination likewise suggests a strong correlation between the biomass of lichen species and forest age (Fig. 5).

The twenty species showing the majority of their biomass in old growth have been integrated with the nine species restricted to old growth (above) to create a list of species showing strong affinity for old growth (Table 6). Since older forests have many times

Table 4. Estimated mean standing biomass (kg/ha) of epiphytic macrolichen species, standard error of the means, and percent of a species' total biomass in all age classes (pooled). Data are presented in order of descending biomass in old growth. Means were derived from 3 study sites in each age class (n=3 sites/age class) in and around H. J. Andrews Experimental Forest, Willamette National Forest, western Cascades, Oregon. Statistics for functional groups are summarized in Table 8.

	FOREST AGE (YEARS)											
	510			140			70			40		
	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes
LICHEN SPECIES												
<i>Lobaria oregana</i>	2576.50	559.51	80.28	513.21	173.35	15.99	108.12	106.22	3.37	11.46	6.53	0.36
<i>Lobaria pulmonaria</i>	721.50	447.88	72.42	273.89	141.04	27.49	0.00	0.00	0.00	0.93	0.93	0.09
<i>Alectoria sarmentosa</i>	330.58	153.59	59.70	40.96	38.26	7.40	169.45	62.88	30.60	12.75	7.72	2.30
<i>Platismatia glauca</i>	222.42	32.01	50.25	144.81	72.90	32.72	59.26	16.14	13.39	16.12	8.75	3.64
<i>Usnea spp. pendant</i>	182.24	51.85	76.20	33.87	19.30	14.16	16.61	3.85	6.94	6.45	6.29	2.70
<i>Sphaerophorus globosus</i>	169.72	86.72	55.86	123.35	14.77	40.60	10.61	5.91	3.49	0.13	0.13	0.04
<i>Pseudocyphellaria anthraspis</i>	84.33	31.61	73.35	30.64	29.26	26.65	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hypogymnia inactiva</i>	80.01	23.70	20.53	84.78	29.97	21.75	186.96	70.00	47.97	37.96	24.25	9.74
<i>Platismatia herrei</i>	58.84	18.14	63.61	27.19	4.34	29.39	4.77	2.56	5.16	1.70	0.81	1.84
<i>Pseudocyphellaria anomala</i>	44.67	23.12	53.90	31.62	13.11	38.16	0.11	0.11	0.13	6.47	4.40	7.81
<i>Hypogymnia enteromorpha</i>	40.40	7.83	19.77	87.14	25.51	42.64	56.93	13.36	27.85	19.91	5.63	9.74
<i>Hypogymnia imshaugii</i>	37.13	5.82	26.27	31.83	7.35	22.52	52.89	3.23	37.42	19.50	10.39	13.79
<i>Platismatia stenophylla</i>	17.72	9.39	21.02	32.44	12.84	38.47	31.70	26.03	37.59	2.47	1.69	2.93
<i>Nephroma helveticum</i>	15.84	7.97	54.47	12.44	10.13	42.79	0.00	0.00	0.00	0.80	0.80	2.74
<i>Hypogymnia physodes</i>	13.61	2.07	34.83	14.43	5.45	36.93	3.40	1.51	8.69	7.64	4.70	19.55
<i>Alectoria vancouverensis</i>	10.61	10.61	88.89	0.00	0.00	0.00	0.85	0.85	7.12	0.48	0.48	3.99
<i>Usnea spp. tufted</i>	9.60	3.25	29.96	11.14	9.63	34.75	8.59	5.97	26.81	2.72	1.27	8.48
<i>Pseudocyphellaria rainierensis</i>	8.49	5.06	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nephroma bellum</i>	5.91	1.99	58.66	4.17	1.83	41.34	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lobaria scrobiculata</i>	4.11	1.65	32.82	8.15	4.60	65.05	0.00	0.00	0.00	0.27	0.27	2.13
<i>Hypogymnia tubulosa</i>	3.71	1.78	33.10	3.77	2.71	33.57	1.46	1.46	13.01	2.28	1.69	20.32
<i>Parmelia sulcata</i>	2.81	0.98	41.07	3.05	2.29	44.57	0.64	0.33	9.29	0.35	0.03	5.06
<i>Nephroma resupinatum</i>	2.31	2.31	74.33	0.80	0.80	25.67	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cetraria idahoensis</i>	1.88	1.88	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cetraria chlorophylla</i>	1.49	0.89	45.51	0.16	0.12	4.90	0.53	0.27	16.33	1.09	1.05	33.27
<i>Bryoria oregana</i>	1.30	0.96	68.90	0.24	0.12	12.72	0.27	0.14	14.14	0.08	0.05	4.24
<i>Bryoria pikei</i>	1.09	0.51	77.25	0.24	0.20	17.06	0.05	0.05	3.79	0.03	0.03	1.90
<i>Bryoria capillaris</i>	1.06	1.06	44.41	0.35	0.21	14.53	0.98	0.98	41.06	0.00	0.00	0.00

TABLE 4 CONTINUED

LICHEN SPECIES	FOREST AGE (YEARS)											
	510			140			70			40		
	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes	Biomass (kg/ha)	± S.E.	% of Σ species' biomass in all age classes
<i>Bryoria friabilis</i>	0.90	0.86	39.97	0.80	0.27	35.25	0.45	0.24	20.06	0.11	0.07	4.72
<i>Parmelia pseudosulcata</i>	0.90	0.68	51.52	0.03	0.03	1.52	0.80	0.80	45.44	0.03	0.03	1.52
<i>Bryoria fuscescens</i>	0.82	0.54	29.02	0.40	0.36	13.98	0.93	0.38	32.67	0.69	0.69	24.32
<i>Pseudocyphellaria crocata</i>	0.80	0.80	24.61	1.94	1.94	59.84	0.00	0.00	0.00	0.50	0.50	15.55
<i>Hypogymnia metaphysodes</i>	0.53	0.19	24.73	1.33	0.74	61.67	0.00	0.00	0.00	0.29	0.29	13.60
<i>Cladonia coniocraea</i>	0.53	0.53	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hypogymnia occidentalis</i>	0.53	0.53	11.39	3.99	3.95	85.75	0.13	0.13	2.86	0.00	0.00	0.00
<i>Nephroma laevigatum</i>	0.53	0.53	10.52	4.51	3.74	89.48	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nephroma parile</i>	0.29	0.29	17.56	1.38	0.94	82.44	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cladonia squamosa</i>	0.27	0.27	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hypogymnia apinnata</i>	0.21	0.21	5.43	3.71	3.71	94.57	0.00	0.00	0.00	0.00	0.00	0.00
<i>Bryoria pseudofuscescens</i>	0.13	0.13	33.33	0.00	0.00	0.00	0.27	0.27	66.68	0.00	0.00	0.00
<i>Cetraria orbata</i>	0.13	0.13	1.90	3.95	2.14	56.21	2.65	1.33	37.73	0.29	0.29	4.17
<i>Parmeliopsis hyperopta</i>	0.05	0.05	11.76	0.13	0.07	29.41	0.03	0.03	5.89	0.24	0.24	52.95
<i>Cavernularia hultenii</i>	0.03	0.03	10.01	0.05	0.03	19.99	0.03	0.03	10.01	0.16	0.12	59.99
<i>Sticta fuliginosa</i>	0.03	0.03	0.79	1.91	1.46	56.63	0.05	0.05	1.58	1.38	1.38	40.99
<i>Cetraria pallidula</i>	0.00	0.00	0.00	0.27	0.27	50.00	0.00	0.00	0.00	0.27	0.27	50.00
<i>Evernia prunastri</i>	0.00	0.00	0.00	0.27	0.27	58.82	0.03	0.03	5.89	0.16	0.16	35.29
<i>Hypotrachyna sinuosa</i>	0.00	0.00	0.00	0.13	0.13	55.54	0.00	0.00	0.00	0.11	0.05	44.46
<i>Nephroma occultum</i>	0.00	0.00	0.00	1.33	1.33	100.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Parmelia saxatilis</i>	0.00	0.00	0.00	0.13	0.07	71.44	0.00	0.00	0.00	0.05	0.05	28.56
<i>Ramalina farinacea</i>	0.00	0.00	0.00	0.29	0.25	52.38	0.27	0.27	47.63	0.00	0.00	0.00
<i>Sticta limbata</i>	0.00	0.00	0.00	1.06	1.06	57.09	0.00	0.00	0.00	0.80	0.80	42.91
TOTAL CYANOLICHENS	3465.20	1035.50	77.3	887.29	280.04	19.8	108.28	106.38	2.4	22.57	15.14	0.5
<i>Lobaria oregana/L. pulmonaria</i>	3298.00	978.52	78.4	787.10	222.81	18.7	108.12	106.22	2.6	12.39	7.34	0.3
TOTAL OTHER	652.83	164.18	37.4	567.33	89.81	32.5	413.05	117.68	23.7	110.67	57.20	6.3
TOTAL ALECTORIOD	538.00	202.58	63.5	87.78	17.73	10.4	198.44	60.33	23.4	23.34	11.11	2.8
TOTAL FOR AGE CLASS	4656.30	743.88	65.81	1542.30	183.02	21.80	719.77	156.74	10.17	156.61	58.62	2.21

Table 5. Estimated mean standing biomass of epiphytic macrolichens in *Pseudotsuga-Tsuga* forests of four ages, arranged in order of percent of species' biomass of the total species' biomass in all age classes (pooled). Means were derived from the 12 study sites in and around H. J. Andrews Experimental Forest, Willamette National Forest, western Cascades, Oregon; n= 3 sites/age class. The first division of the table separates species containing greater than 75% of their biomass in old growth. The second division separates species containing greater than 50% of their biomass in old growth. A dagger (†) signifies species containing greater than 50% of their biomass in forests of 140 years old or older. Standard errors of the means are presented in Table 4.

LICHEN SPECIES	FOREST AGE (years)							
	510		140		70		40	
	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes
<i>Pseudocyphellaria rainierensis</i>	8.49	100.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cetraria idahoensis</i>	1.88	100.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cladonia coniocraea</i> **	0.53	100.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cladonia squamosa</i> **	0.27	100.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Alectoria vanconverensis</i>	10.61	88.89	0.00	0.00	0.85	7.12	0.48	3.99
<i>Lobaria oregana</i>	2576.50	80.28	513.21	15.99	108.12	3.37	11.46	0.36
<i>Bryoria pikei</i>	1.09	77.25	0.24	17.06	0.05	3.79	0.03	1.90
<i>Usnea sp. pendant</i>	182.24	76.20	33.87	14.16	16.61	6.94	6.45	2.70
<i>Nephroma resupinatum</i>	2.31	74.33	0.80	25.67	0.00	0.00	0.00	0.00
<i>Pseudocyphellaria anthraspis</i>	84.33	73.35	30.64	26.65	0.00	0.00	0.00	0.00
<i>Lobaria pulmonaria</i>	721.50	72.42	273.89	27.49	0.00	0.00	0.93	0.09
<i>Bryoria oregana</i>	1.30	68.90	0.24	12.72	0.27	14.14	0.08	4.24
<i>Platismatia herrei</i>	58.84	63.61	27.19	29.39	4.77	5.16	1.70	1.84
<i>Alectoria sarmentosa</i>	330.58	59.70	40.96	7.40	169.45	30.60	12.75	2.30
<i>Nephroma bellum</i>	5.91	58.66	4.17	41.34	0.00	0.00	0.00	0.00
<i>Sphaerophorus globosus</i>	169.72	55.86	123.35	40.60	10.61	3.49	0.13	0.04
<i>Nephroma helveticum</i>	15.84	54.47	12.44	42.79	0.00	0.00	0.80	2.74
<i>Pseudocyphellaria anomala</i>	44.67	53.90	31.62	38.16	0.11	0.13	6.47	7.81
<i>Parmelia pseudosulcata</i>	0.90	51.52	0.03	1.52	0.80	45.44	0.03	1.52
<i>Platismatia glauca</i>	222.42	50.25	144.81	32.72	59.26	13.39	16.12	3.64
<i>Cetraria chlorophylla</i> †	1.49	45.51	0.16	4.90	0.53	16.33	1.09	33.27
<i>Bryoria capillaris</i> †	1.06	44.41	0.35	14.53	0.98	41.06	0.00	0.00
<i>Parmelia sulcata</i> †	2.81	41.07	3.05	44.57	0.64	9.29	0.35	5.06
<i>Bryoria friabilis</i> †	0.90	39.97	0.80	35.25	0.45	20.06	0.11	4.72
<i>Hypogymnia physodes</i> †	13.61	34.83	14.43	36.93	3.40	8.69	7.64	19.55
<i>Bryoria pseudofuscescens</i>	0.13	33.33	0.00	0.00	0.27	66.68	0.00	0.00
<i>Hypogymnia tubulosa</i> †	3.71	33.10	3.77	33.57	1.46	13.01	2.28	20.32
<i>Lobaria scrobiculata</i> †	4.11	32.82	8.15	65.05	0.00	0.00	0.27	2.13

TABLE 5 CONT'D

	FOREST AGE (years)							
	510		140		70		40	
	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes	Mean Biomass (kg/ha)	% Σ sp. biomass in all age classes
LICHEN SPECIES								
<i>Usnea</i> sp. tufted †	9.60	29.96	11.14	34.75	8.59	26.81	2.72	8.48
<i>Bryoria fuscescens</i>	0.82	29.02	0.40	13.98	0.93	32.67	0.69	24.32
<i>Hypogymnia imshaugii</i>	37.13	26.27	31.83	22.52	52.89	37.42	19.50	13.79
<i>Hypogymnia metaphysodes</i> †	0.53	24.73	1.33	61.67	0.00	0.00	0.29	13.60
<i>Pseudocyphellaria crocata</i> †	0.80	24.61	1.94	59.84	0.00	0.00	0.50	15.55
<i>Platismatia stenophylla</i> †	17.72	21.02	32.44	38.47	31.70	37.59	2.47	2.93
<i>Hypogymnia inactiva</i>	80.01	20.53	84.78	21.75	186.96	47.97	37.96	9.74
<i>Hypogymnia enteromorpha</i> †	40.40	19.77	87.14	42.64	56.93	27.85	19.91	9.74
<i>Nephroma parile</i> †	0.29	17.56	1.38	82.44	0.00	0.00	0.00	0.00
<i>Parmeliopsis hyperopta</i>	0.05	11.76	0.13	29.41	0.03	5.89	0.24	52.95
<i>Hypogymnia occidentalis</i> †	0.53	11.39	3.99	85.75	0.13	2.86	0.00	0.00
<i>Nephroma laevigatum</i> †	0.53	10.52	4.51	89.48	0.00	0.00	0.00	0.00
<i>Cavernularia hultenii</i>	0.03	10.01	0.05	19.99	0.03	10.01	0.16	59.99
<i>Hypogymnia apinnata</i> †	0.21	5.43	3.71	94.57	0.00	0.00	0.00	0.00
<i>Cetraria orbata</i> †	0.13	1.90	3.95	56.21	2.65	37.73	0.29	4.17
<i>Sticta fuliginosa</i> †*	0.03	0.79	1.91	56.63	0.05	1.58	1.38	40.99
<i>Cetraria pallidula</i> †	0.00	0.00	0.27	50.00	0.00	0.00	0.27	50.00
<i>Evernia prunastri</i> †	0.00	0.00	0.27	58.82	0.03	5.89	0.16	35.29
<i>Hypotrachyna sinuosa</i> †	0.00	0.00	0.13	55.54	0.00	0.00	0.11	44.46
<i>Nephroma occultum</i> †*	0.00	0.00	1.33	100.00	0.00	0.00	0.00	0.00
<i>Parmelia saxatilis</i> †	0.00	0.00	0.13	71.44	0.00	0.00	0.05	28.56
<i>Ramalina farinacea</i> †	0.00	0.00	0.29	52.38	0.27	47.63	0.00	0.00
<i>Sticta limbata</i> †*	0.00	0.00	1.06	57.09	0.00	0.00	0.80	42.91
<i>Lobaria oregana</i> & <i>L. pulmonaria</i>	3298.00	78.42	787.10	18.72	108.12	2.57	12.39	0.29
TOTAL CYANOLICHENS	3465.20	77.29	887.29	19.79	108.28	2.42	22.57	0.50
TOTAL ALECTORIOD	538.00	63.48	87.78	10.36	198.44	23.41	23.34	2.75
TOTAL OTHER	652.83	37.44	567.33	32.53	413.05	23.69	110.67	6.35
TOTAL FOR AGE CLASS	4656.30	65.81	1542.30	21.80	719.77	10.17	156.61	2.21

† Species with a majority of biomass (>50%) in forests of 140 years old or older.

* Species thought to have been undersampled by litterfall methods because of their preference for large, high limbs. These species appear from direct access to be highly old growth associated.

** Found non-epiphytically in other age classes.

POLAR

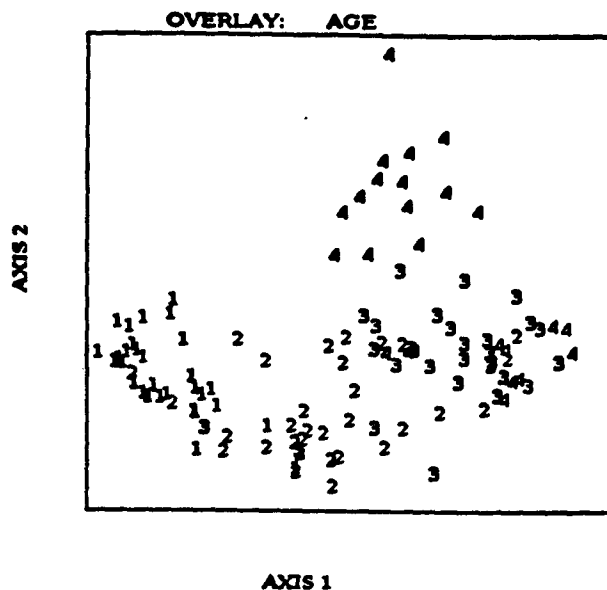


Fig. 5. Results of Bray-Curtis polar ordination of macrolichen biomass of 37 primary species found in litterfall plots, in and around the H. J. Andrews Experimental Forest, western Cascades, OR. Age classes displayed are: (1) 510 year forests, (2) 140 year old forests, (3) 70 year-old forests, (4) 40 year old forests; $n=30$ plots/age class. Axis 1 is presumed to be an age axis. The gradient described by axis 2 is unknown.

