AN ABSTRACT OF THE DISSERTATION OF

Shanti D. Berryman for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on October 8, 2002.
Title: Epiphytic Macrolichens in Relation to Forest Management and Topography in a Western Oregon Watershed.

Abstract approved: ____

Bruce McCune

This dissertation describes patterns in epiphytic macrolichen community composition, diversity, and biomass across various stand types in the Blue River watershed of western Oregon. It first examines the relative importance of ecological factors such as stand age, remnant tree retention, and topography to lichen communities in the landscape. It then develops models for estimating epiphytic macrolichen biomass and uses these models to assess potential impacts of forest management strategies on future lichen biomass in the watershed.

Epiphytic macrolichen communities were sampled in 117 coniferous stands in uplands and riparian areas. Stands were typed by stand age (young, <20; pole, 21-80; mature, 81-200; and old-growth, >200 yrs) and by the degree of remnant tree retention (older trees that survived the most recent disturbance). Lichen biomass (oven-dried, kg/ha) was estimated for three functional groups: nitrogen-fixing cyanolichens, forage lichens, and matrix lichens in 63 of the 117 stands. Elevation was the leading factor related to differences in macrolichen communities and biomass. Cyanolichens (dominated by *Lobaria oregana*) were largely limited to lower elevations and were most abundant in old growth (median 1,377 kg/ha).

Lichen community composition changed with stand age. Remnant presence was related only to lichen community differences in young stands. Lichen biomass increased with stand age and with remnant retention. Stands along perennial streams were cyanolichen hotspots compared to uplands. Lichen biomass was unrelated to uplands and riparian areas.

Regression models estimating lichen biomass by functional group were developed from topography, stand structure, and lichen communities. The model for cyanolichen biomass had the strongest predictive power ($R^2 = 0.85$), whereas models for forage and matrix lichen biomass were less powerful ($R^2 = 0.55$ and $R^2 = 0.58$, respectively).

We estimated cyanolichen and forage lichen biomass in the present watershed and forecasted lichen biomass in 200 yrs for two different management scenarios: the Landscape Plan (LP) and the Northwest Forest Plan (NWFP). Under both scenarios, lichen biomass was predicted to increase substantially from current levels due to increased remnant tree retention and the elimination of clear-cutting. The LP scenario yielded 12% higher forage lichen biomass and 8% higher cyanolichen biomass than the NWFP.

Epiphytic Macrolichens in Relation to Forest Management and Topography in a Western Oregon Watershed

by

Shanti D. Berryman

A DISSERTATION

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degree of

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APPROVED:

Major Professor, representing Botany and Plant Pathology

Chair of the Department of Botany and Plant Pathology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Shanti D. Berryman, Author

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CONTRIBUTION OF AUTHORS

Dr. Bruce McCune contributed considerably to this dissertation by assisting with the study design and by providing guidance on lichen identification, analysis, model development, and presentation of results. John Cissel contributed to the work presented in Chapter 4. John played a key role in developing and evaluating the two forest management plans addressed in this chapter. In addition, he provided maps of stand structure used for modeling the changes in lichen biomass under two alternative management plans in the Blue River watershed.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (CONTINUED)

TABLE OF CONTENTS (CONTINUED)

Page

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

LIST OF TABLES

LIST OF TABLES (CONTINUED)

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

DEDICATION

This dissertation is dedicated to my parents, Bob and Shelly Berryman, who have given me incredible support, love, guidance, and friendship.

Epiphytic Macrolichens in Relation to Forest Management and Topography in a Western Oregon Watershed

Chapter 1

Introduction

This dissertation relates patterns in epiphytic macrolichen communities among forest stands to topography and forest management in the Blue River watershed of western Oregon. Important factors from these relationships are used to develop models for estimating epiphytic macrolichen biomass in forest stands. Using these models, I evaluate potential impacts of different forest management practices on future lichen biomass in the Blue River watershed.

I focus on three functional groups of epiphytic macrolichens in this dissertation. These groups include nitrogen-fixing cyanolichens, forage lichens, and matrix lichens. Cyanolichens are important contributors of fixed nitrogen in forests of the Pacific Northwest (Antoine 2001; Denison 1979; Pike 1978), especially in old-growth Douglas fir/western hemlock forests where cyanolichens are abundant (McCune 1993; Neitlich 1993; Pike et al. 1977). Forage lichens are used as food and nesting-material for many forest animals including the northern flying squirrel (*Glaucomys sabrinus;* Rosentreter et al. 1997; Zabel & Waters 1997; Hayward & Rosentreter 1994) and many ungulates, such as the black-tailed deer (Stevenson & Rochelle 1984; Stevenson 1978) and woodland caribou (Rominger & Oldemeyer 1989; Servheen & Lyon 1989; Edwards et al. 1960). Matrix lichens include the remaining leafy macrolichens that are generally considered early colonizers of young stands. Matrix lichens are known to provide habitat and food for many arthropods (Pettersson et al. 1995).

In the Pacific Northwest (PNW), surveys for several lichen species associated with old growth are mandated on federal forests under the Northwest

Forest Plan (NWFP) within the range of the northern spotted owl (USDA & USDI 1994*a*). Prior to the NWFP, much of the importance of non-vascular plant species in PNW forest ecosystems had been overlooked. As the NWFP was developed and implemented, managers and ecologists learned that certain lichen species are more sensitive to forest management practices and habitat loss than other lichen species. Part of their sensitivity may be due to inherent dispersal-limitations (Sillett et al. 2000*a*, 2000*b*). In order to properly manage for the long-term diversity and ecosystem-level contributions of these lichen species, it is important to better understand their distribution and factors influencing their distribution in the forest landscape.

This dissertation is part of the multidisciplinary Blue River Landscape Project (LP) in the Central Cascades Adaptive Management Area (AMA), which encompasses the Blue River watershed (Cissel et al. 1999). The AMA was allocated under the NWFP as a site for research and experimental forest management. The LP management team (Cissel et al. 1999) developed both the LP and NWFP management scenarios in detail, including projections of forest structure and maps of the watershed for the next 200 years (Figure 1.1). The two management scenarios (NWFP and LP) are projected to result in very different future forest landscapes.

Under the NWFP, old growth will be allocated primarily to reserve areas such as riparian reserves (all streams will be buffered) and other special reserve areas (e.g., late-successional reserves, wilderness areas; USDA & USDI 1994*a*). Approximately 80% of the federal lands managed under the NWFP will be in these reserve areas. Young forests will dominate between the reserve areas and will be harvested on an 80-year rotation, leaving 15% live remnant tree retention with each harvest. Alternatively, the LP is based in part on fire history and will result in a future landscape with varying levels of live remnant tree retention (15 to 50%) and forests of varied ages (Cissel et al. 1999). Riparian areas along perennial non fish-

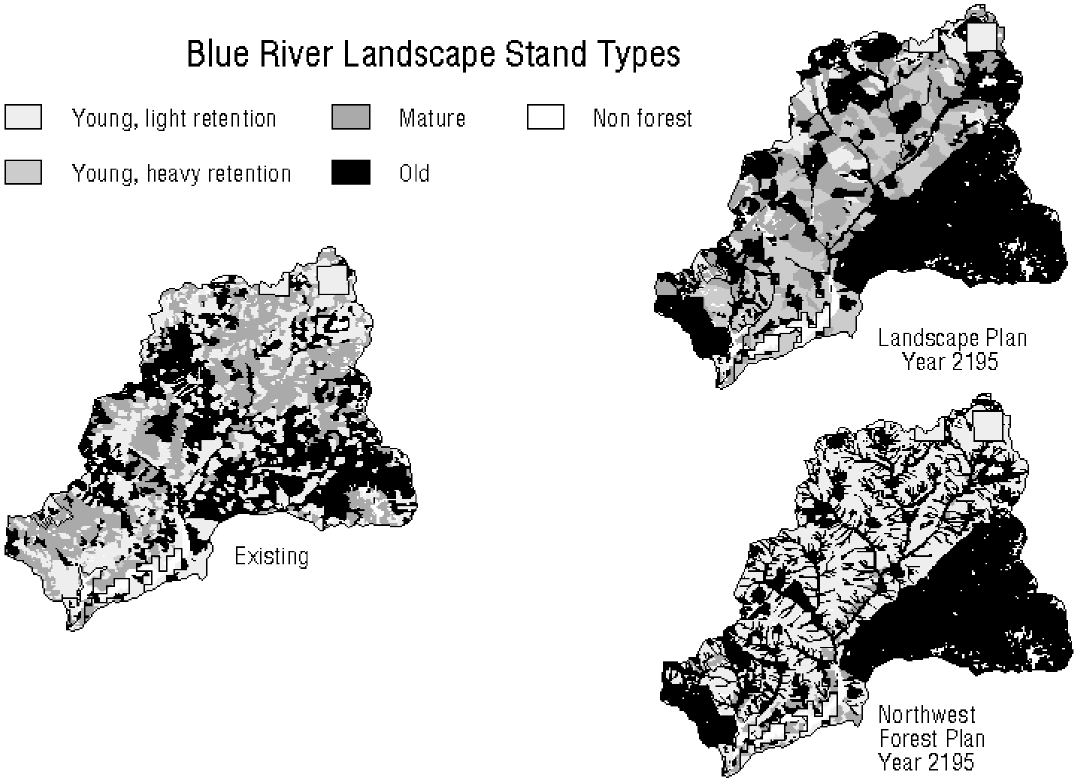


Figure 1.1. Maps of the present stand types in the Blue River watershed and forecasted maps of projected stand types in the future landscape managed under the Northwest Forest Plan and the Landscape Plan (modified from Cissel et al. 1999).

bearing streams and intermittent streams will not be buffered in the classic sense, except for leaving trees on the bank that are necessary for stability.

The intent of this dissertation is to document present patterns in lichen communities across the landscape and use predictive models to assess possible impacts of these two management scenarios on future lichen biomass. A related study (not included in this dissertation) examines differences in the probability of lichen species' occurrences under the two management scenarios (McCune et al. 2002*b*, *in review*). Results from these studies can be used to select forest management strategies that may promote lichen communities in the future landscape.

Chapter Two of this dissertation describes variation in lichen communities in relation to stand age, remnant tree retention, and topography. I evaluate these factors simultaneously to determine relationships with lichen community composition and lichen species diversity for all macrolichens combined and for each functional group. Understanding these relationships can help forest managers identify and manage for important habitat and forest features that are related to lichen diversity and abundance.

The third chapter of this dissertation describes patterns in epiphytic macrolichen biomass by functional group in relation to topography and to factors of stand structure addressed in Chapter Two. Lichen biomass is also related to patterns in lichen community composition and species richness. Sampling lichen biomass across a landscape is a tedious and time-consuming task. I develop regression models for estimating lichen biomass by functional group based on relevant factors of topography, stand structure, and lichen communities. Such models can be used to understand and map the distribution of lichen biomass across the landscape without directly sampling each stand. These maps can serve as a guide for forest managers to identify which areas have abundant lichens and warrant protection. These biomass models also provide a basis for modeling lichen contributions to ecosystem function. For example, *L. oregana* is the most abundant cyanolichen in the forests of the Cascade Range and is a significant contributor of new nitrogen to the system (Antoine 2001). We can estimate annual nitrogen fixation in forest stands using our model to estimate cyanolichen biomass and Antoine's (2001) model to estimate nitrogen fixation by *L. oregana.*

Chapter Four of this dissertation examines the potential impacts of the NWFP and LP scenarios on future lichen biomass in the Blue River watershed. Cyanolichen and forage lichen biomass is estimated for the present watershed using models based on relevant factors of forest structure and topography. The same models are then used to predict changes in lichen biomass 200 years into the future under each management plan. We compare changes in predicted lichen biomass for each functional group between the present watershed and two future landscape scenarios. In addition, we compare differences in predicted lichen biomass between the two future management scenarios. Differences in lichen biomass are related to different management prescriptions, such as the elimination of clear-cutting under both scenarios and the degree of remnant tree retention in stands.

Results from this dissertation contribute to a better understanding of the variation of lichen communities across the landscape and present the relative importance of stand structure characters (i.e., stand age, remnant tree retention) and topography to lichen communities. Forest managers can use the outcome of this research to prioritize lichen habitat in need of conservation and to consider management practices that may enhance epiphytic macrolichen diversity and abundance in the landscape. Findings from this study are specific to the forests in the Blue River watershed, however the patterns in lichen communities may be generalized elsewhere in similar forests of the PNW.

Chapter 2

Epiphytic Macrolichen Communities Along Gradients in Topography and Forest Structure in a Western Oregon Landscape, USA

Shanti Berryman and Bruce McCune

For submission to *The Bryologist*

ABSTRACT

Epiphytic macrolichen communities were compared among forest stand types in the Blue River watershed of western Oregon. Stand types were defined by stand structure, according to age classes of the younger tree cohort and remnant tree retention. Old growth was not stratified by age of the younger cohort or by remnant tree retention. Remnant trees were those trees in the older cohort that remained following a stand disturbance that initiated tree regeneration, such as a timber harvest or natural forest fire. Stands were located in upland and riparian forests of two vascular plant series (western hemlock and true fir). Presence and abundance of all epiphytic macrolichen species were sampled in a 0.4 ha circular plot in 117 stands. Non-metric multidimensional scaling (NMS) ordination revealed that the strongest differences in lichen community composition were related to the elevation gradient, which was correlated with vascular plant series. Cyanolichens were largely limited to lower elevation forests (470 – 950 m) of the western hemlock series, while matrix lichens and forage lichens with green-algal photobionts dominated high elevation stands (950 – 1470 m) of the true fir series. Lichen communities differed with stand age. In even-aged young stands, lichen communities were species poor and lichen community composition was very different from all other stand types. In general, macrolichen species richness varied little among stand types. However, cyanolichen species were most diverse in old-growth and mature stands at lower elevations. Lichen communities in young stands (< 20 yrs) with remnants were very different from those in even-aged young forests in both plant series. As a stand develops, the presence of remnant trees may accelerate the development of the lichen community towards those found in older stands. Remnant trees might serve as refugia for lichens through a disturbance and may provide lichen inoculum to younger trees in the stand following the disturbance. Hardwood patches were hotspots for lichen diversity, particularly cyanolichens that are not commonly found on conifers. Hardwood patches were most prevalent along channels of perennial streams. In order to maintain and

enhance lichen species diversity at a landscape level, forest managers must consider the importance of features such as late-successional stands, remnant trees, hardwoods, and riparian areas to lichen communities. These features are especially important to retain in or near regenerating forests to promote colonization by dispersal-limited lichens.

INTRODUCTION

This study examines the importance of various ecological factors, such as stand age, remnant tree retention, and topography to lichen communities across a forested landscape in western Oregon. Others have documented relationships between these factors individually and lichen communities in the Pacific Northwest (Peterson & McCune 2001; Pipp et al. 2001; Peck & McCune 1997; McCune 1993; Neitlich 1993); however, relationships to combinations of these factors have not been examined at the landscape scale. In this study, we evaluate the relative strengths and interactions of these factors in relation to epiphytic macrolichen communities. In addition, we document changes in lichen communities along a topographic gradient. Understanding the relative importance of forest features and topography as influences on lichen communities is an important step towards making successful management decisions for the conservation of lichen habitat within the landscape.

There is increasing concern regarding the maintenance of biodiversity in forest ecosystems, since many forest habitats are highly fragmented as a result of human development and forest management practices such as clear-cutting and suppression of natural wildfires (Harris 1984; Norse 1990). Lichens have become a focus of interest because they represent a responsive component of biodiversity in forests of the Pacific Northwest of North America (Peterson & McCune 2001; Neitlich & McCune 1997; Rosentreter 1995; Neitlich 1993) and in forests throughout the world (Price & Hochachka 2000; Pharo et al. 1999; Holien 1998; Kuusinen & Siitonen 1998; Dettki & Esseen 1998; Brown & Kantivilas 1994;

Kuusinen 1994; Selva 1994). In addition, lichens play important roles in ecosystems. For example, lichens containing cyanobacteria are important contributors of fixed nitrogen (N) in forest ecosystems (Antoine 2001; Pike 1978) and may be particularly important in old-growth temperate forests of North America that are considered N-limited (Sollins et al. 1980). Additionally, many epiphytic macrolichens are important in the food-web of terrestrial organisms, providing nutrition for mollusks, small mammals, and large ungulates (summarized in McCune 1993).

Old-growth forests support diverse epiphytic macrolichen communities and provide habitat for many rare lichens in the PNW (Keon & Muir 2002; Peterson & McCune 2001; Rosso et al. 2000; Sillett & Goward 1998; Rosentreter 1995; McCune 1993; Neitlich 1993) and in other forests of the world (Holien 1998; Kuusinen & Siitonen 1998; Brown et al. 1994; Selva 1994). In addition, epiphytic macrolichens are abundant in old-growth forest canopies (Chapter 3; Dettki & Esseen 1998; McCune et al. 1997*a*; Esseen et al. 1996; McCune 1993; Neitlich 1993; Esseen 1985; Rhoades 1981; Pike et al. 1977, 1972). Biomass of old-growth associated lichens develops slowly in the old-growth conifer forests of the PNW (Sillett et al. 2000*a,* 2000*b*; Sillett & McCune 1998), in which cyanolichen biomass can exceed one metric ton per hectare (Chapter 3; McCune 1993; Neitlich 1993; Sillett 1995).

In the Pacific Northwest (PNW) forests, there is special concern for conservation of old-growth habitat since much has been lost due to cutting. The remaining old growth is restricted to federal lands where it has been reduced by logging disturbance (Harris 1984; Spies et al. 1994). The loss of old-growth forests could result in the decline or local extinction of some old-growth-associated lichen species (Rosso et al. 2000; Sillett & Goward 1998; Rosentreter 1995; Goward 1993, 1994). Additionally, forest continuity and propagule availability needed for successful lichen dispersal may be reduced by the loss of older forests in the present landscape (Rose 1976; Tibell 1992; Goward 1993, 1994, 1995).

Lichen communities in very young forests differ from those in late-seral forests. Lichens may be slow to colonize young forests because the quality of substrate is poor (Esseen et al. 1996; Lesica et al. 1991) or because of unsuitable habitat due to microclimate conditions or simply because they need time to develop. However, recent transplant and sowing studies have shown that certain old-growth associated lichens grow just as well or better in young stands as compared to old stands (Keon & Muir 2002; Sillett et al. 2000*a,* 2000*b*). Habitat and substrate suitability may not be the factors restricting certain old-growth-associated lichens (such as *Lobaria oregana*) to older forests and dispersal may be the leading factor limiting lichen colonization in younger forests (Dettki et al. 2000).

Management strategies can address the lichen dispersal-limitation problem. Maintaining remnant trees in forest stands during timber harvest may promote epiphytic macrolichen diversity and biomass in the landscape. Remnant trees may serve as refugia for lichens during timber harvest, may ameliorate the microclimate following harvest, and can provide lichen inoculum to the regenerating trees (Chapter 3; Peck & McCune 1997; Sillett & Goslin 1999). In addition, managing to create or maintain structural variability in stands, such as small forest gaps, large snags and wolf trees may also provide important microhabitat for epiphytic lichens, thereby enhancing lichen diversity and biomass in managed forests (Peterson & McCune 2001; Pipp et al. 2001; Neitlich & McCune 1997). Maintaining natural diversity "hotspots" in the landscape, such as hardwoods and riparian areas, may also promote lichen diversity at the landscape level (McCune et al. 2002*a*; Peterson & McCune 2001; Rolstad et al. 2001; Rosso 2000; Neitlich & McCune 1997).

In this study we compared epiphytic macrolichen communities among a broad spectrum of forest structural types in the Blue River watershed of the western Cascade Mountains. Forest stands were typed by stand age, degree of remnant tree retention, uplands or riparian areas, and vascular plant series. Results from this study can be used to establish monitoring and management recommendations for maintaining and enhancing future lichen diversity and abundance in the Blue River watershed. In addition, the relationships between lichen communities and stand structure that were revealed here will be used to predict the likely consequences of alternative forest management strategies for epiphytic lichen presence and biomass in the future landscape (Chapter 4; McCune et al. 2002*b*, *in review*).

METHODS

Study area

The study site is located in the Blue River watershed of the Central Cascades Adaptive Management Area (AMA) in the Willamette National Forest, Oregon (Figure 2.1). Stands were sampled between 44.0 and 44.5° N, and 122.0 and 123.0° W. The Blue River watershed consists of 23,900 hectares of conifer-dominated forest on steep volcanic terrain of the Cascade Mountain Range, ranging from 317 – 1,639 m in elevation (Cissel et al. 1999). Average annual precipitation is approximately 2,500 mm, deposited as rain or snow in higher elevations, mainly between October and April. The winters are mild and wet with average temperature of 2°C in January, and the summers are warm and dry with average temperature of 22°C in July. The northern section of the watershed consists of a narrow band of high elevation, *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) and *Abies procera* Rheder (Noble fir) dominated forest (hereafter, “true fir series”). Most of the watershed is lower elevation forest dominated by *Pseudotsuga menziesii* Mirb. Franco. (Douglas fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock; hereafter, “western hemlock series;” Logan et al. 1987).

The Blue River watershed is a site for experimental forest management as part of the Central Cascades AMA, managed under the Landscape Plan (LP; Cissel et al. 1999). The current approach uses some features of natural fire regimes as a basis for forest management. In addition, the LP management strategies integrate

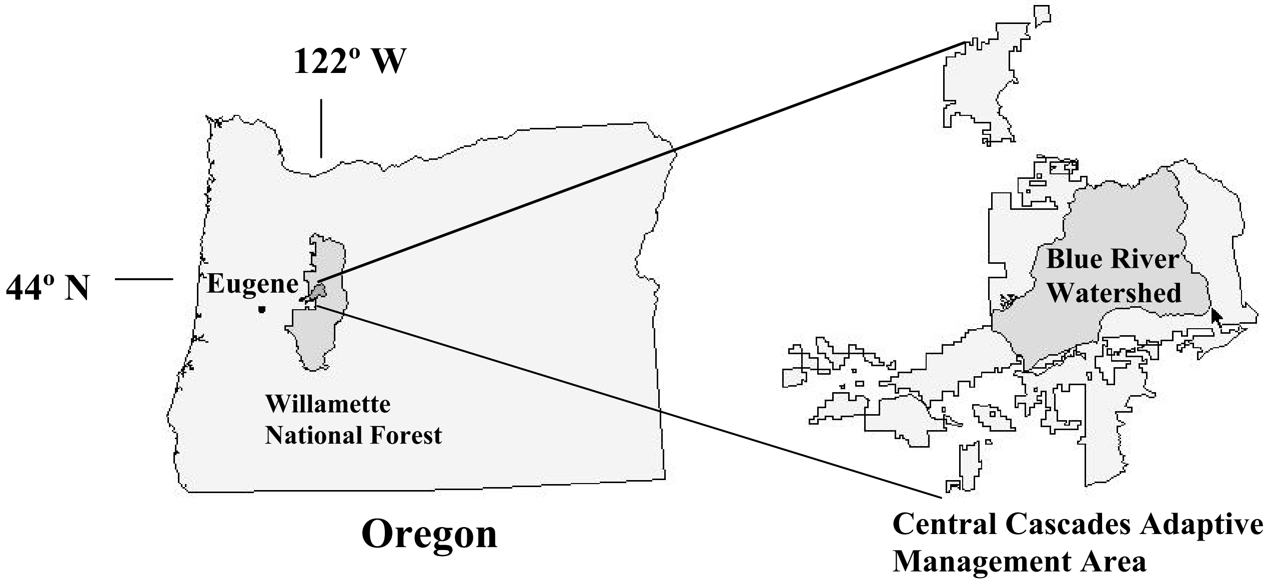


Figure 2.1. Map of the Blue River watershed (gray area on the right) in the Central Cascades Adaptive Management Area of the Willamette National Forest, Oregon, USA.

other historical landscape disturbances, conservation biology, and assessments of watershed processes (Cissel et al. 1999). The LP management strategy is expected to result in a future forest landscape with variable tree ages and varied levels of remnant retention (15 to 50 % green tree retention). This plan differs from the Northwest Forest Plan (NWFP), under which most federal forests in the PNW are currently being managed (USDA & USDI 1994*a*). Under the NWFP plan, forests in riparian reserves and other reserve areas (i.e., late-successional reserves) will not be harvested. The remaining upland forest matrix (which composes approximately 19% of the federal forest lands managed under the NWFP) will be harvested on 80 yr rotations, leaving light green tree retention (15% retention) between harvests.

The Blue River watershed has undergone decades of fire suppression and timber extraction. Historical fire regimes varied in frequency and severity within the watershed (Weisberg 1998). Forests in true fir series burned infrequently (mean fire interval of 260 yrs), but fires were severe with high mortality (> 80%). The fire return interval for the western hemlock series ranged from 100 to 180 yrs with less severe burns (40-80% mortality). Consequently, under the LP, forests in the two plant series will be managed differently in the Blue River watershed.

Sample design

Lichen communities were sampled in forest stands according to a stratified random design. Forest stands were stratified by four attributes, modified from the LP (Cissel et al. 1999; Figure 2.2):

(1) two plant series (western hemlock and true fir);

(2) four age classes (the younger tree cohort; young < 20 yrs, pole 21-80 yrs, mature 81-200 yrs; and old growth > 200 yrs);

(3) four classes of remnant retention based on the percent canopy cover of remnant trees that survived from the previous stand, following a disturbance that initiated tree regeneration: 0 = 0 - 7.5%; 15 = 7.5 - 22.5%; 30 = 22.5 - 37.0%; 50 = 37.0 - 62.0%. Remnant trees included the older live trees that

remained following the most recent timber harvest or those old trees that survived a natural forest fire (e.g., wolf trees). The characteristics of remnant trees (i.e., size, crown structure) varied among stands because remnants from a timber harvest were often smaller and younger than those remnants surviving forest fires. Old-growth stands were not stratified by remnant classes. Only 0% and 15% retention classes were sampled in the true fir series, since future management strategies will prescribe only these retention levels in the true fir series (Cissel et al. 1999);

(4) four topographic classes (upland, and three riparian stream classes: intermittent; perennial non fish-bearing; and perennial fish-bearing, stream order < 5). Only even-aged stands along perennial streams were sampled because few stands with remnant trees were located along such streams.

Upland stands were at least two tree-heights (~ 105 m) from perennial fish-bearing streams (hereafter referred to as "perennial stream < 5^{th} order") and one tree-height (~ 52 m) from all other streams (USDA & USDI 2001). Riparian stands were defined as having some part of the stream within or immediately bordering the plot boundary. Intermittent streams formed narrow channels and the stream-bank vegetation was similar to that of upland slopes. Perennial streams formed wider channels and vegetation along the stream banks was characteristic of riparian areas including hardwood trees and shrubs. Stands along perennial streams had very few remnants present and hence, were stratified by the age-class of the co-dominant tree cohort, ignoring the remnant stratum (Figure 2.2).

The design yielded 34 possible stand types for the western hemlock series and 22 for the true fir series, of which we sought to sample three stands each. However, some stand types were sampled with fewer stands or were not sampled all due to their scarcity or absence in the landscape (such as stands with remnant retention ≥ 30%). The 50% remnant retention class was uncommon in the

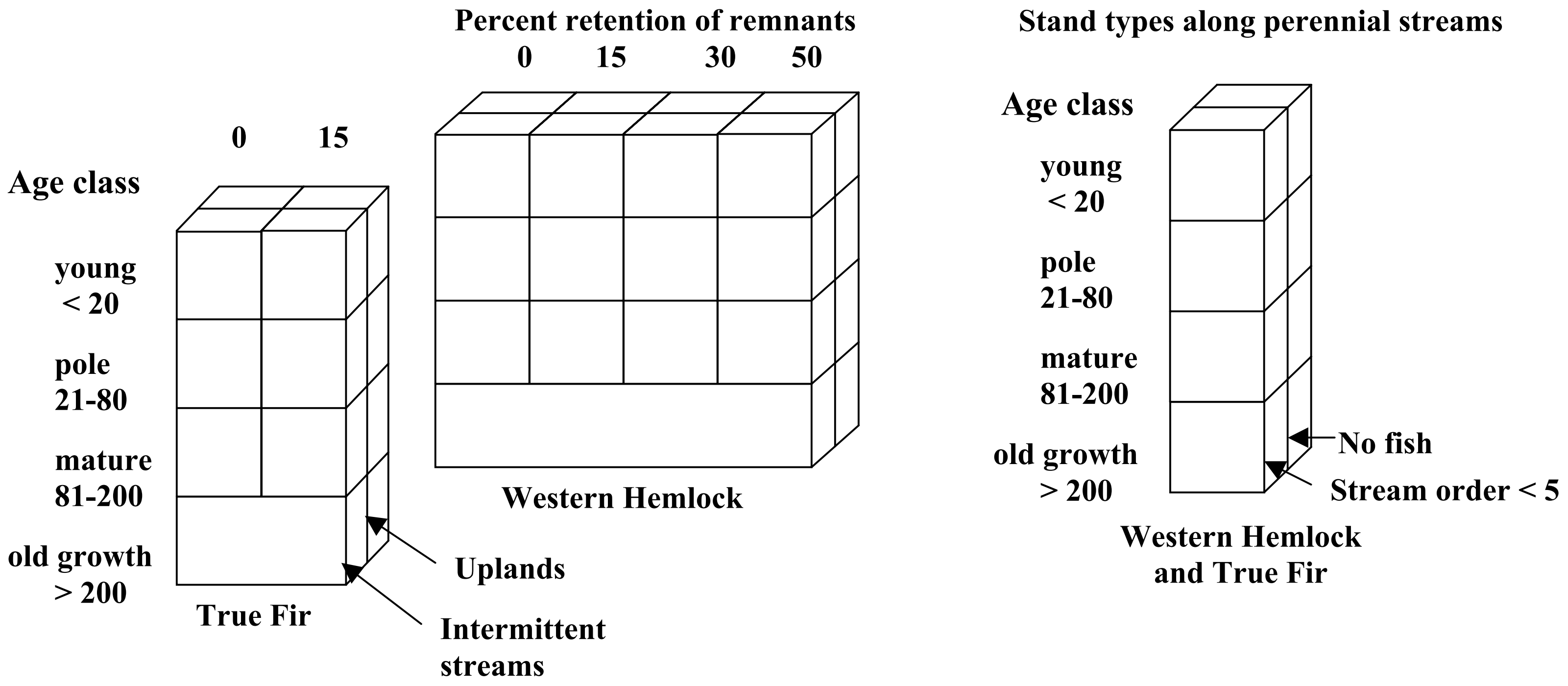


Figure 2.2. Sample design for stand types sampled in the Blue River watershed, modified from the Blue River Landscape Plan. Each cell in the sample design matrix represents a stand type. When possible, three stands were sampled per stand type in both the western hemlock and true fir vascular plant series. Stands in uplands and in areas along intermittent streams were stratified by age class and the percent retention of older remnant trees following the most recent disturbance. Stands located in areas along perennial fish-bearing (stream order < 5) and perennial non fish-bearing (no fish) streams were stratified by the age class of the co-dominant cohort, ignoring retention class. Old growth was not stratified by retention classes. Stand types in the true fir plant series were sampled only in two remnant retention classes (0 and 15%).

landscape at the time of sampling and was therefore under-represented compared to other retention classes. The 50% retention class will become more prominent in the future landscape as managed under the LP (Cissel et al. 1999). We sampled 27 stand types in the western hemlock series, 6 of which were sampled with < 3 stands. In the true fir series we sampled 18 stand types, 10 of which were sampled with < 3 stands.

Stand selection and plot installation

We located stands of various stand types from aerial photos. Most stands were within the Blue River watershed, however some stands were located outside of the watershed, but still on the Willamette National Forest and within the AMA boundaries (Appendix A, Figure A1). Stands sampled outside of the Blue River watershed represented stand types that were scarce or absent in the watershed (Figure A1). Stands were sampled in the summers of 1997-1999 using one permanent plot (37.4 m radius, 0.4 ha area) per stand.

