AN ABSTRACT OF THE THESIS OF

Andrea M. Ruchty for the degree of Master of Science in Botany and Plant Pathology presented on October 6, 2000. Title: The Association of Epiphytic Macrolichens and Bryophytes with Riparian Stand Types along a Valley Continuum, Oregon Coast Range.

Abstract Approved: *Redacted for Privacy*

Bruce P. McCune

I surveyed epiphytic macrolichens and bryophytes in six stands in each of seven riparian stand types in the Oregon Coast Range. This study (Chapter 2) describes the association of epiphytes with stand types and the corresponding potential of forest canopy conversions to affect epiphyte communities. Species composition, diversity, and representation of functional groups differed among stand types. Epiphyte communities changed along a valley continuum, from higher elevation, older, conifer-dominated stands along constrained stream reaches bounded closely by slopes, to lower elevation, hardwood-dominated stands on broad floodplains along unconstrained rivers or streams. Epiphyte communities also appear to be affected by bark pH. We conclude that riparian canopy conversions in the Oregon Coast Range have great potential to affect epiphyte communities.

A transplant study (Chapter 3) examined whether canopy environment is important in determining associations between lichen species and canopy type in Oregon Coast Range riparian forests. The growth of four lichen species was compared beneath three canopy types. If canopy environment is important in determining the distribution of individual transplant species, then transplant species should show growth response patterns under the different canopy treatments that correspond to their known habitat preferences. We found that the survival, health and growth of individual transplant species did not differ by canopy type, though, as a group, lichen transplants were less healthy and did not survive as often under bigleaf maple canopies. *Hypogymnia inactiva* grew less well and was less healthy than the other three lichen species, though its survival rate was similar to that of the other transplant species.

Chapter 4 supplements data presented in Chapter 2 by, (1) describing where and with what abundance ROD-listed epiphyte species were found, (2) reporting species found to be rare and, (3) reporting absent species that we had expected to find. Of the nine ROD-listed "riparian" lichens, five were encountered in our surveys. Sixteen additional ROD-listed lichen and 2 bryophyte species were encountered during surveys. Of all the ROD-listed riparian species that were encountered more than once, none were restricted to a specific stand type. Many rare species (present in less than 5% of sampled stands) are more common on other substrates or in nearby habitats. Though suitable habitat was available, we found some lichen and bryophyte species less often than expected; these species may be

more rare than has been previously recognized. This information improves our understanding of the habitat requirements of riparian epiphyte species and allows us to assess their rarity within the Oregon Coast Range.

The Association of Epiphytic Macrolichens and Bryophytes with Riparian Stand
Types along a Valley Continuum, Oregon Coast Range

by

Andrea M. Ruchty

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Andrea M. Ruchty, Author

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Chapter 1. Introduction

Until relatively recently, knowledge of the species diversity and ecology of

epiphytic lichens and bryophytes living in the forests of the Pacific Northwest was

confined to a handful of researchers and academics that took a special interest in

these groups. With increasing recognition of the roles epiphytes play in ecosystems

(Denison 1979, Maser et al. 1986, McCune 1993, Nadkarni 1984, Pettersson et al.

1995, Pike et al. 1972, Pike et al. 1975, Rominger and Oldemeyer 1989,

Rosentreter and Eslick 1993), greater focus has been placed on these organisms.

Concurrently, concern has grown regarding the effects of forest management

practices on these organisms, and additional research has explored these issues

(McCune et al. 1997, Neitlich and McCune 1997, Peck 1997, Peterson 2000, Rosso

2000, Sillett 1998, Sillett and McCune 1998, Sillett et al. 2000). Little research has

focused, however, on epiphytes in riparian zones, though riparian zones have been

heavily impacted by land management practices in the Pacific Northwest.

Riparian forests in the Oregon Coast Range vary along a coniferous –

deciduous continuum in canopy composition (COPE 1990). The main canopy

species include red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*),

Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), western

hemlock (*Tsuga heterophylla*) and in the coastal fog belt, Sitka spruce (*Picea sitchensis*) (Franklin and Dyrness 1973, Hibbs 1987, Nierenberg 1996).