Table 6. Epiphytic macrolichens closely associated with late successional forests by biomass or species presence. Listed species are those which were restricted to forests at least 140 years old or showed greater than 50% of their pooled biomass from all age classes in old growth (510 year old stands). Lichens were sampled in the H. J. Andrews Experimental Forest and vicinity, Willamette National Forest, western Cascades, Oregon. Distributions follow Goward et al. (1992).

Species Restricted to Forests \geq 140 Years Old or With Greater Than 50% of Their Pooled Biomass from All Age Classes in Old Growth

<i>Alectoria sarmentosa</i> */**	<i>Nephroma occultum</i>
• <i>Alectoria vancouverensis</i>	<i>Nephroma parile</i> **
• <i>Bryoria oregana</i>	<i>Nephroma resupinatum</i> **
• <i>Bryoria pikei</i>	<i>Omphalina</i> sp.
<i>Cetraria platyphylla</i> *†	<i>Parmelia pseudosulcata</i>
• <i>Hypogymnia apinnata</i> **	<i>Parmelia squarrosa</i> **
<i>Hypogymnia austerodes</i> **	<i>Platismatia glauca</i> */**
• <i>Hypogymnia oceanica</i> **	• <i>Platismatia herrei</i> **
• <i>Lobaria oregana</i> **	• <i>Pseudocyphellaria anomala</i> **
• <i>Lobaria oregana</i> (blue green morph)	• <i>Pseudocyphellaria anthraxis</i> **
<i>Lobaria pulmonaria</i> **	• <i>Pseudocyphellaria rainierensis</i>
<i>Nephroma bellum</i> **	<i>Sphaerophorus globosus</i> **
<i>Nephroma helveticum</i> **	• <i>Sticta beauvoisii</i>
<i>Nephroma laevigatum</i> **	<i>Usnea</i> spp.*/**

Additional Species Which Showed Greater Than 50% of Their Pooled Biomass from All Age Classes in Forests \geq 140 Years Old

<i>Bryoria capillaris</i> *	<i>Hypogymnia tubulosa</i> **
<i>Bryoria friabilis</i>	<i>Hypotrachyna sinuosa</i> **
<i>Cetraria chlorophylla</i> **	<i>Lobaria scrobiculata</i> */**
<i>Cetraria idahoensis</i> *	<i>Parmelia saxatilis</i> */**
<i>Cetraria orbata</i> **	<i>Parmelia sulcata</i> */**
• <i>Cetraria pallidula</i>	• <i>Platismatia stenophylla</i>
<i>Evernia prunastri</i> ***	<i>Pseudocyphellaria crocata</i> *
<i>Hypogymnia enteromorpha</i> **	<i>Ramalina farinacea</i> ***
• <i>Hypogymnia metaphysodes</i>	<i>Sticta fuliginosa</i> **
<i>Hypogymnia occidentalis</i> *	<i>Sticta limbata</i> **
<i>Hypogymnia physodes</i> */**	

- * significant range east of Cascades or eastern North America
- ** significant boreal and/or coastal range, mostly Oregon coast north to coastal Alaska
- *** significant Willamette Valley distribution
- † outlier (not recommended for list of associates in western Cascades)
- endemic to Pacific Northwestern North America

more lichen biomass than younger forests, most lichens that appear across an age spectrum will nonetheless develop greater biomass in older forests. A list of all species that showed greater than 50% of their biomass in forests older than 140 years shows 49 species--most of the 59 epiphytic macrolichens found in the stands.

Thirty-one of the macrolichens listed by the interagency Forest Ecosystem Management Assessment Team (FEMAT 1993) as closely associated with old growth in spotted owl habitat (i.e., Cascades and Coast Range old growth from northern California to Washington) occurred in this study area. Although the FEMAT team lacked fundamental quantitative data, their list represents a good attempt at characterizing old growth associated lichens. Only 3 of the lichens on their list--*Hypogymnia oceanica*, *Pseudocyphellaria rainierensis* and *Sticta beauvoisii*--were restricted to old growth in this study area. Of the remaining 28 species, only 8 were restricted to stands of 140 years or older. The use of abundance to indicate association brings the FEMAT list and results of this study much closer. When species are considered whose old growth lichen biomass is greater than 50% of the biomass in all age classes, this study lacks 8 species on FEMAT's list but includes three species not on FEMAT. When species are considered whose mature forest (140 year old) lichen biomass is greater than 50% of the biomass in all age classes, this study lacks only 3 species on FEMAT's list, *but includes 17 others not listed by FEMAT*. Ideally, old growth-associated lichen conservation lists should combine species presence and biomass data from both Cascadian and coastal forests.

From the perspective of forest management, it appears likely that the conversion of old growth forests into young rotation stands has dramatic effects on lichen populations. Whereas only nine species in this study appear to be restricted to old growth in the

western Cascades, 20 species develop the majority of their biomass in old growth forests. These species would develop only a small fraction of their potential late successional biomass even 140 years after old growth liquidation. On the landscape level, if we assumed equal land area covered in these different age classes, removal of the old growth would eliminate two thirds of the lichen biomass in the forest. The age structure of western Oregon and Washington forests has shifted dramatically toward young forests over the past 70 years and, consequently, has eliminated the vast majority of former lichen biomass in these forests. Even 140 year rotations appear to be entirely inadequate in maintaining the thriving lichen populations present in old growth.

Lichen Community Composition along a Chronosequence

During forest development, cyanolichen biomass increased dramatically while the Alectoriod and "other" lichen biomass increased only modestly (Fig. 6).

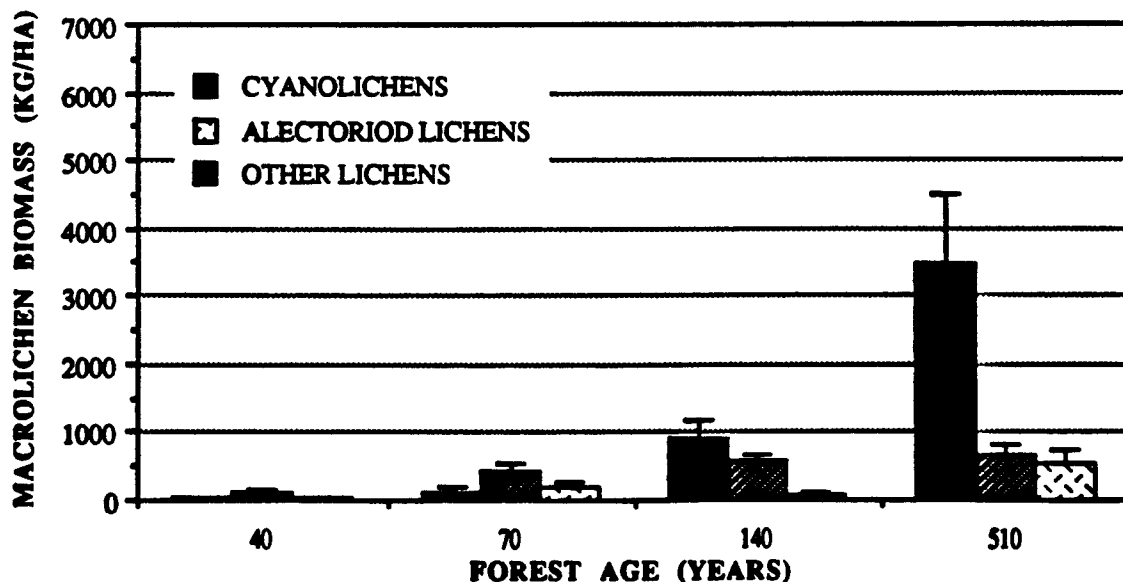


FIG. 6. Functional macrolichen groups constituting the mean biomass of each age class displayed as a function of time, H. J. Andrews Experimental Forest, OR; n= 3 stands per age class. Error bars display the standard error of the means.

The dramatic increase in overall lichen biomass over time is primarily due to cyanolichen growth, most notably of *Lobaria oregana*, which constitutes 55% of the lichen biomass in old growth (Fig. 7; Table 7). Cyanolichens showed significant differences ($p < 0.05$) between all age classes except 40 and 70 (Table 8, Appendices 5a and d).

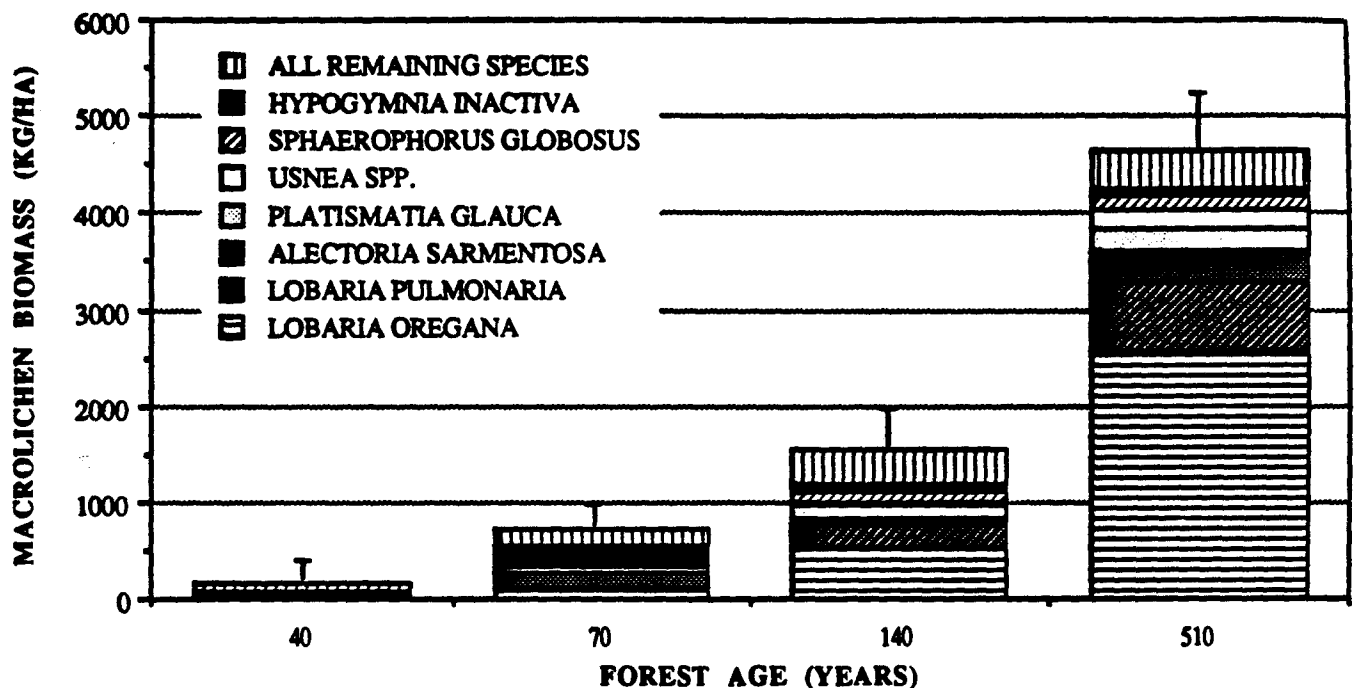


Fig. 7. Macrolichen species composition of major biomass contributors in each forest age class, H. J. Andrews Experimental Forest and vicinity, western Cascades, OR; $n = 3$ sites/age class. Error bars display the standard error of the total mean biomass.

Causes for the high cyanolichen species richness and biomass in old growth are complex and poorly understood, but appear to involve microclimate, substrate, canopy architecture, and long-term branch stability which allows sufficient time for propagule dispersal and slow lichen growth (McCune 1993b; Howe 1978; Lesica et al. 1991). Working in the same watersheds as those sampled here, Howe (1978) found that the abundance of cyanolichens in old growth is strongly related to the vertical distance from a

Table 7. Estimated mean standing biomass of epiphytic macrolichens in a forest age class expressed as a percent of total biomass in that age class. Lichens were collected in *Pseudotsuga-Tsuga* forests of four ages, and are presented in order of descending biomass in old growth, with corresponding rank in that age class. Means represented come from the 12 study sites in and around H. J. Andrews Experimental Forest, Willamette National Forest, western Cascades, Oregon; n= 3 sites/age class.

LICHEN SPECIES	FOREST AGE (YEARS)							
	510		140		70		40	
	% of Total Biomass in Age Class	Rank	% of Total Biomass in Age Class	Rank	% of Total Biomass in Age Class	Rank	% of Total Biomass in Age Class	Rank
<i>Lobaria oregana</i>	55.33	1	33.28	1	15.02	3	7.32	6
<i>Lobaria pulmonaria</i>	15.50	2	17.76	2	0.00		0.59	16
<i>Alectoria sarmentosa</i>	7.10	3	2.66	7	23.54	2	8.14	5
<i>Platismatia glauca</i>	4.78	4	9.39	3	8.23	4	10.29	4
<i>Usnea spp. pendant</i>	3.91	5	2.20	8	2.31	8	4.12	9
<i>Sphaerophorus globosus</i>	3.64	6	8.00	4	1.47	9	0.09	30
<i>Pseudocyphellaria anthraxis</i>	1.81	7	1.99	12	0.00		0.00	
<i>Hypogymnia inactiva</i>	1.72	8	5.50	6	25.97	1	24.24	1
<i>Platismatia herrei</i>	1.26	9	1.76	13	0.66	11	1.09	13
<i>Pseudocyphellaria anomala</i>	0.96	10	2.05	11	0.01	26	4.13	8
<i>Hypogymnia enteromorpha</i>	0.87	11	5.65	5	7.91	5	12.71	2
<i>Hypogymnia imshaugii</i>	0.80	12	2.06	10	7.35	6	12.45	3
<i>Platismatia stenophylla</i>	0.38	13	2.10	9	4.40	7	1.58	11
<i>Nephroma helveticum</i>	0.34	14	0.81	15	0.00		0.51	17
<i>Hypogymnia physodes</i>	0.29	15	0.94	14	0.47	12	4.88	7
<i>Alectoria vancouverensis</i>	0.23	16	0.00		0.12	17	0.30	21
<i>Usnea spp. tufted</i>	0.21	17	0.72	16	1.19	10	1.74	10
<i>Pseudocyphellaria rainierensis</i>	0.18	18	0.00		0.00		0.00	
<i>Nephroma bellum</i>	0.13	19	0.27	19	0.00		0.00	
<i>Lobaria scrobiculata</i>	0.09	20	0.53	17	0.00		0.17	25
<i>Hypogymnia tubulosa</i>	0.08	21	0.24	22	0.20	14	1.46	12
<i>Parmelia sulcata</i>	0.06	22	0.20	24	0.09	19	0.22	22
<i>Nephroma resupinatum</i>	0.05	23	0.05	31	0.00		0.00	
<i>Cetraria idahoensis</i>	0.04	24	0.00		0.00		0.00	
<i>Cetraria chlorophylla</i>	0.03	25	0.01	40	0.07	20	0.69	15
<i>Bryoria oregana</i>	0.03	26	0.02	38	0.04	23	0.05	33
<i>Bryoria pikei</i>	0.02	27	0.02	39	0.01	28	0.02	36
<i>Bryoria capillaris</i>	0.02	28	0.02	34	0.14	15	0.00	
<i>Bryoria friabilis</i>	0.02	29	0.05	32	0.06	21	0.07	31
<i>Parmelia pseudosulcata</i>	0.02	30	≤ 0.01	44	0.11	18	0.02	35
<i>Bryoria fuscescens</i>	0.02	31	0.03	33	0.13	16	0.44	19
<i>Pseudocyphellaria crocata</i>	0.02	32	0.13	25	0.00		0.32	20
<i>Hypogymnia metaphysodes</i>	0.01	33	0.09	28	0.00		0.19	24
<i>Cladonia coniocraea</i>	0.01	34	0.00		0.00		0.00	
<i>Hypogymnia occidentalis</i>	0.01	35	0.26	20	0.02	25	0.00	
<i>Nephroma laevigatum</i>	0.01	36	0.29	18	0.00		0.00	

TABLE 7 CONT'D

LICHEN SPECIES	FOREST AGE (YEARS)							
	510		140		70		40	
	% of Total	Rank	% of Total	Rank	% of Total	Rank	% of Total	Rank
<i>Nephroma parile</i>	0.01	37	0.09	27	0.00		0.00	
<i>Cladonia squamosa</i>	0.01	38	0.00		0.00		0.00	
<i>Hyopogymnia apinnata</i>	≤ 0.01	39	0.24	23	0.00		0.00	
<i>Cetraria orbata</i>	≤ 0.01	40	0.26	21	0.37	13	0.19	23
<i>Bryoria pseudofuscescens</i>	≤ 0.01	41	0.00		0.04	24	0.00	
<i>Parmeliopsis hyperopia</i>	≤ 0.01	42	0.01	41	0.00		0.15	27
<i>Sticta fuliginosa</i>	≤ 0.01	43	0.12	26	0.01	27	0.88	14
<i>Cavernularia hultenii</i>	≤ 0.01	44	≤ 0.01	44	0.00		0.10	29
<i>Nephroma occulium</i>	0.00		0.09	29	0.00		0.00	
<i>Sticta limbata</i>	0.00		0.07	30	0.00		0.51	18
<i>Ramalina farinacea</i>	0.00		0.02	35	0.04	22	0.00	
<i>Evernia prunastri</i>	0.00		0.02	37	0.00		0.10	28
<i>Cetraria pallidula</i>	0.00		0.02	36	0.00		0.17	26
<i>Hypotrachyna sinuosa</i>	0.00		0.01	42	0.00		0.07	32
<i>Parmelia saxatilis</i>	0.00		0.01	43	0.00		0.03	34
<hr/>								
TOTAL CYANOLICHENS	74.42	1	57.53	1	15.04	3	14.41	3
<i>Lobaria oregana</i> & <i>L. pulmonaria</i>	70.83	2	51.03	2	15.02	4	7.91	4
TOTAL OTHER	14.02	3	36.78	3	57.39	1	70.67	1
TOTAL ALECTORIOD	11.55	4	5.69	4	27.57	2	14.91	2
<hr/>								
TOTAL FOR AGE CLASS	100.00		100.00		100.00		100.00	

Table 8. Summary of ANOVA and regression results for biomass of epiphytic macrolichen functional groups, H. J. Andrews Experimental Forest, Willamette National Forest, western Cascades, OR; n=12 sites. P values are derived from data square root transformed to normalize residuals. Full statistical summaries are provided in Appendices 1-5.