Once the stand was located on the ground, a reference point (RP) was established along the road to assist in future plot relocation. From the RP (e.g., typically a tree) we chose an approximate azimuth into the stand. The RP was labeled with metal tags indicating the azimuth and distance to plot center. This azimuth was followed for 46.0 m (not slope-corrected) plus a two-digit random integer. Plot center was located no less than 46.0 m from: designated reserve areas in timber sales (other than stream buffers); the stand edge; roads; campgrounds; and power lines. Failing this, another random number was chosen and the same azimuth was followed until plot center was located outside of these exclusive areas and at least within 46.0 m of the stand edge. In addition, if a large perennial stream was within the plot, another random number was chosen to relocate plot center so that a significant percentage of the plot was not occupied by water.

Plot center was marked with steel rebar and PVC pipe to increase the possibility of plot relocation after major disturbances, such as a fire or timber harvest. Three RP trees near plot center were tagged to reference the plot center with an azimuth and distance. In timber sale units, tagged RP trees were those preferably marked to remain after harvest.

Lichen community survey

The Forest Health Monitoring (FHM) lichen method was used to sample lichen communities in each stand. These data will be used as a baseline for long-term monitoring of lichen communities in the managed landscape. In each FHM plot, the surveyor completed a maximum two-hour ocular lichen community survey. The survey method consisted of two parts performed simultaneously (McCune et al. 1997*b*): 1. The field surveyor collected specimens of each species present for identification in the lab. The collection represented the species diversity and composition of epiphytic macrolichens in the plot as fully as possible. The population sampled consisted of all macrolichens occurring on woody plants, excluding the 0.5 m basal portions of trees and shrubs below 0.5 m. Given the large plot area, lichen litter and fallen branches provided a sample of the canopy lichens. 2. The abundance of each species was estimated using a five-step scale (modified from McCune et al. 1997*b* and from L. Geiser, Sampling Protocol, unpublished):

0 = absent
1 = rare (< 3 individuals per plot);
2 = uncommon (4-10 individuals per plot);
3 = common (>10, but < 40 individuals per plot);
4 = very common (> 40 individuals per plot, but less than half of the available substrate was covered by the species);
5 = abundant (more than half of the available substrate had the species present).

The FHM method has been used to sample lichen communities in over 1,000 plots for the FHM program nationwide (McCune 2000) and has been used by the Pacific Northwest Forest Service Air Quality Biomonitoring Project for nearly 1,000 lichen community plots in Oregon and Washington (L. Geiser, unpublished data). Field methods are described in McCune et al. (1997*b*) and have been documented for repeatability and quality assurance.

Lichen nomenclature followed McCune and Geiser (1997), and McCune's key (unpublished online key) to the genus *Usnea* in the Pacific Northwest. Voucher specimens were deposited in the Oregon State University Herbarium (OSC).

Stand variables

Latitude and longitude coordinates and topographic features such as slope, aspect, and elevation were recorded for each stand. We calculated the heat load index and potential direct incident radiation for each stand. The heat load index represents the amount of heat a site potentially receives and is derived from models based on latitude, slope, and aspect (McCune & Keon 2002). Potential direct incident radiation ($MJ/cm^2/yr$) represents the amount of light a site potentially receives, and is also derived from latitude, slope, and aspect. Stand basal area (BA, m^2/ha) was measured for all live and dead trees, separating hardwoods and conifers. BA was measured with an angle gauge in five variable-radius subplots within each stand: one at plot center and the other four at 23.0 m in each cardinal direction from plot center. A consistent BA factor was used for all subplots within one stand, though the factor varied across all stands, depending on tree size and density. Mean BA was calculated for each stand. Diameter at breast height (dbh), crown width, and tree species were measured for the trees recorded in the BA subplots.

The age class of the younger cohort was estimated for the stand, or, if the age class was difficult to determine, we cored representative trees. Old growth was defined as stands > 200 yrs with highly variable canopy layers. Total percent canopy cover of remnant trees was used as an estimate of total percent retention of remnants for a stand, as defined by the LP (Cissel et al. 1999). We estimated canopy cover of remnants from dbh and crown width. J. Mayo (unpublished data) developed a table for estimating canopy cover of trees from dbh. This table is based on the relationship of dbh to crown width, from which percent canopy cover by each remnant tree was calculated. Remnants were typically *Pseudotsuga menziesii*, and in some cases *Tsuga heterophylla*, *Thuja plicata,* or *Abies procera*. Remnant tree age was not measured, but we documented remnant characteristics and estimated remnant tree age in our field observations.

Analysis

NMS ordination

We used non-metric multidimensional scaling (NMS) to ordinate stands in lichen species space. The ordination was used to assess gradients in lichen community composition and their relationships with topography and stand structure. An arbitrary cut-off of $R^2 \geq 0.3$ was used when assessing correlations of environmental variables and species richness with the ordination axes. Correlations of 0.3 or greater were biologically meaningful in the ordinations. NMS is an iterative technique that is capable of extracting non-linear gradients in species space (Kruskal 1964; Mather 1976). Sørensen distance measure was used with the Slow-and-Thorough autopilot settings in PC-ORD 4.0 (40 runs of 400 iterations; McCune & Mefford 1999). Lichen species present in < 5% of the plots were excluded from the analysis, eliminating 41 rare species to reduce noise in the data ("reduced species matrix").

Multivariate outlier analysis of all 117 stands found nine potential outliers, three of which had average distances to other stands > 3 standard deviations from the grand mean of distances among stands. These three outliers were examined in the NMS ordination (Kruskal 1964; Mather 1976) of stands in lichen space. When the outliers were excluded from the ordination analysis, the patterns of the stands in the ordination did not change appreciably. We concluded that the outliers were non-influential in the ordination and did not disrupt patterns in the other points. Therefore, these stands were included in the subsequent analyses.

NMS was run on the reduced species matrix across vascular plant series. This ordination was rotated to align the elevation gradient with an axis because this was the strongest environmental gradient separating lichen communities in the watershed. The vascular plant series were correlated with the elevation gradient. The species and environmental matrices were then partitioned by vascular plant series to more closely examine the relationship of lichen communities to forest structure and topographic classes. This partitioning diminished the overwhelming influence of elevation on lichen communities. Sampling was limited by the availability of stand types in the watershed and therefore, it was not possible to stratify by elevation within the two plant series.

The ordination of all 117 stands in lichen species space revealed ten high elevation stands classified in the western hemlock series (young *Pseudotsuga menziesii* plantations) that positioned with the true fir stands. These ten stands were thereafter included in the true fir species matrix, because their lichen epiphytes were more similar to those in the true fir series than to those in the western hemlock series. Thus, the final species matrix for the western hemlock series consisted of 67 stands and the true fir series species matrix consisted of 50 stands.

NMS was run separately on the species matrix for each vascular plant series. The western hemlock species matrix had four outliers; one stand was extreme (3.75 standard deviations from the grand mean of distances among stands). This stand was further examined with Bray-Curtis ordination (Bray & Curtis 1957; Beals 1984) and in the NMS ordination. The stand was an outlier due to the absence of many common species; however, we chose to retain it in the species matrix since, when excluded, it did not affect the overall patterns of the NMS ordination. Similarly, the true fir matrix had five non-influential outlying stands in the NMS ordination.

We also evaluated differences in lichen communities in the ordinations along a stand structural gradient for each plant series. To achieve this, we developed an age index to integrate the many stand types into a single continuous variable, representing the biological significance of the influence of old trees on lichen communities. The age index combines age credits for the age classes and for the remnant trees in each stand and expresses them as a percentage of old growth.

Age credits were assigned according to the median tree age for the age classes of the younger cohort and for old growth (Table 2.1). The *a priori* median age for old growth was arbitrarily selected as 300 yrs based on estimates for old-growth forests we sampled in the Blue River watershed. The age credits for the age classes were the "base age credits." If remnant trees were present in a stand, we added the percent of remnants (15, 30, or 50%) to the "base age credits." This sum was the age index value for the stand (Table 2.1). Each stand type received a value between 3 and 100, where 100 represented old growth and 3 represented an even-aged young stand. We $\log_{10}$-transformed the age index (hereafter referred to as "age index" or "AI") to improve linearity with lichen response variables (see Chapter 3).

Each 2-dimensional ordination was rotated to maximize the correlation of the age index with one axis. The scores from the axis represented the lichen community composition gradient in relation to the age index. We compared ordination scores from the age index axis among stand types. This allowed us to assess differences in lichen composition among stages of stand development (i.e., young, pole, mature, old-growth). We averaged the ordination score by stand type for all even-aged stands and for young stands (< 20 yrs) with 15% remnants and young stands with ≥ 30% remnants (combining the 30 and 50% retention classes) to assess how the presence of remnants following a disturbance is related to lichen community composition in regenerating young stands. When making these calculations for the western hemlock series, we omitted one anomalous young stand with 50% remnant retention (this stand was not an outlier overall). The lichen community in this stand was anomalous compared to those in other stands of the same stand type. In addition, our field observations indicated that the remnants in this stand appeared to be relatively younger than those present in other stands of the same stand type.

Table 2.1. Definition of the age index, where the median age of the stand is calculated as a percentage of the median age of old growth (300 yrs assumed for all old growth, see text). Raw age index = ((median age/median age of old growth)*100) + % remnants. AI represents $\log_{10}$(raw age index).

Stand Type	Median age	Raw age index	AI
Young, < 20 yrs, no remnants	10	3	0.48
Young, < 20 yrs, 15% remnants	10	18	1.26
Young, < 20 yrs, 30% remnants	10	33	1.52
Young, < 20 yrs, 50% remnants	10	53	1.72
Pole, 21-80 yrs, no remnants	50	17	1.23
Pole, 21-80 yrs, 15% remnants	50	32	1.51
Pole, 21-80 yrs, 30% remnants	50	47	1.67
Pole, 21-80 yrs, 50% remnants	50	67	1.83
Mature, 81-200 yrs, no remnants	140	47	1.67
Mature, 81-200 yrs, 15% remnants	140	62	1.79
Mature, 81-200 yrs, 30% remnants	140	77	1.89
Mature, 81-200 yrs, 50% remnants	140	97	1.99
Old growth, > 200 yrs	300	100	2.00

Epiphytic macrolichens were divided into three functional groups (McCune 1993) to analyze patterns in lichen community structure from a functional perspective. These groups included "cyanolichens," which consist of all N-fixing lichens with cyanobacteria present as either the primary or secondary photobiont; "forage lichens," which consisted of all alectorioid lichens (i.e., fruticose) used as forage by wildlife, primarily the genera *Alectoria, Bryoria,* and *Usnea*; and "matrix lichens," which included all remaining green-algal lichens, primarily foliose lichens. Patterns of lichen composition and diversity for each functional group were assessed in the ordinations with respect to topographic gradients and stand structure.

Lichen community composition

In addition to the ordinations, Multi-Response Permutation Procedures (MRPP; Berry et al. 1983; Mielke 1984) were performed in PC-ORD 4.0 (McCune & Mefford 1999) to test for differences in lichen community composition between groups (e.g., between plant series, among topographic classes, and among even-aged stands and stands with remnants). This procedure tested for multivariate differences among groups, based on the average within-group Sørensen distance. MRPP was used for testing compositional differences among groups across all macrolichens combined and separately for forage and matrix lichen functional groups. We were unable to use MRPP to test for differences in cyanolichen composition because cyanolichens were absent from many stands.

When comparing lichen communities among topographic classes (i.e., uplands and riparian classes), we used both even-aged stands and stands with remnants. Differences in lichen communities among topographic classes were weak, so we chose to ignore topographic class in our analyses of lichen communities and stand structure.

Within each plant series, we compared differences in lichen composition across all stand types and separately for stands with remnants and even-aged stands without remnants. To further clarify differences in lichen communities with stand types, we made multiple pair-wise comparisons between stand types using MRPP, comparing differences in lichen composition for all macrolichens and for each functional group. MRPP can be used for more than two groups, however, pair-wise comparisons revealed differences in lichen communities between specific stand types. A total of 36 multiple pair-wise comparisons were made for the western hemlock series and significant differences in lichen communities were reported at the 0.05 level. Of these 36 comparisons, we would expect approximately two to be significant by chance at the 0.05 level. Of the fifteen pair-wise comparisons made for the true fir series, we expected approximately one to be significant by chance at the 0.05 level.

Indicator species analysis (ISA; Dufrêne & Legendre 1997) was used to calculate indicator values for lichen species, for the two plant series, for even-aged stands, and for topographic classes. The species indicator value (IV) is a combination of species relative frequency and abundance within a given group. The indicator value reflects the faithfulness of a species to a particular group. MRPP and ISA analyses were performed in PC-ORD 4.0 (McCune & Mefford 1999) and stand types with fewer than three stands were excluded from the analyses.

Species diversity

We calculated several measures of species diversity (Whittaker 1972). Alpha (α) diversity is the average species richness per stand. Gamma (γ) diversity is the total number of species found across all stands in the landscape. Two measures of beta diversity were calculated: Whittaker's beta diversity (γ/α) and average half changes (HC) among stands. Whittaker's beta diversity measures compositional heterogeneity across plots, using the ratio of the total number of species, to the average number of species per stand (γ/α). The second measure of beta diversity is the average Sørensen distance among stands, transformed to half changes by: $HC = \log(1-D)/\log(0.5)$, where D is the average distance (one HC equals a 50% change of community composition). All diversity measures were calculated for the non-transformed species matrices, which included all rare species.

We evaluated differences in lichen species richness between plant series for all 117 stands, indicating differences for all macrolichens, cyanolichens, forage lichens, and matrix lichens (analyses performed in SPSS 8.0; Anon. 1998). Differences in macrolichen richness between plant series were tested using an independent sample t-test. Subsequent analyses of lichen species richness were performed on the species matrices partitioned by plant series to account for the influence of elevation. In each plant series, we assessed differences in epiphytic lichen species richness among stand types and among topographic classes using one-way ANOVA and Tukey's honestly significant difference test (Tukey's HSD) of multiple comparisons between groups. As mentioned above, we ignored topographic class when assessing lichen species richness in relation to stand structure and we combined stand types when assessing lichen species richness in relation to topographic classes. Stand types with fewer than three stands were excluded from the ANOVA. Correlations of species richness with environmental factors were assessed using Pearson's correlation coefficient.

RESULTS

Lichen communities across all stands

Elevation gradient

Differences in lichen community composition in the Blue River watershed were most strongly related to elevation (Figure 2.3; Table 2.2). The 2-dimensional NMS ordination of 117 stands in species space described 82% of the cumulative variance in the community structure (axis 1 = 33% and axis 2 = 49%) and axis 2 was highly correlated with elevation ($R^2 = 0.66$). Axis one was correlated with the age index ($R^2 = 0.54$ and live tree BA ($R^2 = 0.36$). Stands in the true fir series generally positioned low on axis 2 (higher elevations, 950 – 1470 m) while stands in the western hemlock series tended to be higher on axis 2 (lower elevations, 470 –

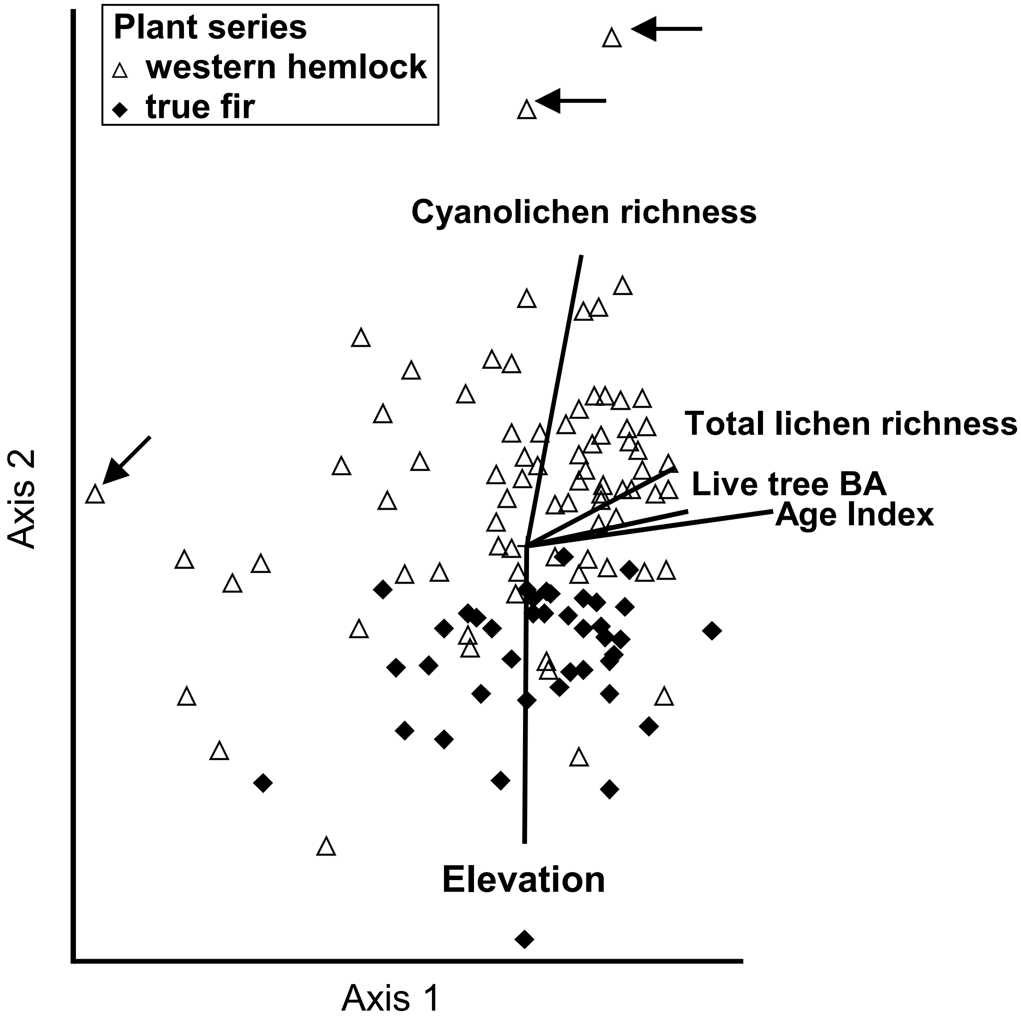


Figure 2.3. Rotated NMS ordination of stands (N = 117) in lichen species space and joint plot showing correlations of environmental and lichen community variables with each axis (all R^2 correlations ≥ 0.3; see Table 2.3 for correlations of variables with the ordination axes). Vector length corresponds to the strength of the correlation. Arrows indicate non-influential outliers.

Table 2.2. Correlations (R^2) of environmental and lichen community variables with NMS ordination axes (see Figure 2.3). Correlations were reported if $R^2 \geq 0.3$ for one axis.

Variables	**Axis 1**	**Axis 2**
Elevation	0.004	0.66
Log age index	0.54	0.08
Live tree BA	0.36	0.08
Total lichen richness	0.33	0.17
Cyanolichen richness	0.12	0.65

950 m). Lichen communities in stands at intermediate elevations (940 – 1285 m) were similar between the two plant series. The absence of cyanolichens in the high elevation stands and their abundance at lower elevations was largely responsible for the differences in lichen community composition in stands of the two plant series (MRPP, T = -28.07, $p << 0.001$, A = 0.05). Other topographic variables such as heat load index, potential direct incident radiation, slope, and aspect were weakly correlated with the ordination axes (maximum $R^2 = 0.05$).

A total of 111 taxa were found across the 117 stands (Table 2.3, including all rare species). Many lichen species were significant indicators for each plant series (Table 2.3), of which cyanolichens were dominant indicators for the western hemlock series at lower elevations (12 cyanolichen indicators). *Lobaria oregana* was present in 90% of the lower elevation stands and therefore, was a dominant indicator for the western hemlock series (IV = 77.8, p = 0.001). In contrast, *Lobaria* species were found only in four stands in the true fir series at higher elevations and *Pseudocyphellaria anomala*, *P. crocata*, and *Nephroma parile* were present in only a few true fir stands (Table 2.3). Cyanolichens were always in very low abundance when found in the true fir series.

Several forage lichens indicated the higher elevation, true fir series, including three *Bryoria* spp. and *Nodobryoria oregana* (Table 2.3). Very little

Table 2.3. Abundance and indicator values for epiphytic macrolichen species in the 117 stands. AV = average abundance class for each species over all stands; FG = lichen functional group: cyanolichens (C), forage lichens (F), or matrix lichens (M); T = total number of stands in which each species occurred; FR = percent frequency of occurrence. Indicator species for western hemlock (WH) and true fir (TF) plant series, topographic classes, and even-aged stands and old growth are reported for those species with indicator values of $p \leq 0.05$. No indicators are reported for stands with remnants. One species can be an indicator for more than one group.

Lichen species	**AV**	**FG**	**T**	**FR**	**Indicators**
Alectoria imshaugii	0.5	F	29	25	
Alectoria sarmentosa	3.6	F	114	97	TF
Alectoria vancouverensis	0.1	F	4	3	
Bryoria	0.0	F	2	2	
Bryoria capillaris	1.2	F	53	45	TF
Bryoria fremontii	0.0	F	1	1	
Bryoria friabilis	0.9	F	45	38	
Bryoria fuscescens	0.2	F	12	10	TF
Bryoria glabra	1.0	F	44	38	WH mature
Bryoria mystery olive sp.	0.7	F	35	30	TF
Bryoria pseudofuscescens	0.4	F	17	15	
Bryoria tortuosa	0.0	F	1	1	
Bryoria trichodes	0.1	F	4	3	
Candelaria concolor	0.0	M	1	1	
Cavernularia hultenii	0.6	M	37	32	TF, TF pole, TF stream < 5th order
Cetraria canadensis	0.1	M	5	4	
Cetraria chlorophylla	1.4	M	71	61	TF, TF pole,
Cetraria merrillii	0.2	M	13	11	
Cetraria orbata	1.1	M	67	57	TF mature, WH mature
Cetraria pallidula	0.3	M	22	19	WH
Cetraria platyphylla	1.2	M	62	53	TF old growth
Cetraria subalpina	0.1	M	2	2	
Cladonia	0.0	M	3	3	
Cladonia albonigra	0.0	M	1	1	
Cladonia carneola	0.0	M	4	3	
Cladonia fimbriata	0.0	M	2	2	
Cladonia norvegica	0.0	M	1	1	
Cladonia ochrochlora	0.2	M	12	10	

Table 2.2 (continued)

Cladonia squamosa	0.1	M	3	3	
Cladonia squamosa v. *subsquamosa*	0.4	M	19	16	WH
Cladonia transcendens	0.7	M	33	28	TF old growth
Cladonia umbricola	0.1	M	47	40	
Esslingeriana idahoensis	0.9	M	47	40	WH mature, TF mature, WH no fish
Evernia prunastri	0.3	M	24	21	WH no fish
Fuscopannaria pacifica	0.2	C	12	10	WH, WH stream < 5th order
Fuscopannaria leucostictoides	0.0	C	3	3	
Hypogymnia	0.0	M	1	1	
Hypogymnia apinnata	1.4	M	60	51	TF
Hypogymnia enteromorpha	3.2	M	109	93	
Hypogymnia imshaugii	2.6	M	100	85	TF
Hypogymnia inactiva	3.5	M	115	98	WH, WH upland
Hypogymnia metaphysodes	1.0	M	56	48	WH mature, TF mature
Hypogymnia occidentalis	0.5	M	27	23	TF, WH mature
Hypogymnia oceanica	0.4	M	35	30	TF, TF stream < 5th order
Hypogymnia physodes	2.3	M	105	90	TF pole
Hypogymnia rugosa	0.5	M	19	16	TF, TF old growth, WH no fish
Hypogymnia tubulosa	1.4	M	79	68	
Hypotrachyna sinuosa	0.2	M	15	13	WH young
Leptogium cyanescens	0.0	C	1	1	
Leptogium polycarpum	0.0	C	2	2	
Letharia columbiana	0.0	M	1	1	
Letharia vulpina	0.3	M	20	17	
Lobaria oregana	1.8	C	63	54	WH, WH old growth
Lobaria pulmonaria	1.1	C	45	38	WH, WH old growth
Lobaria scrobiculata	0.4	C	29	25	WH
Melanelia	0.0	M	4	3	
Melanelia elegantula	0.0	M	1	1	
Melanelia exasperatula	0.2	M	14	12	
Melanelia fuliginosa	0.1	M	3	3	
Melanelia multispora	0.0	M	2	2	

Table 2.2 (continued)

Melanelia subaurifera	0.1	M	8	7	WH young, TF pole
Nephroma	0.0	C	2	2	
Nephroma bellum	0.3	C	19	16	WH
Nephroma helveticum	0.6	C	29	25	WH, WH old growth
Nephroma laevigatum	0.1	C	8	7	
Nephroma occultum	0.1	C	7	6	
Nephroma parile	0.1	C	13	11	WH stream < 5th order
Nephroma resupinatum	0.3	C	17	15	WH
Nodobryoria abbreviata	0.0	F	1	1	
Nodobryoria oregana	2.4	F	98	84	TF
Parmelia	0.1	M	5	4	
Parmelia hygrophila	0.9	M	58	50	TF
Parmelia pseudosulcata	0.5	M	25	21	
Parmelia saxatilis	1.1	M	69	59	
Parmelia sulcata	1.2	M	70	60	
Parmeliopsis ambigua	0.3	M	18	15	TF, TF mature
Parmeliopsis hyperopta	2.8	M	103	88	TF, WH mature, TF mature
Peltigera britannica	0.0	C	1	1	
Peltigera collina	0.2	C	11	9	WH
Physcia adscendens	0.0	M	4	3	
Physcia aipolia	0.0	M	2	2	
Physcia tenella	0.0	M	1	1	
Platismatia glauca	3.6	M	116	99	TF, WH mature
Platismatia herrei	2.8	M	102	87	WH mature, TF old growth
Platismatia norvegica	0.1	M	8	7	TF stream < 5th order
Platismatia stenophylla	2.7	M	106	91	WH mature
Pseudocyphellaria	0.0	C	1	1	
Pseudocyphellaria anomala	0.9	C	46	39	WH
Pseudocyphellaria anthraspis	0.6	C	27	23	WH, WH old growth
Pseudocyphellaria crocata	0.3	C	25	21	
Pseudocyphellaria rainierensis	0.2	C	10	9	WH, WH old growth
Ramalina dilacerata	0.2	M	10	9	
Ramalina farinacea	0.2	M	12	10	
Sphaerophorus globosus	2.3	M	83	71	WH, WH mature, TF old growth
Sticta fuliginosa	0.2	C	16	14	WH
Sticta limbata	0.1	C	6	5	
Sticta weigelii	0.1	C	8	7	WH stream < 5th order

Table 2.2 (continued)

Usnea	0.7	F	35	30	
Usnea chaetophora	0.0	F	3	3	
Usnea cornuta	0.0	F	3	3	
Usnea diplotypus	0.1	F	3	3	
Usnea filipendula	1.0	F	54	46	
Usnea glabrata	0.1	F	7	6	
Usnea glabrescens	0.0	F	1	1	
Usnea scabrata	2.5	F	103	88	WH, WH mature
Usnea substerilis	0.1	F	2	2	
Usnea wirthii	0.2	F	8	7	
Vulpicida canadensis	0.1	M	8	7	
Xanthoria	0.0	M	1	1	
Xanthoria polycarpa	0.0	M	3	3	

Bryoria was found in the lower elevation forests and when present, it was less abundant than in the true fir series. *Alectoria sarmentosa* was also a strong indicator (IV = 54.8, p = 0.003) for the true fir forest, where it was especially abundant (covering > 50% of tree boles and branches) in old growth. *Alectoria* and *Bryoria* typically co-occurred in matted clumps on tree boles and branches in the true fir series. Many matrix lichens (e.g., *Hypogymnia* and *Platismatia*) were indicators of the true fir series (Table 2.3).

Nearly ubiquitous lichens such as *Alectoria sarmentosa*, *Hypogymnia inactiva, H. enteromorpha, H. imshaugii, H. physodes, Platismatia glauca, P. herrei, P. stenophylla, Nodobryoria oregana*, *Parmeliopsis hyperopta*, and *Usnea scabrata* occurred in most stands regardless of stand structure or plant series. *Alectoria sarmentosa* and *U. scabrata* were two of the most common and abundant forage lichens found in the watershed (Table 2.3). *Hypogymnia enteromorpha, H. inactiva*, and *Platismatia glauca* were the most frequent matrix lichens in the watershed (Table 2.3).

Species diversity

Cyanolichen diversity differed greatly between the two plant series (Table 2.4). Cyanolichens were more diverse in the lower elevation western hemlock series than in the true fir series at higher elevations. Gamma diversity was 25% lower in the true fir forests than in the western hemlock series. However, the number of stands sampled in the true fir series (N = 50) was less than in the western hemlock series (N = 67). Consequently, the differences in gamma diversity between the two plant series may be a reflection of differences in the area sampled. In addition, average alpha diversity (α) was slightly higher for stands in the western hemlock series as compared to stands in the true fir series (95% CI for the difference in average alpha diversity between the two plant series = 1.65 to 6.17; Table 2.4). Average forage lichen species richness was slightly higher in stands of the true fir series as compared to stands in the western hemlock series (95% CI for the difference in alpha diversity of forage lichens = 0.48 to 1.78), however, beta diversity and gamma diversity of forage lichens was similar between the two plant series. Average matrix lichen diversity measures were similar between both plant series. Matrix lichen species richness was higher than that of cyanolichens and forage lichens in both plant series.

<u>Western hemlock series</u>

While we evaluated lichen community composition and lichen diversity in relation to stand structure separately for each plant series to control partially for the influence of elevation, lichen communities did vary considerably with elevation (range 469 – 1286 m) within this series. The second 2-dimensional ordination described a cumulative variance of 83% in lichen community structure and was rotated to maximize the correlation of the age index with axis 1 (axis 1 = 58% and axis 2 = 25%; Figure 2.4A; Table 2.5). The relationship of the elevation gradient to the age index gradient was orthogonal in the ordination. Cyanolichens were most

Table 2.4. Diversity of epiphytic macrolichens across all stands and for stands within the western hemlock and true fir series (N = number of stands). Alpha diversity (α) is average species richness, with the standard deviation in parentheses. Beta diversity is shown as γ/α and as average half changes (HC), HC were not calculated for cyanolichens because cyanolichens were absent from some stands. Gamma diversity (γ) is the total number of species found.

Diversity Measures

	alpha	**beta**		**gamma**
		γ/α	**HC**	
Overall				
N = 117				
All macrolichens	26.5 (6.4)	4.2	0.9	111
Cyanolichens	3.4 (4.1)	7.1	---	24
Forage lichens	5.8 (1.8)	4.3	0.9	25
Matrix lichens	17.2 (3.8)	3.6	0.7	62
Western hemlock				
N = 67				
All macrolichens	28.2 (6.8)	3.7	0.9	104
Cyanolichens	5.8 (4.0)	4.1	---	24
Forage lichens	5.3 (1.7)	4.5	0.9	24
Matrix lichens	17.1 (3.9)	3.3	0.7	56
True fir				
N = 50				
All macrolichens	24.2 (5.0)	3.2	0.8	78
Cyanolichens	0.3 (0.9)	20.0	---	6
Forage lichens	6.5 (1.8)	3.1	0.8	20
Matrix lichens	17.5 (3.7)	3.0	0.8	52

abundant in low elevation stands with higher age-indices. Total BA of the stand generally increased with stand age and with increased remnant retention (Table 2.6), but was weakly correlated with lichen communities in the ordination (R^2 = 0.24, with axis 1 and R^2 = 0.08, with axis 2). Other topographic variables such as

Figure 2.4. Rotated NMS ordination of stands in lichen species space for the western hemlock series (A) and the true fir series (B). For the western hemlock series, two axes explained 83% of the variation in lichen community structure: axis 1 = 58% and axis 2 = 25%. For the true fir series, two axes explained 81% of the variation in lichen community structure: axis 1 = 50% and axis 2 = 31%. Joint plots show correlations of environmental and lichen community variables with each axis, showing only those with $\geq R^2 = 0.3$. Vector length corresponds to the strength of the correlation (see Table 2.5 for correlations). Symbols indicate stand types: Y = young (< 20 yrs); P = pole (21-80 yrs); M = mature (81-200 yrs); OG = old growth (> 200 yrs); and 0, 15, 30, and 50 represent the remnant retention classes (see sample design).

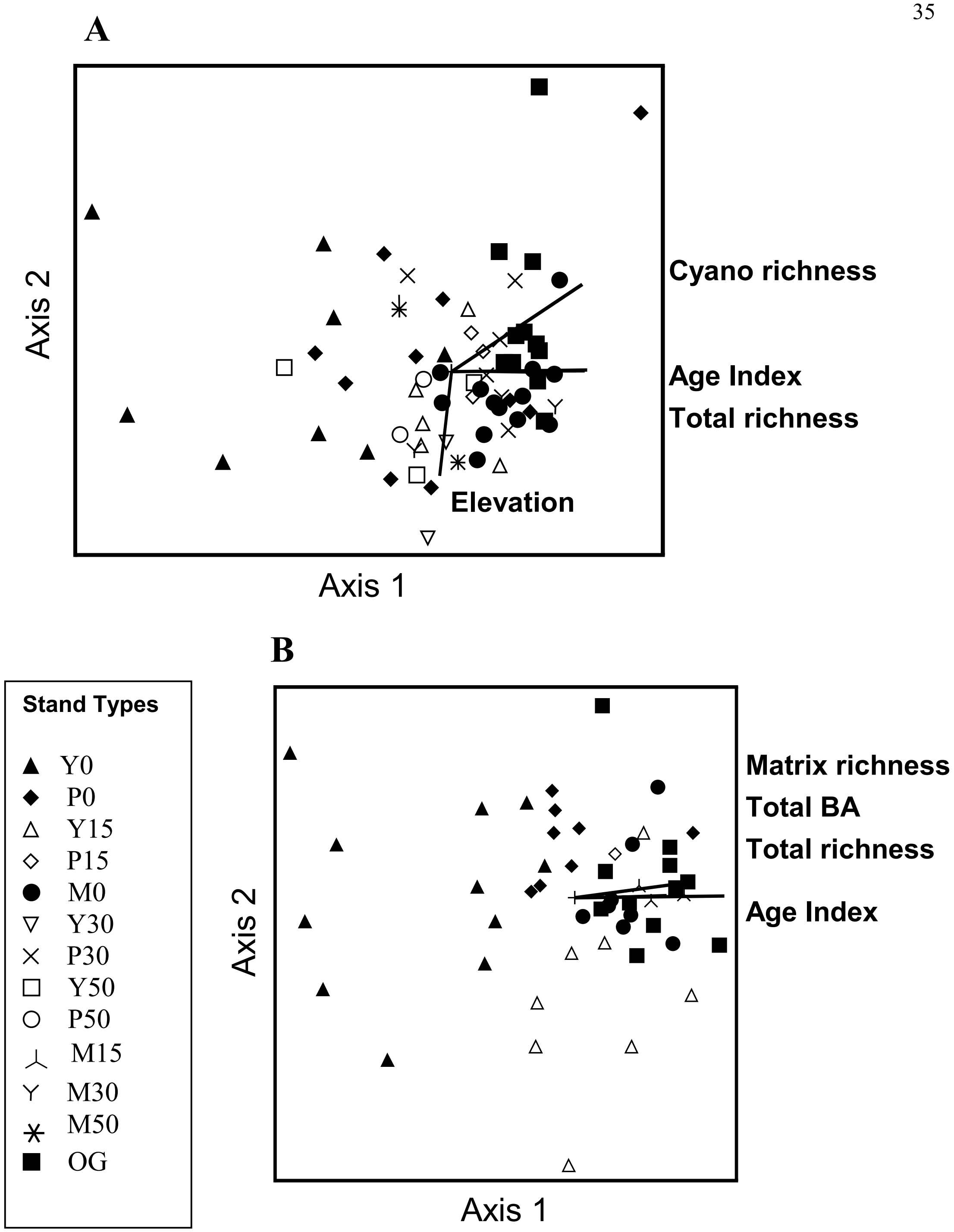

A
Axis 2
Axis 1
Cyano richness
Age Index
Total richness
Elevation
B
Stand Types
▲ Y0
◆ P0
△ Y15
◇ P15
● M0
▽ Y30
× P30
□ Y50
○ P50
⅄ M15
Y M30
⚹ M50
■ OG
Axis 2
Axis 1
Matrix richness
Total BA
Total richness
Age Index

Figure 2.4

Table 2.5. Correlations (R^2) of environmental and lichen community variables with NMS ordination axes (see Figure 2.4) for two ordinations: one for each plant series. Correlations were only reported for variables with correlations of $R^2 \geq 0.3$ for one axis

	Axis 1	**Axis 2**
Western Hemlock		
Age index	0.45	0.001
Elevation	0.04	0.38
Total lichen richness	0.50	0.07
Cyanolichen richness	0.47	0.32
True Fir		
Age index	0.66	0.003
Total BA	0.46	0.07
Total lichen richness	0.32	0.01
Matrix lichen richness	0.32	0.21

the heat load index, potential direct incident radiation, slope, and aspect were again unrelated to lichen communities (maximum $R^2 = 0.08$).

Lichen composition in relation to stand structure

Lichen community composition differed among stand types (MRPP, T = -7.46, A = 0.08, p << 0.001; Table 2.8). The small A statistic from MRPP comparing lichen community composition among stand types indicates high heterogeneity of lichen community composition within stand types and also indicates overlap in lichen communities among stand types (Figure 2.4A). This variation of lichen communities within stand types may be related in part to the influence of elevation. For example, older stands present at higher elevations in the western hemlock series typically had fewer cyanolichens present than similar aged stands at lower elevations (see Table 2.7 for elevation ranges for each stand type).

Lichen communities differed among all even-aged stand classes and old growth (T = -10.00, A = 0.09, p << 0.001) with the most prominent differences

Table 2.6. Basal area (BA, m^2/ha) measurements for stand types in each plant series, excluding stand types with < 3 stands. Young = < 20 yrs, pole = 21-80 yrs, mature = 81-200 yrs, and old growth = > 200 yrs; percentages refer to percent remnants retained. N = number of stands. Live and dead BA includes remnant trees.

	N	**Live BA**	**Dead BA**	**% BA Conifers**	**Remnant BA**
Western Hemlock					
Young, 0%	8	12	0	90	0
Young, 15%	10	14	4	100	14
Young, 50%	3	31	2	99	31
Pole, 0%	5	41	4	94	0
Pole, 15%	3	51	4	100	14
Pole, 30%	5	49	8	100	24
Mature, 0%	13	58	3	98	0
Mature, 30%	3	101	10	100	40
Old Growth	11	70	5	98	0
True Fir					
Young, 0%	11	10	0	100	0
Young, 15%	8	11	3	100	11
Pole, 0%	8	35	3	97	0
Mature, 0%	8	54	7	100	0
Mature, 15%	3	71	15	100	21
Old Growth	11	61	13	100	0

between young (< 20 yrs) and old stands (Figure 2.4A). Forage and matrix lichen species composition also differed with stand age classes ($T = -1.74$, $A = 0.03$, $p = 0.05$ and $T = -7.13$, $A = 0.08$, $p << 0.001$, respectively). Lichen community composition of even-aged young stands was most different from all other stands, because these stands had few species (Figures 2.5 & 2.6, see below) and those were present in low abundance. Lichen populations in even-aged pole stands were usually more developed (i.e., larger populations) than in even-aged young stands, however, the lichen communities did differ from those in old growth and even-aged mature stands (Table 2.8).

Even-aged mature (81-200 yrs) and old-growth (> 200 yrs) stands differed somewhat in species composition (T = -4.05, A = 0.04, p = 0.003), primarily due to greater abundance of cyanolichens in old growth. However, in the ordination,

Table 2.7. Elevation minimum, maximum, and median values for each stand type in the western hemlock and true fir series. The number of stands (N) sampled in each topographic class by stand type: U is uplands; PF is perennial fish-bearing stream order < 5; PnF is perennial stream no fish; and Inter is intermittent streams. Abbreviations of stand types are described in Figure 2.4.

Stand type	**N**	**Elevation (m)**			**Topographic position**			
		Min.	Max.	Median	U	PF	PnF	Inter
Western hemlock								
Y0	8	701	1097	838	2	3	2	1
Y15	5	616	896	872	3	0	0	2
Y30	2	981	1286	1134	2	0	0	0
Y50	3	579	963	914	3	0	0	0
P0	10	604	938	764	3	1	2	4
P15	3	683	835	744	3	0	0	0
P30	5	457	853	732	5	0	0	0
P50	2	615	1085	850	2	0	0	0
M0	13	610	970	799	4	3	3	3
M15	0	----	----	----	--	--	--	--
M30	3	814	1201	853	2	0	0	1
M50	2	762	1213	988	2	0	0	0
OG	11	469	914	735	3	3	2	3
True fir								
Y0	11	1000	1469	1225	4	0	4	3
Y15	8	945	1463	1262	6	0	0	2
P0	8	1079	1311	1181	3	2	2	1
P15	1	1250	1250	----	1	0	0	0
M0	8	1158	1341	1266	3	0	1	4
M15	3	1289	1335	1298	3	0	0	0
OG	11	1128	1347	1238	4	1	3	3

Table 2.8. Pairwise multiple comparisons (MRPP) between lichen community composition for all epiphytic macrolichens in stand types of the western hemlock and true fir series based on the age class of the stand and the percent retention class of remnants, across all topographic classes. Each cell represents a stand type. One of the cell letters must be the same as another cell to indicate p-value > 0.05 for the null hypothesis of no difference in lichen communities between stand types. One asterisk indicates stand types excluded from the analysis, with < 3 stands. Two asterisks indicate stand types not present in the landscape.

Western hemlock

Age class (yrs)		**Percent remnant retention**			
		0	15	30	50
Young	< 20	a	e	*	abce
Pole	21 – 80	b	bcde	bcde	*
Mature	81 – 200	c	**	bcde	*
Old growth	> 200	d			

True fir

Age class (yrs)		**Percent remnant retention**	
		0	15
Young	< 20	a	c
Pole	21 – 80	b	*
Mature	81 – 200	d	d
Old growth	> 200	d	

lichen communities of mature and old-growth stands overlapped broadly in composition (Figure 2.4A). Cyanolichens such as *Lobaria oregana*, *L. pulmonaria*, *Nephroma helveticum*, *Pseudocyphellaria anthraspis*, and *P. rainierensis* were strong indicators of old-growth stands, while cyanolichens did not indicate even-aged mature stands (ISA, Table 2.3). Cyanolichens were often present in mature stands, but were in lower abundance than in old growth. Even-aged mature and old-growth stands at higher elevations in the western hemlock series had fewer cyanolichens than similar-aged stands at lower elevations in the same plant series. Cyanolichen species richness was correlated with elevation in the western hemlock series ($R^2 = 0.27$).

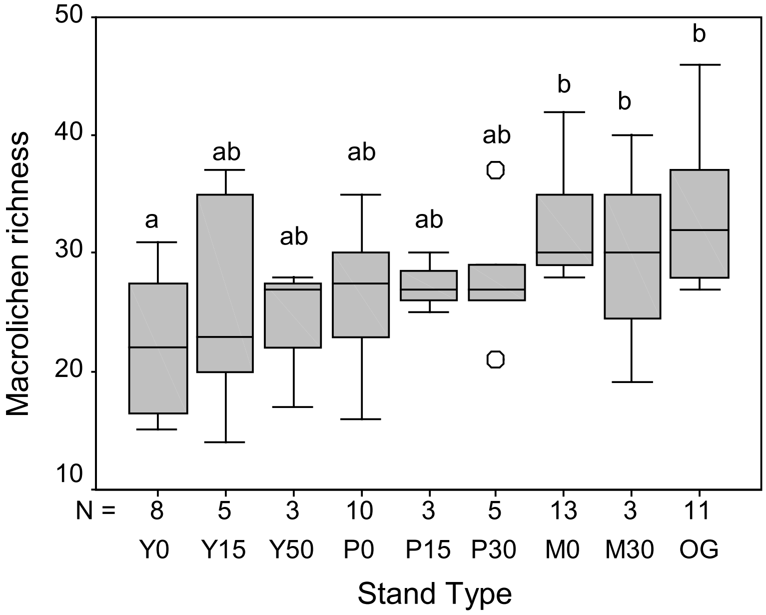
Patterns of lichen communities in stands with remnant trees were not as clear as in even-aged stands. There was considerable variability in lichen community composition within stands with remnant trees. Lichen communities in young stands (< 20 yrs) with remnant retention differed from those in even-aged young stands (< 20 yrs) and were more similar to those in pole stands with and without remnants (21-80 yrs; Figure 2.4A). Lichen communities in young stands with 50% retention of remnants were highly variable (Figure 2.4A) and differed from those in old growth (Table 2.8). Unlike young stands, lichen communities in pole and mature stands with remnants were more similar to those of old-growth stands (Table 2.8).

Lichen diversity in relation to stand structure

Total epiphytic macrolichen species richness differed slightly among stand types (across all topographic classes) in the western hemlock series (one-way ANOVA, F = 2.9, p = 0.01; Figure 2.5). Mean species richness of epiphytic macrolichens was highest in old-growth stands (mean = 33.2, st.dev. = 6.0) and lowest in even-aged young stands (mean = 22.3, st.dev. = 6.1). Lichen diversity was significantly lower in even-aged young stands as compared to even-aged mature stands (Tukey's HSD, 95% CI for the difference = 1.1 to 19.0) and old-

Figure 2.5. Box plots show the distribution of macrolichen species richness in different stand types of the western hemlock and true fir series. Stand types are abbreviated as: Y0 = even-aged young (< 20 yrs), Y15 = young with 15% remnants, Y50 = young with 50% remnants, P0 = even-aged pole (21-80 yrs), P15 = pole with 15% remnants, P30 = pole with 30% remnants, M0 = even-aged mature (81-200 yrs), M15 = mature with 15% remnants, M30 = mature with 30% remnants, OG = old growth (> 200 yrs). 50% of the data falls within the interquartile range of the box, with the top of the box representing the 75th percentile and the bottom the 25th percentile. The horizontal line in the box represents the sample median. The whiskers on either end of the box represent the range of values that fall within 1.5 box lengths, showing extreme values that are not considered outliers. Circles indicate moderate outliers (> 3 box lengths from either end). Stand types with N < 3 were are not shown. Letters that differ from each other represent significant differences at $p \leq 0.05$ from Tukey's HSD. N = number of stands per stand type.

Western Hemlock



True Fir

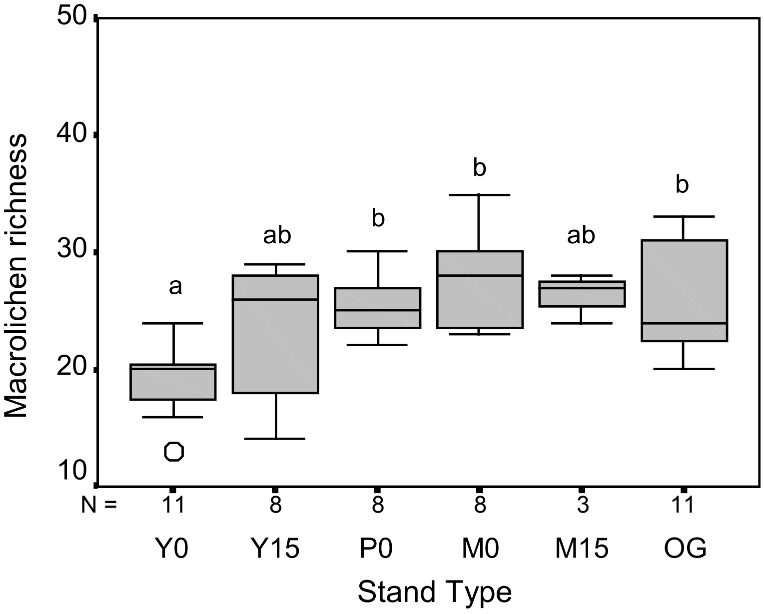


Figure 2.5

growth stands (Tukey's HSD, 95% CI for the difference = 1.7 to 20.2; Figure 2.5). The presence of remnant trees was not related to differences in lichen species richness (Figures 2.5 and 2.6).

Average cyanolichen species richness was highest in old-growth stands and differed significantly from young stands with and without remnants (see Figure 2.6 for effect sizes). Average forage lichen species richness was similar among stand types (Figure 2.6). Matrix lichens were most diverse in mature stands without remnants, differing significantly from even-aged young stands (Tukey's HSD, 95% CI for the difference = 0.3 to 11.2).

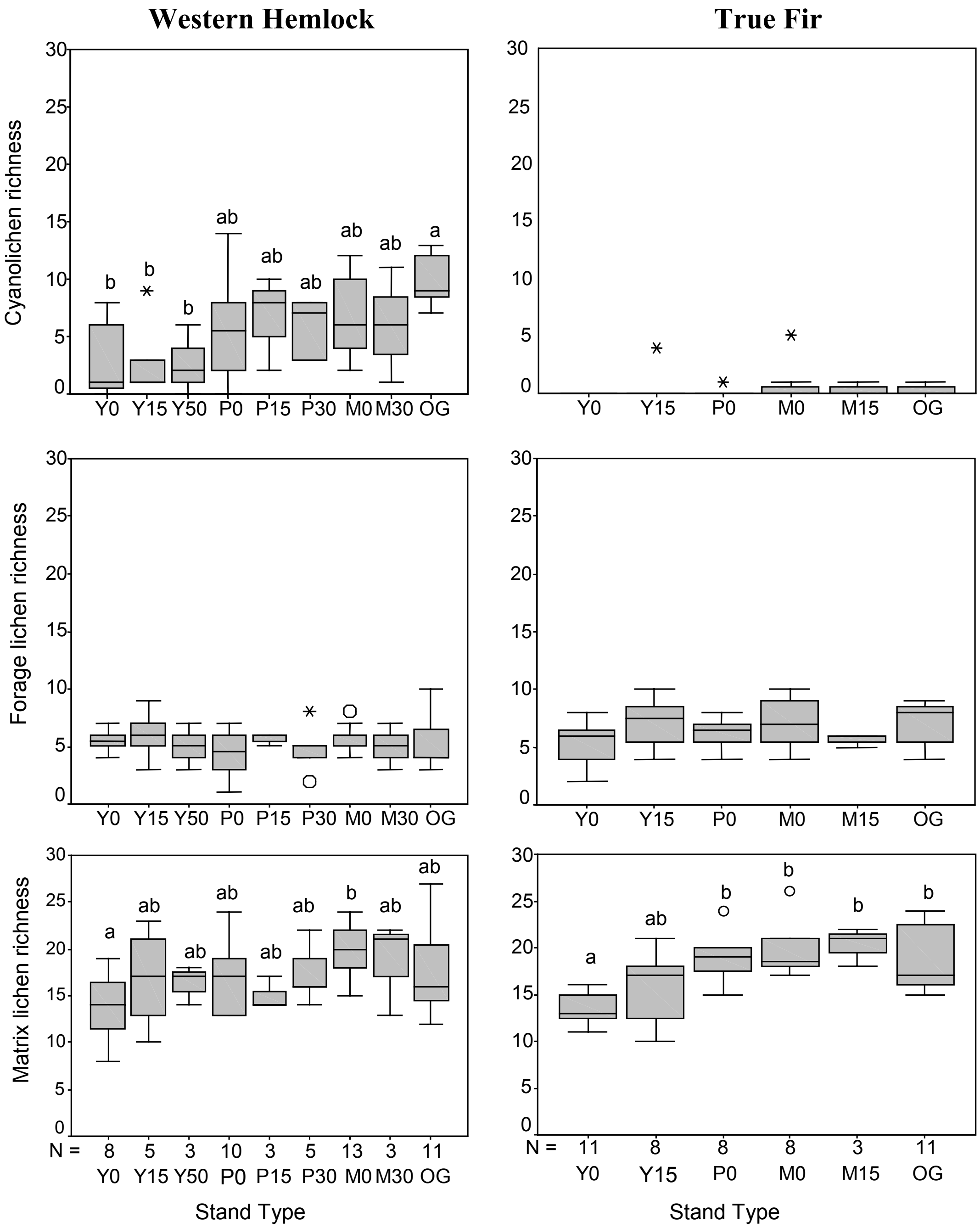
True fir series

Elevation was not a strong gradient separating lichen communities within the true fir series because the true fir forests represent a narrow portion of the upper Blue River watershed (elevation ranging from 950 –1470 m; Table 2.7). Similarly, no other topographic variables (i.e., heat load, potential direct incident radiation, slope, aspect) were related to patterns in lichen communities of the true fir series (maximum $R^2 = 0.07$). The NMS ordination of stands in lichen species space for the true fir series resulted in a 2-dimensional solution describing 81% of the community variance, rotated to maximize the correlation of the age index with axis 1 (axis 1 = 50% and axis 2 = 31% after rotation; Figure 2.4B).

Stand structure

The strongest gradient in lichen communities in the true fir forests was correlated with the age index in the ordination (Figure 2.4B; Table 2.5). As in the western hemlock series, BA generally increased with stand age and with increased remnant retention (Table 2.6). Macrolichen community composition overall differed among even-aged stands (MRPP, T = -10.0, A = 0.11, $p \ll 0.001$), as did species composition of matrix lichens (T = -11.48, A = 0.15, $p \ll 0.001$), whereas forage lichen composition did not differ across even-aged stands (T = -0.16, A =

Figure 2.6. Box plots show the distribution of epiphytic macrolichen species richness by functional groups in stand types of the western hemlock and true fir series. Stand type abbreviations are described in Figure 2.5. 50% of the data falls within the interquartile range of the box, with the top of the box representing the 75th percentile and the bottom the 25th percentile. The horizontal line in the box represents the sample median. The whiskers on either end of the box represent the range of values that fall within 1.5 box lengths, showing extreme values that are not considered outliers. Circles indicate moderate outliers (1.5 to 3 box lengths from either end) and asterisks indicate extreme outliers (> 3 box lengths from either end). Stand types with $N < 3$ were are not shown. Letters that differ from each other represent significant differences at $p \leq 0.05$ from Tukey's HSD. No differences were found for forage lichens. N = number of stands per stand type.


Western Hemlock
True Fir
Cyanolichen richness
Forage lichen richness
Matrix lichen richness
0
5
10
15
20
25
30
b
b
b
ab
ab
ab
ab
ab
a
Y0 Y15 Y50 P0 P15 P30 M0 M30 OG
Y0 Y15 P0 M0 M15 OG
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ab
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ab
ab
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ab
b
b
b
b
N = 8 5 3 10 3 5 13 3 11
N = 11 8 8 8 3 11
Stand Type
Stand Type

Figure 2.6

0.003, $p = 0.41$). Cyanolichens were absent from many stands, thus we could not assess compositional differences for this group.

Lichen community composition in even-aged young (< 20 yrs) stands differed from that in even-aged pole (21-80 yrs) stands (Figure 2.4B; Table 2.8). In addition, lichen communities in even-aged young and pole stands were different from all other stand types (Figure 2.4B; Table 2.8). Lichen communities in young stands with 15% remnants differed in composition from even-aged young stands and were more similar to lichen communities of pole and mature stands (Figure 2.4B). Pole stands with remnants were few in the watershed ($N = 1$) and therefore, were not included in the analyses. Lichen communities were similar between old-growth and even-aged mature stands ($T = -0.12$, $A = 0.001$, $p = 0.42$; Figure 2.4B; Table 2.8) and did not differ from mature stands with 15% remnants (Figure 2.4B; Table 2.8).

Lichen diversity in relation to stand structure

Matrix lichens were the most abundant and diverse group in the true fir series. Consequently, matrix lichen species richness was strongly correlated with macrolichen species richness ($R^2 = 0.88$; Figure 2.4B; Table 2.5). Average species richness for all macrolichens differed among stand types (one-way ANOVA, $F = 8.41$, $p << 0.001$). Even-aged young stands (< 20 yrs) were the least diverse compared to all other stands (Figure 2.5). Lichen species richness for all macrolichens and for matrix lichens increased with total BA and with the age index (Figure 2.4B; Table 2.5). Remnant tree retention was unrelated to lichen species richness in the true fir series (Figures 2.5 & 2.6). Matrix lichen diversity in young stands with and without remnants was similar, but differed from all other stand types (Figure 2.6). Forage lichen diversity was consistent across stand types and cyanolichens were nearly absent from true fir stands.

Hardwood trees and shrubs

The presence of hardwood trees in the stand was recorded in the BA counts. However, many hardwood trees were small in diameter relative to the conifers, resulting in poor representation of hardwoods in the BA measurements (Table 2.6). Hardwood shrubs were not included in the BA measurements, however, they provide important substrate for lichens. Hardwood abundance may have been more effectively represented by a density count, since field observations showed that the presence of even a few hardwoods seemed to enhance lichen diversity. Field observations suggested that common hardwoods such as *Acer circinatum* Pursh*,* *Acer macrophyllum* Pursh, *Alnus rubra* Bong., *Castanopsis chrysophylla* (Dougl.) A.DC., *Cornus nuttallii* Aud.*, Corylus cornuta* Marsh var. *californica* (A.DC.) Sharp, and *Rhododendron macrophyllum* G. Don provided unique substrates for lichens that were uncommon on the surrounding conifers. Hardwood patches were lichen diversity "hot spots" and were often found in disturbed areas along stream banks or in open rocky areas of upland forest stands. Lichens commonly found on hardwoods included species in the genera *Nephroma*, *Pseudocyphellaria*, and green-algal lichen genera such as *Melanelia*, *Parmelia*, *Ramalina*, *Evernia,* and *Hypotrachyna.*

Upland and riparian stands

Lichen community composition differed in uplands and riparian stands across all 117 stands (MRPP, T = -2.99, A = 0.01, p= 0.01). Lichen community patterns in the upland and riparian classes were evaluated separately for each plant series to account for the influence of elevation on lichen communities.

Lichen communities differed between uplands and stands along perennial streams < 5th order in the western hemlock series (MRPP, T = -4.56, A = 0.02, p = 0.001; Table 2.9; see Table 2.7 for summary of topographic classes by stand type). There were no strong differences in lichen communities among the other riparian stream classes or between them and upland sites (Table 2.9; low A-statistics indicate heterogeneous lichen communities within the topographic classes and also indicate overlap in the lichen communities between topographic classes). Average total macrolichen richness was similar among stands in uplands (mean species richness was 27.0) and riparian areas (mean species richness for perennial streams < 5th order = 30.5, for perennial non-fish bearing = 29.3, and for intermittent streams = 28.4) for the western hemlock series (from one-way ANOVA, F = 0.80, p = 0.50)**.** Although, cyanolichen species richness was higher in stands along perennial streams < 5th order than in uplands (Tukey's HSD, 95% CI for the difference = 1.35 to 8.48). Cyanolichens such as *Fuscopannaria pacifica, Nephroma parile*, and *Sticta weigelii* were primary indicators of sites with perennial streams < 5th order (Table 2.3). Many of the cyanolichens found in stands along perennial streams were more commonly found on hardwoods and were not typically present on conifers. We were unable to determine if differences in lichen communities along perennial streams was related to hardwoods, to environmental factors, or to a combination of both.

Table 2.9. Chance-corrected within-group agreement (*A*) for comparisons among lichen communities in the four topographic classes (MRPP). Comparisons were made only for stands in the western hemlock series. Asterisk indicates significant differences ($p \leq 0.05$).

	Upland	**Intermittent**	**Perennial (no fish)**
Upland	——		
Intermittent	0.001	——	
Perennial (no fish)	0.007	0.006	——
Perennial (< 5th order)	0.024*	0.008	0.012

In the western hemlock series, individual lichen species responded differently with respect to topographic class. Lichen species such as *Hypogymnia oceanica*, *Nephroma occultum*, *N. resupinatum*, *Pseudocyphellaria crocata,* and *P. rainierensis* increased in frequency and abundance from uplands to perennial streams (Figure 2.7), but were not significant indicators of any particular topographic position (ISA: all $p > 0.05$). In contrast, species such as *Fuscopannaria pacifica*, *N. parile,* and *Sticta weigelii* were found predominantly in stands along perennial streams and were significant indicators for sites along perennial streams < 5th order (ISA: all $p \leq 0.05$; Figure 2.7). *Esslingeriana idahoensis*, *Evernia prunastri,* and *Hypogymnia rugosa* were indicators for sites with perennial non fish-bearing streams (Table 2.3). *Hypogymnia inactiva* was the only lichen indicator for upland sites in the western hemlock series; this lichen was frequent in all stands in the watershed, but more abundant in uplands.

Upland and riparian stands did not separate in the ordination for the true fir series, nor did lichen communities in upland and riparian classes differ by MRPP ($T = -0.93$, $A = 0.01$, $p = 0.17$). In general, there were fewer hardwoods found in stands in the true fir series (Table 2.6). In the true fir series, 26 of 50 stands were riparian (3 along perennial fish-bearing streams, 10 along perennial non fish-bearing streams, and 13 along intermittent streams; see Table 2.7 for summaries by stand type). In addition, there were no obvious differences in lichen species richness among stands in uplands and riparian areas (one-way ANOVA, $F = 0.51$, $p = 0.68$). When cyanolichens were found in the true fir series, there was no clear relationship with topographic class.

DISCUSSION

Many ecological factors, such as stand age, remnant trees, and topography have been demonstrated to be important to temperate forest epiphytes (Peterson & McCune 2001; Pipp et al. 2001; Rolstad et al. 2001; Hazell & Gustafsson 1999; Sillett & Goslin 1999; Peck & McCune 1997; Halpern & Spies 1995; McCune

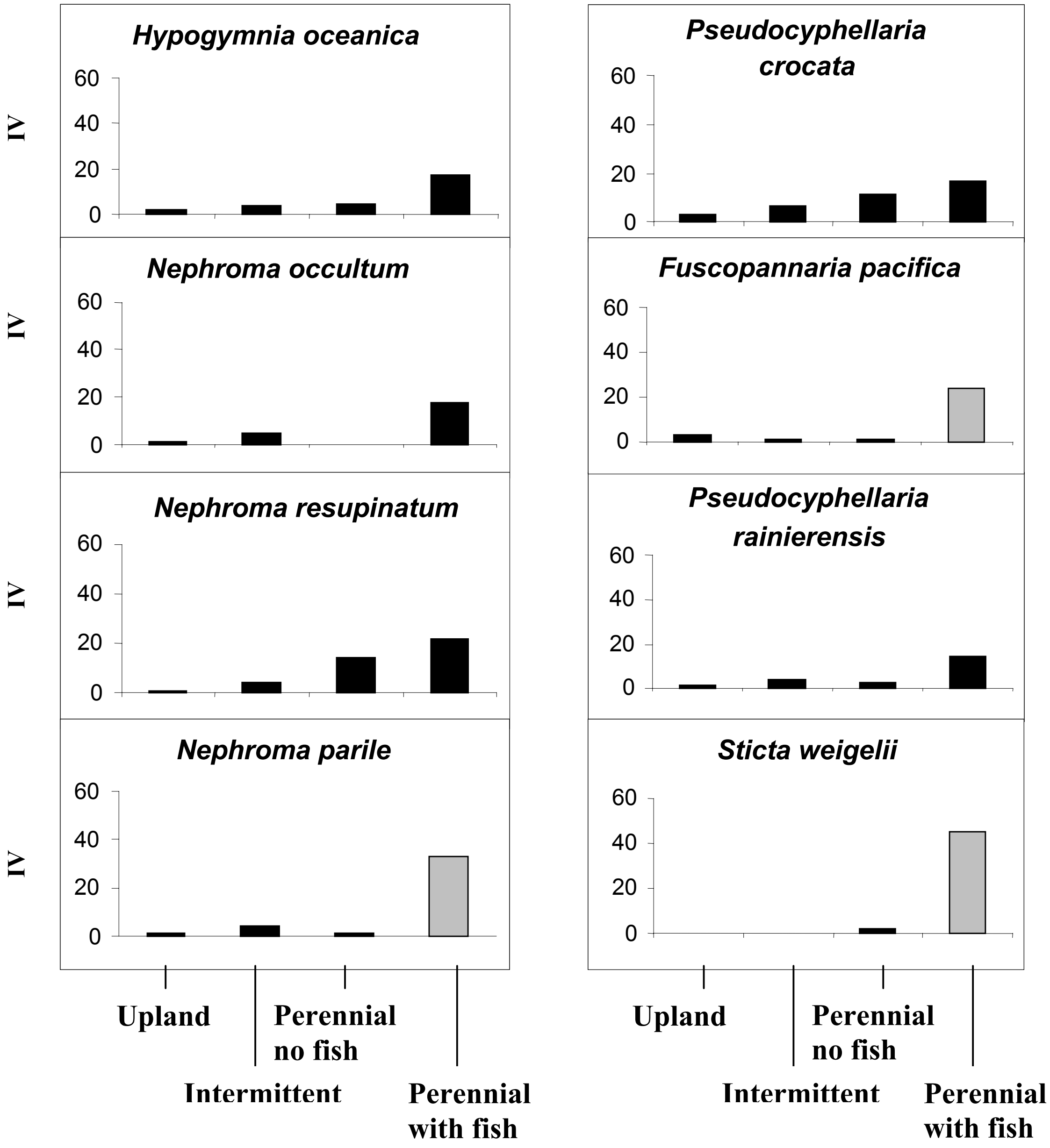

Figure 2.7. Indicator values (IV) for lichens in the four topographic classes of the western hemlock series, across all stand types. Indicator values represent a combination of species frequency and abundance. Indicator values for these species were high only in areas along perennial streams. Gray bars indicate significant species indicators for the topographic class ($p \leq 0.05$ from a randomized test from Indicator Species Analysis; see also Table 2.3).