TEST	FUNCTIONAL GROUP			TOTAL BIOMASS
	<u>Cyanolichens</u> p	<u>Alectoriod</u> p	<u>Other</u> p	p
FUNCTIONAL GROUP ANOVA	0.0006 ***	0.01*	0.02*	0.0001***
LEAST SQUARE MEANS TESTS				
40 vs. 70	NS†	0.05*	NS	0.02*
140	0.020*	NS	0.03*	0.0007***
510	0.0002***	0.003**	0.008**	0.0001***
70 vs. 140	0.03*	NS	0.004**	0.037*
510	0.0003***	NS	NS	0.0001***
140 vs. 510	0.009**	0.01**	NS	0.0005***
R-SQUARED (Functional Group v. Forest Age Class)	0.77	0.56	0.33	0.90

†NS = not significant at the $p \leq 0.05$ level

stream. McCune (1993b) hypothesized that vertical, moisture and temporal gradients all foster similar zonation of macrolichen communities. It is likely that the open canopy, abundant, water-retaining moss mats, and coarse woody debris of old growth forests maintain the bright but moist environment supporting the diverse and abundant community of cyanolichens found even in non-riparian environments.

The seven most dominant lichen species in the study reflected the dramatic changes in functional group composition with forest development (Fig. 7). *Hypogymnia inactiva* and *Alectoria sarmentosa*, which showed affinity for young stands, high vertical placement in the canopy, and low moisture requirements (McCune 1993b), change less than such species as *Lobaria* spp. which require conditions found more widely in old growth. Multivariate correlations between the biomass of lichen species and two ordination axes reflect similar, but more diluted, trends (Table 9). Using multivariate methods *Lobaria oregana* shows an r^2 of 0.59 against the presumed time axis. This contrasts to this species' r^2 of 0.86 using simple linear regression. Other species correlations are weaker than those of the functional groups overall (Table 8), possibly because a variety of species in a functional group may fill similar niches.

Changes in Environmental Gradients through Time

Stand age *per se* cannot be considered a direct causal agent influencing lichen diversity and abundance; rather, it is a convenient summary of many direct agents to which it is intimately linked. The diversity and abundance of epiphytic lichens depend partly on the biology of the lichens and partly on their ever-changing microenvironment. Lichens grow slowly and disperse poorly (Bailey 1976). Establishment and growth of

Table 9. Pearson and Kendall correlations of macrolichen biomass of 37 species with 2 Bray-Curtis ordination axes, H. J. Andrews Experimental Forest, western Cascades, OR; n=114 biomass plots. Rare species were purged from the data set to avoid extraneous signals (Gauch 1982). The first two letters of the abbreviations are the first two letters of the lichen genus; the last three represent the first three letters of the species epithet. For species names, see Appendix 4. Axis 1 is presumed to represent forest age. The meaning of axis 2 is not clear.

PEARSON AND KENDALL CORRELATIONS WITH ORDINATION AXES

AXIS:	1			2		
	r	r-sq	tau	r	r-sq	tau
ALSAR	-.340	.115	-.151	-.151	.023	-.114
ALVAN	-.125	.016	.076	.044	.002	.079
BRCAP	.000	.000	.120	-.092	.008	-.058
BRFRI	-.085	.007	.043	-.061	.004	-.128
BRFUS	.043	.002	.025	-.017	.000	.003
BRORE	-.203	.041	-.053	-.061	.004	-.005
BRPIK	-.299	.089	-.242	-.070	.005	.000
CECHL	-.026	.001	-.041	-.056	.003	-.034
CEORB	.038	.001	.112	-.042	.002	.007
HYAPP	-.026	.001	-.105	.016	.000	.034
HYENT	.061	.004	.041	-.328	.108	-.278
HYIMS	.011	.000	.008	-.263	.069	-.216
HYINA	.079	.006	.042	-.135	.018	-.147
HYMET	-.214	.046	-.246	.023	.001	.059
HYOCC	-.034	.001	-.048	-.104	.011	-.115
HYPHY	-.171	.029	-.080	-.211	.044	-.221
HYTUB	-.162	.026	-.201	-.116	.013	-.094
LOORE	-.768	.589	-.788	-.097	.009	-.263
LOPUL	-.302	.091	-.453	.069	.005	-.032
LOSCR	-.246	.060	-.244	-.058	.003	-.037
NEBEL	-.270	.073	-.286	-.025	.001	-.078
NEHEL	-.253	.064	-.419	.018	.000	-.003
NELAE	-.086	.007	-.089	.017	.000	.048
NEPAR	-.102	.010	-.172	-.041	.002	-.057
NERES	-.130	.017	-.141	.022	.001	.037
PAPSE	-.075	.006	-.110	-.029	.001	-.098
PASUL	-.122	.015	-.159	-.026	.001	-.056
PLGLA	-.375	.141	-.366	-.154	.024	-.280
PLHER	-.499	.249	-.408	-.132	.017	-.128
PLSTE	-.044	.002	-.018	-.051	.003	-.094
PSANA	-.413	.170	-.383	-.018	.000	.040
PSANT	-.326	.106	-.414	.032	.001	.006
PSCRO	-.064	.004	-.056	.081	.006	.111
PSRAI	-.171	.029	-.132	-.020	.000	.024
SPGLO	-.475	.225	-.509	-.205	.042	-.249
USPEN	-.411	.169	-.361	-.112	.013	-.162
USTUF	-.066	.004	.016	-.104	.011	.026

lichens depend on adequate time for propagule dispersal, suitable germination substrate, stability of the substrate over many years, proper wetting and drying regime, moisture, light, and temperature (McCune 1993b; Brodo 1973). Many factors controlling these conditions are strongly associated with forest age (e.g., canopy architecture, forest humidity, substrate condition, and temporal stability of the substrate). These factors also appear to have strong associations with independent vertical and moisture gradients within a forest, the latter owing largely to landscape level moisture patterns related to riparian, upland or ridgeline fog belt locations (McCune 1993b).

Several time-related structural attributes are associated with lichen biomass (Figs. 8a-d). Crown volume and mean height of the closest canopy tree to plot center showed the strongest correlations with lichen abundance ($r^2 = 0.78$ and 0.77 respectively). With increasing stand age, the mean tree height increased from 20+ to 60+ m (see Table 10 for summary of environmental gradients). Crown volume similarly increased from approximately 1000 m^3 to 4000 m^3 . Both of these variables were highly correlated with stand age ($r^2 = 0.73$ and 0.76 respectively). Crown volume showed significant differences ($p < 0.05$) only between the three younger stands versus old growth but not between these three stands, a result nearly duplicated in comparing tree height with stand age. The great differences between the lichen biomass in old growth versus younger stand probably owe largely to factors associated with different stand structures.

Stand density and percent canopy closure, both of which are probably strongly associated with the microclimate and light levels in a stand, had a surprisingly modest influence on lichen biomass in this study. Stand density correlated moderately with lichen biomass ($r^2 = 0.47$) and with age ($r^2 = 0.44$). Percent canopy closure correlated

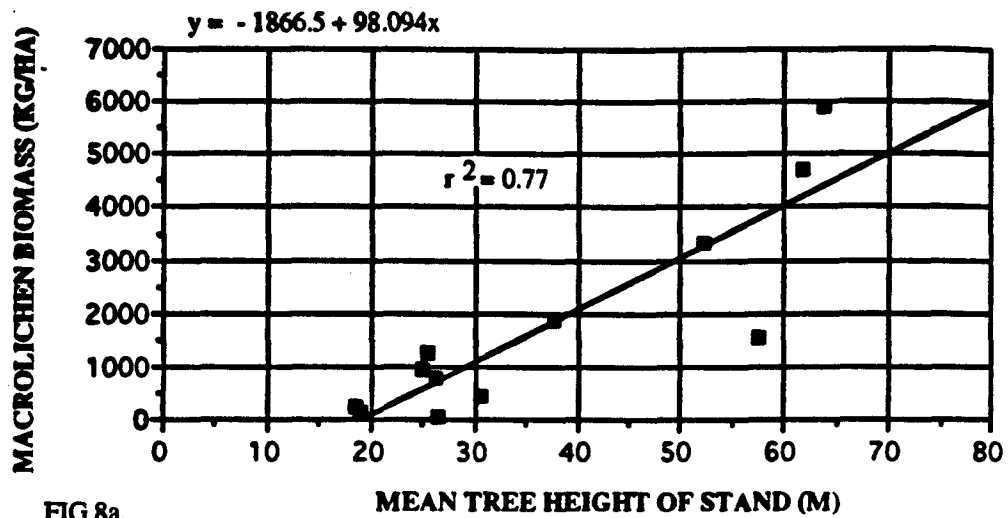


FIG 8a.

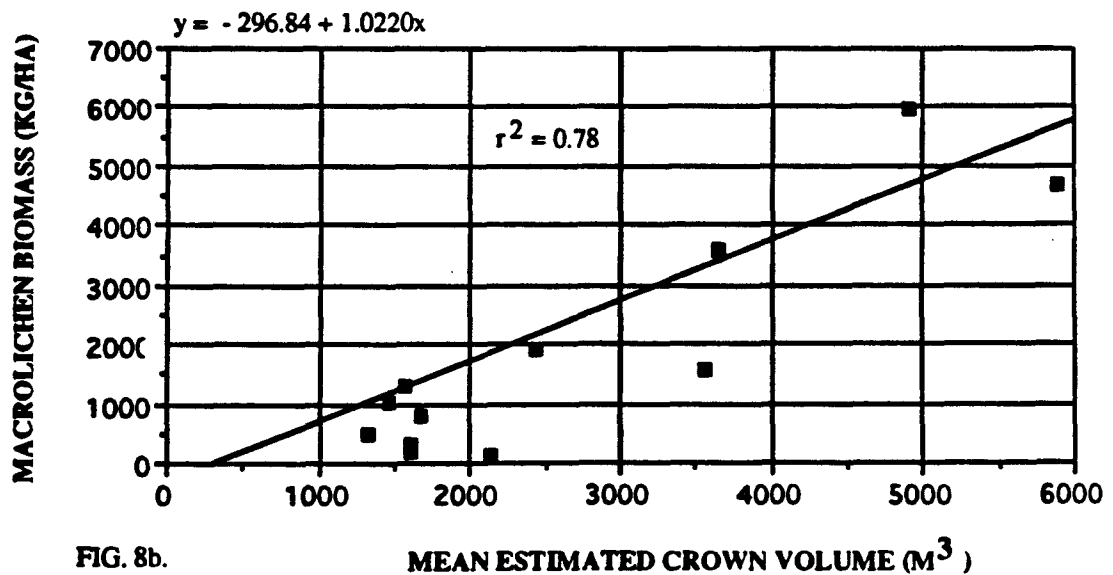


FIG. 8b.

Fig. 8a-b. (8a): Regression of macrolichen biomass on mean tree height of closest tree to plot center in stand; $n=10$ trees per site. (8b): Regression of epiphytic macrolichen biomass on mean crown volume based on measurements of tree closest to plot center; $n=10$ trees/site. Both data sets based on 120 plots in H. J. Andrews Experimental Forest and vicinity, western Cascades, OR.

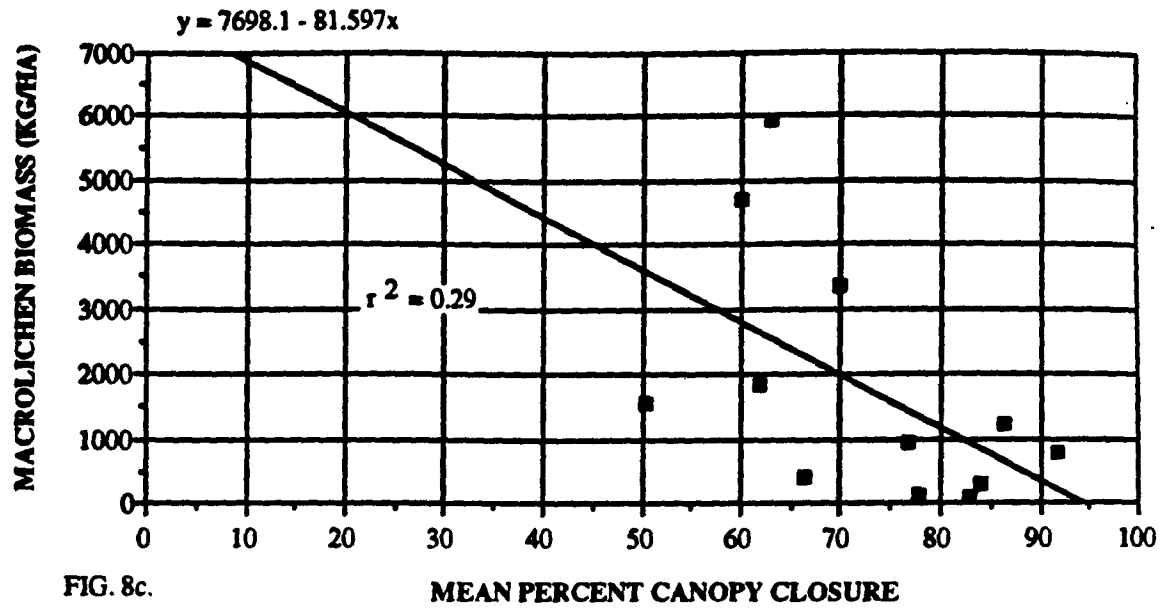


FIG. 8c.

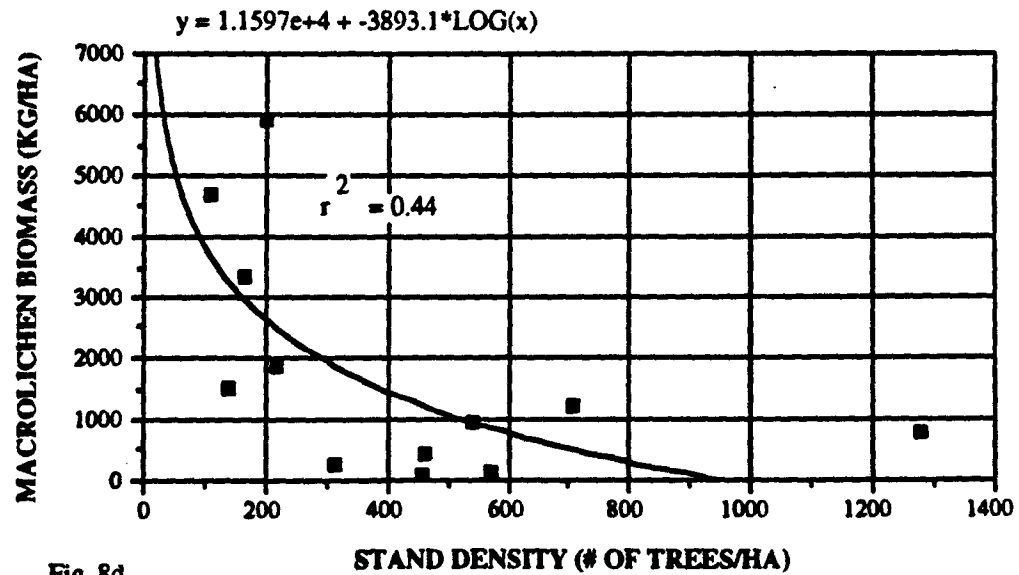


Fig. 8d.

FIG. 8c-d. (8c) Regression of macrolichen biomass on mean percent canopy closure; $n=10$ plots/site. (8d) Regression of macrolichen biomass on mean stand density (no. of trees/ha); $n=10$ plots/site. Both figures from H. J. Andrews Experimental Forest and vicinity, western Cascades, OR. Data based on 120 sample plots.

Table 10. Summary of environmental gradients in stands of four ages, H. J. Andrews Experimental Forest and vicinity, western Cascades, OR; n=30 trees/age class.

GRADIENT	FOREST AGE (years)								STATISTIC		
	510		140		70		40		F	p	r-sq
	Mean	±S.E.	Mean	±S.E.	Mean	±S.E.	Mean	±S.E.			
Number of Trees per hectare	157.33	12.12	354.67	50.99	760.00	75.85	446.67	36.04	2.4	0.140	0.44
Height of Closest Canopy Tree	59.27	2.41	40.33	3.42	27.27	1.15	21.37	1.16	10.3	0.004	0.77
Percent Canopy Closure	64.33	2.49	66.33	3.48	78.33	2.87	81.67	1.88	1.6	0.250	0.29
Maximum Crown Width	9.20	0.47	7.64	0.29	6.60	0.25	7.00	0.26	5.6	0.230	0.63
Height of Lowest Branch >1m	22.43	2.02	11.29	1.64	11.67	0.82	0.93	0.32	12.2	0.002	0.64
Crown Volume (cu. m)	4352.74	630.09	1837.52	242.47	800.72	99.57	1093.63	105.82	9.60	0.005	0.78

poorly with biomass ($r^2 = 0.30$), although my canopy closure data were (by virtue of ground-based sampling) based on closure of the lower crown . Lower crown conditions may have little effect on the abundant lichen populations above .

In trying to move from indirect to direct factors influencing lichen distribution, it would be fruitful to study the effect of branch age on lichen biomass. As branches appear to support the majority of the lichen biomass, the two are probably highly correlated. It appears likely that stand age and tree height should correlate strongly with branch age, but may vary among tree species. As lichens face dispersal and colonization problems (Bailey 1976), temporal continuity of large horizontal limbs may be among the most critical age-related factors influencing their diversity and abundance.

Lichen microhabitat and substrate on a given branch or point along the bole change rapidly as a young forest ages. Young stands, especially dense plantations, make poor environments for epiphytes. Tree density is high, making light levels low (Table 10; Hunter 1993). Potential host branches are dense among Douglas-firs, but most will be shed before the tree reaches maturity (e.g., 140 years old). McCune (1993b) and Pike et al. (1975) found that epiphyte distribution is stratified vertically, with bryophytes and cyanolichens dominant in the lower crown, Alectorioid lichens dominant in the mid to upper crown, and "other" lichens dominant toward the apex. As McCune predicted (1993b), these vertical zones correspond very closely to the temporal zonation found in this study . With increasing age, therefore, the colonizable branches of young trees hosting "other" lichens such as *Hypogymnia inactiva* soon become more appropriate for Alectorioids; and if these original branches persist, they eventually become most suited for cyanolichens or bryophytes. The rapid changes in stand structure and hence lichen

microhabitat evidently disfavor heavy accumulation of lichen biomass until microhabitats begin to stabilize in old growth.