1993; Neitlich 1993; Hyvärinen & Kauppi 1992; Lesica et al. 1991; Spies 1991; Rose 1976). However, the influences of these factors on lichen communities have rarely been studied simultaneously. In this study, we did so to allow an appraisal of the relative strengths of these factors in relationship to epiphytic macrolichens in the Blue River watershed of the Cascade Mountains.

Elevation gradient

Lichen communities differed more strongly across the 1,000 m span of elevation than for any other single factor. Lower elevation forests (470 – 950 m) differed in species composition from lichen communities in the true fir forests at higher elevations (950 – 1470 m). The vascular plant series were related to the elevation gradient. We showed 16 species to be indicators of the higher elevation true fir series across all stand types and 17 species to be indicators of the lower elevation western hemlock series across all stand types.

The elevation differences were mostly due to the abundance and diversity of cyanolichens in low elevation stands and their scarcity in the higher elevation stands. These findings agree with other studies that show cyanolichens to be absent from higher elevation forests in the PNW (1220-1340 m; Peck & McCune 1997) and abundant in old growth at lower elevations (500-1000 m; Peterson & McCune 2001; Sillett & Neitlich 1996; Sillett 1995; McCune 1993; Neitlich 1993; Pike et al. 1972,1977). Additionally, compositional differences between the two plant series reflected forage lichen dominance in old forests in the true fir series, primarily by *Alectoria sarmentosa*. The great abundance of *A. sarmentosa* may limit available substrate for other lichen species to colonize such forests.

Lichen communities in relation to stand structure

Stand age

Epiphytic macrolichen community composition clearly changes through time in even-aged stands. Differences in lichen community composition with stand age were more apparent than differences in lichen species richness. Lichen community composition in even-aged young stands (< 20 yrs) was considerably different from all other even-aged stands. Furthermore, lichen species richness was generally poor in even-aged young stands. Lichen communities in young stands were primarily composed of small numbers of matrix lichens, such as the genera *Platismatia* and *Hypogymnia*. Cyanolichens were absent from young stands, with the exception of a few cases in which cyanolichen propagules appeared to have dispersed from nearby old growth. When selecting even-aged young stands for sampling, we did not consider the proximity to old growth. Close proximity to old growth may enhance lichen dispersal to young stands. Average total lichen species richness was higher in even-aged pole stands (21-80 yrs) than in even-aged young stands in the true fir series, however this was not seen in similar-aged stands of the western hemlock series.

Lichen community composition in even-aged young and pole stands may be different from older stands because it may simply take time for lichens to reach these forests and they may be slow to establish (Sillett et al. 2000*b*). Even-aged young and pole stands in the PNW forest matrix are predominantly plantations from past clearcuts, many of which were overstocked. These plantations are typically very dense, which may limit lichen establishment in the stand. In addition, low light and infrequent wetting/drying cycles may result in slow lichen growth in such dense stands.

Lichen communities in older stands (> 80 yrs, with and without remnants) were composed of lichens across all functional groups (with the exception of cyanolichens in the true fir forests). Lichen communities in old-growth and mature stands of the western hemlock series were diverse, providing habitat for many cyanolichens. *Nephroma occultum* and *Pseudocyphellaria rainierensis* are two cyanolichens in the Blue River watershed that were only found in old-growth stands of the western hemlock series and have been documented by others as old-growth associates (Rosso et al. 2000; Sillett & Goward 1998; Goward 1994, 1995). Cyanolichens can also be abundant in hardwood patches and riparian forests along large streams (McCune et al. 2002*a*; Peterson & McCune 2001; Rosso 2000; Ruchty 2000; Sillett & Neitlich 1996; Neitlich & McCune 1997).

Lobaria oregana is a dominant cyanolichen in mid-elevation old growth of the western Cascades (McCune 1993; Spies 1991; Pike et al. 1977) and was found to be an old growth-associate in our study as well as in others (Neitlich 1993; Peterson & McCune 2001). However, *L. oregana* is capable of growing well in young stands and may, therefore, be old-growth-associated because of dispersal limitations, rather than a dependence on the environment associated with older forests (Sillett & McCune 1998; Sillett et al. 2000*a,*2000*b*). Sillett et al. (2000*a,*2000*b*) suggested that dispersal often limits establishment of old-growth associated lichens in young stands, primarily for lichens that reproduce asexually by fragmentation or coarse soredia that are not easily dispersed. As a result, the longer a stand persists without disturbance, the more likely it is to be colonized by dispersal-limited lichens. In addition, the close proximity of a propagule source enhances the likelihood of dispersal-limited lichens colonizing younger forests (Dettki 1998).

Dispersal does not limit all old-growth associated lichens. In some cases substrate may be a limiting factor, as demonstrated by Caliciales (pin-lichens) that colonize old bark and old snags (Tibell 1992). Other lichens may be old-growth associates due to specific microsites required for growth. Sillett (1995) suggested that the cyanolichens *Pseudocyphellaria rainierensis* and *Peltigera britannica* as an epiphyte were strongly associated with old growth due to the abundance of moss mats, which they colonize in such forests in the PNW.

Remnant tree retention

The presence of remnant trees in forest stands may change the forest structure to resemble that of older stands and remnant trees may also enhance forest connectivity in a dissected landscape (Franklin et al. 1997). In the Blue River watershed, remnant tree retention was generally less important to lichen communities than stand age in both plant series. In this study, the presence of remnants was most important to lichen communities in young forests, whereas the importance of remnants in older stands was less clear. The presence of remnant trees in young stands was related to significant differences in lichen community composition as compared to even-aged young stands across both plant series (Figure 2.8). For example, in the western hemlock series, lichen community composition in young stands with remnant retention of 15% or greater was similar to that of even-aged pole forests (21-80 yrs) in the Blue River watershed. This pattern was also true for young stands with 15% remnant retention in the true fir series. The presence of remnants in young stands following a tree-regenerating disturbance in old growth may accelerate the development of the lichen community towards that of older stands (Figure 2.8).

Remnant trees may provide refugia from a disturbance, increasing survival of lichen populations following a disturbance. Peck & McCune (1997) suggested that remnants may buffer the microclimate extremes of a stand in the early years following a disturbance. This microclimate buffering may help surviving lichen populations to rebound after the disturbance. Remnants may also serve as a propagule source for lichens in the young regenerating stands following a disturbance (Sillett & Goslin 1999; Peck & McCune 1997; Neitlich & McCune 1997). The influence of remnants on lichen communities will vary, however, depending on the density and quality of remnants, such as remnant age, size, and wind-firmness. Although we did not measure remnant age, we estimated remnant tree age in our field observations. In general, it seemed that large old remnant trees seemed to host more abundant lichens than younger remnant trees.

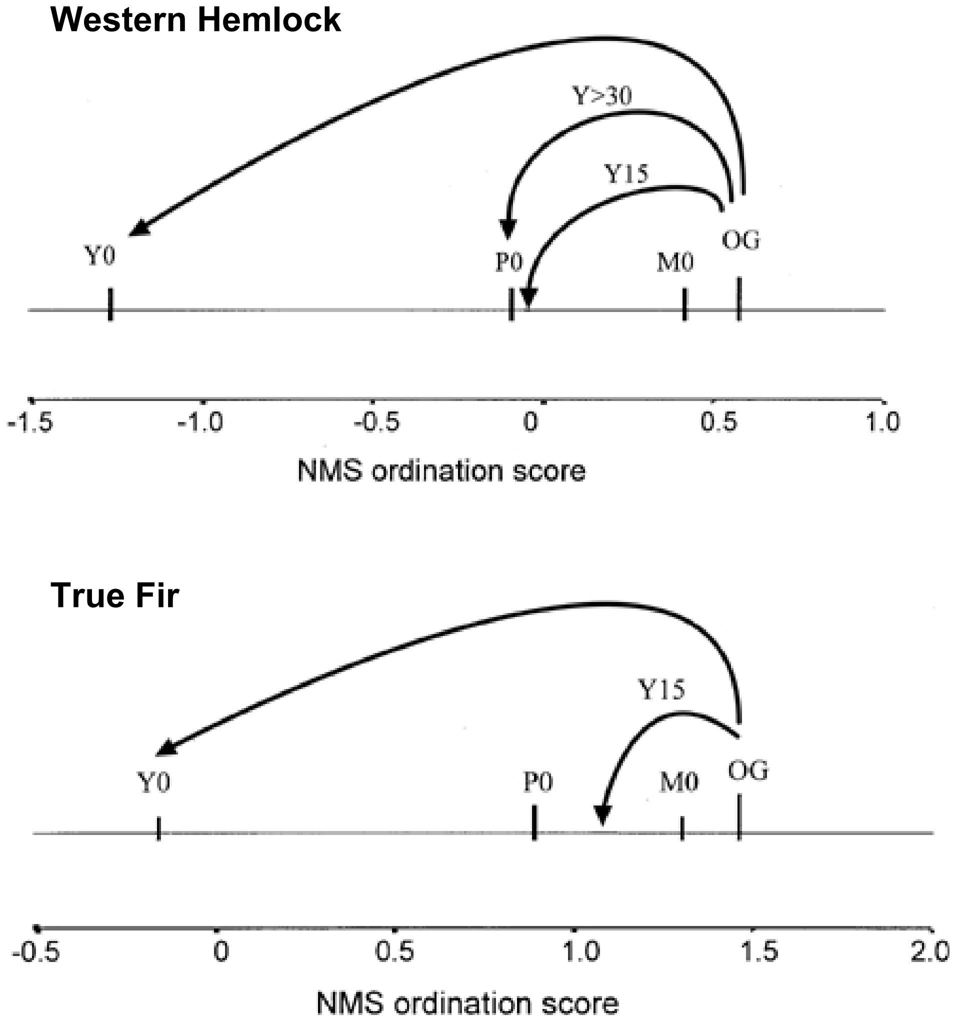

Figure 2.8. Diagram representing changes in lichen community composition along a gradient in stand structure and stand development within the western hemlock and true fir series (average ordination scores by stand type from axis 1 in each ordination; Figure 2.4). The lichen community composition gradient was extracted from rotated ordinations for each plant series, for which axis one in each ordination was correlated with the age index. The relative distance between stand types represents the relative difference in lichen community composition based on the averaged ordination scores from axis one by stand type. Arrows represent a disturbance event occurring in an old-growth stand and some possible scenarios that could occur following the disturbance, such as: total tree mortality, light remnant retention (15%), high remnant retention (> 30%). Y0 = even-aged young stand (< 20 yrs), Y15 = young stand with 15% remnant tree retention, Y > 30 = young stand with > 30% remnant tree retention, P0 = even-aged pole stand (21-80 yrs), M0 = even-aged mature stand (81-200 yrs), OG = old growth (> 200 yrs).

Hardwood and riparian areas

Riparian and hardwood areas provide microhabitat for many cyanolichens, old-growth-associates, and other species not commonly found in conifer forests (McCune et al. 2002*a*; Keon & Muir 2002; Rosso 2000; Ruchty 2000; Neitlich & McCune 1997; Sillett & Neitlich 1996). Lichen diversity is often higher in hardwood patches of young and managed stands than in the more homogeneous conifer-dominated portions of these stands (Peterson 2000; Rosso 2000). In our study, lichens typically found on hardwood trees and shrubs included species in the genera *Evernia*, *Hypotrachyna*, *Lobaria*, *Melanelia, Nephroma*, *Parmelia, Pseudocyphellaria, Ramalina,* and *Sticta*. For example, lichen communities in the western hemlock series along perennial streams < 5th order were cyanolichen rich "hot spots." Perennial streams < 5th order usually formed large channels in which hardwood shrubs and trees dominated the floodplain. The increased presence of hardwoods was confounded with the presence of perennial streams and therefore, it was difficult to determine which factors were influencing patterns of lichen communities along perennial streams.

Lack of differences in lichen communities with topographic classes in the true fir series may result in part from the small sample size of stands along perennial streams. Riparian stands, especially those with perennial streams < 5th order, were scarce in the true fir series since these forests are at higher elevations where many of the stream headwaters occur.

Over the range of stream sizes included in this study, lichen communities differed subtly. Extending the riparian gradient outside of the Blue River watershed to large valley bottom streams in the McKenzie River watershed, however, resulted in much larger differences in lichen communities (McCune et al. 2002*a*). They found that lichen communities in forests along very large streams were more diverse than upland forests, due to increased abundance of cyanolichens and abundant nitrophilous lichens that are presumably stimulated by air pollution (N-based) in the lower valley bottoms.

Forest management implications

In federal forests of the Cascade Range, maintaining intact old-growth stands in the landscape can provide a viable lichen propagule source, preserve habitat continuity for old-growth-associates (Rosso et al. 2000; Goward 1995), and can help maintain large cyanolichen populations at lower elevations that are important to nutrient cycles in the forest ecosystem (Antoine 2001; Denison 1979; Pike 1978). In addition, mature stands (80-200 yrs) are important to maintain in the landscape because they also provide habitat for cyanolichens and for other abundant macrolichens.

The presence of remnants in young stands may enhance lichen communities. Remnants provide temporal continuity of habitat during forest development in managed forests (Hazell & Gustafsson 1999). Remnant retention is especially important for lichens that are dispersal-limited and may prove effective for maintaining long-term old-growth associated lichens in managed forests (Sillett & Goslin 1999). In this study, the remnant trees were both old wolf trees that survived from historical wildfires and old trees that remained after timber harvests. Consequently, there was a range in remnant tree size and age, in which those trees left following harvests were occasionally younger relative to remnant trees from wildfires. More research is needed to determine if the quality of remnant trees is important to lichen communities following timber harvest.

Riparian areas are often buffered during harvest in federal forests of the Cascade Range and are recognized as important habitat for forest and aquatic species. Hardwoods are prevalent along streams and are often "hot spots" for epiphytic macrolichen diversity. Other hardwood gaps located in open areas or rocky areas and understory shrubs are also important lichen habitat. Forest managers often overlook the importance of hardwood shrubs to lichen communities. The loss of hardwood trees and shrubs (especially older individuals) could contribute to the loss of hardwood-associated lichen species in a given area (Peterson 2000; Rosso 2000). Recognizing the importance of hardwood patches and managing for them in the landscape is likely to assist in the maintenance of lichen diversity across the landscape (Neitlich & McCune 1997).

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Chapter 3

Estimating Epiphytic Macrolichen Biomass from Topography, Stand Structure and Lichen Community Data in the Central Cascade Forests of Western Oregon, USA

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ABSTRACT

We collected data on epiphytic macrolichen communities and biomass in forest stands with various structural characteristics in the central Cascades of western Oregon. Sampling was stratified by the age class of the younger cohort and by the retention of remnant trees present as an older cohort. Old growth was not stratified by the younger cohort or remnant tree retention. Remnants were those trees that survived the most recent disturbance. Forests in this area will be managed according to these two structural and age-related characteristics and our goal was to assess how lichen biomass is related to forest structure and lichen composition. Lichen biomass was estimated for three functional groups: cyanolichens, forage lichens, and matrix lichens. We used lichen litter to estimate epiphytic lichen biomass in forest stands based on a previously published ratio. Lichen biomass changed along an elevation gradient, with highest cyanolichen biomass at low elevations (470 – 950 m) and highest forage lichen biomass at higher elevations (950 – 1470 m). Lichen biomass was related to stand types; lowest lichen biomass in even-aged young stands and highest in old-growth and mature stands with remnant trees. Lichen biomass was higher in stands with high remnant retention as compared to similar even-aged stands. We developed models for estimating epiphytic macrolichen biomass (oven-dried; 10^x kg/ha) using stepwise-linear regression and nonlinear regression. We followed a three-step approach to develop the predictive models, each step demanding an additional class of variables. First, we created models from topographic predictors that are easily extracted from GIS data. We then developed models based on both topographic and stand structure variables. Finally, we developed models based on topography, stand structure, and lichen community data. Models with the greatest explanatory power were: cyanolichen biomass predicted as a function of elevation, stand age index, the sum of abundance for *Lobaria oregana* and *L. pulmonaria*, and cyanolichen species richness ($R^2 = 0.85$); forage lichen biomass predicted as a function of stand age index and the abundance of *Alectoria sarmentosa* ($R^2 = 0.55$);

and matrix lichen biomass predicted as a function of stand age index and the sum of abundances for matrix lichen species in the stand ($R^2 = 0.58$).

INTRODUCTION

We described patterns of epiphytic lichen biomass in temperate conifer forests of the western Oregon Cascades as they relate to topography, stand structure, and lichen communities. Sampling epiphytic macrolichen biomass in forests is slow and tedious. We developed models for estimating epiphytic macrolichen biomass that will save time in efforts to assess large-scale patterns of lichen abundance. The models provide a method for estimating stand-level biomass for three lichen functional groups (cyanolichens or "nitrogen-fixers," forage lichens, and matrix lichens) from topography, stand structure, and lichen community data. The models based on topographic variables can be applied when only Geographic Information Systems (GIS) data are available. Models based on stand structural variables and lichen community data provide better estimates of biomass, but require visiting the stands for data collection.

Lichen community data (e.g., species richness and community composition) are easily collected, but do not necessarily reflect the contribution of these species to forest ecosystem function. It is important to understand the distribution of lichen biomass in the forest landscape, since contributions of lichens, such as nitrogen fixation and provision of forage, are likely proportional to their biomass (Pike 1978). Our models can be used to identify areas in the landscape with abundant lichens, which may assist managers in prioritizing lichen habitat in need of conservation and can help managers devise management plans for the future forests. This is the first attempt at developing models for estimating lichen biomass on the landscape scale.

Epiphytic macrolichens are important components of forest ecosystems. Lichens contribute to forest biodiversity (Pharo et al. 1999; Dettki & Esseen 1998; Kuusinen & Siitonen 1998; Lesica et al. 1991) and are used for forage by many animals. The genera *Alectoria* and *Bryoria* are important food sources for deer (Stevenson & Rochelle 1984; Stevenson 1978), woodland caribou (Rominger & Oldemeyer 1989; Servheen & Lyon 1989; Edwards et al. 1960), and flying squirrels (Rosentreter et al. 1997; Zabel & Waters 1997; Maser et al. 1986; Maser et al. 1985). Lichens provide nesting material for birds (Starkey & Hagar 1999) and flying squirrels (Hayward & Rosentreter 1994) and are used for habitat by many invertebrates (Pettersson et al. 1995). Lichens may also play important roles in productivity and nutrient cycling of forest ecosystems (Esseen et al. 1996; Knops et al. 1991; Boucher & Nash 1990; Pike 1978). Lichens with cyanobacteria as a photobiont (cyanolichens), such as *Lobaria oregana*, fix atmospheric nitrogen and are especially important to nutrient cycles of Pacific Northwest forest ecosystems (Antoine 2001; Denison 1979; Pike 1978). In addition, lichen epiphytes are useful indicators of forest health (McCune 2000) because they are sensitive to forest management practices and they serve as indicators of air quality (L. Geiser, unpublished data; Richardson 1989).

Epiphytic lichen biomass of temperate forests slowly increases with stand age, typically reaching high levels in mature and old-growth forests (McCune 1993; Neitlich 1993) and in stands that are more structurally complex (Pipp et al. 2001; Clement & Shaw 1999; McCune et al. 1997*a*). In the Pacific Northwest (PNW), cyanolichens are major components of lichen biomass in old-growth forests at low elevations (~1,000 kg/ha dry weight, McCune 1993; Neitlich 1993; Pike et al. 1977), comprising 60-80% of the total lichen biomass in such stands (Sillett 1995; McCune 1994; Neitlich 1993; Pike et al. 1977). Cyanolichen biomass in the PNW conifer forests is dominated primarily by *Lobaria oregana* (McCune 1993; Neitlich 1993; Pike et al. 1977). *L. oregana* is considered old-growth associated, but is also capable of growing well in young stands (Sillett et al. 2000*a*, 2000*b*; Sillett & McCune 1998). Cyanolichens are nearly absent in young, regenerating conifer forests and when present they are in very low abundance (Chapter 2; Sillett & Neitlich 1996; Neitlich 1993). Recent studies suggest that some cyanolichens, such as *Lobaria oregana*, are dispersal-limited (Sillett et al. 2000*a*, 2000*b*) and as a result, are well established in old-growth forests simply because they had more time to get there.

Lichen diversity and abundance may be maintained by preserving existing populations and suitable habitat in the landscape and by managing to promote dispersal of lichen propagules among forest stands, especially to young even-aged forests where lichen diversity and biomass are low (Peterson & McCune 2001; Dettki & Esseen 1998; Neitlich & McCune 1997; Neitlich 1993). Various management practices, such as leaving old remnant trees during harvest, may benefit the survival and propagation of lichen communities in managed landscapes. Canopy structure is enhanced with increased remnant tree retention, and is positively related to greater cyanolichen biomass (Sillett & Goslin 1999; Peck & McCune 1997) and increased overall lichen biomass (Pipp et al. 2001). Maintenance of other forest structural features such as hardwood patches and snags may also enhance forest lichen diversity and biomass (Pipp et al. 2001; Rosso 2000; Sillett & Neitlich 1996). We must better understand the relationships between epiphytic lichen communities and lichen biomass to manage for both at the landscape scale.

In this paper, we evaluate patterns in epiphytic macrolichen biomass by functional group as they relate to topography, stand age, remnant tree retention, and lichen communities in the Blue River watershed of western Oregon. We use these relationships to develop regression models for estimating epiphytic macrolichen biomass by functional group in forest stands. There are three classes of regression models: those based only on topographic variables that can be derived from GIS; those based on topographic variables and stand structure; and those models that were developed from topographic variables, stand structure, and lichen community data. These models are useful tools for understanding and predicting the distribution of epiphytic macrolichen biomass at a landscape scale.

METHODS

Study area

We studied forests that were, for the most part, in the Blue River watershed of the Central Cascades Adaptive Management Area in the Willamette National Forest, Oregon, USA (Figure 3.1; see Chapter 2 for site details). The Adaptive Management Area is currently managed under the experimental Blue River Landscape Plan (LP), in which management is based, in part, on historical fire regimes (Cissel et al. 1999). The Blue River watershed consists of 23,900 hectares of mainly conifer forest on steep terrain ranging from 317 – 1639 m in elevation. The watershed receives an average annual precipitation of 250 cm. The winters are cold and wet with a mean temperature of 2° C in January, and the summers are warm and dry with a mean temperature in July of 22° C. The northern part of the watershed consists of a narrow band of high elevation forests (> 950 m) dominated by *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) and *Abies procera* Rheder (Noble fir) (hereafter, "*Abies* series;" Logan et al. 1987). Most of the watershed is lower elevation forests (< 950 m) dominated by *Pseudotsuga menziesii* Mirb. Franco. (Douglas fir) and *Tsuga heterophylla* (Raf.) Sarg. (hereafter, "*Tsuga* series;" Logan et al. 1987).

Sample design

This study was part of an extensive lichen community study implemented in the Blue River watershed (Chapter 2). Lichen communities and biomass were sampled in forest stands using a stratified random design based on the following attributes:

(1) two plant series (*Tsuga* and *Abies*);

(2) four age classes (the younger tree cohort; young < 20 yrs, pole 21-80 yrs, mature 81-200 yrs; and old growth > 200 yrs);

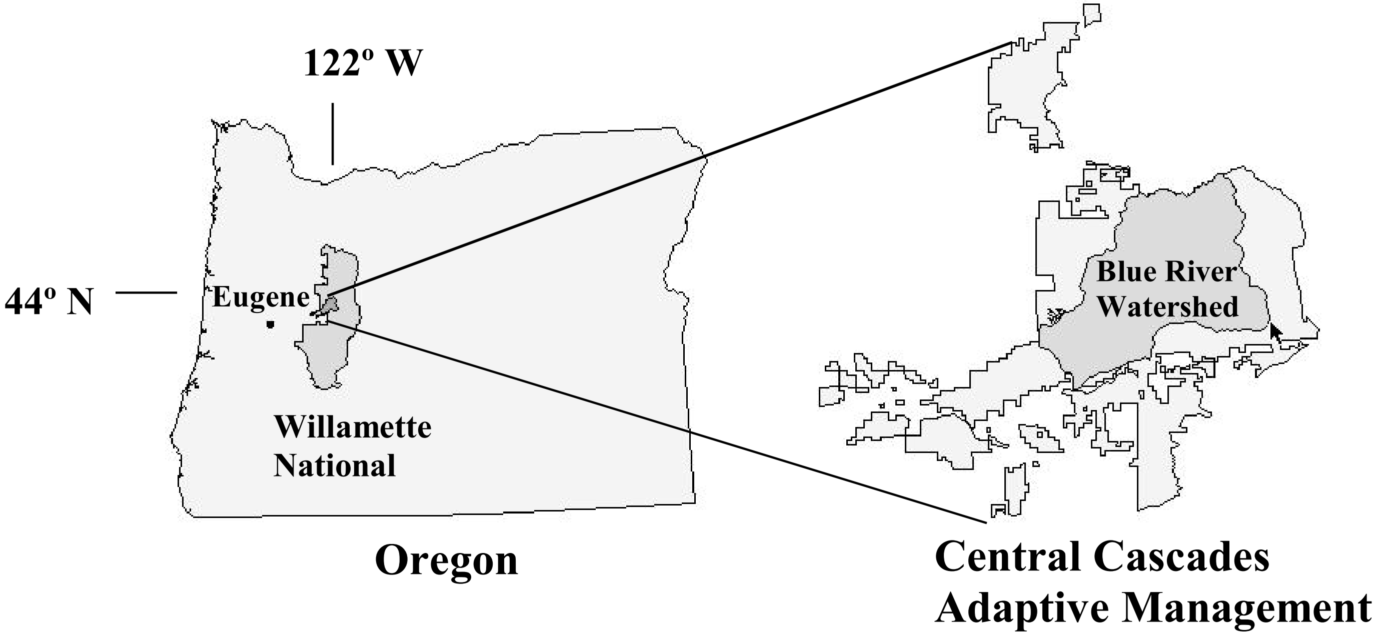


Figure 3.1. Map of the Blue River watershed (gray area on the right) in the Central Cascades Adaptive Management Area of the Willamette National Forest, Oregon, USA.

(3) four classes of remnant tree retention based on the percent canopy cover of remnant trees that survived from the previous stand following a disturbance that initiated tree regeneration: 0 = 0 - 7.5%; 15 = 7.5 - 22.5%; 30 = 22.5 - 37.0%; 50 = 37.0 - 62.0%. Remnant trees included the older live trees that remained following the most recent timber harvest or those old trees that survived a natural forest fire (e.g., wolf trees). The characteristics of remnant trees (i.e., size, crown structure) varied among stands because remnants from a timber harvest were often smaller and younger than those remnants surviving forest fires. Old-growth stands were not stratified by remnant classes. Only 0% and 15% classes were sampled in the true fir series, since future management strategies will prescribe only these retention levels in the true fir series (Cissel et al. 1999);

(4) four topographic classes (upland, and three riparian stream classes: intermittent, non-fish bearing; perennial non fish-bearing; and perennial fish-bearing, stream order < 5). Only even-aged stands along perennial streams were sampled because few stands with remnant trees were located along such streams.

Each combination of the four attributes defines a stand type. While we sought to sample lichen communities in three stands for each stand type, many combinations of these strata were not present in the landscape and thus, were not sampled. In addition, some stand types were scarce in the watershed, and were therefore sampled in areas outside of it, while still on the Willamette National Forest.

We located stand types using aerial photos. We then located the stands on the ground and verified the stand type classification. The age class was estimated for the stand, or, if the age class was difficult to determine, we cored representative trees. Total percent canopy cover of remnant trees was used as an estimate of total percent retention of remnants for a stand, as defined by the LP (Cissel et al. 1999). We estimated canopy cover of remnants from tree diameter at breast height (dbh) and crown width. J. Mayo (unpublished data) developed a table for estimating canopy cover of trees from dbh, based on the relationship of dbh to crown width. The percent canopy cover of each remnant tree was then calculated from the crown width.

Lichen communities

The Forest Health Monitoring (FHM) lichen community method was used for the permanent installation and sampling of the lichen community plots (see McCune et al. 1997*b* for detailed methods). Each of the 117 stands was sampled for lichen community data using one FHM plot (see Chapter 2; see also Appendix A, Figure A1). The FHM plot center was randomly located within the stand. The FHM method is a time-constrained ocular survey of epiphytic macrolichens that occur on woody plants (including tall shrubs) in a 0.4 ha circular plot (37.4 m radius). The survey includes all epiphytic macrolichens that occur in the forest litter and on boles and branches that are visible from the ground, excluding the lower 0.5 m of tree boles and shrubs. Species abundance was recorded in five coarse abundance classes (modified from L. Geiser, unpublished Methods and from McCune et al. 1997*b*). Each species was assigned an abundance class as follows:

0 = absent
1 = rare (< 3 individuals per plot);
2 = uncommon (4-10 individuals per plot);
3 = common (> 10, but < 40 individuals per plot);
4 = very common (> 40 individuals per plot, but less than half of available substrate covered by the species);
5 = abundant (present on more than half of the available substrate).

Lichen nomenclature follows McCune and Geiser (1997) and McCune's online key (unpublished key) to the genus *Usnea* in the Pacific Northwest. Lichen voucher specimens are in the Oregon State University herbarium (OSC).

Litter plots

It is difficult and time consuming to estimate epiphytic lichen biomass by directly sampling the forest canopy and forest understory. Therefore, we estimated epiphytic lichen biomass from lichen litterfall on the forest floor. We then converted our lichen litter biomass estimates to estimates for epiphytic lichen biomass using a 100:1 relationship between lichen epiphyte biomass and biomass of epiphytic lichen litter ($R^2 = 0.89$) collected in late summer in forests of the western Cascades (McCune 1994). Epiphytic lichen biomass includes all epiphytic lichens growing on boles and branches of trees and tall shrubs.

Collecting lichen litter in late summer (during late August through October) avoids the large and variable amounts of litter that can occur in winter months due to large storm events (Esseen 1985; Stevenson & Rochelle 1984). Late summer litter does not represent annual litterfall because lichen litter in the forests of the western Cascades is eaten and decomposes rapidly (McCune & Daly 1994). However, such samples can be used to estimate epiphytic lichen biomass at the stand level (Sillett & Goslin 1999; Peck & McCune 1997; McCune 1994; Neitlich 1993). Annual variation in litterfall is one source of error in such estimates. Hence, this method should be based on samples collected during one late-summer period and is best used for estimating large relative differences in epiphytic lichen biomass among stands over a large area (McCune 1994).

Lichen litter was collected in a minimum of one stand per stand type. Of the 117 stands in which we collected lichen community data, we sampled 63 stands for lichen litter biomass (see Appendix A, Figure A2 for stand locations). The 63 stands were chosen to include the full range of stand types included in the 117 stands. In each stand, epiphytic macrolichen litter was sampled in 2 m radius circular plots ("litter plots"). Depending on the stand age and complexity of canopy structure, ten to fifteen litter plots were sampled for each stand (Figure 3.2; McCune 1994). Stands with obviously low lichen biomass (e.g., even-aged young stands, < 20 yrs) were sampled with 10 litter plots. Old growth (> 200 yrs), mature stands (81-200 yrs), and most stands with remnants were sampled with 15 litter plots.

Litter plots were placed along three transects per stand at randomly selected intervals, but constrained to ≥ 12 m to 30 m from the last litter plot (two transects if sampling only 10 litter plots). This achieved interspersion throughout the stand. Some litter plots were placed outside of the FHM plot boundaries, though still within the stand. Five litter plots were sampled per transect. Transects were established on the contour, using the FHM plot center as a starting point for the first transect. The other two transects were parallel to the first, separated by 12 m.

Sampling lichen litter biomass by functional group

Epiphytic macrolichens were divided into three functional groups based on their roles in the forest ecosystem (McCune 1993). These groups include "cyanolichens," which consist of all nitrogen-fixing lichens with cyanobacteria present as either the primary or secondary photobiont; the major contributors to this group included primarily *Lobaria oregana* and to a lesser degree *L. pulmonaria*. "Forage lichens" consist of all pendulous fruticose lichens used for forage by wildlife, primarily the genera *Usnea, Alectoria,* and *Bryoria*. "Matrix lichens" account for all remaining green-algal macrolichens, primarily foliose in growth form, and for which the genera *Platismatia* and *Hypogymnia* were most common in our study area.

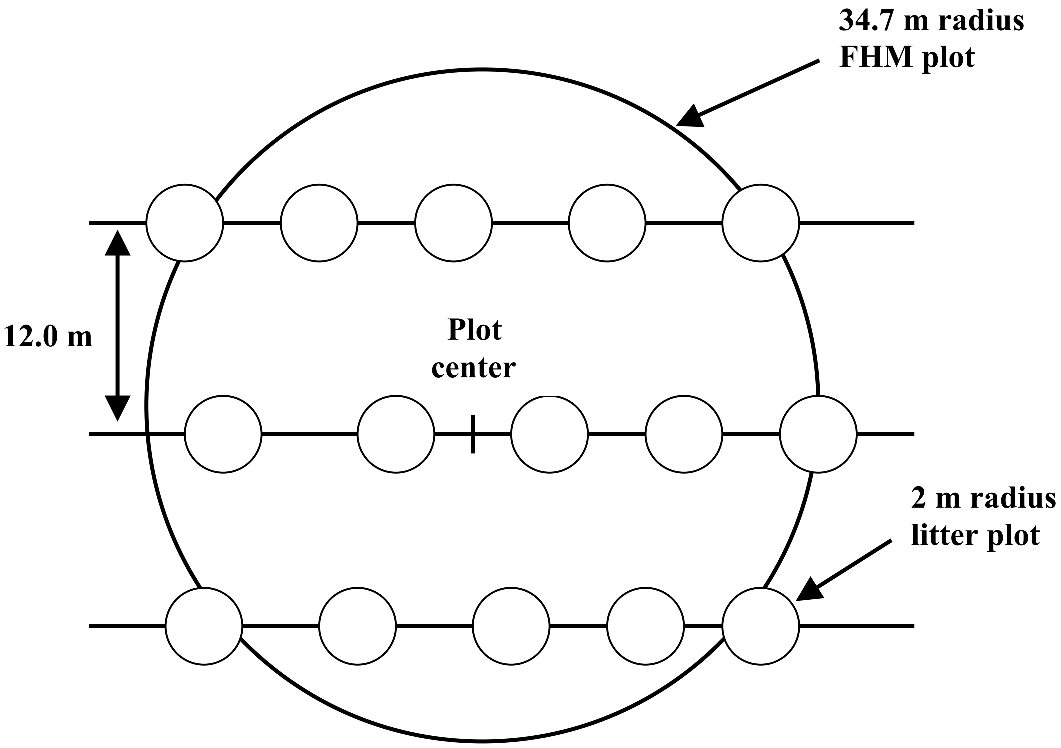


Figure 3.2. Sampling schematic, showing the placement of lichen litter plots within the stand.

We modified McCune’s (1994) litter-pickup method for estimating stand-level lichen biomass to expedite sampling across many stands at the landscape scale. The "reference method" was developed to sample lichen litter biomass from the forest floor more rapidly, while maintaining a similar level of accuracy to that obtained with the litter-pickup method. This method was adapted from Rosso et al. (2000) in which they visually estimated biomass of lichens and bryophytes in the forest canopy using air-dried reference samples for calibration. The reference method is also a modification of the abundance classes (defined by grams of lichen) used by Stevenson et al. (1998) to estimate arboreal forage lichen biomass. We combined modifications of these two approaches to visually estimate lichen litter biomass by functional group on the forest floor.

We estimated lichen litter biomasses during the late summers of 1997 – 1999, during which each of the 63 stands were sampled once for lichen litter. Within each litter plot, oven-dried samples from each functional group (0.1, 1.0, 5.0, 10.0 g) were used as references for calibrating estimates of lichen litter biomass in the field. To assess reliability of the method, estimates from the reference method were calibrated against true litter-pickup masses, using both litter-pickup and reference methods for one litter plot in each of 16 different stands. Two field collectors calibrated their biomass estimates from the lichen litter plot to true lichen masses (16 litter plots per field collector). The “picked-up” specimens were air-dried, then oven-dried at 60°C for 24 hours, and then weighed to the nearest milligram in the lab.

Daily calibrations were also made between estimates of biomass for individual clumps of lichen litter and true lichen masses for each functional group. These calibrations allowed field collectors to gauge the accuracy of their litter estimates. We also calibrated litter estimates between field collectors to improve precision of the estimates.

Analysis

The biomass of lichen litter for each functional group was averaged for each stand and then converted to epiphytic lichen biomass using the 100:1 ratio of epiphyte biomass to litter biomass (McCune 1994). The average epiphytic macrolichen biomass values were log-transformed [$\log_{10}(x + 1)$; where x was an estimate of oven-dried epiphyte biomass, kg/ha, based on lichen litter estimates] to reduce skewness in the analyses and for model development because epiphyte biomass values ranged across one to five orders of magnitude. All results are reported as biomass of epiphytic macrolichens (oven-dried; 10^x kg/ha).

Comparison of biomass sampling methods

Our minimum data quality objective was to visually estimate the true lichen litter biomass to the nearest order of magnitude. We compared visual estimates of biomass (collected with the reference method) with true litter masses (collected with the litter-pickup method) across 16 arbitrarily selected litter plots collected by each field observer. The biomass values from the litter pick-up method were considered "true values" when comparing the two sampling methods. Percent bias was calculated as the signed percent deviation from the true weight of lichen litter, while percent inaccuracy was the absolute value of the percent deviation from the true weight of the lichen litter:

$$\% \text{ Bias} = 100(x_{obs} - x_{true}) / x_{true}$$

$$\% \text{ Inaccuracy} = 100 \left| x_{obs} - x_{true} \right| / x_{true}$$

where x = grams of lichen litter (transformed to $\log_{10}(x+1)$ to reduce skewness), x_{obs} = biomass estimated visually, and x_{true} = actual biomass. Functional groups with zero biomass were not included in the percent bias and inaccuracy calculations.

For each collector, we calculated the signal-to-noise ratio for sampling lichen litter biomass (oven-dried; 10^x kg/ha) with the reference method. The "signal" was the range in biomass values from the litter-pickup method for all 16 litter plots in which both methods were employed. The "noise" was the mean squared error (s_{diff}^2) of the difference between estimated and true biomass values:

$$\text{Signal-to-noise ratio} = \text{range} / s_{diff}^2$$

A high signal-to-noise ratio indicates a biomass signal that is larger than the error associated with the sampling method.

Patterns of lichen biomass in the landscape

Non-metric multidimensional scaling (NMS; Mather 1976; Kruskal 1964) was used to ordinate forest stands in lichen species space, using lichen abundances from the community surveys. Ordination allows us to relate patterns in lichen biomass to gradients in lichen community composition and to environmental gradients. NMS is an iterative technique that is useful for detecting nonlinear gradients in community data. Stand scores from the rotated ordinations form the basis for estimating lichen biomass from lichen community composition.

We ordinated lichen community data from 117 stands in the Blue River watershed (63 of these stands were also sampled for lichen biomass). A total of 111 epiphytic macrolichens were found in the 117 stands (see Chapter 2 for species list). Only 71 of the 111 species were used in the ordination because we deleted species present in less than 5% of the stands to reduce noise in the data. The Sørensen distance measure was used in NMS with the Slow and Thorough autopilot mode in PC-ORD (best of 40 runs; McCune & Mefford 1999).

The ordination was rotated to maximize the correlation of canopy biomass for each lichen functional group with one axis. This required a separate rotation for each group, resulting in three different rotations of the one ordination. Overlays of environmental variables on the ordination were used to assess patterns in epiphytic lichen biomass in relation to environmental and lichen community gradients using Pearson's correlations (see Chapter 2 for lichen community gradient results). An arbitrary cut-off of $R^2 \geq 0.5$ was used when assessing correlations of environmental variables and species richness with the ordination axes. Correlations of 0.5 or greater were biologically meaningful in the ordinations.

We compared total lichen biomass and lichen biomass for each functional group among stand types for the 63 stands in which lichen biomass was sampled, ignoring the distinction among topographic classes (upland and riparian areas). Lichen biomass did not differ with respect to topographic class. Comparisons of lichen biomass in relation to all stand types were made separately for the two plant series using one-way analysis of variance in SPSS 8.0 (Anon. 1998). Stand types with fewer than two stands were omitted from the analysis.

Predictive models for estimating biomass

We developed predictive regression models using SPSS 8.0 (Anon. 1998) for estimating epiphytic macrolichen biomass for each functional group. Models were developed in three stages, each stage demanding more field data. The dependent variable in these models was epiphytic macrolichen biomass (oven-dried; 10^x kg/ha) by functional group. Models were developed based on the 63 stands in which lichen biomass was gathered. We did not use the models to make biomass estimates for the remaining stands in which we did not sample lichen biomass.

First, we developed models from topographic variables that can be derived from a digital elevation model (DEM) in GIS (the topographic variables we used, however, were collected on site). Second, we developed models based on both topography and stand structure. Obtaining the stand structure variables requires a site visit or access to a well-developed database that contains information on tree ages and remnant tree retention. The third step in our model building included variables based on topography, stand structure, and lichen communities. These models can be used only at sites where lichen community data have been collected.

In the third step, all classes of variables were not always represented in the best models.

Models based on lichen community data included abundance codes for the lichen species that dominated that functional group. For example, in PNW forests where cyanolichens are present, the majority of cyanolichen biomass consists of *Lobaria oregana* and *L. pulmonaria*. Therefore, abundances of *L. oregana* and *L. pulmonaria* were predictors that were considered when building the regression models for estimating cyanolichen biomass. Similarly, *Alectoria sarmentosa* is the most predominant forage lichen in the Blue River watershed and is the main contributor to forage lichen biomass. Therefore, abundance of *A. sarmentosa* was considered as a predictor when making models for forage lichen biomass.

Topographic predictors included: elevation, slope, potential incident radiation, heat load index, and topographic position (Table 3.1). Stand structure predictors included average total basal area of live and dead trees (m^2/ha) and the age index (AI; Table 3.1). Stand types were not used as predictors in the regression models because stand types are categorical and in some cases only one or two stands were sampled per stand type. The age index integrates the many stand types into a single continuous variable, representing what we conceive as a single biological phenomenon: the influence of old trees on lichen communities and biomass.

The age index is a combination of age credits for the stand age class and the retention of remnant trees, expressed as a percentage of old growth. In the field, stands were assigned to age classes based on age estimates. We used the median age of the younger cohort and of old growth to assign "age credits" to a stand (Table 3.2). The median age was calculated as a percentage of the median age for old growth (i.e., 300 yrs). The median age for old growth was an *a priori* estimate based on an estimate of the median age of old-growth forests in the Blue River watershed. This percentage represented the base age credits for each age class.

Table 3.1. Topography, stand structure, and lichen community descriptors considered as predictors (independent variables) in regression models estimating epiphytic macrolichen biomass for functional groups. Table shows the range or minimum and maximum values for each predictor across all 63 stands in which lichen biomass was collected.

Symbol	**Description**			
Topography predictors			**Min.**	**Max.**
E	elevation (m)		469	1469
PDIR	potential direct incident radiation ($MJ/cm^2/yr$); represents the amount of light a site potentially receives, derived from latitude, slope, and aspect		0.28	1.04
HLI	heat load index measures the amount of heat a site potentially receives during the day, derived from models based on latitude, slope, and aspect (McCune & Keon 2002)		0.39	1.04
SLP	slope (degrees)		0.9	36.0
Stand structure predictors			**Min.**	**Max.**
BA	total basal area of live and dead trees from prism measurements (m^2/ha)		4	129
AI	$\log_{10}$ (age index) of trees in a stand (see Table 3.2)		0.48	2
Interaction term			**Min.**	**Max.**
BA* E			4,455	117,570
Lichen community predictors		**Functional Group**	**Min.**	**Max.**
L	sum of abundance classes for *Lobaria oregana* and *L. pulmonaria* by stand	cyano	0	8

Table 3.1 (continued)

AL	abundance class for *Alectoria sarmentosa* in each stand	forage	0	5
S	NMS ordination scores for stands in lichen species space from the axis most strongly correlated with biomass of the lichen functional group	cyano forage matrix	-1.29 -0.87 -1.27	0.78 0.54 0.61
R	species richness of lichens in each functional group by stand	cyano forage matrix	0 2 10	12 10 26
A	sum of abundance classes for all lichens in each functional group by stand	cyano forage matrix	0 4 20	34 32 78

If remnants were present, the percent canopy cover class by remnants (15, 30, or 50%) was added to the base credits. Values for the raw age index ranged between 3 and 100, where 3 represented even-aged young stands and 100 represented old growth (Table 3.2). The age index was $\log_{10}$-transformed to improve linearity in the models (hereafter "$\log_{10}$ age index" will be referred to as "age index" or "AI").

The lichen community predictors included: species richness of each lichen functional group for a stand, the sum of abundance classes for all observed species in each lichen functional group, stand scores from the NMS ordination rotated for each functional group, and the abundance classes for selected individual species within a lichen functional group (usually the dominant species; Table 3.1). There were three stand scores from the ordination, one for the rotation for each lichen functional group. Meaningful interaction terms were retained if they contributed significantly ($p \leq 0.05$) to the model (only one interaction term, BA*E; Table 3.1).

Table 3.2. Definition of the age index, where the median age of a stand is calculated as a percentage of the median age of old growth (300 yrs assumed for all old growth, see text). Raw age index = ((median age/median age of old growth)*100) + % remnants. AI represents $\log_{10}$(raw age index).

Stand Type	Median age	Raw age index	AI
Young, < 20 yrs, no remnants	10	3	0.48
Young, < 20 yrs, 15% remnants	10	18	1.26
Young, < 20 yrs, 30% remnants	10	33	1.52
Young, < 20 yrs, 50% remnants	10	53	1.72
Pole, 21-80 yrs, no remnants	50	17	1.23
Pole, 21-80 yrs, 15% remnants	50	32	1.51
Pole, 21-80 yrs, 30% remnants	50	47	1.67
Pole, 21-80 yrs, 50% remnants	50	67	1.83
Mature, 81-200 yrs, no remnants	140	47	1.67
Mature, 81-200 yrs, 15% remnants	140	62	1.79
Mature, 81-200 yrs, 30% remnants	140	77	1.89
Mature, 81-200 yrs, 50% remnants	140	97	1.99
Old growth, > 200 yrs	300	100	2.00

Because patterns in lichen biomass differed among functional groups, predictive models for estimating lichen biomass were determined separately for each group using each of the three classes of predictors described in the steps above. We calculated the standard deviation of the unstandardized residuals for each regression model. The standard deviation of the biomass estimate was reported for each model using a 95% confidence interval.

Scatterplots of cyanolichen biomass and the predictors revealed that both nonlinear (3-parameter sigmoid) and linear terms were needed in the models. We combined these by first using nonlinear regressions, obtaining the residuals from those regressions, then using stepwise-linear regression of the residuals against the remaining predictors. The total coefficient of determination was combined for both models:

Overall $R^2 = R_Y^2 + (1 - R_Y^2) * R_Z^2$

where R_Y^2 is the coefficient of determination from the nonlinear model based on topography and forest structure, and R_Z^2 is the coefficient of determination from the stepwise-linear model used to predict the residuals from the nonlinear regression. The form of the nonlinear equation was:

$$B = \frac{ax_1}{1 + \left(\frac{x_2}{b}\right)^c}$$

where x_1 is the AI, x_2 is elevation, b is a fitted parameter controlling the steepness of the elevation response, and c is a fitted parameter controlling the elevation of the inflexion point of the biomass response. The lower asymptote is fixed at zero biomass. The upper asymptote (maximum biomass at a given elevation) is controlled by the parameter a.

Stepwise-linear regression was used to develop predictive models for forage and matrix lichen biomass. Scatterplots did not suggest a need for nonlinear terms. Initial models from these regressions had many statistically significant parameters ($p \leq 0.05$), but their inclusion in the models explained very little additional variation. Consequently, for the sake of parsimony, we included a term in a model if it resulted in a minimum increase of the coefficient of determination (adjusted R^2) by 0.05.

RESULTS

Comparison of biomass sampling methods

The reference method was both reliable and expeditious for sampling lichen litter biomass. Our objective was to estimate epiphytic lichen biomass to the nearest order of magnitude, and we achieved much better accuracy than this using the reference method. The average percent inaccuracy of the reference method ranged from 4 – 11% across functional groups and collectors, where 100% inaccuracy represented one order of magnitude difference between samples (Table 3.3). In general, inaccuracy was low and varied little between collectors. The reference method slightly overestimated lichen litter (positive % bias). The degree of positive bias varied between collectors for each functional group (Table 3.3).

Table 3.3. Comparisons of two methods for sampling lichen litter biomass on a log-scale: reference method and litter-pickup method. True lichen litter mass was based on the litter-pickup method. Average percent bias and inaccuracy of lichen biomass estimates from the reference method are shown for each functional group. Inaccuracy and bias were measured as percentages and positive bias is indicated by a plus sign. Standard errors (SE) are reported for each calculation. The value *sdiff*^{2} is the variance of the difference between the estimates based on each sampling method. Signal-to-noise is the ratio of the range in estimates from the litter-pickup method across all samples to the mean squared error of the difference between sampling methods. Sample sizes (N) vary because some plots had zero biomass, and were not included in the comparisons. SB and DM are the two collectors.

		Bias		**Inaccuracy**		**Signal-to-Noise**	
Collector	**N**	**%**	**SE**	**%**	**SE**	***sdiff*^{2}**	**ratio**
Forage lichens							
SB	15	+2.8	0.1	11.2	3.4	0.09	39.47
DM	15	+6.9	3.4	10.4	2.7	0.07	60.11
Cyanolichens							
SB	7	+5.9	5.0	11.4	3.0	0.12	22.66
DM	6	+1.5	1.8	4.0	0.7	0.02	85.59
Matrix lichens							
SB	15	+1.5	3.4	7.3	2.8	0.04	77.46
DM	14	+4.1	3.3	9.2	2.4	0.12	27.25

The inaccuracies (4 – 11%) are inconsequential, considering the huge range of estimated biomass values (over 4 orders of magnitude). This contrast can be quantified with signal-to-noise ratios. These ratios were high overall, indicating that the range of estimated biomasses was much larger than the error associated with the reference method. The signal-to-noise ratio varied by observer and by lichen functional group (Table 3.3).

The reference method was expeditious, requiring approximately 5 to 15 minutes to sample one litter plot. Consequently, when sampling 15 litter plots per stand, we were able to sample a total of 2 to 3 stands per day. In comparison, the litter-pickup method averaged approximately 30 to 65 minutes per litter plot (one stand per 1 to 2 days), and was especially slow in complex older stands with heavy litter. The slowest aspect of the reference method was training field collectors for sampling and regularly calibrating estimates to actual oven-dried weights of lichen.

Patterns of lichen biomass in the landscape

Elevation gradient

Elevation was the strongest environmental gradient in the ordination describing patterns in lichen communities and biomass in the Blue River watershed (Figure 3.3; Table 3.4; see also Chapter 2). The elevation gradient was related to the vascular plant series, where most stands at higher elevations were in the *Abies* series and low elevation stands were in the *Tsuga* series. Epiphytic cyanolichens were nearly absent from high elevation *Abies* stands, dropping off at approximately 900 – 1,000 m (Figure 3.4A). Biomass of forage lichens increased slightly with elevation (Figure 3.4B), reaching the highest biomass in high elevation old-growth stands (median biomass in *Abies* old-growth stands, 1,443 kg/ha). Forage lichens in higher elevation stands were typically present in large, dense clumps, covering

Figure 3.3. Three different rotations of the NMS ordination of stands in lichen species space based on the 71 species that occurred in more than 5% of the 117 stands. The ordination was rotated three times, each time maximizing the correlation of biomass of a lichen functional group with axis 1 (see Table 3.4). Vector overlays show the directional correlations of elevation and cyanolichen species richness with the ordination, radiating from the ordination centroid (only showing vectors for variables with $R^2 \geq 0.5$). The length of the vectors is proportional to the strength of the correlation (R^2) between the axis scores and the indicated variable. Symbols code plant series: open triangles = *Tsuga*; solid triangles = *Abies*). **(A)** Ordination rotated to maximize the correlation of epiphytic **cyanolichen** biomass (oven-dried; 10^x kg/ha) with axis 1 ($R^2 = 0.65$). **(B)** Ordination rotated to maximize the correlation of epiphytic **forage lichen** biomass (oven-dried; 10^x kg/ha) with axis 1 ($R^2 = 0.33$). **(C)** Ordination rotated to maximize the correlation of epiphytic **matrix lichen** biomass (oven-dried; 10^x kg/ha) with axis 1 ($R^2 = 0.40$).

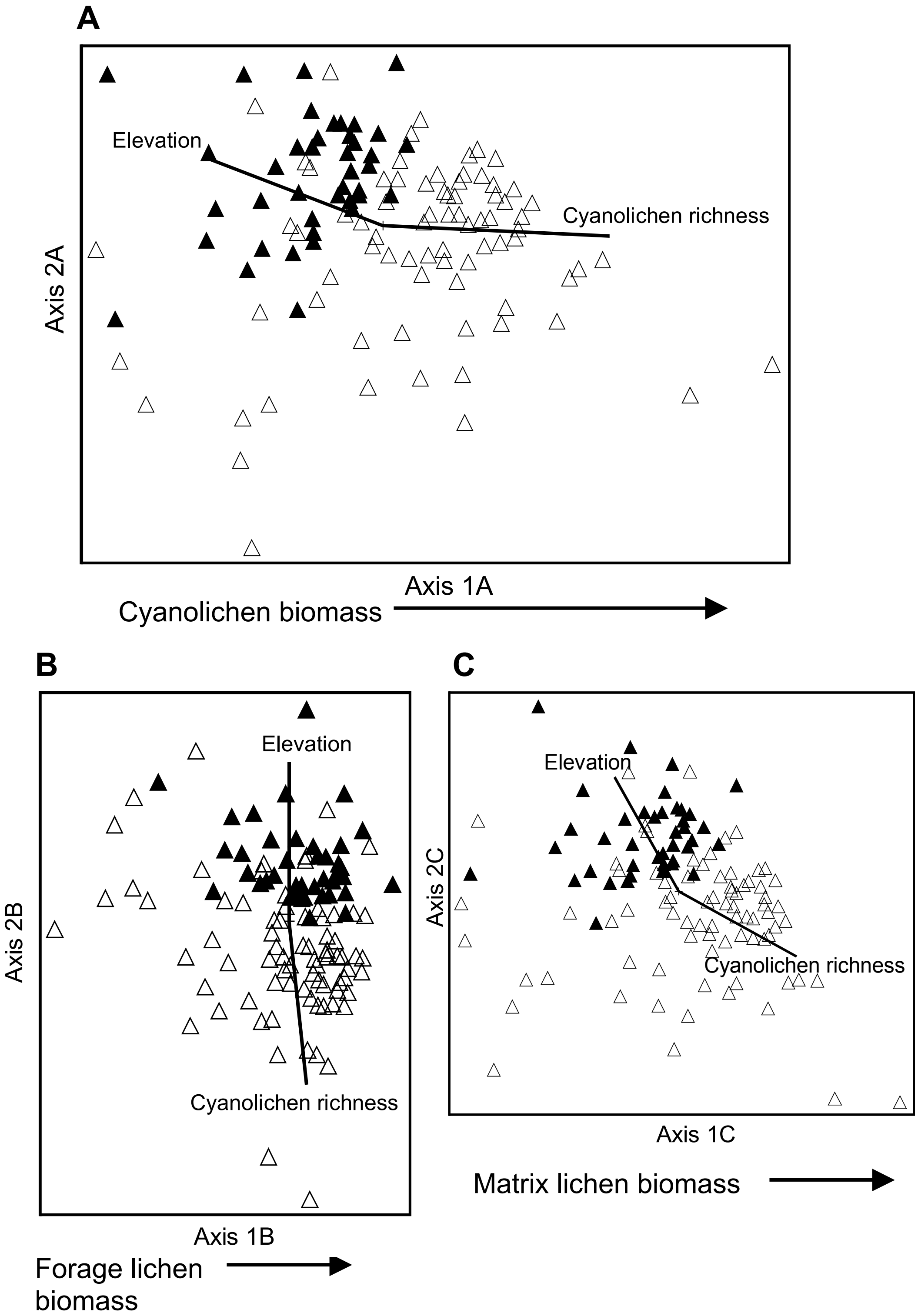

A
Elevation
Cyanolichen richness
Axis 2A
Axis 1A
Cyanolichen biomass
B
Elevation
Cyanolichen richness
Axis 2B
Axis 1B
Forage lichen biomass
C
Elevation
Cyanolichen richness
Axis 2C
Axis 1C
Matrix lichen biomass

Figure 3.3

Table 3.4. Variance explained by the axes of three separate rotations of a 2-dimensional NMS ordination solution, each rotation maximizing the correlation of epiphytic lichen biomass (oven-dried; 10^x kg/ha) for a particular functional group with axis 1 (see Figure 3.3 for ordinations). R^2 is the coefficient of determination for lichen biomass with ordination scores from axis 1.

		Variance explained in original distances (%)		
Rotation for functional group	**R^2**	**axis 1**	**axis 2**	**Total**
Cyanolichens	0.65	57.5	24.6	82.1
Forage lichens	0.33	31.5	50.7	82.1
Matrix lichens	0.40	57.3	24.9	82.1

over 50% of the boles and branches in the stand. Matrix lichen biomass did not change with elevation (Figure 3.4).

Stand types

Overall comparisons of lichen biomass with stand types were made for the 63 stands in which epiphytic macrolichen biomass was visually estimated. Total epiphytic macrolichen biomass across all functional groups differed among stand types in both the *Tsuga* (from a one-way ANOVA; F = 10.47, p = << 0.001) and *Abies* series (F = 7.17, p = 0.001; Figure 3.5). Cyanolichen biomass differed among stand types in the *Tsuga* series (F = 6.03, p = <<<0.001; Figure 3.6). In contrast, there was very little cyanolichen biomass in the *Abies* forests and when found, it did not seem related to stand types. Forage lichen biomass differed among stand types in both the *Tsuga* (F = 7.88, p = << 0.01) and *Abies* series (F = 5.21, p = 0.01), as did matrix lichen biomass (*Tsuga*, F = 5.55, p = << 0.001; and *Abies,* F = 10.88, p = << 0.001; Figure 3.6).

Figure 3.4. Estimated biomass (oven-dried; 10^x kg/ha) of epiphytic macrolichens by functional group in stands versus elevation (m). Symbols code plant series: open triangles = *Tsuga*; solid triangles = *Abies*. Biomass values are shown for all stands with the exception of even-aged young stands (< 20 yrs); in general these stands have very little or zero lichen biomass.

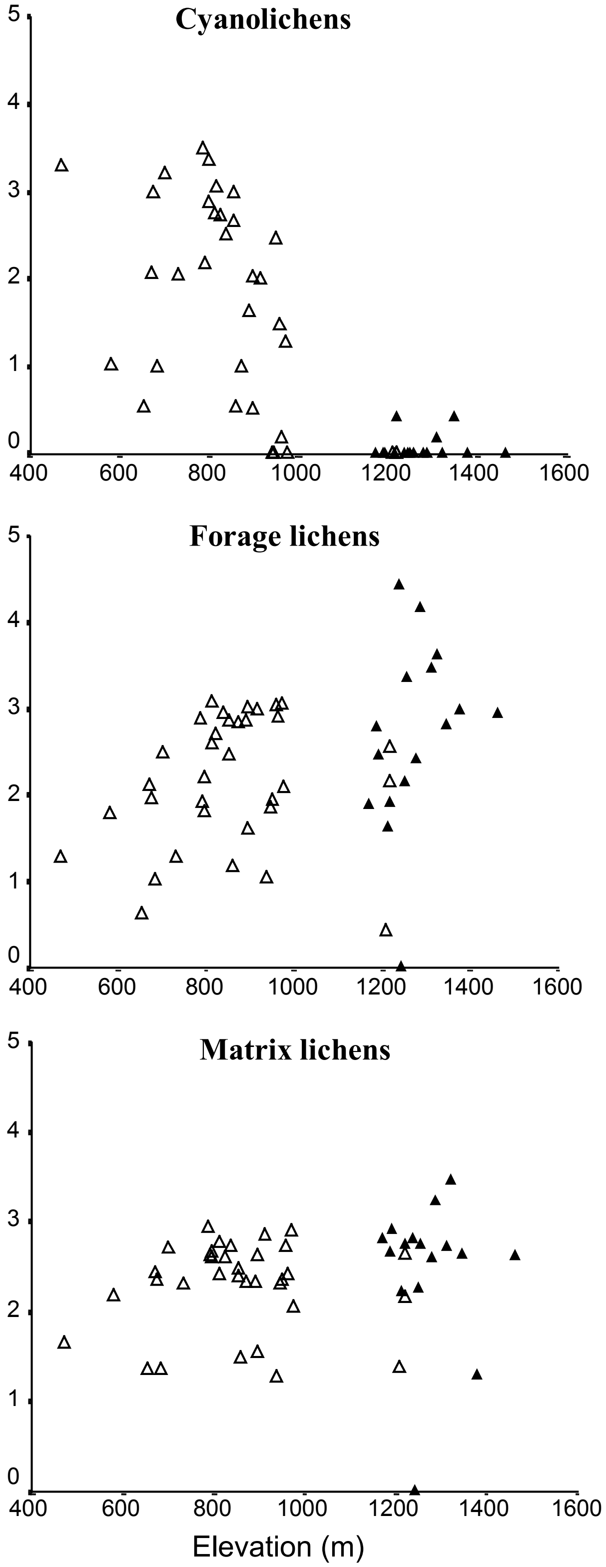
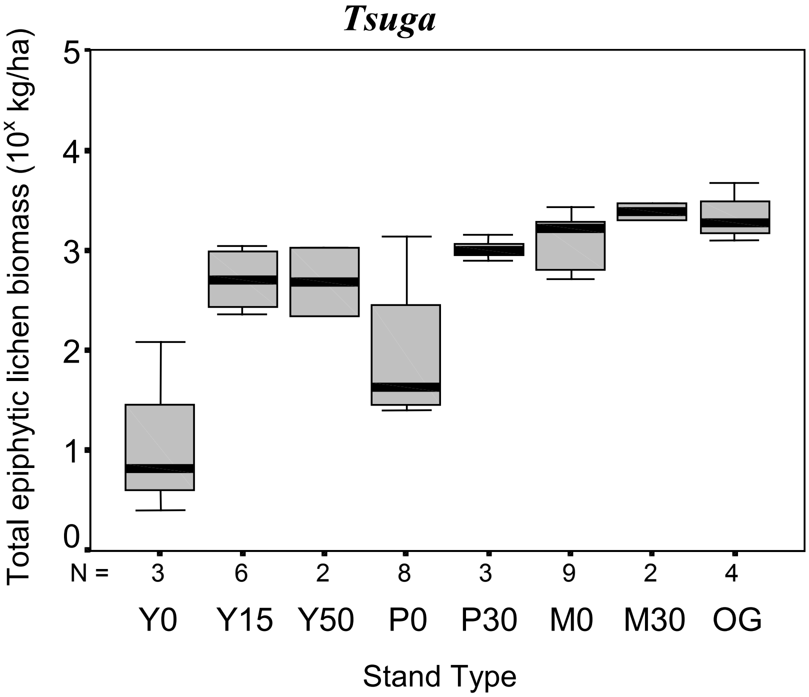

Cyanolichens
Forage lichens
Matrix lichens
0
1
2
3
4
5
400
600
800
1000
1200
1400
1600
Elevation (m)

Figure 3.4

Figure 3.5. Distribution of estimated total epiphytic lichen biomass (oven-dried; 10^x kg/ha) in different stand types for the *Tsuga* and *Abies* series. Stand types are abbreviated as: Y0 = even-aged young (< 20 yrs), Y15 = young with 15% remnants, Y50 = young with 50% remnants, P0 = even-aged pole (21-80 yrs), P15 = pole with 15% remnants, P30 = pole with 30% remnants, M0 = even-aged mature (81-200 yrs), M15 = mature with 15% remnants, M30 = mature with 30% remnants, OG = old growth (> 200 yrs). 50% of the data falls within the interquartile range of the box, with the top of the box representing the 75th percentile and the bottom the 25th percentile. The horizontal line in the box represents the sample median. The whiskers on either end of the box represent the range of values; all fell within 1.5 box lengths and none were considered outliers. Stand types with N < 2 are not shown.