Other factors may also help block the accumulation of high biomass in younger forests. First, the density of branches in young stands probably blocks the influx of wind-dispersed propagules. Second, although deep shade may lessen evaporation from young stands, middle and lower branches probably receive less moisture than in older age classes because of interception by the dense crown. Other than abundant crustose lichen coverage, young stand epiphytes are few. Field observations suggest exceptions to this condition in young stands (1) on exposed ridgetops and roadsides, both with different microclimates than the stand interior; and (2) within a few meters of old growth edges where young stands receive a steady shower of lichen fragments and propagules.

As a forest matures, tree growth slows and dominant branches strengthen their hegemony. The microclimate in the crown begins to stabilize and leaching of the exposed bark improves substrate favorability for many lichens (Brodo 1973). As some surrounding trees die of suppression or windthrow the crown opens, allowing the entry of more propagules, light, and direct precipitation. As the forest ages to old growth, stable upper branches become heavily stocked with large lichens. Large live branches persisting for over 200 years become widespread. Forest structure continues to diversify, leading to a wide variety in microhabitats (Hansen et al. 1991). Cyanolichens, extremely limited and patchy in younger stands, begin to dominate in the increasingly moist microclimate of the lower crown. Lichens with broader tolerances (e.g., *Alectoria sarmentosa*, *Platismatia glauca*) also achieve their peak abundance in this optimal, stable

environment. Bryophytes such as *Antitrichia curtipendula* and *Isothecium myosuroides* begin to cover many branches in the lower crown, sometimes even excluding lichens.

Lichen Conservation and Forest Management

Approximately 350,000 acres of mature and old growth forest have been harvested in the Willamette National Forest in the last 50 years (Hunter 1993). High rates of old growth liquidation have also characterized recent land management by other agencies in the Pacific Northwest as foresters have sought to replace "unproductive" forests with vigorous, young stands. Longer rotations have been proposed to allow for greater biodiversity, but rotation times needed to protect different forest components may differ, and are often unknown (FEMAT 1993). From the objective of maximizing lichen species diversity and abundance, it appears that short successive rotations of even 70 to 140 years would have a devastating effect. This corroborates observations by Rose (1988) that even *selective* cutting has had a dire impact on British cyanolichen communities.

Great attention has been focused recently on the new silvicultural practice of retaining live, old trees ("green trees") in cutting units (FEMAT 1993). The effectiveness of green tree retention hinges upon the *reasons* old growth supports richer and more abundant epiphyte communities than young stands. If epiphyte limitations in young stands owe primarily to dispersal limitations, retained trees might have a dramatic effect. If, on the other hand, epiphyte paucity owes to lack of proper substrate or microclimate, green tree retention may have relatively little effect until the young stand begins to acquire

structural and microclimatic conditions of old growth. This change typically occurs in 200 years in the western Cascades (Hansen et al. 1991).

Several field observations offer support for the second hypothesis, underscoring the importance of substrate in determining lichen diversity and abundance. First, the modest volume of cyanolichens in the upper reaches of the canopy (McCune 1993b) amidst a probable shower of cyanolichen propagules from heavily stocked, adjacent lower crowns suggests that this paucity owes to microhabitat. Factors possibly limiting cyanolichens in the upper crown include substrate suitability, moisture regime, light, and branch duration. Second, observations in Glacier Bay, Alaska (Neitlich and Campbell unpublished data) revealed an abundant community of cyanolichens on Sitka alder (*Alnus sinuata*) amidst a young matrix of cyanolichen-poor Sitka spruce (*Picea sitchensis*). Third, Sillett and Neitlich (1993 unpublished data) report on an "island" of diverse and abundant cyanolichens growing on the young *Salix* and *Symphoricarpos* shrubs of an abandoned homesite amidst a 200 year old *Pseudotsuga* forest devoid of such lichens. The spores and/or vegetative diaspores must have traveled great distances to arrive at the site, suggesting good dispersal ability. Propagules probably landed in the depauperate forest, as well, but did not establish because of a lack of proper substrate or microclimate.

Support for the counter-hypothesis that lichen poverty in young stands owes to dispersal limitations has been offered by Rose (1976, 1992), but treats only species presence, not abundance. Based on extensive research on the relationship between lichen species richness and forest age, Rose (1992) and Goward (1991) hypothesized that the age of a stand may influence lichen species richness less than its temporal

continuity through individual trees. Thus a 300 year old tree may support more taxa than a 150 year old forest matrix in which it lives; likewise, a 150 year old tree living in a 300 year old forest will probably host more taxa (because of increased dispersal opportunities) than a tree in an even-aged 150 year old forest. A study currently underway is attempting to compare epiphytes of 70 year old post-fire stands possessing remnant green trees with pure 70 year old stands without such remnants (Acker, et al., 1993). Although green tree retention appears to create few differences in epiphytic communities after 70 years to 90 years (J. Peck, personal communication; S. Sillett, personal communication), it is possible that effects might become more pronounced as the stand matures. Still, as the close association of lichen biomass with late successional forests suggests, increases in the species richness of a regenerating unit via green trees doesn't necessarily imply functionally viable communities of these taxa.

My field observations of boundaries between 40 year old post-clearcut stands and old growth reveal that young trees within 5 m of old growth have a greater lichen species richness and biomass than the interior of the young stands. This increased species richness and abundance appears to decline rapidly after 5 m. If enough green trees could be retained in a cutting unit, increases in lichen species richness and biomass above clearcut stands are conceivable. Unfortunately, this desired effect hinges both on the economics of how many trees might be retained and on the condition of epiphytes in retained trees facing a new microclimate. Again, field observations suggest that retained old growth green trees in the Andrews Experimental Forest lack the epiphyte loads of their neighbors in adjacent old growth. Reasons for this relative poverty may include direct damage in broadcast burning, removal by wind, or mortality due to exposure.

Clearly, the ability of green tree retention to enrich post-harvest lichen communities is highly questionable, at best, and requires much additional study on the *causes* of slow development of lichen communities in young stands.

Since some green tree retention is currently underway, I propose some ideas for mitigating its impacts on lichens. Clustering green trees is probably preferable to scattering trees for two reasons. First, observations above suggest that clusters better preserve the old growth microhabitat likely necessary for the growth, reproduction and maintenance of cyanolichen populations. Cyanolichens constitute approximately 75% of the high biomass in old growth, but form the rarest component of young stands (Table 7). Additionally, my field observation that 10-20% of retained trees fall to wind during the first 5 years following cutting suggests that clustering of trees may be needed to keep them standing.

Other measures may also help with mitigation of silvicultural impacts on lichens. Retention of Pacific yew (*Taxus brevifolia*) is highly recommended. Owing perhaps to its very slow growing, stable habit, yew hosts a very rich understory community of mosses and lichens often including *Pseudocyphellaria rainierensis*, a rare old growth and Pacific Northwest endemic. Retaining as much coarse woody debris as possible on site is also of critical importance in fostering rich communities of dead wood specialists. The Caliciales and dozens of epixylic *Cladonia* species, are abundant on coarse woody debris in various stages of decomposition, but are otherwise scarce. Forty year old stumps and downed logs, for instance, were typically brimming with as many as 6-10 species of *Cladonia*.

Although no studies have yet addressed the effects of young stand management on lichens, several field observations suggest that leaving hardwoods in young stands may help enhance lichen communities. Leaving broadleaf trees has been advocated for increasing bird diversity in young stands (Hunter 1993). Detailed field observations during this study revealed that big leaf maple (*Acer macrophyllum*) in 70 and 140 year old stands supported a significantly greater density of *Lobaria* spp. and of the epiphytic bryophytes *Isothecium myosuroides*, *Antitrichia curtipendula*, and *Porella navicularis* than did other tree species in these age classes. Campbell and Neitlich (1992 unpublished data) likewise found that 95 year old Sitka alders (*Alnus sinuata*) hosted a far more diverse and abundant lichen community than the 95 year old conifers with which they grew, including a far greater presence of cyanolichens in the genera *Lobaria*, *Nephroma*, *Pseudocyphellaria* and *Sticta*. Observations of the striking lichen communities even on young hardwoods in the Willamette Valley offer additional evidence of their value in boosting abundance and diversity. Explanations for the rich and abundant lichen communities on hardwoods may include: (1) a less acidic bark pH than in conifers (Hale 1967); (2) absence of leaves during the rainiest seasons, permitting abundant direct precipitation and light; and (3) long term stability of exposed, unshed horizontal bark. Bark pH and stability begins to improve for epiphytes in conifers only as trees reach old age.

Avoiding dense plantation may also help to speed the accumulation of high lichen biomass. Field observations reveal that 40 year-old roadside trees host a far greater lichen load than interior forest trees just a few meters away. This effect is presumably due to greater access to direct precipitation, light, and propagules. In the forest interior,

where stand densities vary less than at edges, this study found a moderate correlation between stand density and lichen biomass ($r^2 = 0.47$). Observations that open grown trees typically host greater (though potentially different) lichen biomass than sheltered trees (Campbell and Neidlich 1992), and that exposed ridgetops harbor great volumes of lichen biomass (FEMAT 1993) provide additional support for reduced stocking . One factor probably impeding a more rapid accumulation of lichen biomass in young stands is early colonization by crustose lichens. It has been demonstrated that crustose lichens can inhibit germination of lichen spores and can allelopathically outcompete germinating vegetative diaspores (Lawrey 1984). It is likely that macrolichens in a more sparsely stocked, brighter environment could outcompete these crustose lichens, thus allowing more rapid colonization than in the dark environment of unthinned stands. The major unresolved question preceding full recommendation of thinning is whether the increase in lichen biomass in retained trees offsets losses from culled trees.

AMPLIFICATIONS

Conservation of old growth forests is essential to ensure the perpetuity of many of the lichens in this study. In a web so tightly woven as a forest ecosystem, implications of lichen disappearance also extend far beyond these taxa. The endangerment of lichen communities holds consequences for arboreal invertebrates and a large number of vertebrates.

Invertebrates

Lichens are used by a wide variety of invertebrates for food and/or shelter (Gerson and Seaward 1977). In a preliminary investigation, analysis of 495 g of the eight most abundant lichens collected in the canopy of a 75 m Douglas-fir in the H. J. Andrews Experimental Forest yielded 773 invertebrates (Table 11; Piechnik et al. unpublished data). Sixty percent of these were oribatid mites (Acari); 30 percent were Collembolans. Approximately 90 percent of the genera, and 70 percent of the individuals were exclusively arboreal.

Links between lichens, arthropods and other components of the ecosystem are extensive. Many arboreal oribatid mites feed primarily on lichens and other fungi and survive the desiccation in the canopy without drinking by synthesizing and efficiently using water (A. Moldenke, personal communication). Many also use the lichens for shelter, excavating minute burrows in the medullary hyphae. As they digest and defecate lichen thalli, they quickly make nitrogenous and other nutrient rich materials available to plants and soil organisms below. The Collembolans, also largely fungivorous, constitute

Table 11. Arthropods found in 8 lichen species gathered in canopy of a 75 m *Pseudotsuga menziesii* near study stand number 2, a 510 year old *Pseudotsuga* - *Tsuga* stand, H. J. Andrews Experimental Forest, western Cascades, OR. (After Piechnik et al., unpublished data). Matrix values represent the number of individuals of each arthropod genus associated with lichen.

ARTHROPOD	LICHEN SPECIES								TOTAL
	<i>Alectoria sarmentosa</i>	<i>Hypogymnia enteromorpha</i>	<i>Hypogymnia inactiva/ imshaugii</i>	<i>Platismatia glauc</i>	<i>Sphaero- phorus globosus</i>	<i>Lobaria oregana</i>	<i>Lobaria scrobiculata</i>	<i>Pseudo- cyphellaria anomala</i>	
COLEMBOLLA									
Hypogastura	10	11	4	79	61	18	7	40	230
Isotoma	1	0	0	0	0	1	0	0	2
Uzellia	0	2	0	0	0	2	0	0	4
ACARI									
Achipteria	2	0	1	8	70	6	1	24	112
Bdella	1	0	0	7	1	4	0	0	13
Camisia	0	2	3	2	2	2	0	0	11
Coropaculla	0	0	0	7	0	3	0	3	13
Cunaxid	1	1	0	1	1	0	0	0	4
Eremacus	1	1	1	0	0	0	0	1	4
Eremacus (Aircraft carrier)	2	0	0	1	0	0	0	1	4
Odontodamaeus	7	0	0	4	1	2	0	0	14
Ommatocephus	0	0	0	0	0	3	0	0	3
Oppiella	0	1	0	0	0	2	0	0	3
"Oppiella"	0	0	0	0	0	1	0	0	1
Oribatula/Phauloppla	8	21	2	24	13	24	0	8	100
Platylodes	0	0	2	4	3	2	0	0	11
Scapheremaeus	0	0	2	0	0	1	0	0	3
Scheloribates	1	9	0	1	0	4	0	5	20
Sphaerozetoid	0	1	0	0	0	0	0	0	1
Orbatid general--Immature	6	2	7	55	15	32	10	22	149

	LICHEN SPECIES								
	<i>Alectoria sarmentosa</i>	<i>Hypogymnia enteromorpha</i>	<i>Hypogymnia inactiva/ imshaugii</i>	<i>Platismatia glauca</i>	<i>Sphaero- phorus globosus</i>	<i>Lobaria oregana</i>	<i>Lobaria scrobiculata</i>	<i>Pseudo- cyphellaria anomala</i>	TOTAL
ARTHROPOD									
ARANEA									
Clubiona (Clubionae)	0	0	0	0	0	1	0	0	1
INSECTA									
Agulla (Raphidioptera)	0	0	0	0	2	1	0	0	3
Cecidomyiid (Diptera)	0	1	1	0	0	1	1	0	4
Chironomid (Diptera)	0	0	0	1	0	0	2	0	3
Dipteran - general	0	0	0	0	0	0	1	1	2
Earwig (Dermaptera)	0	0	0	0	0	0	0	1	1
Elaterid (immature)	0	5	0	1	0	1	0	0	7
Geometer (Lepidoptera)	0	0	0	0	0	2	0	0	2
Liposcelis (Pscocoptera)	2	5	1	5	1	5	0	1	20
Micromoth (Lepidoptera)	0	0	0	1	0	0	0	0	1
Moth (Lepidoptera)	0	0	0	0	0	0	0	1	1
Mycetophilid (Diptera)	0	0	0	0	0	0	1	0	1
Orange Thrips (Pthiraptera)	2	4	1	10	2	2	0	1	22
Parasitic Wasp (Hymenoptera)	0	0	0	1	0	0	0	0	1
Psychodid (Diptera)	0	0	1	0	0	0	0	0	1
Other	0	0	1	0	0	0	0	0	1
Number of Individuals	44	66	27	212	172	120	23	109	773
Lichen biomass (g)	115.22	16.60	10.00	50.60	31.10	260.30	1.60	9.90	495.3
Density (Individuals/g lichen)	0.38	0.40	2.70	4.18	5.53	0.46	14.40	11.00	1.56
Number of Genera	14	14	13	18	12	23	7	13	37
Genus richness (Genera/g lichen)	0.12	0.84	1.30	0.36	0.39	0.09	4.38	1.30	0.07

the primary food source for many arboreal spiders (Halaj 1993). These spiders, in turn, constitute a major food source for the gleaning and hawking birds seen foraging in the canopy, e.g., Hermit warbler, Swainson's and Hermit Thrushes, Western Tanager (Ehrlich et al. 1988).

Based on the lichen biomass of the species found in each age class and the arthropod densities in these lichen species, old growth stands appear to host 4 times more lichen-associated canopy arthropods than rotation age stands (Fig. 9). It is fascinating

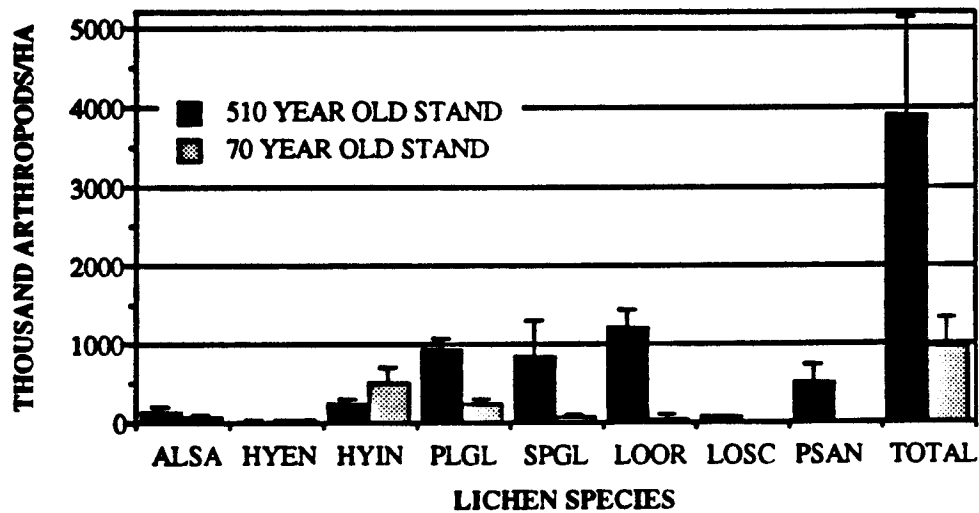


FIG. 9. Comparison of the number of arthropods in 510 year old v. 70 year old douglas fir forest based on the biomass of these forests and arthropod richness of major species, H. J. Andrews Experimental Forest, western Cascades, OR; n=3 stands/age class; n= 1 canopy arthropod sample. Four letter codes represent first two letters of genus, and first two letters of species: ALSA (*Alectoria sarmentosa*); HYEN (*Hypogymnia enteromorpha*); HYIN (*Hypogymnia inactiva*); PLGL (*Platismatia glauca*); SPGL (*Sphaerophorus globosus*); LOOR (*Lobaria oregana*); LOSC (*Lobaria scrobiculata*); PSAN (*Pseudocyphellaria anomala*). Arthropod data from Piechnik et al., unpublished; lichen data from this study.

that the density and genus richness of arthropods found in *Lobaria oregana* was among the two lowest of the eight common lichen species (Fig. 10). It is the sheer volume of *Lobaria oregana* in old growth that nonetheless allows this species to harbor more

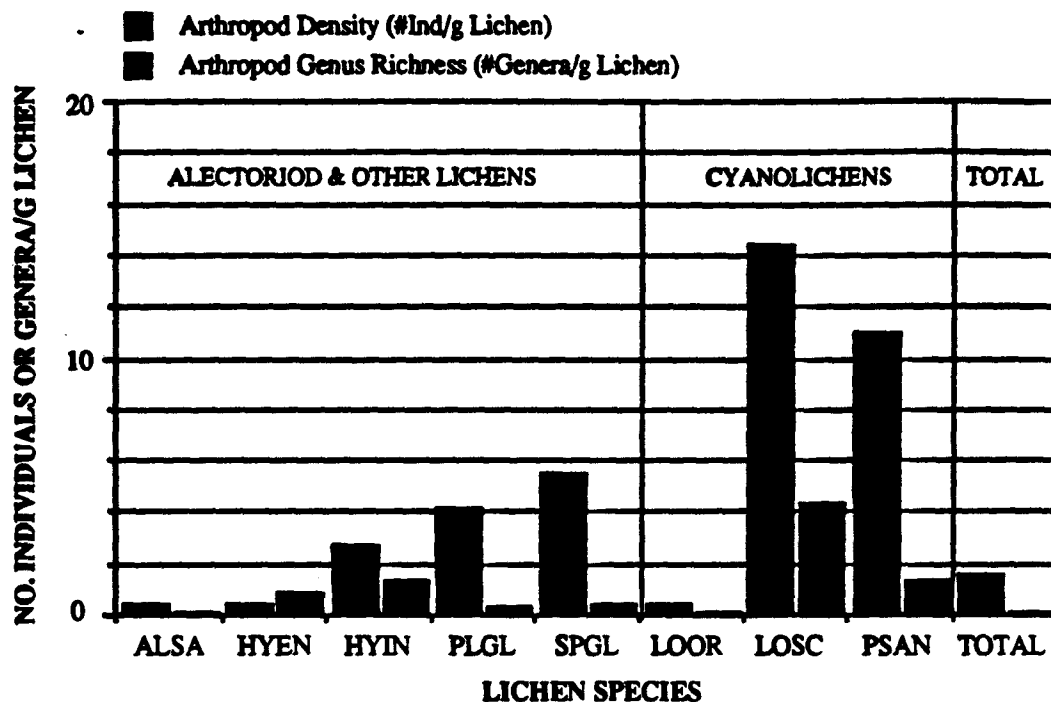


FIG. 10. Density and genus richness of arthropods in 8 species of lichens from canopy of 510 year old douglas fir, H. J. Andrews Experimental Forest, western Cascades, OR. Data from Piechnik et al. unpublished data. Species codes are interpreted in Fig. 9.

arthropods than other lichens. The actual arthropod density in the lichen species of younger stands may differ from that of old growth, but is likely to be lower than that presented because of the poorly developed arthropod habitat in young stands compared to old growth (A. Moldenke, personal communication).

Using a mean arthropod density of 1.56 individuals/g lichen (all species combined), we predicted arthropod densities in the lichen species based only on their biomass in old growth, thus assuming no differences between the lichens' ability to host arthropods. *Lobaria oregana*, *Alectoria sarmentosa*, and *Hypogymnia enteromorpha*, all of which harbored fewer than 1.56 arthropods/g of lichen, had fewer arthropods than

predicted (Fig. 11). Primarily due to the high contribution of *Lobaria* to the total biomass, the total observed density of arthropods is less than that predicted. Reasons for

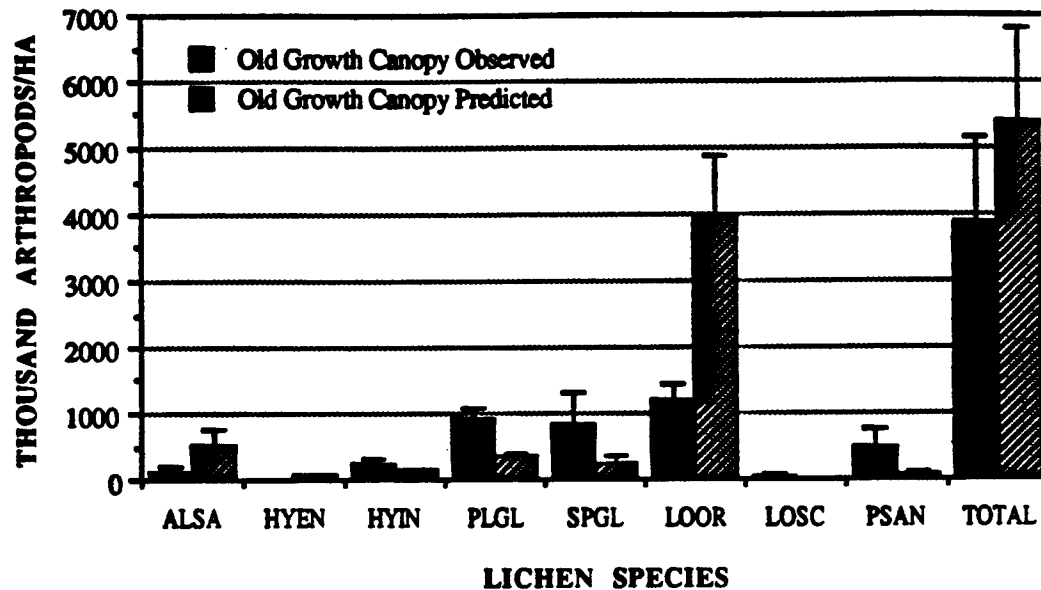


FIG. 11. The number of arthropods observed in the canopy of an old growth Douglas-fir v. that predicted given no differences in arthropod density for different lichens (e.g., all values based on lichen biomass alone). From Piechnik and Neitlich, unpublished; H. J. Andrews Experimental Forest, western Cascades, OR; $n=3$ stands. Error bars display standard error of the mean lichen biomass multiplied by arthropod density. Species codes are interpreted in Fig. 9

differences in richness and density of arthropods among different lichen species are not clear but may involve defensive secondary compounds, lichen morphology, palatability, and the microsite in which the lichens are found (Shorrocks et al. 1991; Gerson 1977). Lichen species harboring fewer arthropods than predicted based on biomass (e.g., *Lobaria oregana*) may be employing defensive chemicals to advantage against herbivory. The most abundant lichen species in the canopy have low densities of arthropods, suggesting that strategies inhibiting herbivory may increase these lichens' success in

growing, surviving and reproducing. Our findings of two orders of magnitude differences in arthropod richness between lichen species holds great promise for further investigation. Replication and sampling in younger stands would permit a better sense for the reliability of these data.

Vertebrates

Many rodents, ungulates, and birds use lichens for food and shelter, although it is difficult to determine the extent to which these animals could substitute alternate forage and construction materials if needed.

The northern flying squirrel (*Glaucomys sabrinus*) has received a great deal of attention in Pacific Northwestern forests as a dietary staple of the northern spotted owl (*Strix occidentalis*), and for its role in curing and dispersing spores of many mycorrhizal fungi (Maser et al. 1986). Forsman et al. (1984) found that the flying squirrel constituted 60% of the spotted owl's winter diet in the western Cascades. The interagency spotted owl recovery team (Thomas et al. 1990) likewise concluded that the flying squirrel is especially important to the spotted owl in the western hemlock-Douglas-fir zone of the lower elevation western Cascades forests.

Maser et al. (1986) report that in southwestern Oregon, lichens constituted 64% of the winter stomach contents of the flying squirrel. East of the Cascade crest and in Idaho, the favored lichen for forage and nest material is *Bryoria fremontii* (Maser et al. 1986; Rosentreter 1993). Lichen species upon which the squirrel feeds west of the Cascade crest are unknown, but are thought to be Alectorioid (McCune 1993b). Several other small mammals of the western Cascade forests including the red tree vole

(*Phenacomys longicaudus*) and the Douglas squirrel (*Tamiasciurus douglasi*) have been reported to use lichens for food and nesting material (Carey 1991; Denison 1973; Campbell and Neitlich, unpublished)

Black-tailed deer (*Odocoileus hemionus columbianus*) and elk (*Cervus elaphus*) both forage on lichens, especially in winter when few other energy sources are available (Robbins 1987). Lichens of the study area used for forage by deer include *Alectoria sarmentosa*, *Bryoria* spp., *Usnea* spp., *Lobaria oregana*, *Platismatia glauca*, and *Sphaerophorus globosus*. Field observations revealed that whereas *Lobaria oregana* was widespread on the forest floor in old growth stands, it was sparse to absent along deer trails. It appears that, where this lichen is abundant, it constitutes an important food source for deer.

At least 19 birds common west of the Cascade Crest use lichens in their nests (Table 12). Uses appear to fill four basic needs: structural materials, camouflage, sanitation, and waterproofing (Ehrlich et al. 1988). Hummingbirds often coat the outside of their nests with lichens, typically *Parmelia* spp. (USDA 1928). As lichens both absorb and lose water very readily (Blum 1973), they serve as wicks, absorbing moisture from the interior of the nest and quickly transmitting it to the atmosphere. The antibiotic properties of lichens including *Usnea* have been widely recognized by many cultures (Richardson and Young 1977) and may serve as the basis for use as a sterilizing agent. Declining lichen populations in our forests may potentially affect chick survival among some bird species by decreasing the adults' control of nest-borne pathogens (Ehrlich et al. 1988).

Table 12. Bird species west of the Cascade Crest in Oregon and Washington utilizing lichens in nest construction. Data come from field observations during this study and Richardson and Young 1977.

Bushtit	(<i>Psaltiriparus minimus</i>)
Wrentit	(<i>Chamaea fasciata</i>)
Boreal chickadee	(<i>Parus hudsonicus</i>)
White-winged crossbill	(<i>Lotia leucoptera</i>)
Olive-sided flycatcher	(<i>Nuttallornis borealis</i>)
Swainson's hawk	(<i>Buteo swainsoni</i>)
Anna's hummingbird	(<i>Calypte anna</i>)
Black-chinned hummingbird	(<i>Archilochus alexandri</i>)
Rufous hummingbird	(<i>Selasphorus rufus</i>)
Golden-crowned kinglet	(<i>Regulus satrapa</i>)
Common merganser	(<i>Mergus merganser</i>)
Marbled murrelet *	(<i>Brachyramphus marmoratus</i>)
American redstart	(<i>Setophaga ruticilla</i>)
Swainson's thrush	(<i>Hylocichla ustulata</i>)
Varied thrush	(<i>Ixoreus naevius</i>)
Solitary vireo	(<i>Vireo solitarius</i>)
Warbling vireo	(<i>Vireo gilvus</i>)
Hermit warbler	(<i>Dendroica occidentalis</i>)
Townsend's warbler	(<i>Dendroica townsendi</i>)

* Threatened in range (USFWS 1992 in FEMAT 1993)

Nitrogen Fixation

Lichens are thought to supply the bulk of the annual nitrogen budget in lower elevation (≤ 950 m) and riparian forests (B. Griffiths, personal communication). N fixation levels by lichens in old growth forests were approximately 145 times those of 40 year old stands (Table 13). Lichens of rotation-aged stands (70 years old) and mature stands (140 years old) contributed approximately 32 and 4 times less than those of old growth, respectively. These rates are approximately 5 times higher than those presented by Pike (1978) and Howe (1978) because of a discrepancy between litterfall and direct access estimates of lichen biomass. As direct sampling estimates were based on only a few intensively studied trees, whereas McCune's (1993b) litterfall to standing biomass

Table 13. Estimated nitrogen fixation rates (kg/ha/yr) by cyanolichens in the H. J. Andrews Experimental Forest based on old growth cyanolichen n-fixation estimates by Howe (1978) and throughfall and litterfall estimates provided by Pike (1978). Zones are as follows: (1) Elevation <1000m, vertical distance from a stream <150m ; (2) Elevation <1000m, vertical distance from a stream >150m (3) Elevation >1000m, vertical distance from a stream <150m (4) Elevation >1000m, vertical distance from a stream >150m .

ZONE	% (in area) of H. J. Andrews Experimental Forest	FOREST AGE (years)							
		40		70		140		510	
		Kg Fixed N/ha/yr	% Annual Throughfall + Litterfall N budget (kg N/ha/yr)	Kg Fixed N/ha/yr	% Annual Throughfall + Litterfall N budget (kg N/ha/yr)	Kg Fixed N/ha/yr	% Annual Throughfall + Litterfall N budget (kg N/ha/yr)	Kg Fixed N/ha/yr	% Annual Throughfall + Litterfall N budget (kg N/ha/yr)
1	71	0.14	≤1	0.65	3	5.32	22	20.79	88
2	12	0.02	≤1	0.11	≤1	0.89	4	3.47	15
3	15	0.05	≤1	0.22	1	1.77	7	6.93	29
4	2	<0.01	≤0.01	0.01	≤0.1	0.08	0	0.30	1
TOTAL	100	0.11	≤0.01	0.50	2	4.14	17	16.17	68

regression was based on 18 trees, litterfall estimates probably provide a better approximation. Howe (1978) presented data gathered by litterfall but extrapolated them to stand level with a multiplier of 20 rather than 100, as suggested by litterfall study. In Table 13, I used Howe's original estimates for arboreal cyanolichens in different zones of the Andrews Experimental Forest, but multiplied them by 5. The annual nitrogen budget estimates for throughfall and litterfall came from Pike (1978). The annual production rate for cyanolichens were based on that for *Lobaria oregana*, or 0.3 g/g. Nitrogen content of cyanolichens came from Pike's estimate of 1.73% of dry weight for *Lobaria oregana*, the most abundant of all cyanolichens.

Litterfall biomass estimates suggest that epiphytic cyanolichens contribute 68% of the annual throughfall and litterfall nitrogen budget in the H. J. Andrews Experimental Forest as a whole, a strikingly different result than Pike's (1978) estimate of 19%. Pending further study, the two sets of estimates should probably be considered as lower and upper limits.

Lichen Dispersal

In recent years, increasing attention has also been focused on dispersal of lichens by invertebrates, small mammals and birds. Lawrey (1984) reports that viable lichen propagules have been germinated from slug feces. Bailey (1976) reports that both Collembolans and mites have served as lichen dispersers, and that lichen fragments have been found clinging electrostatically to birds' feet in mist nets. It is likely that flying squirrels using *Bryoria* for food and nest materials inadvertently disperse lichen propagules. Declines in animal populations in some manner dependent upon lichens may

have negative effects on lichen dispersal for taxa which disperse poorly by wind (e.g., those relying on heavy vegetative diaspores).

CONCLUSION

Forests of different ages differ dramatically in the abundance and diversity of their epiphytic macrolichens. Findings presented herein suggest that conversion of old growth forests into young rotational stands threatens many lichen taxa and most lichen populations. The vast differences between the lichen populations of different forest age classes deserve attention in considering forest management in the Pacific Northwest. Lichens warrant concern not only because of the biodiversity they represent, but because of the important roles they play in the ecosystem. Not surprisingly, the findings in this study mirror those in Montana (Lesica et al. 1991) and in the United Kingdom (Rose 1992). This study has greatest application for forest management in the inland forests of the Pacific Northwest, but appears to be relevant to coastal forests, as well. A similar study in coastal and Alaskan forests would be extremely useful to explore the nature and extent of regional differences.

This study elicits the question of what factors are responsible for the differences in lichen abundance and diversity along the course of forest development. Dispersal limitations and the slow growth rate of lichens have often been cited to explain the paucity of lichens in younger forests (FEMAT 1993; Rose 1992), but may be less important than changes in microclimate and substrate associated with increasing forest age. Resolving this debate is of primary importance as we attempt to fill gaps not only in our basic knowledge of lichen ecology, but in our skills as forest stewards. Better understanding of this issue will enable a more rigorous evaluation of several applied questions in epiphyte conservation. Most prominent among these are the impacts of proposed logging of old growth fragments perceived to be of little importance as animal habitat, and the

much questioned potential of green tree retention to speed lichen recovery in young stands.

Future studies in lichen ecology which strive to quantify standing lichen biomass face an important methodological problem. The biomass estimates in this study, and those in McCune (1993) are approximately three to five times higher than those of earlier studies (e.g., Pike 1978; Howe 1978). While the true standing biomass of lichens has little bearing on the differences in biomass among age classes presented herein, greater confidence in our absolute biomass values would enable better quantification of ecosystemic components ranging from N-fixation to canopy arthropods. It is of primary importance that we replicate studies such as McCune's (1993) over space and time to assure that the 1:100 litterfall-to-standing crop ratio is correct.

The many roles of lichens in the ecosystem have received far less study in conservation biology than deserved because of the difficulties in taxonomy and canopy access. As these roles are elucidated, interdependencies between different components of the system become increasingly appreciated (e.g., Maser et al. 1986). The role of lichens as critical winter forage for the flying squirrel is illustrative. The remainder of the flying squirrel's winter diet comes largely from hypogeous mycorrhizal fungi, which require the squirrel for spore dispersal (Maser et al. 1985). The squirrel depends upon lichens; hypogeous mycorrhizal fungi have based their reproductive strategy upon dispersal by squirrels; forest health and reproduction depend heavily upon mycorrhizal fungi; both the lichens and the squirrels live by the grace of a healthy forest. The interdependence of these players highlights the importance of interdisciplinary studies in understanding forest ecosystems. It reinforces, moreover, an important idea emerging in

conservation biology that many of the critical players in a system are not the most obvious ones.