Tsuga
Total epiphytic lichen biomass (10^x kg/ha)
5
4
3
2
1
0
N =
3
6
2
8
3
9
2
4
Y0
Y15
Y50
P0
P30
M0
M30
OG
Stand Type

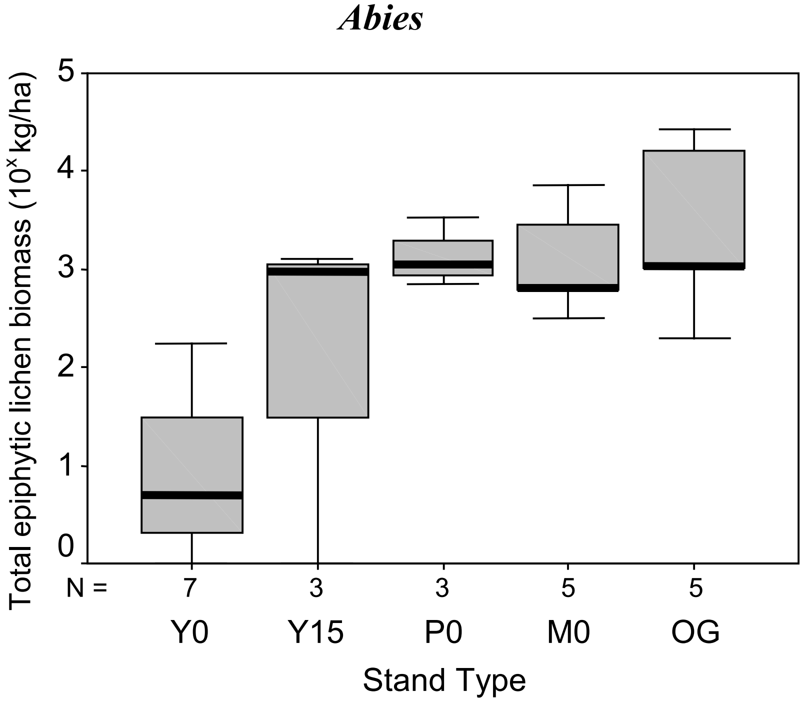

Abies
Total epiphytic lichen biomass (10^x kg/ha)
5
4
3
2
1
0
N =
7
3
3
5
5
Y0
Y15
P0
M0
OG
Stand Type

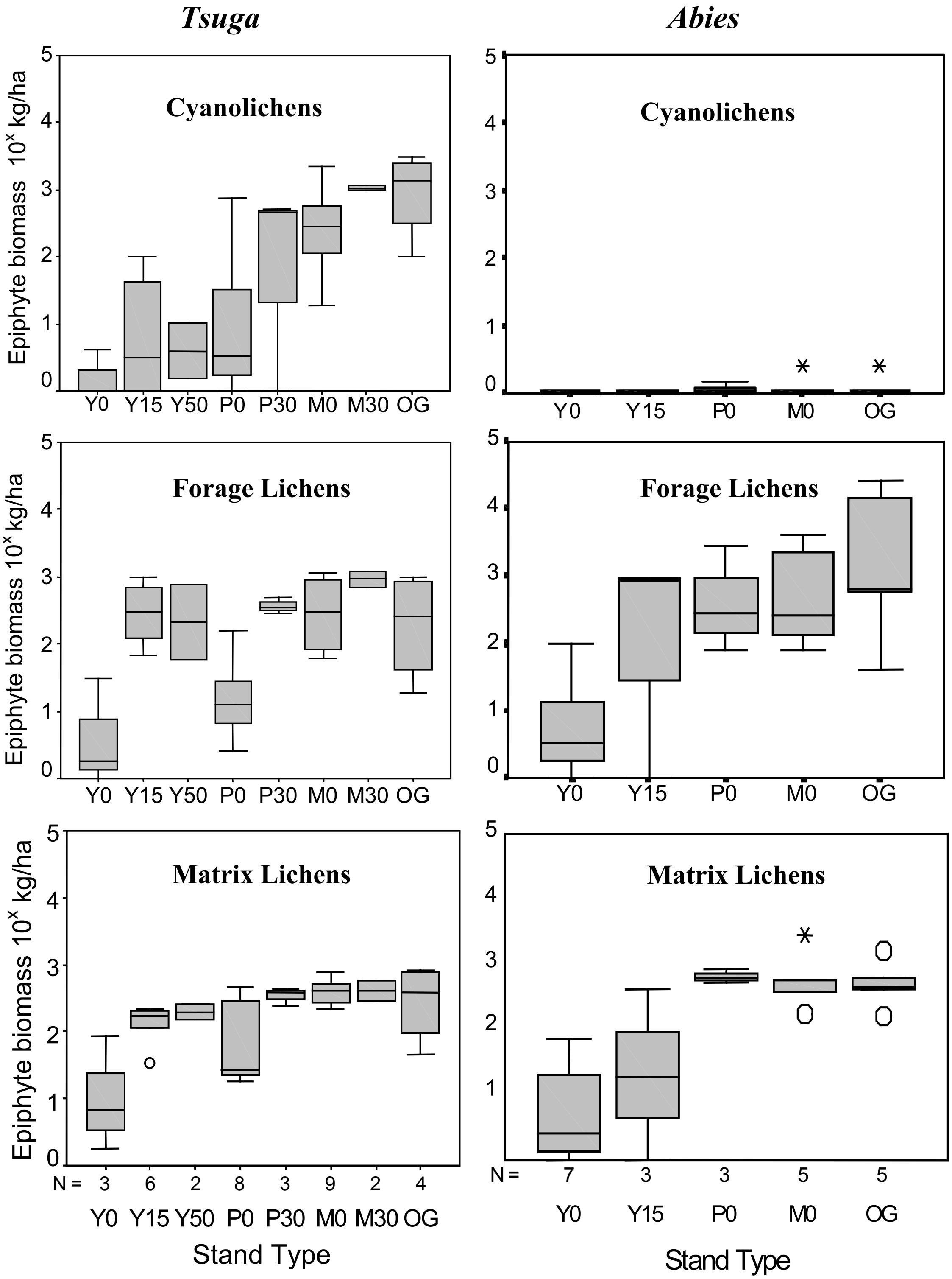
Figure 3.5

Stand age

Differences in total epiphytic macrolichen biomass were related to stand age in both plant series (Figure 3.5). Total lichen biomass differed across all even-aged stands and old growth in the *Abies* series. However, in the *Tsuga* series, total lichen biomass did not differ between even-aged young and pole stands, but biomass in these stands was different from that in even-aged mature stands and in old growth. In both plant series, lichen biomass was lowest in even-aged young stands (Figure 3.5). Total lichen biomass was similar in even-aged mature and old-growth stands in both plant series (Figure 3.5). Biomass was very high in some even-aged mature stands and old-growth stands in the *Abies* series, our estimates reaching a maximum of approximately 26,915 kg/ha, most of this being forage lichens (primarily *Alectoria sarmentosa*). However, the median total biomass for old growth was slightly higher in the *Tsuga* series (1,905 kg/ha) than in the *Abies* series (1,070 kg/ha; Figure 3.5).

In the *Tsuga* series, cyanolichen biomass was highest in older stands (Figure 3.6). Cyanolichens were absent from most young stands (< 20 yrs; median biomass 0 kg/ha), while the highest levels of cyanolichen biomass were in old-growth stands (ranging from 99 to 3,089 kg/ha; median 1,377 kg/ha). Four old-growth stands were sampled for lichen biomass in the *Tsuga* series, three of which were sampled between 450 and 800 m elevation, these stands had cyanolichen biomass ≥ 1,000 kg/ha. The fourth old-growth stand was sampled at 916 m and had much lower cyanolichen biomass (99 kg/ha) than the other stands at relatively lower elevations. Cyanolichen biomass was positively correlated with cyanolichen species richness ($R^2 = 0.72$; Figure 3.3A) and with richness of all macrolichens ($R^2 = 0.32$) in the *Tsuga* series, suggesting that older stands host both abundant and diverse lichen communities. In contrast, only 8 of the 50 stands sampled for lichen communities in the *Abies* series supported cyanolichens and when present, they

Figure 3.6. Distribution of estimated epiphytic macrolichen biomass (oven-dried; 10^x kg/ha) by functional groups in even-aged stands and stands with remnants in both the *Tsuga* and *Abies* series. Stand type abbreviations are described in Figure 3.5. 50% of the data falls within the interquartile range of the box, with the top of the box representing the 75th percentile and the bottom the 25th percentile. The horizontal line in the box represents the sample median. The whiskers on either end of the box represent the range of values that fell within 1.5 box lengths; these are extreme values that were not considered outliers. Circles indicate moderate outliers (1.5 to 3 box lengths from either end of the box) and asterisks indicate extreme outliers (> 3 box lengths from either end). Stand types with N < 2 are not shown.



Tsuga
Abies
Cyanolichens
Forage Lichens
Matrix Lichens
Epiphyte biomass 10^x kg/ha
0
1
2
3
4
5
Y0 Y15 Y50 P0 P30 M0 M30 OG
Y0 Y15 P0 M0 OG
N = 3 6 2 8 3 9 2 4
N = 7 3 3 5 5
Stand Type
Stand Type

Figure 3.6

were always in low abundance. Cyanolichen biomass was found in only 4 of these 8 stands.

In even-aged stands of the *Tsuga* series, forage lichen biomass increased with stand age and leveled off in mature and old-growth stands. Similarly, forage lichen biomass in the *Abies* series increased with age, but was greatest in old-growth stands, in some stands reaching very high levels (26,915 kg/ha of forage lichen biomass in one old-growth stand; Figure 3.6). Forage lichen biomass was not correlated with forage lichen species richness ($R^2 = 0.01$) or with species richness of all macrolichens ($R^2 = 0.07$). *Alectoria sarmentosa* was the leading contributor to forage biomass in the Blue River watershed; other forage species such as *Bryoria* and *Usnea* were only minor contributors. Forage lichen biomass in even-aged pole stands was greater in the *Abies* series (median biomass 286 kg/ha) than in the *Tsuga* series (median biomass 11.0 kg/ha).

The matrix lichen functional group includes many ubiquitous lichen species that are considered early colonizers (e.g., the genera *Hypogymnia* and *Platismatia*). These genera are often abundant across stands of various ages. Matrix lichen biomass in even-aged stands generally increased with stand age, but leveled off in mature and old-growth stands for both plant series (reaching 500 – 600 kg/ha; Figure 3.6). Matrix lichen biomass was positively correlated with matrix lichen species richness ($R^2 = 0.30$) and with species richness of all macrolichens ($R^2 = 0.25$).

Remnant tree retention

In the *Tsuga* series, the presence of remnant trees in young and pole stands was related to increased lichen biomass from similar even-aged stands (Figure 3.5). However, the presence of remnant trees in mature stands was not related to differences in total lichen biomass from even-aged mature stands. Similarly, greater macrolichen biomass was related to remnant tree retention in young stands of the *Abies* series (Figure 3.5). Pole and mature stands with remnants were few (N < 2 per stand type) in the *Abies* series and were not included in these analyses.

In the *Tsuga* series, cyanolichen biomass was greater in stands with remnants than in even-aged stands. In young stands (< 20 yrs) with 15% retention cyanolichen biomass reached 1,000 kg/ha, while cyanolichen biomass only reached 10 kg/ha in young stands with 50% retention (Figure 3.6). Cyanolichen biomass was greater by two orders of magnitude in pole stands (21-80 yrs) with remnants as compared to even-aged pole stands in the *Tsuga* series (Figure 3.6). In the *Tsuga* series, cyanolichen biomass in mature stands with remnants (median ~ 1,000 kg/ha) was similar to that of even-aged mature stands and old growth. Cyanolichens were nearly absent in the *Abies* series, for which no clear patterns emerged with respect to remnant retention.

In both plant series, stands with remnant retention had greater forage lichen and matrix lichen biomass than even-aged stands in the same age class. In the *Tsuga* series, forage and matrix lichen biomass was much higher in young and pole stands with remnants than in similar even-aged stands (Figure 3.6). In the *Abies* series, forage biomass was much higher in young stands with 15% remnant retention (median forage lichen biomass 850 kg/ha) than in even-aged young stands (median forage lichen biomass 2.4 kg/ha; stands with > 15% remnant retention were not sampled in the *Abies* forests; Figure 3.6). However, matrix lichen biomass was only slightly higher in young stands with 15% remnant retention (median 18.0 kg/ha) as compared to even-aged young stands (median 1.6 kg/ha) in the *Abies* series. *Tsuga* pole stands with 30% remnant retention had forage biomass one order of magnitude higher than even-aged pole stands. Differences in forage and matrix lichen biomass between even-aged mature stands and mature stands with remnants in the *Tsuga* series were less dramatic (Figure 3.6).

Riparian and upland stands

We found no clear differences in epiphytic lichen biomass in relation to upland and riparian forests. Only 5 of the 63 stands in which we sampled lichen biomass were along perennial fish-bearing streams and 8 stands were along perennial non fish-bearing streams. The remaining stands were in uplands or were located along small intermittent streams. The small number of stands along perennial streams may have limited our ability to detect any differences in epiphytic lichen biomass in these stands when compared to upland forests.

Predictive models for estimating lichen biomass

Estimating cyanolichen biomass

Elevation was the strongest topographic predictor for estimating cyanolichen biomass. We used a nonlinear regression model for this relationship because cyanolichen biomass followed a sigmoid pattern with elevation (Table 3.5). A predictive model for estimating cyanolichen biomass based solely on elevation will overestimate biomass in young forests at low elevations. To account for this, the nonlinear model included both elevation and AI (i.e., the logarithm of the age index, Table 3.2) as predictors (Table 3.5; Figure 3.7A). The AI quantifies stand structure, accounting for the age of the stand and the level of remnant tree retention in a given stand, expressed as a percentage of old growth (see Methods). The model based on elevation and AI had substantial predictive power for cyanolichen biomass ($R^2 = 0.81$).

Epiphytic cyanolichen biomass was related to lichen community composition in the ordination ($R^2 = 0.65$; Figure 3.3A; Table 3.4). However, the ordination scores explained very little beyond that explained by elevation and AI in the predictive models for cyanolichen biomass. Other community variables such as the sum of abundance for *Lobaria oregana* and *L. pulmonaria* and cyanolichen species richness were better predictors for explaining the additional variation in the model. The regression model for predicting cyanolichen biomass from topography, stand structure, and lichen community variables was based on two regression models. The first model was the nonlinear regression in which elevation and the AI were the best predictors of cyanolichen biomass (see Table 3.5). The remaining predictors (including all lichen community predictors) were used in a stepwise-linear regression to predict the unexplained residuals from the nonlinear model. The residuals were best predicted by the sum of abundance classes for *Lobaria oregana* and *L. pulmonaria* and by cyanolichen species richness, explaining additional variation in cyanolichen biomass (Table 3.5). The total variation explained by the combination of these two models was 85% (Table 3.5).

Table 3.5. Predictive equations from nonlinear and stepwise-linear regression for estimating epiphytic macrolichen biomass ("B;" oven-dried, 10^x kg/ha) of functional groups using topographic, stand structure, and lichen community predictors (see Table 3.1 for detailed descriptions of predictors). E is elevation (m), AI is the $\log_{10}$(raw age index), L is the sum of abundance classes for *Lobaria oregana* and *L. pulmonaria*, R is lichen species richness for a given functional group, AL is the abundance class for *Alectoria sarmentosa*, BA*E is the interaction term of average total basal area (m^2/ha) by elevation, and A is the sum of abundance classes for all lichens in a given functional group. Best models are shown with a 95% confidence interval for the estimates (CI). Adjusted R^2 is reported for linear regression models, while R^2 is reported for the nonlinear models (indicated with an asterisk).

Predictors	**Equation**	**CI**	**Adj. R^2**
CYANOLICHENS			
Topography			
E	$B = 2.30 / \left(1 + (E/924.95)^{23.36}\right)$	±1.48	0.64*
Topography and stand structure			
E, AI	$B = (1.50 * AI) / \left(1 + (E/937.75)^{26.99}\right)$	±1.07	0.81*

Table 3.5 (continued)

Topography, stand structure, and lichen community			
E, AI	$B = (1.50 * AI) / (1 + (E/937.75)^{26.99})$	±1.07	0.81*
and			
L, R	[‡]Residuals = $-0.15 + 0.17 L - 0.10 R$	±0.95	0.20
			Overall $R^2 = 0.85$
FORAGE LICHENS			
Topography and stand structure			
AI, E	$B = -1.38 + 1.55 AI + 0.001 E$	±1.53	0.47
Stand structure and lichen community			
AI, AL	$B = -1.26 + 1.26 AI + 0.44 AL$	±1.14	0.55
MATRIX LICHENS			
Topography and stand structure			
AI, BA*E	$B = 0.52 – 0.90 AI + 0.000008 BA*E$	±1.09	0.57
Stand structure and lichen community			
AI, S	$B = -0.10 + 0.95 AI + 0.02 S$	±1.07	0.58

[‡] See Methods section describing the development of predictive models for cyanolichens.

Estimating forage lichen biomass

We found no strong predictive models for estimating forage biomass based on only topographic variables (maximum adjusted $R^2 = 0.19$). However, forage lichen biomass can be predicted from elevation and AI (Table 3.5; Figure 3.7B).

Figure 3.7. Scatterplots for selected predictors from regression models estimating epiphyte biomass (oven-dried; 10^x kg/ha) for lichen functional groups. (**A**) Scatterplot of cyanolichen biomass and age index where solid symbols code stands at < 950 m and open symbols code stands at > 950 m in elevation ($R^2 = 0.55$ for stands < 950 m; $R^2 = 0.06$ for stands > 950 m). (**B**) Scatterplot of forage lichen biomass and age index ($R^2 = 0.43$). (**C**) Scatter plot of matrix lichen biomass and age index ($R^2 = 0.53$). Lines indicate the simple linear relationship between lichen biomass and the selected predictors.

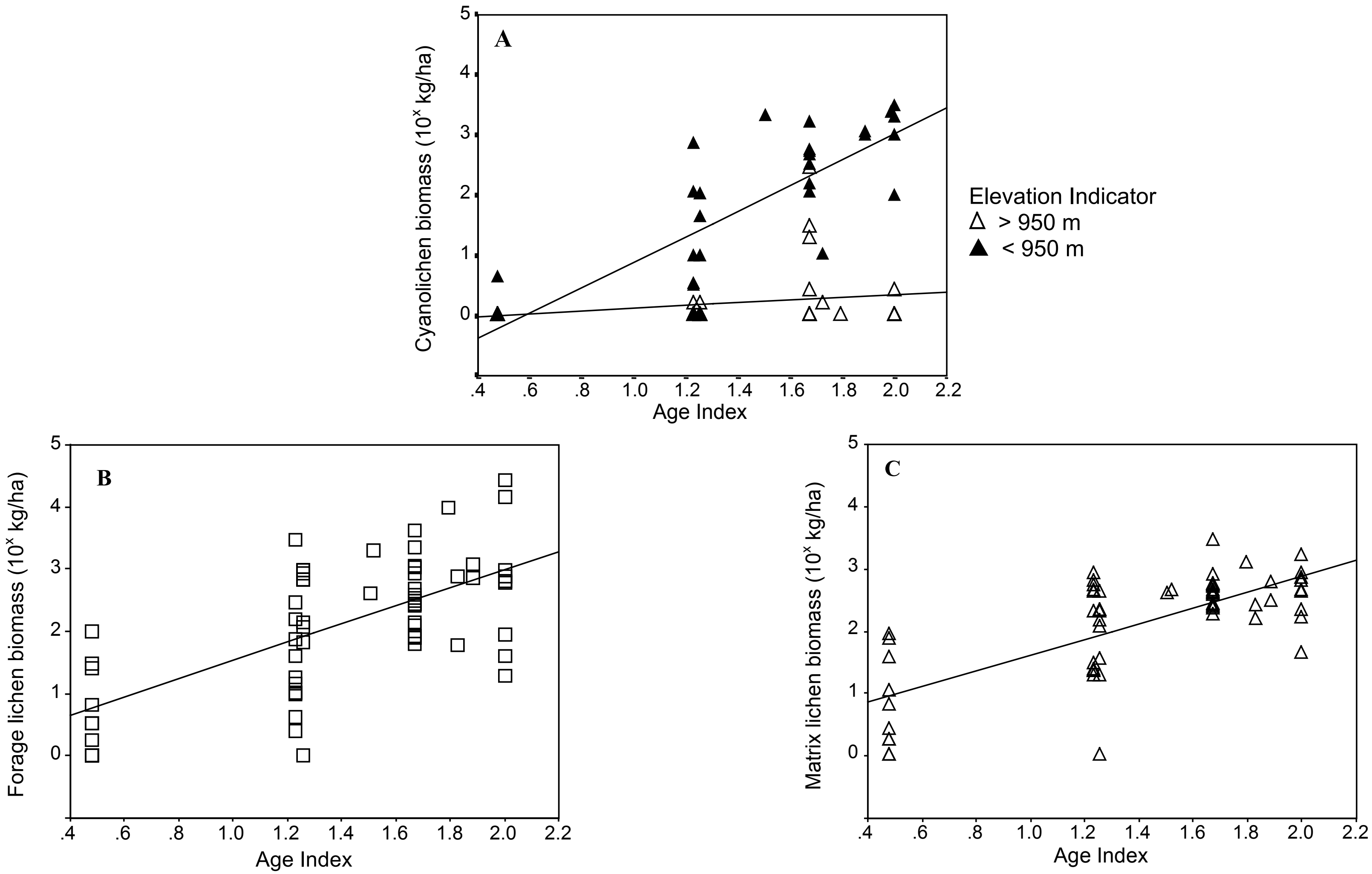

A
Cyanolichen biomass (10ˣ kg/ha)
5
4
3
2
1
0
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
Age Index
Elevation Indicator
△ > 950 m
▲ < 950 m
B
Forage lichen biomass (10ˣ kg/ha)
C
Matrix lichen biomass (10ˣ kg/ha)

Figure 3.7

The best regression model was based on AI and the abundance of *Alectoria sarmentosa.* In this model, no topographic variables were significant (at $p \leq 0.05$) predictors. Most forage lichen biomass was composed of *A. sarmentosa,* especially in the higher elevation stands. Unlike cyanolichens, forage lichen biomass was not as highly correlated with lichen community composition ($R^2 = 0.34$; Table 3.4).

Estimating matrix lichen biomass

Topographic variables were poor predictors for matrix lichen biomass and are not reported (maximum adjusted $R^2 = 0.03$). The model based on AI and the interaction term for total basal area by elevation were the best predictors for estimating matrix biomass when using only topographic and stand structure predictors (Table 3.5; Figure 3.7C). The best model based on all available predictors included the AI and the sum of abundance classes for all matrix lichens found in a stand (no topographic variables were significant at $p \leq 0.05$ in the model; Table 3.5).

Matrix lichens were present and abundant in most stands in the Blue River watershed. Matrix lichen biomass was correlated with lichen community composition in the ordination ($R^2 = 0.41$; Figure 3.3), however the ordination scores explained little variation beyond other variables (such as elevation and AI).

DISCUSSION

Evaluation of sampling methods

The reference method for sampling biomass of lichen litter was more time efficient than the litter-pickup method (McCune 1994). The reference method is useful for biomass estimates that are accurate to within 0.04 to 0.11 orders of magnitude. Annual variation in lichen litterfall introduces additional unmeasured error (McCune 1994; Boucher & Stone 1992; Esseen 1985). To refine the method, we recommend that collectors focus on calibration of visual litter estimates to true lichen weights (litter-pickup) at the litter plot level. Calibrating to individual lichen litter clumps is also useful for training.

In addition, we recommend using individual reference samples for certain lichen species, as well as for each lichen functional group. Some species within a functional group have very different ratios of mass to apparent volume. For example, the matrix lichen functional group included mostly foliose and a few fruticose lichens. It was more difficult to estimate the biomass of this group due to the varied morphology. The matrix lichen *Sphaerophorus globosus* (fruticose lichen) has a dense medulla and is often much heavier than other matrix lichens. Separate reference samples and estimates for *S. globosus* could improve the accuracy of litter estimates for the matrix lichen group. McCune et al. (1997*a*) also suggested separating *S. globosus* and other tufted fruticose lichens from foliose lichens in the matrix lichen group. The between-observer variation of matrix lichen litter estimates may be partly attributed to the variable morphology of species in this group.

Forage lichens are pendulous and tend to clump together in thick mats, especially those in higher elevation forests. Many of these mats become brittle and very dense once they settle into the forest floor. It was difficult to visually estimate the mass of these dense clumps of lichen litter. In an attempt to account for this problem, large clumps of lichen were handled to assess how “dense” they were, improving accuracy of lichen litter estimates. However, the more lichens were handled, the more time it took to sample a litter plot. We made separate reference samples for the dense forage lichen clumps to assist in better calibration of our estimates. In summary, we recommend the reference method as a useful and expeditious method for estimating forest lichen litter at the stand level. Additionally, this method could be used to estimate lichen litter biomass at the species level, rather than by functional group.

Patterns of lichen biomass in the landscape

Epiphytic macrolichen biomass of all functional groups generally increased with stand age. Lichen biomass in young even-aged stands was low (< 10 kg/ha) in both plant series. In the *Tsuga* series, total macrolichen biomass was high (median 1,000 kg/ha) in pole stands with 30% remnants, in mature stands with and without remnants, and in old growth. In the *Abies* series, median macrolichen biomass was ~1,000 kg/ha in young stands with 15% remnant retention, in even-aged pole stands, and in old-growth stands. Total macrolichen biomass in even-aged mature stands of the *Abies* series was lower than in even-aged pole stands (median biomass 630 kg/ha). Our lichen biomass estimates are roughly consistent with and greatly supplement the few estimates available from other studies in the PNW forests (Pipp et al. 2001; McCune et al. 1997*a*; McCune 1993; Neitlich 1993; Rhoades 1981; Pike et al. 1972, 1977).

Cyanolichen biomass in even-aged young stands was often zero or extremely low (< 10 kg/ha) in both plant series. In the *Tsuga* series, highest cyanolichen biomass (median ~1,000 kg/ha) was found in mature stands with remnants and in old growth. Cyanolichen biomass in old-growth stands ranged from 99 to 3,089 kg/ha (median 1,377 kg/ha). Cyanolichen biomass was slightly lower in pole stands with 30% remnant retention (median 458 kg/ha) and in even-aged mature stands (median 278 kg/ha).

Forage lichen biomass was highest in stands with remnants in mature and old-growth stands of the *Tsuga* series. In the *Abies* series, forage lichen biomass was highest in young stands with 15% retention of remnants and in old growth. The high elevation *Abies* forests are important habitat for forage lichens, where they are the dominant epiphytes. We found especially high levels (reaching 26,915 kg/ha) of forage lichen biomass in a few old-growth *Abies* stands. Forests in the *Abies* series contain few cyanolichens and bryophytes, and consequently, there may be more available substrate for forage lichens to colonize. *Alectoria sarmentosa* is the major contributor of forage lichen biomass in the Blue River watershed, consistent with previous findings (Peck & McCune 1997; Neitlich 1993) and is considered old-growth-associated in forests of this region (Peterson & McCune 2001; Neitlich & McCune 1997). This lichen may be dispersal-limited, especially in young dense stands in which wind-dispersed fragments may have difficulty reaching and colonizing appropriate substrates (Dettki et al. 2000; Dettki 1998; Neitlich 1993).

Our estimates of forage lichen biomass are much higher than previously documented estimates for forage lichens (Peck & McCune 1997) or for combined green-algal lichens (Rhoades 1995). Caution must be used in applying our high biomass estimates for forage lichens. These values are based on the ratio of 100:1 lichen epiphyte biomass to lichen litter biomass, which was developed by McCune (1994) in *Pseudotsuga-Tsuga heterophylla* forests at lower elevations. The ratios may not be appropriate for estimating biomass of epiphytic lichens from litterfall in the higher elevation forests of the *Abies* series. Low and high elevation forests may differ in litter decomposition rates, duration of snow burial, in litterfall rates, and abundance of litter herbivores.

Many matrix lichens are early colonizers, such that biomass of this group is generally considered to plateau in younger stands, usually around ~100 yrs (McCune 1993; Neitlich 1993). Biomass for this group persisted throughout mature and old-growth stands in the Blue River watershed (*Tsuga* series: ranging from 43 to 841 kg/ha; *Abies* series: ranging from 161 to 2,883 kg/ha). In both plant series, the median matrix lichen biomass was slightly higher in even-aged mature than in old-growth stands (matrix lichen biomass for *Tsuga* series: even-aged mature = median 415 kg/ha, old growth = median 384 kg/ha; matrix lichen biomass for *Abies* series: even-aged mature = 549 kg/ha, old growth = median 445 kg/ha).

Other studies have shown that lichen biomass increases with stand age, and that in many cases accumulation of epiphytes in a forest is a slow process (Pipp et al. 2001; Esseen et al. 1996; McCune 1993; Neitlich 1993). The slow accumulation of some species may not be attributable to unsuitable habitat in younger forests, but may depend more on time and dispersal. The dispersal-limitation hypothesis is supported by a recent lichen transplant and sowing study that shows *Lobaria oregana*, considered an old-growth-associate, is capable of growing in very young stands if propagules are introduced (Sillett et al. 2000*a*, 2000*b*). However, not all old-growth associated lichens are dispersal-limited; some species appear to require specific microhabitat in old growth (Rosso et al. 2000; Tibell 1992).

Increased forest continuity through maintenance of patches of late-successional habitat throughout the landscape and retention of remnant trees may promote lichen dispersal across a landscape. Lichen biomass increases with the presence of old remnant trees in a stand, however, the contribution of remnant trees to lichen biomass is most pronounced in younger stands (< 80 yrs). Remnant trees apparently serve as refugia for epiphytes during disturbances (e.g., through timber harvests), shed lichen propagules onto younger trees, moderate the microclimate, and create a more complex microhabitat with variable canopy structure, which seems to enhance lichen diversity and biomass (Chapter 2; Pipp et al. 2001; Sillett & Goslin 1999; Peck & McCune 1997). Not only the number of remnants, but also the quality (i.e., age, size, and wind firmness) of the remnant trees may also be a factor influencing lichen abundance. For example, younger remnant trees probably host lower lichen abundance than older remnants. The quality of remnants left after harvest may be important to long-term lichen abundance, but needs further study.

We found no difference in lichen biomass between riparian and upland stands despite differences in lichen community composition (Chapter 2; McCune et al. 2002*a*). However, we sampled lichen biomass in few stands along perennial streams so our inferences are limited. The strong influences of elevation and stand structure combined with our inclusion of small intermittent streams may have masked riparian influences.