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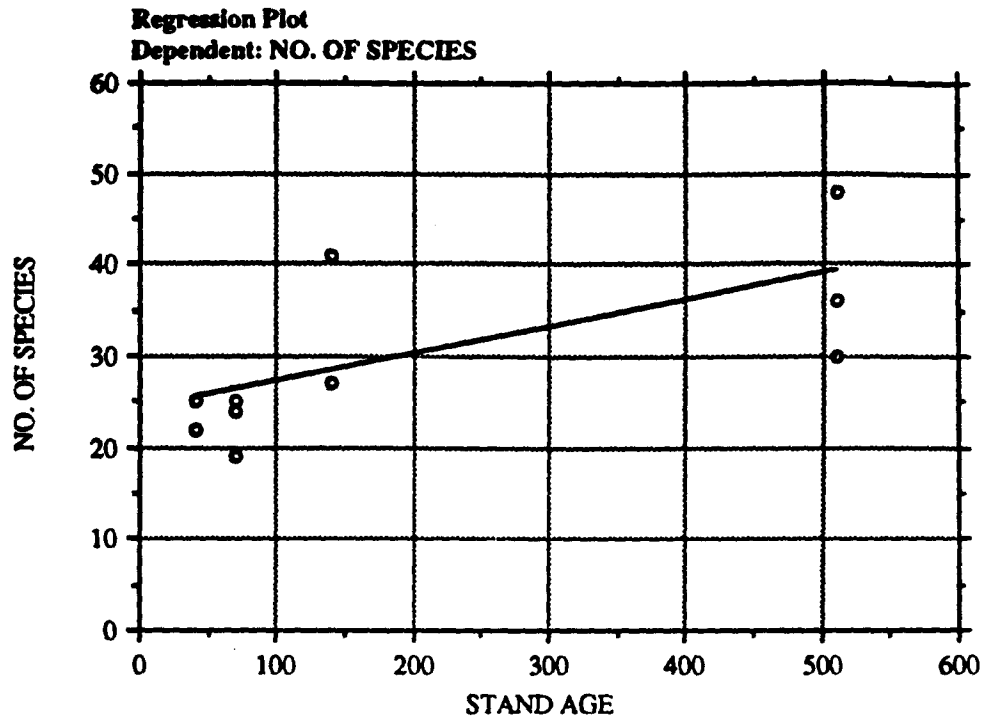
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APPENDIX 1a:
STATISTICAL ANALYSIS OF STAND AGE VERSUS MACROLICHEN SPECIES RICHNESS USING
SIMPLE REGRESSION



Model Summary
Dependent: NO. OF SPECIES

Count 12
R .624
R-Squared .390
Adj. R-Squared .328
RMS Residual 7.599

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	1	368.478	368.478	6.380	.0301
Error	10	577.522	57.752		
Total	11	946.000			

APPENDIX 1b:
STATISTICAL SUMMARY OF DIFFERENCES BETWEEN MEAN MACROLICHEN SPECIES
RICHNESS OF FOUR AGE CLASSES DETECTED BY ANOVA

Type III Sums of Squares

Source	df	Sum of Squares	Mean Square	F-Value	P-V...
STAND AGE	3	594.000	198.000	4.919	.0318
Residual	8	322.000	40.250		

Dependent: NO. OF SPECIES

Fisher's Protected LSD Multiple Range Test

Effect: STAND AGE

Dependent: NO. OF SPECIES

Significance level: .05

	Vs.	Diff.	Crit. diff.	P-Value	
70	40	.333	12.007	.9505	
	140	13.667	12.007	.0304	S
	510	15.333	12.007	.0186	S
40	140	13.333	12.007	.0336	S
	510	15.000	12.007	.0205	S
140	510	1.667	12.007	.7571	

S = Significantly different at this level.

Model Summary

Dependent: NO. OF SPECIES

Count 12

R .810

R-Squared .656

Adj. R-Squared .527

RMS Residual 6.377

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	620.667	206.889	5.087	.0293
Error	8	325.333	40.667		
Total	11	946.000			

APPENDIX 2a:

STATISTICAL SUMMARY OF SQUARE ROOT-TRANSFORMED LICHEN BIOMASS DATA

Significant differences reported in the text come from this analysis, which shows little pattern to the residuals. By contrast, see residual pattern of untransformed data in Appendix 2b.

ANOVA SUMMARY

Dependent: sqrt lichen biomass

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
age	3	5047.627	1682.542	44.143	.0001
Residual	8	304.927	38.116		

Dependent: sqrt biomass

Least Squares Means Table

Effect: age

Dependent: sqrt biomass

	Vs.	Diff.	Std. Error	t-Test	P-Value
40	70	-14.392	5.041	-2.855	.0213
	140	-27.051	5.041	-5.366	.0007
	510	-55.706	5.041	-11.051	.0001
70	140	-12.659	5.041	-2.511	.0363
	510	-41.313	5.041	-8.196	.0001
140	510	-28.655	5.041	-5.684	.0005

Fisher's Protected LSD Least Square Means Multiple Range Test

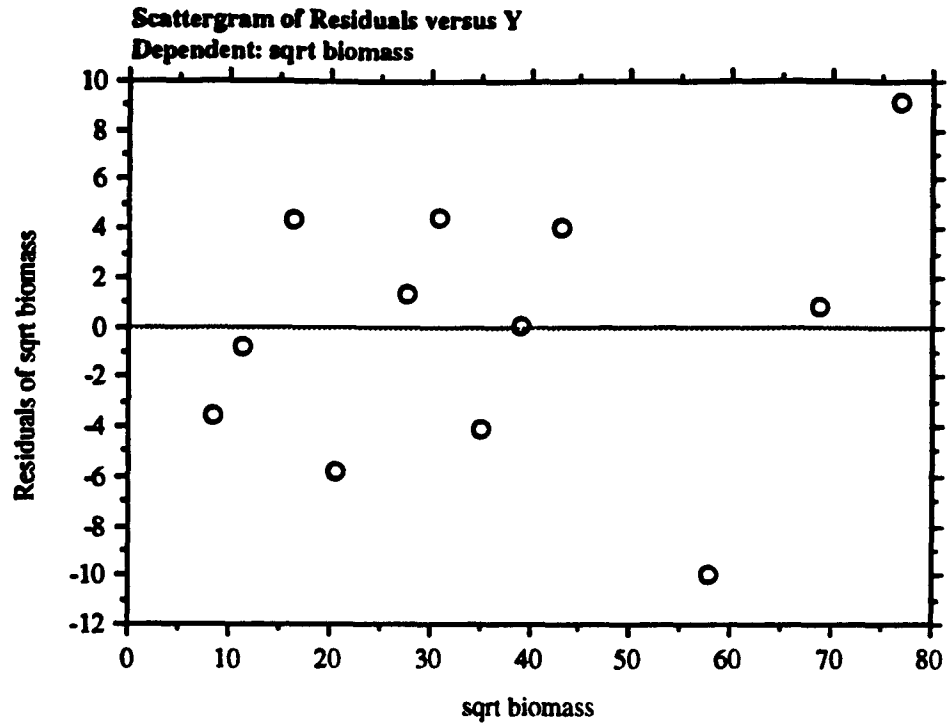
Effect: age

Dependent: sqrt biomass

Significance level: .05

	Vs.	Diff.	Crit. diff.	P-Value	
40	70	14.392	11.624	.0213	S
	140	27.051	11.624	.0007	S
	510	55.706	11.624	.0001	S
70	140	12.659	11.624	.0363	S
	510	41.313	11.624	.0001	S
140	510	28.655	11.624	.0005	S

S = Significantly different at this level.



Means Table
Effect: age
Dependent: sqrt biomass

	Count	Mean	Std. Dev.	Std. Error
40	3	12.082	4.006	2.313
70	3	26.474	5.309	3.065
140	3	39.133	4.055	2.341
510	3	67.787	9.581	5.531

Model Summary

Count	12				
R	.971				
R-Squared	.943				
Adj. R-Squared	.922				
RMS Residual	6.174				
	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	5047.627	1682.542	44.143	.0001
Error	8	304.927	38.116		
Total	11	5352.555			

APPENDIX 2b:

STATISTICAL SUMMARY OF UNTRANSFORMED LICHEN BIOMASS DATA

Note the strong trumpet-shaped character of residuals in untransformed data, a strong indication of the need for transformation. The square root-transformed data (Appendix 2a) exhibits significantly less patterning to the residuals than any other standard transformation attempted. These included log, log-normal, arcsin, and 1/x.

ANOVA SUMMARY

Dependent: lichen biomass

Count 12

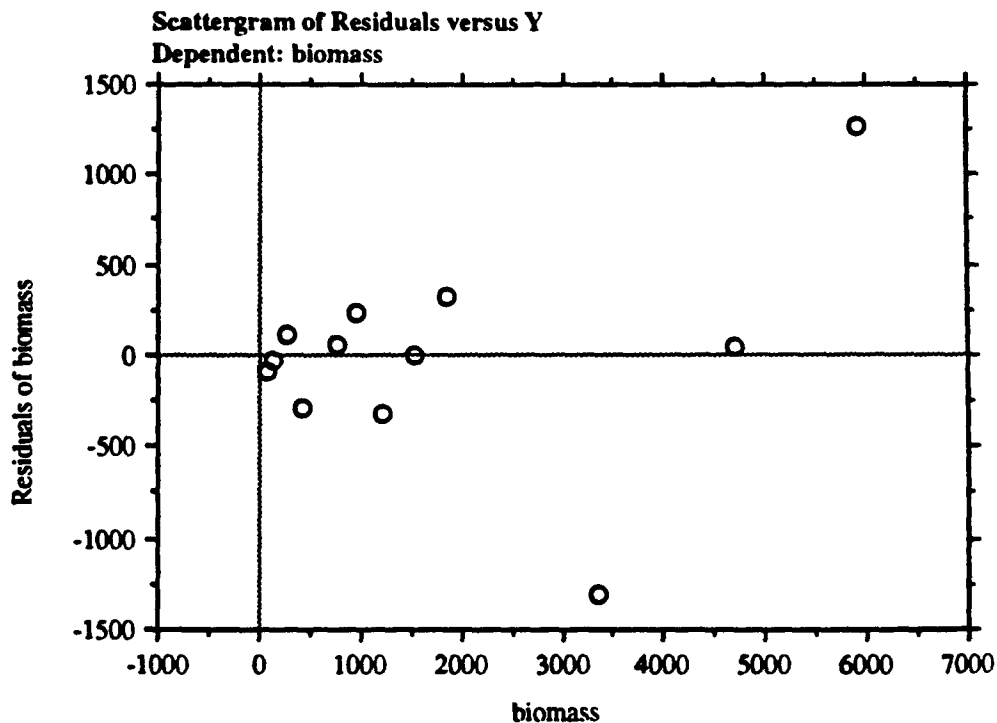
R .953

R-Squared .908

Adj. R-Squared .873

RMS Residual 679.160

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	36266371.583	12088790.528	26.208	.0002
Error	8	3690070.667	461258.833		
Total	11	39956442.250			



Fisher's Protected LSD**Effect: age****Dependent: biomass****Significance level: .05**

	Vs.	Diff.	Crit. diff.	P-Value	
40	70	563.000	1278.753	.3397	
	140	1385.667	1278.753	.0370	S
	510	4499.667	1278.753	.0001	S
70	140	822.667	1278.753	.1762	
	510	3936.667	1278.753	.0001	S
140	510	3114.000	1278.753	.0005	S

S = Significantly different at this level.

Least Squares Means Table**Effect: age****Dependent: biomass**

	Vs.	Diff.	Std. Error	t-Test	P-Value
40	70	-563.000	554.532	-1.015	.3397
	140	-1385.667	554.532	-2.499	.0370
	510	-4499.667	554.532	-8.114	.0001
70	140	-822.667	554.532	-1.484	.1762
	510	-3936.667	554.532	-7.099	.0001
140	510	-3114.000	554.532	-5.616	.0005

Means Table**Effect: age****Dependent: biomass**

	Count	Mean	Std. Dev.	Std. Error
40	3	156.667	101.796	58.772
70	3	719.667	271.266	156.616
140	3	1542.333	317.034	183.039
510	3	4656.333	1288.634	743.993

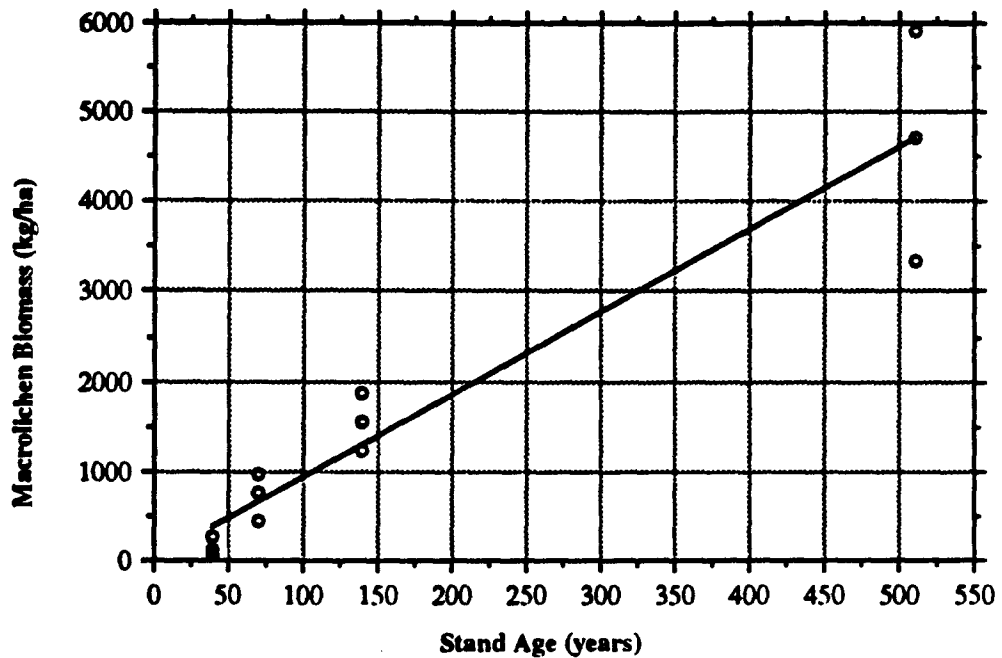
APPENDIX 3:

STATISTICAL SUMMARY OF SIMPLE REGRESSION OF MACROLICHEN BIOMASS ON FOREST AGE

While a non-linear curve probably better represents these data, there is little difference in the best non-linear curve fit and the linear regression. This suggests that for forest ages up to 510, the relationship between lichen biomass and forest age is essentially linear. We predict a significant leveling off of the curve at older forest ages, as stand heterogeneity becomes more pronounced with time.

Regression plot

Dependent: Lichen biomass in 12 stands



Model Summary

Dependent: biomass

Count 12

R .948

R-Squared .899

Adj. R-Squared .889

RMS Residual 635.129

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	1	35922552.239	35922552.239	89.052	.0001
Error	10	4033890.011	403389.001		
Total	11	39956442.250			

APPENDIX 4.

Estimated mean standing biomass (kg/ha), standard error of the means, percent of species' total biomass in all age classes (pooled), and percent of biomass in individual age class. Means were derived from 3 study sites in each age class (n=3 sites/age class) in and around H. J. Andrews Experimental Forest, Willamette National Forest, western Cascades, Oregon.

	FOREST AGE (YEARS)															
	510				140				70				40			
	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class
LICHEN SPECIES																
<i>Alectoria sarmentosa</i>	330.58	153.59	59.70	7.10	40.96	38.26	7.40	2.66	169.45	62.88	30.60	23.54	12.75	7.72	2.30	8.14
<i>Alectoria vancoverensis</i>	10.61	10.61	88.89	0.23	0.00	0.00	0.00	0.00	0.85	0.85	7.12	0.12	0.48	0.48	3.99	0.30
<i>Bryoria capillaris</i>	1.06	1.06	44.41	0.02	0.35	0.21	14.53	0.02	0.98	0.98	41.06	0.14	0.00	0.00	0.00	0.00
<i>Bryoria friabilis</i>	0.90	0.86	39.97	0.02	0.80	0.27	35.25	0.05	0.45	0.24	20.06	0.06	0.11	0.07	4.72	0.07
<i>Bryoria fuscescens</i>	0.82	0.54	29.02	0.02	0.40	0.36	13.98	0.03	0.93	0.38	32.67	0.13	0.69	0.69	24.32	0.44
<i>Bryoria oregana</i>	1.30	0.96	68.90	0.03	0.24	0.12	12.72	0.02	0.27	0.14	14.14	0.04	0.08	0.05	4.24	0.05
<i>Bryoria pikeli</i>	1.09	0.51	77.25	0.02	0.24	0.20	17.06	0.02	0.05	0.05	3.79	0.01	0.03	0.03	1.90	0.02
<i>Bryoria pseudofuscescens</i>	0.13	0.13	33.33	<0.01	0.00	0.00	0.00	0.00	0.27	0.27	66.68	0.04	0.00	0.00	0.00	0.00
<i>Cavernularia hultenii</i>	0.03	0.03	10.01	<0.01	0.05	0.03	19.99	<0.01	0.03	0.03	10.01	<0.01	0.16	0.12	59.99	0.10
<i>Cetraria chlorophylla</i>	1.49	0.89	45.51	0.03	0.16	0.12	4.90	0.01	0.53	0.27	16.33	0.07	1.09	1.05	33.27	0.69
<i>Cetraria idahoensis</i>	1.88	1.88	100.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cetraria orbata</i>	0.13	0.13	1.90	<0.01	3.95	2.14	56.21	0.26	2.65	1.33	37.73	0.37	0.29	0.29	4.17	0.19
<i>Cetraria pallidula</i>	0.00	0.00	0.00	0.00	0.27	0.27	50.00	0.02	0.00	0.00	0.00	0.00	0.27	0.27	50.00	0.17
<i>Cladonia coniocraea</i>	0.53	0.53	100.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cladonia squamosa</i>	0.27	0.27	100.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Evernia prunastri</i>	0.00	0.00	0.00	0.00	0.27	0.27	58.82	0.02	0.03	0.03	5.89	0.00	0.16	0.16	35.29	0.10
<i>Hypogynia apinnata</i>	0.21	0.21	5.43	<0.01	3.71	3.71	94.57	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hypogynia enteromorpha</i>	40.40	7.83	19.77	0.87	87.14	25.51	42.64	5.65	56.93	13.36	27.85	7.91	19.91	5.63	9.74	12.71
<i>Hypogynia inshaugii</i>	37.13	5.82	26.27	0.80	31.83	7.35	22.52	2.06	52.89	3.23	37.42	7.35	19.50	10.39	13.79	12.45
<i>Hypogynia inactive</i>	80.01	23.70	20.53	1.72	84.78	29.97	21.75	5.50	186.96	70.00	47.97	25.97	37.96	24.25	9.74	24.24
<i>Hypogynia metaphysodes</i>	0.53	0.19	24.73	0.01	1.33	0.74	61.67	0.09	0.00	0.00	0.00	0.00	0.29	0.29	13.60	0.19
<i>Hypogynia occidentalis</i>	0.53	0.53	11.39	0.01	3.99	3.95	85.75	0.26	0.13	0.13	2.86	0.02	0.00	0.00	0.00	0.00
<i>Hypogynia physodes</i>	13.61	2.07	34.83	0.29	14.43	5.45	36.93	0.94	3.40	1.51	8.69	0.47	7.64	4.70	19.55	4.88
<i>Hypogynia tubulosa</i>	3.71	1.78	33.10	0.08	3.77	2.71	33.57	0.24	1.46	1.46	13.01	0.20	2.28	1.69	20.32	1.46
<i>Hypotrachyna sinuosa</i>	0.00	0.00	0.00	0.00	0.13	0.13	55.54	0.01	0.00	0.00	0.00	0.00	0.11	0.05	44.46	0.07
<i>Lobaria oregana</i>	2576.50	559.51	80.28	55.33	513.21	173.35	15.99	33.28	108.12	106.22	3.37	15.02	11.46	6.53	0.36	7.32
<i>Lobaria pulmonaria</i>	721.50	447.88	72.42	15.50	273.89	141.04	27.49	17.76	0.00	0.00	0.00	0.00	0.93	0.93	0.09	0.59
<i>Lobaria scrobiculata</i>	4.11	1.65	32.82	0.09	8.15	4.60	65.05	0.53	0.00	0.00	0.00	0.00	0.27	0.27	2.13	0.17

APPENDIX 4- CONTINUED

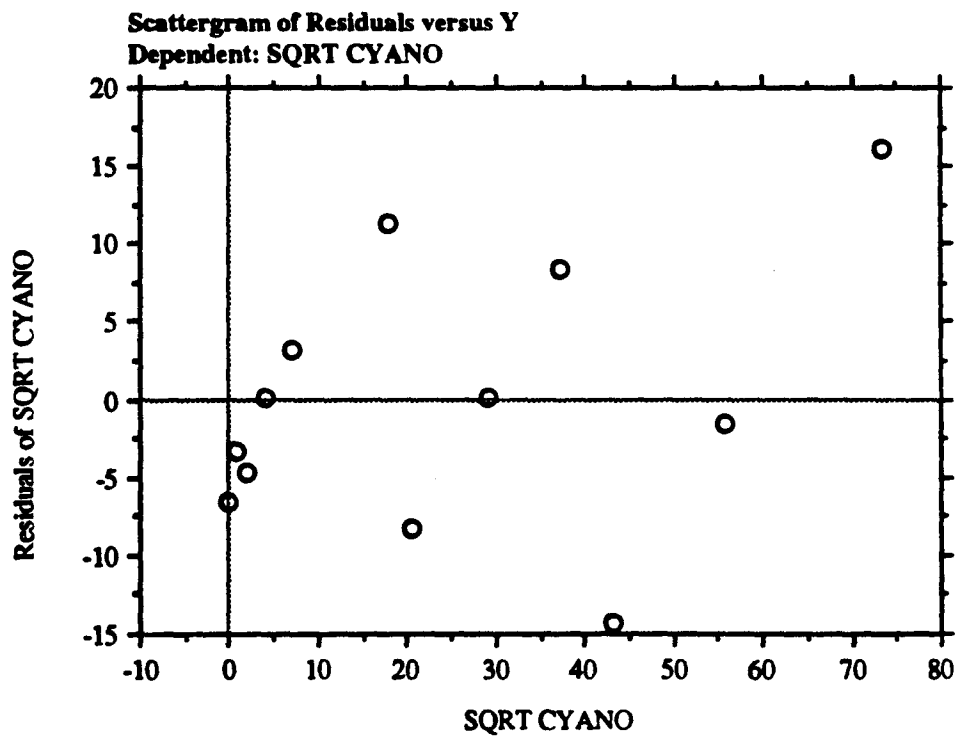
LICHEN SPECIES	FOREST AGE (YEARS)															
	510				140				70				40			
	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class	Biomass (kg/ha)	± S.E.	% of Σ Species' Biomass in All Age Classes	% of Total Biomass in Age Class
<i>Nephroma bellum</i>	5.91	1.99	58.66	0.13	4.17	1.83	41.34	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nephroma helveticum</i>	15.84	7.97	54.47	0.34	12.44	10.13	42.79	0.81	0.00	0.00	0.00	0.00	0.80	0.80	2.74	0.51
<i>Nephroma laevigatum</i>	0.53	0.53	10.52	0.01	4.51	3.74	89.48	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nephroma occultum</i>	0.00	0.00	0.00	0.00	1.33	1.33	100.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nephroma parile</i>	0.29	0.29	17.56	0.01	1.38	0.94	82.44	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nephroma resupinatum</i>	2.31	2.31	74.33	0.05	0.80	0.80	25.67	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Parmelia pseudosulcata</i>	0.90	0.68	51.52	0.02	0.03	0.03	1.52	<0.01	0.80	0.80	45.44	0.11	0.03	0.03	1.52	0.02
<i>Parmelia saxatilis</i>	0.00	0.00	0.00	0.00	0.13	0.07	71.44	0.01	0.00	0.00	0.00	0.00	0.05	0.05	28.56	0.03
<i>Parmelia sulcata</i>	2.81	0.98	41.07	0.06	3.05	2.29	44.57	0.20	0.64	0.33	9.29	0.09	0.35	0.03	5.06	0.22
<i>Parmeliopsis hyperoptera</i>	0.05	0.05	11.76	<0.01	0.13	0.07	29.41	0.01	0.03	0.03	5.89	<0.01	0.24	0.24	52.95	0.15
<i>Platismatia glauca</i>	222.42	32.01	50.25	4.78	144.81	72.90	32.72	9.39	59.26	16.14	13.39	8.23	16.12	8.75	3.64	10.29
<i>Platismatia herrei</i>	58.84	18.14	63.61	1.26	27.19	4.34	29.39	1.76	4.77	2.56	5.16	0.66	1.70	0.81	1.84	1.09
<i>Platismatia stenophylla</i>	17.72	9.39	21.02	0.38	32.44	12.84	38.47	2.10	31.70	26.03	37.59	4.40	2.47	1.69	2.93	1.58
<i>Pseudocyphellaria anomala</i>	44.67	23.12	53.90	0.96	31.62	13.11	38.16	2.05	0.11	0.11	0.13	0.01	6.47	4.40	7.81	4.13
<i>Pseudocyphellaria anthraspis</i>	84.33	31.61	73.35	1.81	30.64	29.26	26.65	1.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pseudocyphellaria crocata</i>	0.80	0.80	24.61	0.02	1.94	1.94	59.84	0.13	0.00	0.00	0.00	0.00	0.50	0.50	15.55	0.32
<i>Pseudocyphellaria rainierensis</i>	8.49	5.06	100.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ramalina farinacea</i>	0.00	0.00	0.00	0.00	0.29	0.25	52.38	0.02	0.27	0.27	47.63	0.04	0.00	0.00	0.00	0.00
<i>Sphaerophorus globosus</i>	169.72	86.72	55.86	3.64	123.35	14.77	40.60	8.00	10.61	5.91	3.49	1.47	0.13	0.13	0.04	0.09
<i>Sticta fuliginosa</i>	0.03	0.03	0.79	<0.01	1.91	1.46	56.63	0.12	0.05	0.05	1.58	0.01	1.38	1.38	40.99	0.88
<i>Sticta limbata</i>	0.00	0.00	0.00	0.00	1.06	1.06	57.09	0.07	0.00	0.00	0.00	0.00	0.80	0.80	42.91	0.51
<i>Usnea spp. pendant</i>	182.24	51.85	76.20	3.91	33.87	19.30	14.16	2.20	16.61	3.85	6.94	2.31	6.45	6.29	2.70	4.12
<i>Usnea spp. tufted</i>	9.60	3.25	29.96	0.21	11.14	9.63	34.75	0.72	8.59	5.97	26.81	1.19	2.72	1.27	8.48	1.74
TOTAL CYANOLICHENS	3465.20	1035.50	77.3	74.42	887.29	280.04	19.8	57.53	108.28	106.38	2.4	15.04	22.57	15.14	0.5	14.41
<i>Lobaria oregana/pulmonaria</i>	3298.00	978.52	78.4	70.83	787.10	222.81	18.7	51.03	108.12	106.22	2.6	15.02	12.39	7.34	0.3	7.91
TOTAL OTHER	652.83	164.18	37.4	14.02	567.33	89.81	32.5	36.78	413.05	117.68	23.7	57.39	110.67	57.20	6.3	70.67
TOTAL ALECTORIOD	538.00	202.58	63.5	11.55	87.78	17.73	10.4	5.69	198.44	60.33	23.4	27.57	23.34	11.11	2.8	14.91
TOTAL FOR STAND	4656.30	743.88	65.81	100.00	1542.30	183.02	21.80	100.00	719.77	156.74	10.17	100.00	156.61	58.62	2.21	100.00

APPENDIX 5a.

STATISTICAL SUMMARY OF SQRT CYANOLICHEN BIOMASS ANOVA. Untransformed data are not presented because patterning of residuals was overwhelmingly strong.

ANOVA Summary
Dependent: SQRT CYANO

Count	12				
R	.934				
R-Squared	.872				
Adj. R-Squared	.824				
RMS Residual	10.103				
	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	5561.208	1853.736	18.160	.0006
Error	8	816.636	102.079		
Total	11	6377.844			



APPENDIX 5a Continued

Fisher's Protected LSD
Effect: AGE
Dependent: SQRT CYANO
Significance level: .05

	Vs.	Diff.	Crit. diff.	P-Value	
40	70	2.679	19.023	.7537	
	140	25.054	19.023	.0161	S
	510	53.595	19.023	.0002	S
70	140	22.374	19.023	.0266	S
	510	50.916	19.023	.0003	S
140	510	28.542	19.023	.0086	S

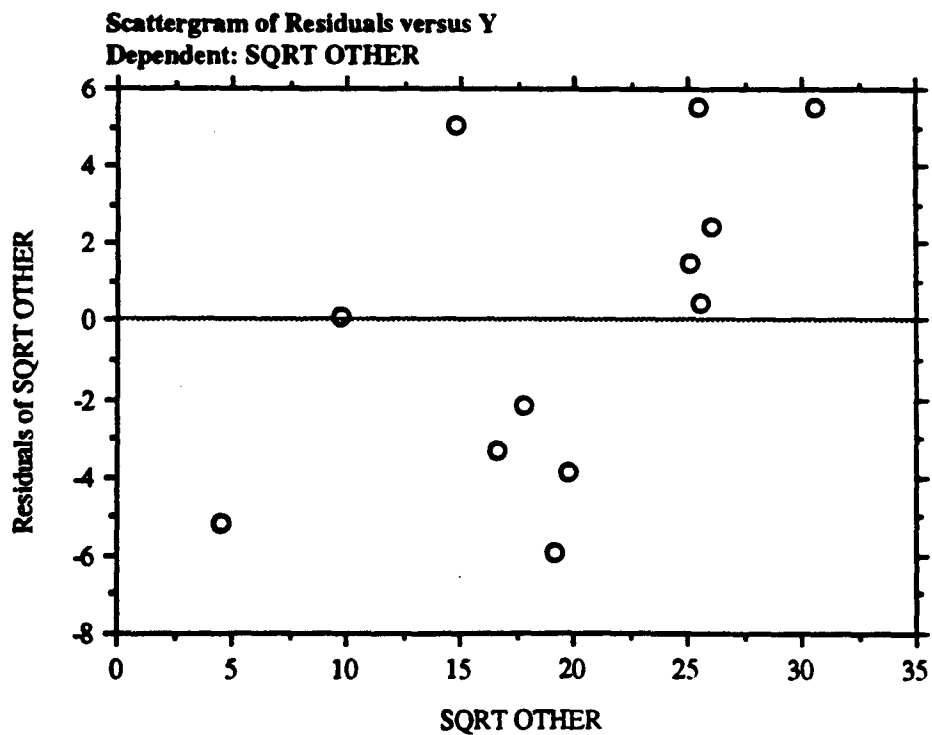
S = Significantly different at this level.

APPENDIX 5b.
STATISTICAL SUMMARY OF SQRT "OTHER" LICHEN BIOMASS ANOVA

Model Summary
Dependent: SQRT OTHER

Count 12
 R .837
 R-Squared .700
 Adj. R-Squared .588
 RMS Residual 4.837

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	437.649	145.883	6.236	.0173
Error	8	187.137	23.392		
Total	11	624.787			



APPENDIX 5b Continued

Fisher's Protected LSD

Effect: AGE

Dependent: SQRT OTHER

Significance level: .05

	Vs.	Diff.	Crit. diff.	P-Value	
40	70	10.286	9.106	.0314	S
	140	13.998	9.106	.0076	S
	510	15.462	9.106	.0044	S
70	140	3.712	9.106	.3748	
	510	5.177	9.106	.2263	
140	510	1.465	9.106	.7203	

S = Significantly different at this level.

APPENDIX 5b Continued.

STATISTICAL SUMMARY OF UNTRANSFORMED "OTHER" BIOMASS ANOVA.
Residuals are not patterned enough to require transformation.

Model Summary

Dependent: OTHER

Count 12

R .788

R-Squared .621

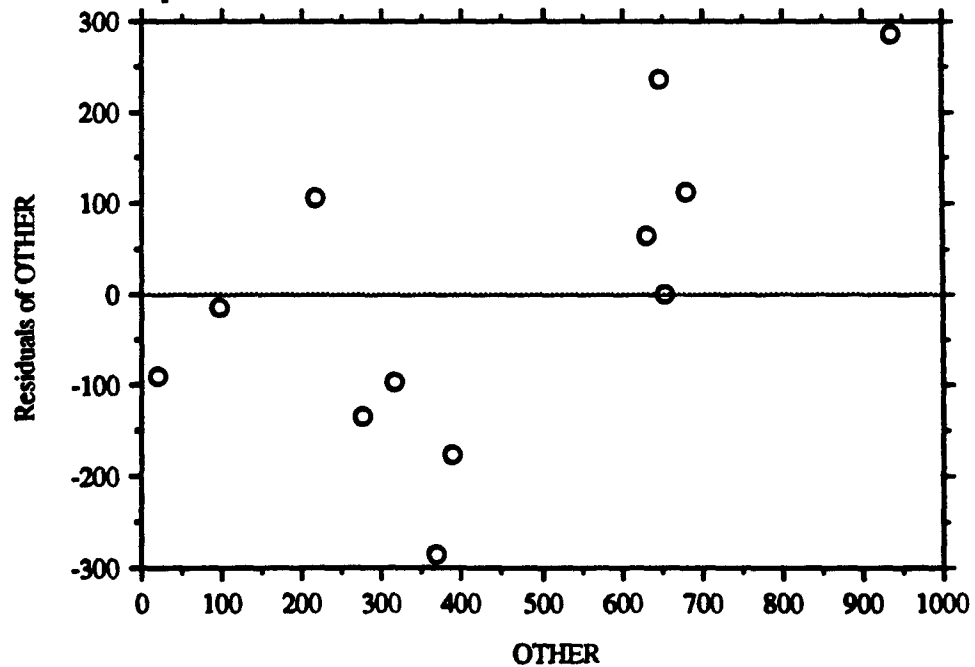
Adj. R-Squared .478

RMS Residual 197.750

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	511880.871	170626.957	4.363	.0425
Error	8	312839.342	39104.918		
Total	11	824720.213			

Scattergram of Residuals versus Y

Dependent: OTHER



APPENDIX 5b Continued

Fisher's Protected LSD

Effect: AGE

Dependent: OTHER

Significance level: .05

	Vs.	Diff.	Crit. diff.	P-Value	
40	70	302.377	372.332	.0980	
	140	456.657	372.332	.0222	S
	510	542.157	372.332	.0100	S
70	140	154.280	372.332	.3673	
	510	239.780	372.332	.1758	
140	510	85.500	372.332	.6108	

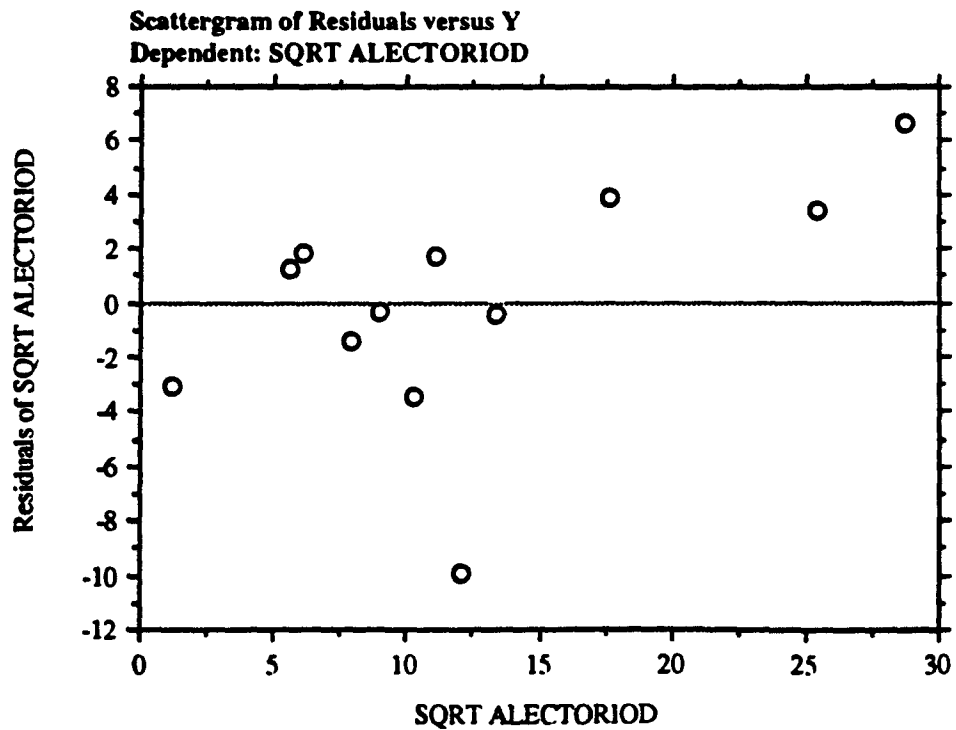
S = Significantly different at this level.

APPENDIX 5c.
STATISTICAL SUMMARY OF SQRT TRANSFORMED ALECTORIOD BIOMASS ANOVA

Model Summary
Dependent: SQRT ALECTORIOD

Count 12
 R .847
 R-Squared .717
 Adj. R-Squared .611
 RMS Residual 5.021

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	511.404	170.468	6.761	.0138
Error	8	201.703	25.213		
Total	11	713.107			



APPENDIX 5c continued

Fisher's Protected LSD

Effect: AGE

Dependent: SQRT ALECTORIOD

Significance level: .05

	Vs.	Diff.	Crit. diff.	P-Value	
40	140	4.977	9.454	.2593	
	70	9.461	9.454	.0499	S
	510	17.757	9.454	.0025	S
140	70	4.483	9.454	.3060	
	510	12.780	9.454	.0143	S
70	510	8.297	9.454	.0776	

S = Significantly different at this level.

APPENDIX 5c continued.

STATISTICAL SUMMARY OF UNTRANSFORMED ALECTORIOD BIOMASS ANOVA

Note strong patterning of residuals.