Predictive models for estimating lichen biomass

We found strong relationships between patterns in lichen communities and lichen biomass in the Blue River watershed. However, the lichen community ordination scores were not selected as the best predictors for lichen biomass because they explained less variation than other predictors. Models including lichen community predictors had slightly more predictive power than models that included only topography and stand structure predictors. Lichen community data are not always available and such data collection requires field personnel who are trained in lichen identification. Predictive models for estimating epiphytic lichen biomass based on topography and stand structure may have a broader application because they eliminate the step of surveying the lichens.

The model for estimating cyanolichen biomass from elevation, AI, cyanolichen species richness, and the abundance codes for *Lobaria oregana* and *L. pulmonaria* had the strongest predictive power overall ($R^2 = 0.85$). Best models estimating forage and matrix lichen biomass had less predictive power ($R^2 = 0.55$ and 0.58, respectively). Matrix lichen biomass may be difficult to predict because matrix lichens are ubiquitous and abundant across the landscape and show a relatively weak correlation with stand structure, while patterns of forage lichen biomass were slightly more distinctive in the landscape.

Our regression models can be validated from other lichen biomass estimates from similar forest stands in the western Cascades. FHM community data have been collected in more than a thousand stands throughout the PNW forests, many of which are located in the western Cascades (L. Geiser, unpublished data; Peterson & McCune 2001; Rosso 2000; Neitlich & McCune 1997; FHM and Forest Inventory Analysis Programs, National Forest Service, unpublished data), allowing the possibility of applying our biomass models to further the understanding of lichen biomass in forests of the PNW region.

Management implications

Biomass models provide a useful tool for describing and understanding the distribution of epiphytic macrolichen abundance at landscape scales. Biomass estimates are important for understanding lichen function at a landscape level. Furthermore, models for estimating lichen biomass can be used to assess probable consequences of alternative management strategies (Cissel et al. 1999) by forecasting future biomass distribution in the landscape based on changes in forest structure (see Chapter 4). Considering impacts of forest management on lichen biomass allows managers to assess possible impacts that management strategies may have on future lichen communities and their contributions to ecosystem functions and properties.

Currently, the Northwest Forest Plan (NWFP) calls for stands in the upland matrix designation of PNW federal forests to be harvested on 80-year rotations leaving 15% green tree retention (USDA & USDI 1994*a*). In the Blue River watershed, young stands with 15% remnants had fairly high levels of lichen biomass (*Tsuga* series, median 500 kg/ha; *Abies* series, median 962 kg/ha), due to abundant matrix and forage lichens. However, cyanolichen biomass was consistently low in young stands with 15% remnants (median 3 kg/ha in the *Tsuga* series and was nearly absent in the *Abies* series). Leaving remnants during timber harvest may enhance lichen biomass in young regenerating stands.

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Chapter 4

Predicting Future Differences in Epiphytic Macrolichen Biomass Under Two Management Plans in a Forested Watershed of the Western Cascades, USA

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ABSTRACT

We used regression models based on stand structure and elevation to estimate epiphytic macrolichen biomass in the present landscape and to forecast changes in lichen biomass 200 yrs into the future for two management scenarios: the Landscape Plan (LP), which is based on natural fire disturbance regimes; and the Northwest Forest Plan (NWFP), which was developed according to silvicultural prescriptions. Predictions were made for the Blue River (BR) watershed (approximately 22,752 hectares of forest) located in the Central Cascade Mountains of western Oregon, USA. Lichen biomass predictions were made for two functional groups, cyanolichens and forage lichens. Forage lichen biomass was estimated at 15,800 metric tons in the present BR watershed (average 695 kg/ha), 2.6 times higher than cyanolichen biomass (6,100 metric tons in the present BR watershed, average 267 kg/ha). Lichen biomass for each functional group should increase in the future under both management scenarios due to the elimination of clear-cutting and to increased remnant retention. However, the LP would yield somewhat higher levels of forage lichens (12% higher at 23,900 metric tons in the BR watershed or on average 1,048 kg/ha) and cyanolichens (8% higher at 9,300 metric tons in the BR watershed or on average 409 kg/ha), due to a relatively larger proportion of mature forests with high remnant tree retention. In contrast, the NWFP landscape would have less diverse forest structure. The forest matrix is to be harvested on 80 yr rotations with 15% remnant retention in the upland landscape matrix, while the remaining forests in riparian reserves and other reserve areas will not be harvested. Lichen biomass has been shown to increase with the presence of remnants in a stand. Remnants may provide refuge for lichens during a disturbance and may promote lichen dispersal following the disturbance. Changes in lichen biomass in the future landscape could have significant implications to lichen contributions to forest ecosystem function (e.g., nitrogen-fixation) and for animals that consume lichens for nutrition. Our predictions provide managers with an understanding of potential long-term consequences that forest management

practices may have on lichen biomass and ecosystem function in the future Blue River watershed.

INTRODUCTION

Epiphytic macrolichens serve important roles in forest ecosystems. For example, they fix atmospheric nitrogen (Antoine 2001; Denison 1979; Pike 1978) and provide forage for many forest animals (Rosentreter et al. 1997; Rominger & Oldemeyer 1989; Servheen & Lyon 1989; Maser et al. 1985; Stevenson & Rochelle 1984; Edwards et al. 1960). We assume that lichens contribute to these roles in proportion to their biomass (Pike 1978). Accurate estimates of lichen biomass in forests are needed to reasonably estimate annual nitrogen (N) fixed by lichens and to better understand lichen contributions to forage. Despite the importance of lichens in these forests, we know of no attempts to model the long-term consequences of forest management practices on lichen biomass, either in the Pacific Northwest (PNW) of North America or elsewhere in the world.

Changes in forest structure may have significant impacts on lichen abundance and function throughout the forest landscape. Historical changes in forest structure in the temperate forests of the PNW were facilitated by natural disturbance regimes, such as wildfires (Agee 1993). However, natural disturbance regimes in these forests have been altered over the past century by fire suppression, logging, and human development (Norse 1990).

Current forest management on federal lands in the PNW emphasizes an ecosystem approach, in which forestry goals are combined with an increased focus on ecosystem integrity and conservation of biodiversity (USDA & USDI 1994*a*; Franklin 1993; Swanson & Franklin 1992). We evaluate the possible impacts that two existing forest management plans may have on future epiphytic lichen biomass in the Blue River watershed of the Central Cascades of western Oregon, USA. The two management plans would result in very different future landscapes (Cissel et al. 1999).

In 1994, the Northwest Forest Plan (NWFP) was implemented for management of federal forests in the PNW region (USDA & USDI 1994*a*). Under this plan, old-growth-associated forest species received special attention for management and conservation. The forest matrix, which occupies approximately 19% overall of the forested landscape in the PNW managed under the NWFP, is to be harvested on 80 yr rotations in the upland landscape matrix, while the remaining forests are in riparian reserves and other reserve areas (e.g., late-successional reserves, wilderness areas). Fifteen percent of standing green trees will be left in upland areas between harvests in the matrix lands, and all streams will be buffered.

The Blue River watershed in western Oregon is within an Adaptive Management Area (USDA & USDI 1994*a*) in which a management plan (Landscape Plan, LP) is currently being implemented (Cissel et al. 1999). The purpose of the Adaptive Management Area (AMA) is to evaluate alternative management approaches on the federal forests. The LP is different from the NWFP in that fire history forms the basis for future management prescriptions in the landscape. The LP will result in forests of different ages and variable levels of remnant tree retention over the long-term (generally far exceeding the 15% green tree retention of the NWFP upland forest matrix). Under the LP, future forests will have a higher percentage of mature stands, old growth, and stands with remnants as compared to forest lands managed under the NWFP and not all riparian areas will be buffered (especially in harvest units along intermittent streams; see Cissel et al. 1999 for further comparisons between the two plans).

The Tool for Exploratory Landscape Scenario Analysis model (TELSA) was used to predict future changes in forest stand structure in the Blue River watershed based on the two management plans (Cissel et al. 1999). The TELSA model forecasted changes in forest structure 200 yrs into the future based on alternative management scenarios and maps of current forest structure. We used predictions of forest structure from TELSA in combination with topographic information to estimate epiphytic macrolichen biomass in the present landscape and to forecast changes in biomass 200 yrs into the future for each management scenario.

Biomass models for epiphytic cyanolichens and forage lichens in temperate conifer forests of the PNW were from Berryman & McCune (Chapter 3). These regression models are based on elevation and stand structure, and can be used to estimate epiphytic macrolichen biomass to better than the nearest order of magnitude (for which biomass values can range over 4 orders of magnitude) in forest stands across a large landscape. These biomass estimates, in turn, provide a basis for further modeling of lichen contributions to ecosystem function (e.g., annual N-fixation by *Lobaria oregana*). We did not forecast biomass estimates for the matrix lichen functional group (i.e., green-algal foliose lichens) because these lichens are ubiquitous across forest stands (Chapter 3; Peterson & McCune 2001; McCune 1993; Neitlich 1993) and their functional roles in the forest ecosystem are less well known.

METHODS

Study area

We mapped lichen biomass in the Blue River watershed located within the Central Cascades AMA in western Oregon, USA (44° 15’ N 122° 15’ W). The watershed is approximately 24,000 hectares of steep terrain resting on volcanic bedrock, of which approximately 22,752 hectares is forested (see Chapter 2 for site details and map). Elevation in the watershed ranges from 317 – 1639 m, with *Pseudotsuga menziesii* Mirb. Franco. (Douglas fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) dominating most of the watershed at lower elevations (< 1,000 m) and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) and *Abies procera* Rheder (Noble fir) forests dominating the higher elevations. Winters are wet and mild (mean 2º C in January) and summers are warm and dry (mean 22º C in July). The mean annual precipitation for the watershed is 2500 mm.

Study design

As part of the LP, current forest stands in the Blue River watershed were classified into structural types based on tree age and retention of remnant trees. These stand types provide the basis for future management prescriptions in the watershed under the LP. Stand types were stratified by four age classes and by four retention classes of remnant trees in a stand. When remnant trees were not present, the stand was typed as even-aged. Age classes were: young < 20 yrs, pole 21-80 yrs, mature 81-200 yrs, and old growth > 200 yrs. Remnant trees were defined as live trees that survived the most recent disturbance that initiated significant tree regeneration (such as a wildfire or timber harvest). Retention classes of remnants were 0, 15, 30, and 50% based on the percent canopy cover by remnant trees in the stand. The percent canopy cover by remnants was determined using a relationship of tree diameter at breast height (dbh) and canopy width to derive percent canopy cover for a given remnant tree based on our dbh measurements (J. Mayo, unpublished data). Old-growth stands were not further stratified by remnant retention.

We sought to estimate epiphytic macrolichen biomass using models based on stand types and elevation. We derived an age index to integrate the many stand types into a single continuous variable representing what we conceive as a single biological phenomenon: the influence of old trees on lichen biomass. This single continuous variable has statistical benefits over a many-state categorical variable (i.e., stand types) because the categories form a partially ordered series. Statistical power was increased in the models by combining the stand type categories in a way that captures the inherent order.

The age index represented forest structure by assigning "age credits" for the age class and the retention class of remnant trees at the site, then combining the age credits into the age index. Age credits were assigned based in part on the median tree age for the younger cohort and for old growth (Table 4.1). The median age was calculated as a percentage of old growth. The *a priori* median age for old growth was 300 yrs based on median age estimates of old-growth forests in the Blue River watershed (trees were not measured for age, only estimated in field observations). The age credits for the younger cohort were the "base age credits." If remnant trees were present in a stand, we added the percent canopy cover by remnants (15, 30, or 50%) to the "base age credits," resulting in the age index value for the stand (Table 4.1). Each stand type received a value between 3 and 100, where 100 represented old growth and 3 was the minimum age index for even-aged young stands (< 20 yrs).

Table 4.1. Definition of the age index, where the median age of the stand is calculated as a percentage of the median age of old growth (300 yrs assumed for all old growth, see text). Raw age index = $\left((\text{median age}/\text{median age of old growth})*100\right)$ + % remnants. AI represents $\log_{10}$(raw age index).

Stand Type	Median age	Raw age index	AI
Young, < 20 yrs, no remnants	10	3	0.48
Young, < 20 yrs, 15% remnants	10	18	1.26
Young, < 20 yrs, 30% remnants	10	33	1.52
Young, < 20 yrs, 50% remnants	10	53	1.72
Pole, 21-80 yrs, no remnants	50	17	1.23
Pole, 21-80 yrs, 15% remnants	50	32	1.51
Pole, 21-80 yrs, 30% remnants	50	47	1.67
Pole, 21-80 yrs, 50% remnants	50	67	1.83
Mature, 81-200 yrs, no remnants	140	47	1.67
Mature, 81-200 yrs, 15% remnants	140	62	1.79
Mature, 81-200 yrs, 30% remnants	140	77	1.89
Mature, 81-200 yrs, 50% remnants	140	97	1.99
Old growth, > 200 yrs	300	100	2.00

Areas without trees would be assigned an age index of zero, although we only sampled forested areas. We $\log_{10}$-transformed the raw age index (hereafter, referred to as "age index" or "AI") to improve linearity in the regression models.

Analysis

The TELSA model was used to compare future forest landscape scenarios in the Blue River watershed as managed under the LP and the NWFP (see Cissel et al. 1999 for results). The TELSA model produces maps of stand structure for the forecasted landscapes under each management scenario, based on current stand structure in the watershed. We used the TELSA stand structure maps to model epiphytic lichen biomass in three landscapes: 1. the present landscape; 2. the future landscape in 200 yrs based on the LP (hereafter, referred to as the "LP scenario"); 3. the future landscape in 200 yrs based on the NWFP (hereafter, referred to as the "NWFP scenario").

We used regression models developed in Chapter 3 to estimate biomass of epiphytic cyanolichens and forage lichens in the Blue River watershed. A non-linear regression model was used for estimating cyanolichen biomass because of a known sigmoid relationship between cyanolichens and elevation across the elevation range (i.e., 470 – 1,470 m) we studied (Chapter 3). A linear regression model was used for estimating forage lichen biomass. These models were developed using GIS data and forest stand structure data that were either measured on site or were available from the GIS database for the LP. GIS grid layers for elevation (E) and the log age index were independent variables in the regression models. The GIS grids were composed of cells 10 by 10 m in size (0.01 ha). Grid cells that represented water, rocky areas, non-forest, or developed areas in the landscape were not included in the analyses.

Models predicted $\log_{10}$-biomass (oven-dried; 10^x kg/ha) of epiphytic forage lichens and cyanolichens separately for each grid cell. To combine these estimates into a single sum for each stand type (or AI) across the whole landscape required back-transforming the predicted $\log_{10}$-biomasses, then summing over all cells for that stand type (AI) in the landscape. To avoid the inherent downward bias in this back-transformation, we reintroduced the error in $\log_{10}$-biomass as a random normal variate with a mean of zero (N) and a variance equal to the variability unexplained by our regression models (MSE of the residuals). Once this variation was incorporated into our lichen biomass predictions, we back-transformed the predictions (10^x, where x was epiphytic macrolichen biomass). The value of one was subtracted from the back-transformed biomass prediction because this constant was originally added to the biomasses before $\log_{10}$-transformation (see Chapter 3, Methods). The back-transformed biomass values were multiplied by the area of the grid cell (0.01 ha) and summed across all grid cells to calculate the best estimate of total lichen biomass for each functional group in each stand type (AI) in the landscape. We also calculated the average oven-dried biomass (10^x kg/ha) of cyanolichens and forage lichens across the landscape.

The regression equations for each lichen functional group were as follows:

Cyanolichens $R^2 = 0.81$

$$B = \left(10\text{\^{}}\left([(1.50*AI) / (1 + (E/937.75)^{26.99})] + N(MSE)\right)\right) - 1$$

Forage lichens $R^2 = 0.47$

$$B = \left(10\text{\^{}}\left([-1.38 + 1.55*AI + 0.001*E] + N(MSE)\right)\right) - 1$$

where B equals the predicted epiphytic lichen biomass of a functional group for a given grid cell, E is elevation (m) as an independent variable, AI is the age index as an independent variable, N is a standard normal random variable, and MSE is the mean squared error of the residual variability unexplained by the regression models.

For each lichen functional group, we produced three maps of predicted lichen biomass on the $\log_{10}$-scale for each landscape. Biomass predictions in the maps included the N(MSE) variation. We do not show maps using the back-transformed values because the range of values was too large (exceeding four orders of magnitude) to map clear patterns of lichen biomass at the 0.01 ha cell resolution. One map represents predicted biomass in the present landscape and the other two maps represent forecasted lichen biomass 200 yrs in the future landscapes under each management scenario (LP and NWFP). The two maps at 200 yrs were used to compare potential impacts the proposed management strategies may have on future epiphytic macrolichen biomass.

RESULTS

Present landscape

Currently, approximately one third of the Blue River watershed is composed of forests with a younger cohort < 80 yrs, many of which are young plantations (Table 4.2). Such young forests host relatively low levels of lichen biomass (Figure 4.1). Old-growth and mature forests dominate the remaining landscape. Few stands have remnant retention and where present, retention is low (Table 4.2).

Our best estimate of epiphytic cyanolichen biomass in the present landscape was 6,100 metric tons (average 267 kg/ha). Forage lichen biomass in the present landscape was estimated at 15,800 metric tons (average 695 kg/ha), 2.6 times higher than cyanolichen biomass. Cyanolichens were limited to lower elevations of the western hemlock series (Figures 4.2 & 4.3). Young plantations and clear cuts in the present forest matrix are clearly areas with very low cyanolichen and forage lichen biomass (Figure 4.1). Old growth hosted abundant cyanolichens in the present landscape (average 550 kg/ha; Figure 4.1A) and hosted even greater abundance of forage lichens (average 1,400 kg/ha; Figure 4.2).

Comparisons between the LP and the NWFP

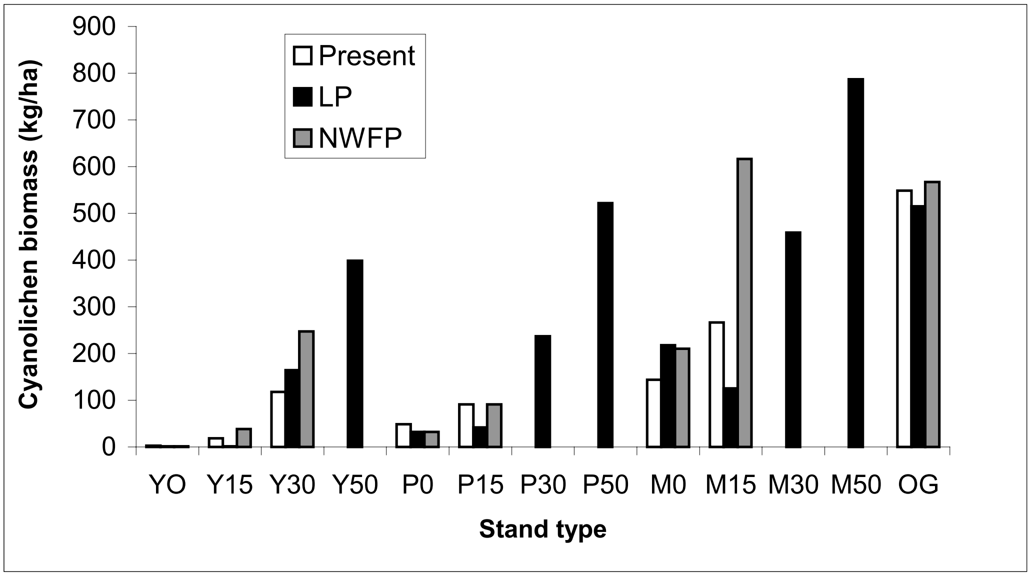
The two management plans would result in different forest structure in the future landscape scenarios 200 yrs from now. The Blue River landscape under the

Table 4.2. Area (ha) of the Blue River landscape covered by each stand type in the present and in the forecasted landscapes 200 yrs in the future. The forecasted area is for the Landscape Plan (LP) and the Northwest Forest Plan (NWFP). The corresponding raw age index (not log-transformed) is shown for each stand type.

		Area (ha)		
			Future	
Stand type	**Raw Age Index**	**Present**	**LP**	**NWFP**
Young, < 20 yrs, no remnants	3	2,262	35	37
Young, < 20 yrs, 15% remnants	18	89	311	2,012
Young, < 20 yrs, 30% remnants	33	140	436	3
Young, < 20 yrs, 50% remnants	53	0	511	0
Pole, 21-80 yrs, no remnants	17	5,231	690	689
Pole, 21-80 yrs, 15% remnants	32	267	916	6,003
Pole, 21-80 yrs, 30% remnants	47	0	1,262	0
Pole, 21-80 yrs, 50% remnants	67	0	1,492	0
Mature, 81-200 yrs, no remnants	47	4,821	126	122
Mature, 81-200 yrs, 15% remnants	62	1,327	1,935	522
Mature, 81-200 yrs, 30% remnants	77	0	2,026	0
Mature, 81-200 yrs, 50% remnants	97	0	513	0
Old growth, > 200 yrs	100	8,615	12,499	13,365
	Total	22,752	22,752	22,753

NWFP scenario would be highly dissected with late-successional habitat limited to riparian reserves and other late-successional reserve areas, such as the H.J. Andrews Experimental Forest in the southeastern corner of the Blue River watershed (USDA & USDI 1994*a*). The H.J. Andrews will be a late-successional reserve under both management plans. These reserve forests would remain undisturbed (at least by intentional human activities) and therefore, most would

A



B

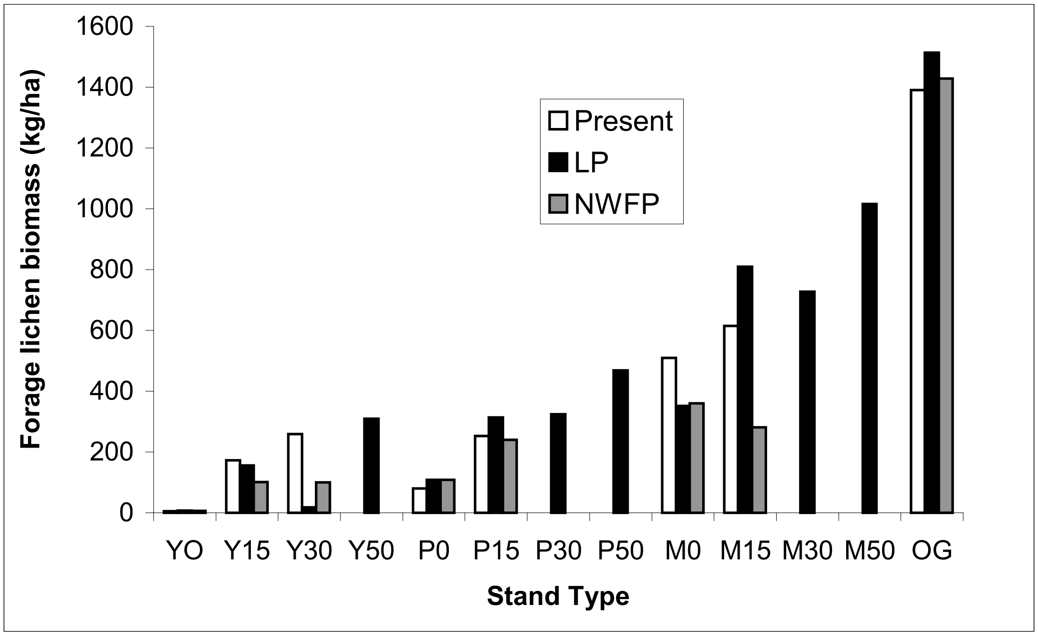


Figure 4.1. Total epiphyte biomass (oven-dried; kg/ha) predicted for cyanolichens (**A**) and forage lichens (**B**) in the present landscape and under the Landscape Plan (LP) and Northwest Forest Plan (NWFP) landscape scenarios projected 200 yrs into the future. Average lichen biomass is calculated by stand type, based on the proportion of area each stand type represents in the landscape.

become old-growth forests with time. The remaining forest matrix (35% of the Blue River watershed) would be young forests (< 80 yrs) with light remnant retention.

The LP scenario would yield more late-successional forests (mature and old growth) and a higher proportion of variable-aged stands with higher remnant retention compared to the present Blue River landscape (Table 4.2). The NWFP would also result in a larger proportion of old-growth forests than in the present landscape (59% versus 38%, respectively), though less acreage in mature (81-200 yrs) and variable-age stands relative to the LP (Table 4.2). Mature stands would comprise 3% of the Blue River landscape under the NWFP and would comprise 20% of the LP landscape scenario.

The most prominent difference between the two plans is related to green tree retention in upland stands. Remnant retention will not exceed 15% under the NWFP and would be present primarily in young stands (1-80 yrs), which would comprise 35% of the future Blue River landscape. In contrast, 42% of the Blue River landscape under the LP would be older variable-aged stands with higher levels of green tree retention (reaching 50% retention in many stands). In both management scenarios, even-aged forests would be nearly eliminated from the landscape (Table 4.2).

Epiphytic lichen biomass for both functional groups should increase in the landscape in both the LP and NWFP scenarios 200 yrs in the future (Figures 4.1-4.3). However, lichen biomass predictions were generally higher in the LP scenario than it is currently and than projected under the NWFP scenario. Cyanolichen biomass would be approximately 8% higher in the landscape managed under the LP as compared to the NWFP. According to our predictions, cyanolichen biomass in the watershed would increase from the current 6,100 metric tons (average 267 kg/ha) to 9,300 metric tons (average 409 kg/ha) under the LP scenario. In comparison, cyanolichen biomass would increase to 8,600 metric tons (average 377 kg/ha) in the future NWFP scenario (Figures 4.1A & 4.2).

Figure 4.2. Maps of predicted cyanolichen biomass (on a $\log_{10}$ scale; kg/ha) in the Blue River watershed. Maps represent the present landscape and the landscape managed under the Landscape Plan (LP) and the Northwest Forest Plan (NWFP) 200 yrs in the future.

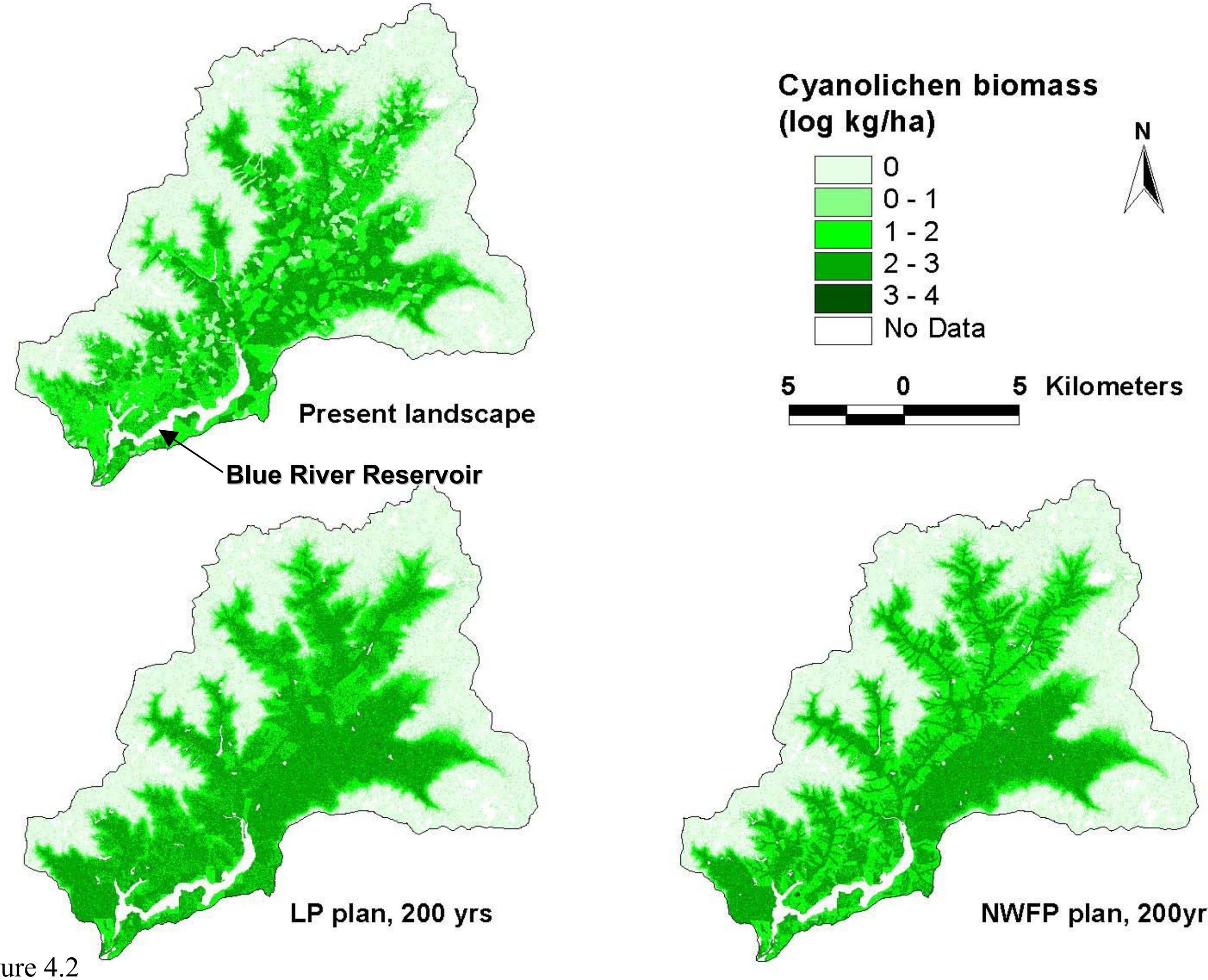

Cyanolichen biomass (log kg/ha)
0
0 - 1
1 - 2
2 - 3
3 - 4
No Data
N
5
0
5
Kilometers
Present landscape
Blue River Reservoir
LP plan, 200 yrs
NWFP plan, 200yrs

Figure 4.2

Figure 4.3. Maps of predicted forage lichen biomass (on a $\log_{10}$ scale; kg/ha) in the Blue River watershed. Maps represent the present landscape and the landscape managed under the Landscape Plan (LP) and the Northwest Forest Plan (NWFP) 200 yrs in the future.

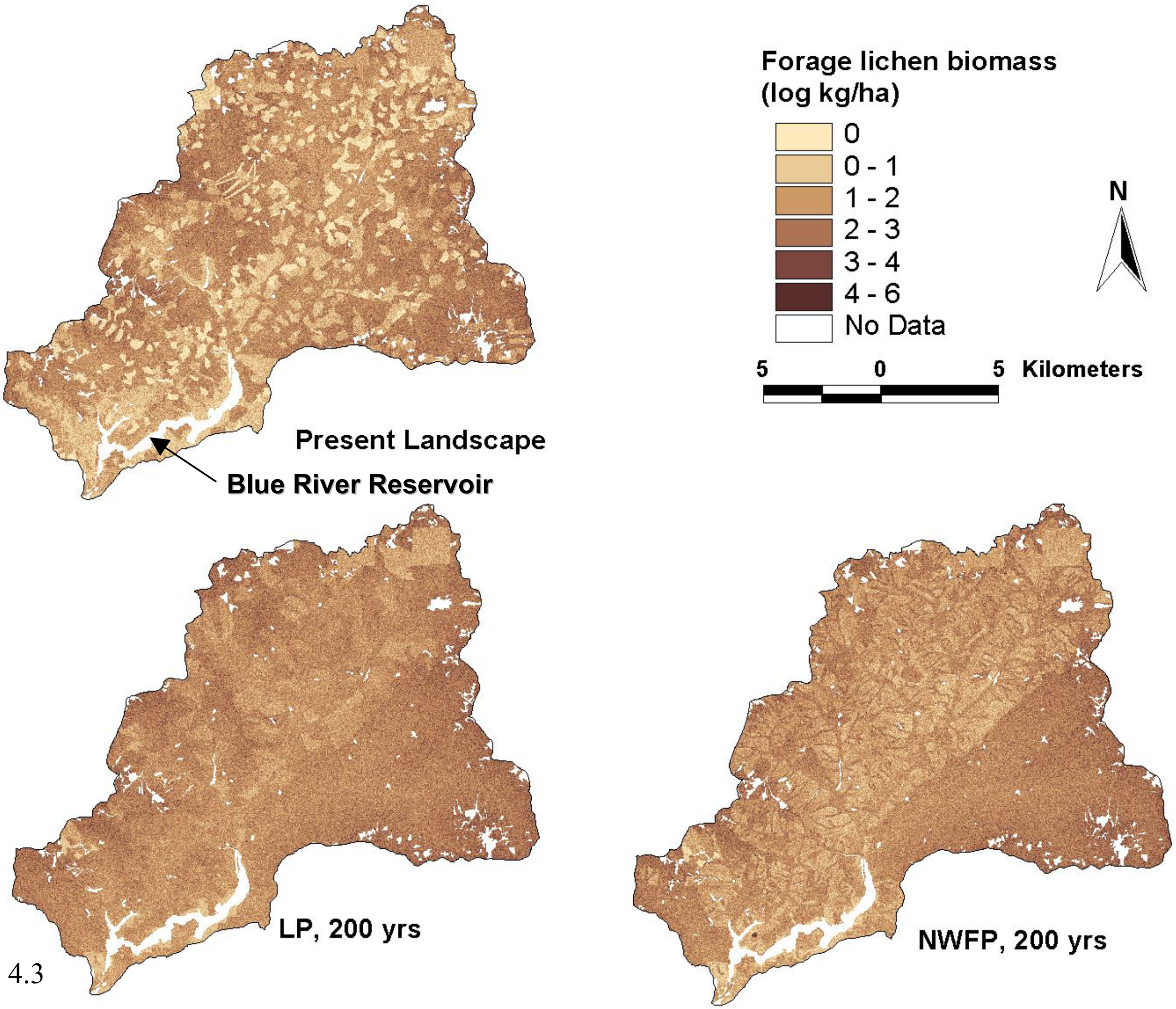

Forage lichen biomass
(log kg/ha)
0
0 - 1
1 - 2
2 - 3
3 - 4
4 - 6
No Data
N
5
0
5
Kilometers
Present Landscape
Blue River Reservoir
LP, 200 yrs
NWFP, 200 yrs

Figure 4.3

Patterns in forage lichen biomass under the two management scenarios in 200 yrs would be similar to patterns for cyanolichens (Figure 4.1B). Under the LP, forage lichen biomass would be approximately 12% greater than under the NWFP scenario. Forecasted forage lichen biomass under the LP would reach 23,900 metric tons (average 1,048 kg/ha), while forecasted forage biomass under the NWFP would be slightly lower at 21,000 metric tons (average 923 kg/ha). This is a substantial increase from the current forage lichen biomass estimated to be 15,800 metric tons (average 695 kg/ha) in the Blue River watershed.

Though total lichen biomass predictions are similar between the two management scenarios for each functional group, the stand types in which lichens would be most abundant differed between each management scenario (Figure 4.1). In the LP scenario, lichen biomass would be highest in mature and old-growth forests and in stands with remnant retention > 30% retention. The spatial distribution of these stand types would be relatively regular throughout the watershed. However, under the NWFP, lichen biomass would be more concentrated in old growth and mature stands with and without remnants, which would be present primarily along riparian corridors and in a few other late-successional reserve areas, such as the H. J. Andrews Experimental Forest (Figures 4.1 - 4.3).

DISCUSSION

Present landscape

Differences in cyanolichen and forage lichen biomass in the present landscape are largely related to an elevation gradient (Chapter 3). Cyanolichens are restricted to lower elevation forests (< 1,000 m) dominated by Douglas fir and western hemlock. As much as 3,000 to 3,500 kg/ha of oven-dried cyanolichen biomass has been estimated for old-growth forests of the Blue River watershed (Chapter 3; Neitlich 1993). As a consequence of past clear-cutting, approximately

10% of the current Blue River landscape is young plantations (< 20 yrs; Table 4.2) with very low lichen abundance (Chapter 3; Neitlich 1993).

Lichen biomass varies across stands of the same age and structure, especially in old-growth stands where structure is complex. Forage lichen biomass reaches very high levels in higher elevation forests where forage lichens are dominant (e.g., occasionally reaching nearly 27,000 kg/ha in true fir old-growth forests, Chapter 3). However, forage lichens are not restricted to the higher elevations and are abundant throughout the Blue River watershed (Chapter 3).

We estimate total forage lichen biomass in the present Blue River watershed to be 15,800 metric tons. Forage biomass is very important to forest wildlife. For example, if approximately 10% of the forage biomass (estimate from Esseen 1985 for annual turnover of *Usnea longissima* litter fall) becomes available to ground-dwelling herbivores, then approximately 1,580 metric tons of forage lichens in the Blue River watershed enter the ground-based food web annually.

Comparisons between the LP and the NWFP

We predict that lichen biomass will increase in both the LP and NWFP scenarios, in which clear-cutting would no longer be a part of forest management. This predicted increase in lichen abundance is related to the decrease in acreage of young even-aged stands in the future landscape, to the increase in late-successional habitat, and to increased remnant tree retention. Epiphytic macrolichens are sparse in young even-aged stands < 80 yrs, where lichen biomass ranges from 1-30 kg/ha (Chapter 3), and lichen biomass increases with stand age (Chapter 3; Esseen et al. 1996; McCune 1993; Neitlich 1993).

Forests managed under the LP would be less dissected than the current landscape and than forests under the NWFP scenario. Most of the late-successional habitat would be present in relatively large forest blocks, resulting in less forest edge and more interior habitat. It is unclear how the loss of forest edge may impact lichen communities. Various studies have shown that lichens respond positively or negatively or show no response to forest edge microhabitats (Kivisto & Kuusinen 2000; Esseen & Renhorn 1998; Renhorn et al. 1997; Sillett 1995, 1994). Lichen response to edge effects may vary by species (Sillett 1994) and our sampling scheme avoided edges, therefore we cannot address them in this study.

Most of the mature forests in the future LP landscape would have high levels of remnant retention (15-50%). Such forests host diverse lichen communities and abundant macrolichens (Chapter 3; Peck & McCune 1997; Sillett & Goslin 1999) and also provide habitat for many old-growth associated species (Chapter 2; Chapter 3; McCune et al. 2002*b*, *in review*). Consequently, the LP scenario would result in somewhat higher lichen biomass than the NWFP scenario (12% higher for forage lichens, 8% higher for cyanolichens).

Remnants are clearly important for maintaining abundant lichens in a stand (Chapter 3; Pipp et al. 2001; Hazell & Gustafsson 1999; Sillett & Goslin 1999; Peck & McCune 1997), however young remnants (typically < 80 yrs) may be less valuable than older remnants. We did not consider the quality or age of the remnant trees in our models. Remnant trees under the LP would be older and larger compared to remnant trees left in upland stands under the NWFP (remnants < 80 yrs). Such young remnant trees may be less valuable as refuges and sources of inoculum for old-growth associated lichens. Consequently, under the NWFP scenario, old-growth associated lichens would have to disperse to upland forests from old growth in riparian reserves and other late-successional reserves. However, leaving the same remnants during consecutive harvests may promote lichen abundance in young stands. We need studies evaluating quality of remnant trees as epiphyte habitat, particularly with respect to tree age, size, wind-firmness, and by species (especially hardwoods versus conifers).

We found that forest structure (e.g., age and remnant retention) is likely to be strongly related to lichen biomass in the future landscape. However, McCune et al. (2002*b*, *in review*) found the probability of lichen species occurrence to be less sensitive to differences in forest structure resulting from the LP and NWFP scenarios. For example, the likelihood of occurrence of *Lobaria oregana* in 0.4 ha plots differed very little between the two scenarios. Increased area of old-growth forests under both plans, compared to the current landscape, did increase the probability of *L. oregana* occurrence throughout the future landscape.

Changes in lichen biomass could have significant implications to contributions of lichens to forest ecosystem function, such as N-fixation. Cyanolichens contribute approximately 50% of the newly fixed N to old forests in the PNW (Sollins et al. 1980). Compared to other biological N-fixers (such as *Alnus* and *Ceanothus* which colonize younger forests), N-fixation by *Lobaria* is considered low in forests other than old growth. However, N-fixing shrubs remain in a stand only for short periods of time in early succession. Whereas, once cyanolichens become well established in a stand, they are likely to remain for many centuries, barring major disturbances such as clear-cutting.

Antoine (2001) estimated that *Lobaria oregana* fixes approximately 2.6 kg/ha of N annually in the H. J. Andrews Experimental Forest of the Blue River watershed (her estimate assumes 550 kg/ha of *L. oregana* canopy biomass). Cyanolichen biomass in old-growth forests of the Blue River watershed ranged from 99 kg/ha to 3,089 kg/ha (see Chapter 3). Most cyanolichen biomass is composed primarily of *L. oregana* in these old forests (Chapter 3). Based on our cyanolichen biomass estimates and Antoine's (2001) model, approximately 0.47 to 14.65 kg/ha/yr of N is fixed by *L. oregana* in these old-growth forests in the present watershed, depending on the cyanolichen biomass present. The input of fixed-N by cyanolichens should increase under each landscape scenario (1.97 kg N/ha/yr under the LP and 1.78 kg N/ha/yr under the NWFP). Average cyanolichen biomass was 267 kg/ha across all stands in the present landscape, which would fix 1.26 kg N/ha/yr according to Antoine's models. Changes in cyanolichen biomass could have significant impacts on long-term forest ecosystem health and productivity in forests where nitrogen is limited (Miller et al. 1996)

In addition to forest management, other factors may influence changes in lichen abundance in the future landscape. For example, increased air pollution could negatively affect the growth of *Lobaria oregana* and other cyanolichens (McCune et al. 2002*b*, *in review*). Changes in climate could also affect lichen abundance, possibly restricting habitat for cyanolichens to moist microsites. Nevertheless, our predictions provide managers with an understanding of potential responses of the biomass of two important functional groups of epiphytic macrolichens to alternative forests management strategies. In addition, such predictions further our understanding of lichen distribution across forest landscapes and provide us with some idea of the consequences of forest management in advance. This work illustrates the potential value of AMAs for evaluating management alternatives that may better enhance lichen biomass across forest the landscape.

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Chapter 5

Conclusions

Epiphytic macrolichen communities varied strongly along an elevation gradient and differed across stand types in the Blue River watershed. Cyanolichens were largely restricted to stands below 1,000 m in the western hemlock series. *Lobaria oregana* was the dominant cyanolichen in these forests and achieved high biomass in old stands. The forage lichen *Alectoria sarmentosa* was a strong indicator for higher elevation stands in the true fir series. *A. sarmentosa* was most abundant in mature and old-growth stands.

Lichen communities changed with stand age in both the western hemlock series and the true fir series. The most prominent differences in lichen communities were between even-aged young stands (< 20 yrs) and old-growth stands (> 200 yrs). Lichen communities were similar in mature (80-200 yrs) and old-growth stands. However, cyanolichens, particularly *Lobaria oregana,* were more frequent and abundant in old growth than in mature stands. Lichen species richness was generally unrelated to stand age, however, cyanolichen species richness was highest in older stands compared to even-aged young stands in the western hemlock series. Lichen biomass increased with stand age, in which lichen biomass was generally high (median biomass approximately 1,000 kg/ha; oven-dried) in mature and old-growth stands for both plant series. Lichen biomass also reached 1,000 kg/ha in even-aged pole stands (21-80 yrs) of the true fir series in which matrix and forage lichens were very abundant.

Differences among lichen communities in relation to remnant tree retention were not as pronounced as differences with stand age. However, lichen community composition in young stands with remnants differed greatly from that in even-aged young stands. Patterns in lichen species richness were unrelated to remnant tree retention. Lichen biomass was substantially higher in stands with remnant retention as compared to similar even-aged stands.

Remnant trees appear to be key features to maintain in the forest landscape and may provide continuity between stands after harvest or other disturbances. The presence of remnant trees in young stands may accelerate the development of lichen communities towards that of older stands. Remnant trees may serve as a refuge for lichens during a disturbance, may inoculate the regenerating stand following the disturbance, and may ameliorate the microclimate by reducing lichen exposure to light, wind, and fluctuating temperatures (Peck & McCune 1997). Additional studies are needed to address the quality of remnant trees as epiphyte habitat with respect to age, size, wind-firmness, and species (in particular, hardwoods versus conifers).

Stands along perennial streams < 5th order were hotspots for cyanolichens. Cyanolichens appeared to be associated with abundant hardwood trees and shrubs along these stream channels. Although these streams were cyanolichen rich, the overall cyanolichen biomass in these stands was not different from that of upland stands where cyanolichens were also abundant.

I developed models for estimating lichen biomass (oven-dried; 10^x kg/ha) by functional group using stepwise-linear regression and nonlinear regression. I followed a three-step approach to develop the models, each step demanding an additional class of variables. First, I created models from topographic predictors that are easily extracted from GIS data. I then developed models based on both topographic and stand structure variables. Finally, I developed models based on topography, stand structure, and lichen community data. Models with the greatest explanatory power were: cyanolichen biomass predicted as a function of elevation, stand age index, the sum of abundance for *Lobaria oregana* and *L. pulmonaria*, and cyanolichen species richness ($R^2 = 0.85$); forage lichen biomass predicted as a function of stand age index and the abundance of *Alectoria sarmentosa* ($R^2 = 0.55$); and matrix lichen biomass predicted as a function of stand age index and the sum of abundances for matrix lichen species in the stand ($R^2 = 0.58$). These models save time in efforts to estimate lichen biomass at the landscape scale and contribute to a better understanding of large-scale patterns in lichen biomass.

I used regression models based on stand structure and elevation to estimate epiphytic cyanolichen and forage lichen biomass in the present Blue River watershed. Projections of stand structure in the future Blue River watershed were used with the biomass models to forecast lichen biomass in the watershed 200 years into the future under two different management scenarios: the Northwest Forest Plan (NWFP) and the Landscape Plan (LP). I evaluated the implications of the NWFP and the LP on future lichen biomass in the watershed and compared changes in biomass from the present watershed to the forecasted levels in the two management scenarios. Clear-cutting would be eliminated under each management scenario and the area of old-growth forests would increase from the present landscape. Consequently, future lichen biomass for both functional groups should increase under either management plan.

A larger percentage of forests will have high remnant retention (15 to 50 %) under the LP than the NWFP. Under the LP, rotations between harvests will be longer than the 80 yr rotations prescribed under the NWFP. Thus, in the Blue River watershed, there will be more forests in the mature age-class under the LP than the NWFP. As a result of higher remnant retention and more mature forests, predictions for cyanolichen and forage lichen biomass were somewhat higher for the LP scenario (8% higher for cyanolichens and 10% higher for forage lichens) than for the NWFP.

Biomass models are important for understanding lichen contributions to ecosystem function and properties, such as nitrogen fixation and provisions to forage. These models can be used to assess the possible consequences of different forest management on lichen communities and project how these changes may impact the function of lichens in these systems. Other factors such as air pollution and potential change in climate could alter our model predictions. Nevertheless, these models are valuable tools for managers to develop a general understanding of potential lichen response to forest management.

Results from studies in this dissertation have broad implications to forest management. Relationships of lichen communities with stand age and remnant trees have been documented in other studies (Peterson & McCune 2001; Pipp et al. 2001; Hazell & Gustafsson 1999; Peck & McCune 1997; Neitlich 1993; McCune 1993; Lesica et al. 1991), however, this is the first attempt to address the relative importance of these factors along with topographic factors at the landscape scale. The studies presented in this dissertation suggest that remnant tree retention is relatively more important to lichen communities in younger stands (< 20 yrs) than in older stands. As the stand develops, the remnants seem to contribute to overall structural diversity and provide important microhabitat for lichens. The retention of remnant trees during harvest and managing for the conservation of older stands should promote lichen biomass across the landscape.

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Appendices

Appendix A

Plot Locations

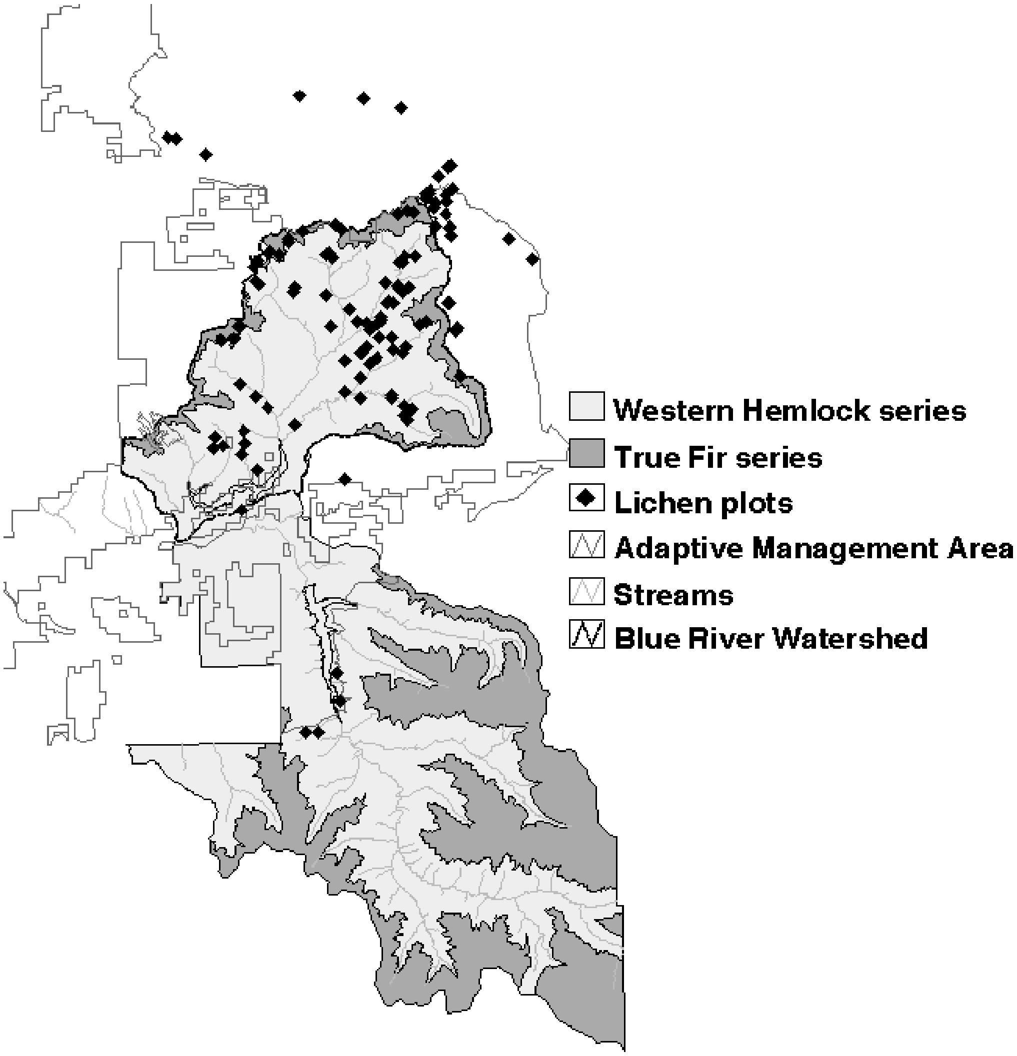

Figure A1. Map of plots (N = 117) sampled for epiphytic macrolichen communities located in the Blue River Ranger District.

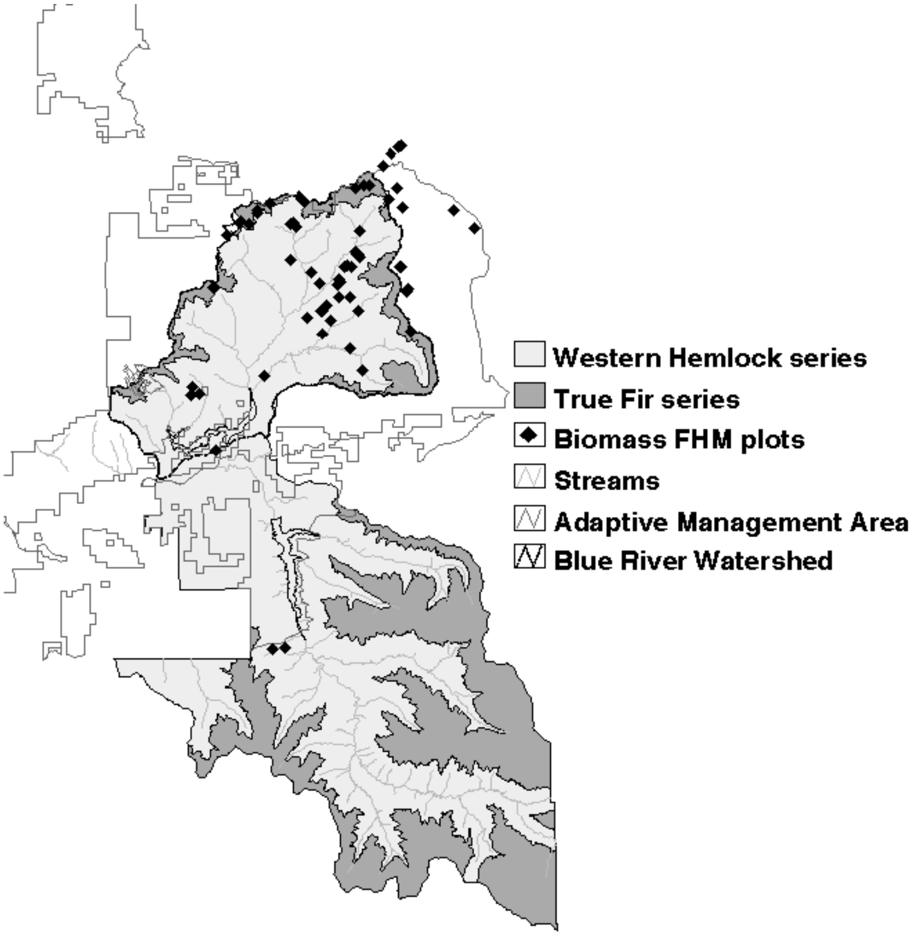

Figure A2. Map of plots (N = 63) sampled for epiphytic macrolichen biomass located in the Blue River Ranger District.

Appendix B

Codes and Descriptions of Environmental and Lichen Community Variables

Table A1. Codes and descriptions of environmental and lichen community variables. This list includes all variables used in the ordination analyses, variables used in other comparative analyses for lichen communities and for lichen biomass, and variables used to build regression models for estimating lichen biomass.

Code	Description
PLOT	plot (stand) name; all beginning with SB followed by a number, 1 through 117
PLTSERIE	vascular plant series: western hemlock = 1; true fir = 2
LAT	latitude (decimal degrees; we used a GPS Plugger in 1997 and we used a GPS Trimble unit in 1998 and 1999) **note: stand SB44 is missing lat. and long. coordinates
LONG	longitude (decimal degrees; we used a GPS Plugger in 1997 and we used a GPS Trimble unit in 1998 and 1999)
TOPOCLA	topographic classes (uplands or riparian areas); 1 = upland sites that do not include or overlap with riparian areas (topocla1); riparian sites were divided into three categories: 2 = perennial fish bearing streams < 5th order (topocla2); 3 = perennial non fish-bearing streams (topocla3); 4 = intermittent streams (topocla4)
TOPOPOS	classes for the topographic position of the stand in relation to the surrounding landscape: 1 = flat or rounded ridge top or peak > 120' wide; 2 = narrow ridge top or peak (120' wide); 3 = side hill, upper 1/3; 4 = side hill, middle 1/3; 5 = side hill, lower 1/3; 6 = canyon bottom < 660' or more wide; 7 = bench or terrace; 8 = broad flat 660' or more wide; 9 = other, describe
ELEV	elevation is altitude measured in meters above sea level, recorded from the GPS unit

Table A1 (continued)

SLOPE	the % slope at plot center, measured with a clinometer
ASPECT	aspect is the direction in which the water flows down hill; degrees east of true north, measured with a compass
PDIR	potential direct incident radiation, (MJ/cm^2/yr); represents the amount of light a site potentially receives, derived from latitude, slope, and aspect
HL	heat load index measures the amount of heat a site potentially receives during the day, derived from models based on latitude, slope, and aspect (McCune & Keon 2002)
AGECLASS	stand age classes; three for the younger cohort (1 = young, < 20 yrs; 2 = pole, 21-80 yrs; and 3 = mature, 81-200 yrs); and 4 = old growth (> 200 yrs)
REMCLASS	retention classes for the percent of remnants in the older cohort (historical retention based on the percent canopy cover of live remnant trees that survived the most recent disturbance): 1 = 0% (0 – 7.5%); 2 = 15% (7.5 – 22.5%); 3 = 30% (22.5 – 37.0%); 4 = 50% (37.0 – 62%); 5 = old growth (not stratified by remnant class)
STRATA	strata based on a combination of the age classes and the remnant retention classes: 1 = young, 0% remnants; 2 = pole; 0% remnants; 3 = young, 15% remnants; 4 = pole, 15% remnants; 5 = mature, 0% remnants; 6 = young, 30% remnants; 7 = pole, 30% remnants; 8 = young, 50% remnants; 9 = pole, 50% remnants; 10 = mature, 15% remnants; 11 = mature, 30% remnants; 12 = mature, 50% remnants; 13 = old growth, not stratified by remnant class
RAWAI	raw age index (see Table 2.1); combines the age class of the stand and the remnant retention and expresses it as a percentage of old growth
AI	$\log_{10}$ raw age index (see Table 2.1)

Table A1 (continued)

DBH75	tree diameter at breast height (cm); 75th percentile for the stand
LOGDBH75	$\log_{10}$ of the tree diameter at breast height (cm); 75th percentile for the stand
DBH50	tree diameter at breast height (cm); 50th percentile for the stand or the median
LOGDBH50	$\log_{10}$ of the tree diameter at breast height (cm); 50th percentile for the stand or the median
LIVEBA	basal area of live trees (m^2/ha), averaged over five variable -radius subplots; measured using a relescope in 1997 and an angle gauge in 1998 and 1999
DEADBA	basal area of dead trees (m^2/ha), averaged over five variable -radius subplots; measured using a relescope in 1997 and an angle gauge in 1998 and 1999
TOTBA	total basal area of live and dead trees (m^2/ha), averaged over five variable-radius subplots; measured using a relescope in 1997 and an angle gauge in 1998 and 1999
REMBA	basal area of live remnant trees (m^2/ha), averaged over five variable-radius subplots; measured using a relescope in 1997 and an angle gauge in 1998 and 1999
BACONIF	percent basal area of conifers in a stand (percentage of total basal area)
BAHARDW	percent basal area of hardwood trees in a stand (percentage of total basal area)
PERBAREM	percent basal area of live remnant trees in a stand (percentage of total basal area)
TOTSPP1	total number of epiphytic macrolichen species (alpha diversity) in a stand based on the original species matrix

Table A1 (continued)

TOTSPP2	total number of epiphytic macrolichen species (alpha diversity) in a stand based on the reduced species matrix in which rare species in < 5% of the stands were deleted
CYANO1	total number of epiphytic cyanolichen species (alpha diversity) in a stand based on the original species matrix
CYANO2	total number of epiphytic cyanolichen species (alpha diversity) in a stand based on the reduced species matrix in which rare species in < 5% of the stands were deleted
FORAGE1	total number of epiphytic forage lichen species (alpha diversity) in a stand based on the original species matrix
FORAGE2	total number of epiphytic forage lichen species (alpha diversity) in a stand based on the reduced species matrix in which rare species in < 5% of the stands were deleted
MATRIX1	total number of epiphytic forage lichen species (alpha diversity) in a stand based on the original species matrix
MATRIX2	total number of epiphytic matrix lichen species (alpha diversity) in a stand based on the reduced species matrix in which rare species in < 5% of the stands were deleted
BIOIND	categorical variable indicating if epiphytic macrolichen biomass was sampled in a stand (0 = no biomass sampled; 1 = biomass was sampled)
CYANOBI	average epiphytic cyanolichen biomass for a stand; oven-dried, $\log_{10}(x+1)$ kg/ha, where x is cyanolichen biomass
FORAGEBI	average epiphytic forage lichen biomass for a stand; oven-dried, $\log_{10}(x+1)$ kg/ha, where x is matrix lichen biomass
MATRIXBI	average epiphytic matrix lichen biomass for a stand; oven-dried, $\log_{10}(x+1)$ kg/ha, where x is forage lichen biomass

Table A1 (continued)

TOTBIO	average total epiphytic macrolichen biomass for a stand; oven-dried, $\log_{10}(x+1)$ kg/ha, where x is lichen biomass
CYANOAV	average epiphytic cyanolichen biomass; oven-dried, kg/ha
FORAGEAV	average epiphytic forage lichen biomass for a stand; oven-dried, kg/ha
MATRIXAV	average epiphytic matrix lichen biomass; oven-dried, kg/ha
CYANOSD	standard deviation of the average epiphytic cyanolichen biomass; oven-dried, kg/ha
FORAGESD	standard deviation of the average epiphytic cyanolichen biomass for a stand; oven-dried, kg/ha
MATRIXSD	standard deviation of the average epiphytic cyanolichen biomass for a stand; oven-dried, kg/ha
CYANOAB	sum of abundance classes for all cyanolichens in a stand from the original species matrix
FORAGEAB	sum of abundance classes for all forage lichens in a stand from the original species matrix
MATRIXAB	sum of abundance classes for all matrix lichens in a stand from the original species matrix
CYANOSC	scores from axis one in the NMS ordination of stands in lichen species space, rotated to correlate cyanolichen biomass with axis one (see Figure 3.3A)
FORAGESC	scores from axis one in the NMS ordination of stands in lichen species space, rotated to correlate forage lichen biomass with axis one (see Figure 3.3B)
MATRIXSC	scores from axis one in the NMS ordination of stands in lichen species space, rotated to correlate matrix lichen biomass with axis one (see Figure 3.3C)

Table A1 (continued)

LOBORPUL	sum of abundance classes for *Lobaria oregana* and *L. pulmonaria* by stand
ALESAR	abundance class for *Alectoria sarmentosa* by each stand
BAXE	total basal area of live and dead trees (m^2/ha) multiplied by elevation (m); used as an interaction term in stepwise-linear regression models for estimating lichen biomass

Appendix C

Archived Data Files

Table A2. Archived data files used in the analyses for this dissertation. All files are archived in the Forest Science Data Bank. Metadata tables are included with each file.

File Name	**File Type**	**Contents**
species.txt	text file	raw epiphytic macrolichen species data. These data are in compact format, for import into PC-ORD.
epiphyte.sps	SPSS syntax file	list of epiphytic lichens scientific names and associated six letter acronyms and number codes; these acronyms were used in the species matrices, and the number codes were used in the species.txt file
sppdata.wk1	PC-ORD spreadsheet	epiphytic macrolichen species abundances for all 117 stands. Species matrix = 111 species by 117 stands.
sppdatatrans.wk1	PC-ORD spreadsheet	reduced epiphytic macrolichen species matrix; deleted species in less than 6 stands. Species matrix = 71 species by 117 stands.
envdata.wk1	PC-ORD spreadsheet	all environmental variables and lichen community and lichen biomass variables for each stand. Environmental matrix = 46 variables by 117 stands.
WHspp.wk1	PC-ORD spreadsheet	epiphytic macrolichen species abundances for all 67 stands in the western hemlock series. Species matrix = 105 lichens by 67 stands

Table A2 (continued)

sppdataWH.wk1	PC-ORD spreadsheet	reduced epiphytic macrolichen species matrix for the western hemlock series; deleted species in less than 4 stands. Species matrix = 71 lichens by 67 stands
TFspp.wk1	PC-ORD spreadsheet	epiphytic macrolichen species abundances for all 50 stands in the true fir plant series. Species matrix = 78 lichens by 50 stands
sppdataTF.wk1	PC-ORD spreadsheet	reduced epiphytic macrolichen species matrix for the true fir series; deleted species in less than 3 stands. Species matrix = 50 lichens by 50 stands
envdataWH.wk1	PC-ORD spreadsheet	all environmental variables and lichen community and lichen biomass variables for each stand in the western hemlock series. Environmental matrix = 35 variables by 67 stands
envdataTF.wk1	PC-ORD spreadsheet	all environmental variables and lichen community and lichen biomass variables for each stand in the true fir series. Environmental matrix = 35 variables by 50 stands
biomodels.sav	SPSS spreadsheet	all environmental and lichen community variables used in building the regression models for estimating lichen biomass by functional group; 63 stands by 31 variables