Model Summary

Dependent: ALECTORIOD

Count 12

R .797

R-Squared .636

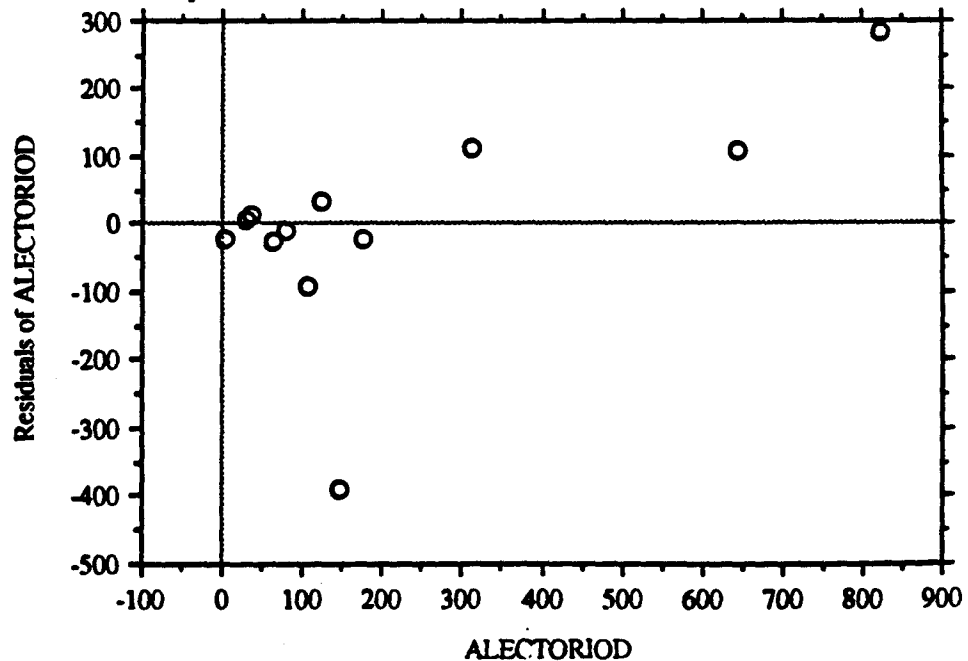
Adj. R-Squared .499

RMS Residual 183.950

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	3	472454.052	157484.684	4.654	.0364
Error	8	270700.097	33837.512		
Total	11	743154.149			

Scattergram of Residuals versus Y

Dependent: ALECTORIOD



APPENDIX 5c continued.

Fisher's Protected LSD
Effect: AGE
Dependent: ALECTORIOD
Significance level: .05

	Vs.	Diff.	Crit. diff.	P-Value	
40	140	64.433	346.349	.6792	
	70	175.100	346.349	.2773	
	510	514.660	346.349	.0090	S
140	70	110.667	346.349	.4823	
	510	450.227	346.349	.0171	S
70	510	339.560	346.349	.0537	

S = Significantly different at this level.

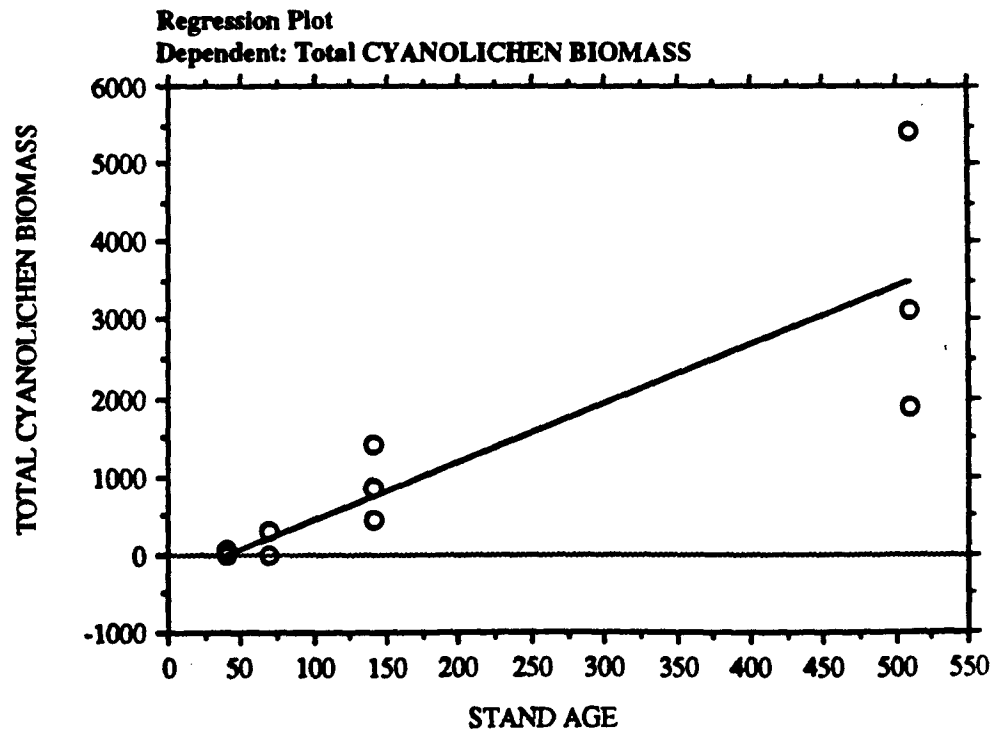
APPENDIX 5d.
CYANOLICHEN BIOMASS REGRESSED ON FOREST AGE CLASS.

Model Summary

Dependent: Total CYANOLICHEN BIOMASS

Count 12
 R .876
 R-Squared .767
 Adj. R-Squared .743
 RMS Residual 841.330

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	1	23241508.113	23241508.113	32.835	.0002
Error	10	7078362.467	707836.247		
Total	11	30319870.580			



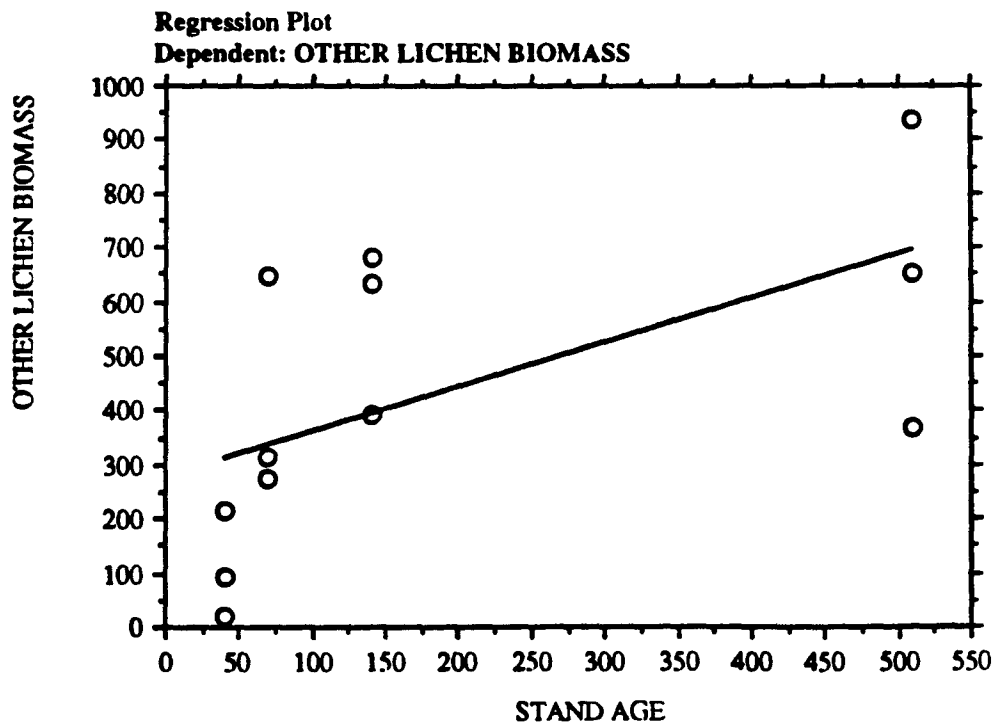
APPENDIX 5c.
REGRESSION OF "OTHER" LICHEN BIOMASS ON FOREST AGE CLASS.

Model Summary

Dependent: OTHER LICHEN BIOMASS

Count 12
 R .579
 R-Squared .336
 Adj. R-Squared .269
 RMS Residual 234.088

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	1	276748.461	276748.461	5.050	.0484
Error	10	547971.752	54797.175		
Total	11	824720.213			



APPENDIX 5f.
REGRESSION OF ALECTORIOD LICHEN BIOMASS ON AGE.

Model Summary

Dependent: ALECTORIOD BIOMASS

Count 12

R .749

R-Squared .562

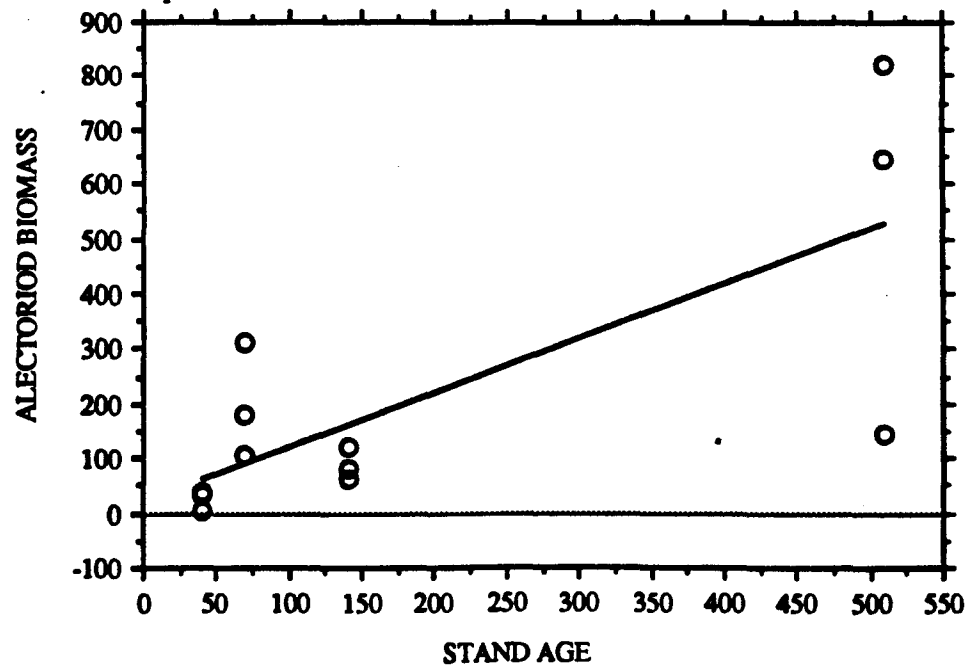
Adj. R-Squared .518

RMS Residual 180.491

	df	Sum of Squares	Mean Square	F-Value	P-Value
Model	1	417383.329	417383.329	12.812	.0050
Error	10	325770.820	32577.082		
Total	11	743154.149			

Regression Plot

Dependent: ALECTORIOD BIOMASS



APPENDIX 6.

Estimated standing biomass (kg/ha) of epiphytic macrolichens in 12 study stands of different ages, H. J. Andrews Experimental Forest and vicinity, western Cascades, OR. The biomass in each stand represents the sum of 10 biomass plots totaling 0.0126 ha.

LICHEN SPECIES	STANDS											
	510			140			70			40		
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Alectoria sarmentosa</i>	59.61	340.76	591.36	1.19	4.22	117.46	63.66	281.24	163.46	0.84	10.19	27.22
<i>Alectoria vancouverensis</i>	0	31.83	0	0	0	0	2.55	0	0	0	1.43	0
<i>Bryoria capillaris</i>	0	3.18	0	0.32	0.72	0	2.94	0	0	0	0	0
<i>Bryoria friabilis</i>	0.08	2.63	0	0.8	1.27	0.32	0.8	0.56	0	0	0.24	0.08
<i>Bryoria fuscescens</i>	0.64	0	1.83	1.11	0.08	0	1.27	1.35	0.16	0	2.07	0
<i>Bryoria oregana</i>	0.72	0	3.18	0.08	0.48	0.16	0.32	0.48	0	0	0.08	0.16
<i>Bryoria pikei</i>	1.43	0.08	1.75	0.64	0.08	0	0	0.16	0	0.08	0	0
<i>Bryoria pseudofuscescens</i>	0	0.4	0	0	0	0	0.8	0	0	0	0	0
<i>Cavernularia hultenii</i>	0	0.08	0	0	0.08	0.08	0	0	0.08	0.4	0	0.08
<i>Cetraria chlorophylla</i>	0.4	3.26	0.8	0.4	0.08	0	0	0.8	0.8	0	3.18	0.08
<i>Cetraria idahoensis</i>	0	0	5.65	0	0	0	0	0	0	0	0	0
<i>Cetraria orbata</i>	0	0.4	0	7.64	0.24	3.98	3.98	3.98	0	0	0	0.88
<i>Cetraria pallidula</i>	0	0	0	0	0.8	0	0	0	0	0	0	0.8
<i>Cladonia coniocraea</i>	0	1.59	0	0	0	0	0	0	0	0	0	0
<i>Cladonia squamosa</i>	0	0.8	0	0	0	0	0	0	0	0	0	0
<i>Evernia prunastri</i>	0	0	0	0.8	0	0	0.08	0	0	0	0.48	0
<i>Hypogymnia apinnata</i>	0	0.64	0	11.14	0	0	0	0	0	0	0	0
<i>Hypogymnia enteromorpha</i>	25.15	51.09	44.96	137.12	53.24	71.06	65.89	74.25	30.64	9.59	28.97	21.17
<i>Hypogymnia imshaugii</i>	29.44	33.42	48.54	17.91	42.89	34.7	50.45	59.29	48.94	0.16	35.73	22.6
<i>Hypogymnia inactiva</i>	32.71	101.07	106.24	140.06	37.08	77.19	144.84	323.65	92.39	1.35	83.8	28.73
<i>Hypogymnia metaphysodes</i>	0.72	0.72	0.16	0.8	2.79	0.4	0	0	0	0.88	0	0
<i>Hypogymnia occidentalis</i>	0	1.59	0	11.89	0	0.08	0	0.4	0	0	0	0
<i>Hypogymnia physodes</i>	13.93	9.87	17.03	17.27	3.9	22.12	2.39	1.43	6.37	2.79	17.03	3.1
<i>Hypogymnia tubulosa</i>	5.41	0.16	5.57	9.15	0.56	1.59	0	0	4.38	1.27	5.57	0
<i>Hypotrachyna sinuosa</i>	0	0	0	0.4	0	0	0	0	0	0.16	0	0.16
<i>Lobaria oregana</i>	3523.24	2619.69	1586.5	274.47	850.31	414.85	3.82	0	320.55	22.6	11.78	0
<i>Lobaria pulmonaria</i>	1614.44	336.46	213.59	479.63	338.13	3.9	0	0	0	2.79	0	0

Continued

APPENDIX 6 Continued

LICHEN SPECIES	STANDS											
	510			140			70			40		
	1	2	3	4	5	6	7	8	9	10	11	12
Lobaria scrobiculata	3.18	1.83	7.32	8.52	15.92	0	0	0	0	0.8	0	0
Nephroma bellum	4.77	9.79	3.18	7.08	4.62	0.8	0	0	0	0	0	0
Nephroma helveticum	26.5	20.77	0.24	3.82	32.63	0.88	0	0	0	2.39	0	0
Nephroma laevigatum	0	1.59	0	1.59	11.94	0	0	0	0	0	0	0
Nephroma occultum	0	0	0	3.98	0	0	0	0	0	0	0	0
Nephroma parile	0	0.88	0	3.18	0.95	0	0	0	0	0	0	0
Nephroma resupinatum	0	6.92	0	0	2.39	0	0	0	0	0	0	0
Parmelia pseudosulcata	0	2.23	0.48	0	0	0.08	2.39	0	0	0	0.08	0
Parmelia saxatilis	0	0	0	0	0.24	0.16	0	0	0	0	0	0.16
Parmelia sulcata	4.06	3.5	0.88	7.64	0.72	0.8	0	0.8	1.11	0.4	0.32	0.32
Parmeliopsis hyperopta	0	0.16	0	0	0.24	0.16	0	0	0.08	0	0.72	0
Platismatia glauca	160.35	266.99	239.93	62.07	82.21	290.15	29.13	84.35	64.3	2.67	32.55	13.13
Platismatia herrei	23.48	83.56	69.47	25.47	20.69	35.41	0	8.75	5.57	0.08	2.55	2.47
Platismatia stenophylla	0.64	33.03	19.5	41.62	7.08	48.62	11.78	83.32	0	0.08	5.73	1.59
Pseudocyphellaria anomala	89.69	31.27	13.05	44.33	45.12	5.41	0	0	0.32	15.04	3.9	0.48
Pseudocyphellaria anthraspis	136.48	89.21	27.3	2.79	89.13	0	0	0	0	0	0	0
Pseudocyphellaria crocata	0	2.39	0	5.81	0	0	0	0	0	1.51	0	0
Pseudocyphellaria rainierensis	7.96	0	17.51	0	0	0	0	0	0	0	0	0
Ramalina farinacea	0	0	0	0.08	0.8	0	0.8	0	0	0	0	0
Sphaerophorus globosus	71.22	342.59	95.34	140.06	136.08	93.9	3.18	6.37	22.28	0.4	0	0
Sticta fuliginosa	0	0.08	0	4.77	0.95	0	0	0	0.16	4.14	0	0
Sticta limbata	0	0	0	3.18	0	0	0	0	0	2.39	0	0
Usnea sp. pendant	80.77	251.47	214.47	27.93	69.87	3.82	13.45	24.27	12.1	0.32	19.02	0
Usnea sp. tufted	3.74	14.96	10.11	30.32	3.1	0	20.45	3.9	1.43	0.2	4.3	3.66
Lobaria oregana & L. pulmonaria	5137.67	2956.15	1800.1	754.1	1188.45	418.75	3.82	0	320.55	25.39	11.78	0
TOTAL CYANOLICHENS	5406	3120.88	1868.69	843.15	1392.89	425.83	3.82	0	321.02	51.56	15.68	0.48
TOTAL ALECTORIOD	146	645.31	822.7	61.99	79.58	121.76	106.24	311.95	177.14	1.43	37.48	31.12
TOTAL OTHER	368	936.73	653.75	631.55	389.94	680.49	314.82	647.38	276.94	20.21	216.54	95.26
TOTAL FOR STAND	5920.74	4702.93	3345.14	1536.69	1862	1228.08	424.88	959.33	775.11	73.29	269.7	126.85