In the Pacific Northwest, historical riparian zones were once probably composed of a mosaic of various species (Maser 1988). In the Oregon Coast Range, canopy species included mature western hemlock, western redcedar and Douglas-fir, as well as other conifer species, with mixed deciduous understories composed of hardwood trees and shrubs (Poage 1995). Red alder most likely dominated frequently disturbed riparian floodplains, while conifers dominated slopes above streams, growing intermixed with hardwoods. The composition and distribution of pre-settlement vegetation in riparian zones was probably quite diverse in pre-settlement times due to the high natural variability of this environment (Nierenberg 1996).

Over the past century, humans have extensively modified the forests of western Oregon's riparian zones and wetlands. Most riparian areas have been logged, burned, or both in the last 100 years (Minore and Weatherly 1994). In the Pacific Northwest, the largest impact on steams and riparian zones has occurred because of logging (Mitsch and Gosselink 1993). These widespread disturbances have led to an increase in the dominance of early successional species, including red alder (Harrington et al. 1994). In fact, most alder stands in existence today originated with these disturbances (Hibbs 1987). With repeated disturbances, red alder populations may expand and come to dominate sites (Newton and Cole 1994). Conversion of riparian zones to housing and agriculture is widespread (Mitsch and

Gosselink 1993) and many bottomlands timbered with Oregon ash (*Fraxinus latifolia*) and other species have been cleared and placed under cultivation (Benner and Sedell 1997). Natural wetlands created by beaver dams have undoubtedly decreased with the near extirpation (by overtrapping) of beaver that occurred throughout North America in the 1800's and early 1900's (Outwater 1996). With growing human populations, and increasing recreational use of riparian zones for campgrounds, parks and trails, the risk of damage to riparian zone vegetation through increased bank erosion and elimination or thinning of riparian vegetation is rising.

Shifts in riparian tree and shrub species composition and canopy structure affect the epiphyte communities that depend on perennial vegetation as substrates, and have undoubtedly caused consequent shifts in epiphytic lichen and bryophyte species composition and abundance. Different kinds of riparian forests host dramatically different lichen communities. For many species, little is known either of their level of habitat specificity or its mechanisms; most of our knowledge is anecdotal. Some lichens, such as the rare riparian forage lichen *Ramalina thrausta*, are usually associated with large old conifers at low elevations, but are unknown from alder stands. Conversely, some riparian lichens such as *Menegazzia terebrata* and *Cetrelia cetrarioides* appear to thrive on red alder but are infrequent on conifers (Culberson and Culberson 1968, McCune and Geiser 1997). Other species, such as *Usnea longissima*, appear to be relatively tolerant of a broad range

of forest types, but limited by their poor dispersal ability (McCune and Geiser 1997, Keon 2000).

In order to understand how changes in tree species composition in riparian zones may affect epiphyte communities, we need to know how diversity and species composition of epiphytic lichens varies among riparian forests with different canopy dominants. Chapter 2 contrasts epiphyte communities among seven riparian stand types in the Oregon Coast Range, including stands dominated by red alder, Oregon ash, conifers and bigleaf maple, as well as stands associated with beaver or wet meadows, waterfalls, and agricultural corridors. This chapter also describes the valley continuum; a continuum of riparian environments along which epiphytic macrolichen and bryophyte communities change.

Chapter 3 describes a lichen transplant study designed to explore potential mechanisms behind epiphytic macrolichen habitat specificity within riparian zones. By monitoring the growth responses of four lichen species exhibiting a range in levels of habitat specificity (including the species *Cetrelia cetrarioides, Hypogymnia inactiva, Lobaria oregana and L. pulmonaria)* we tested whether canopy composition in riparian zones may be important in influencing the distribution of these lichen species.

In 1994, the President's Forest Plan Record of Decision (ROD) (USDA and USDI 1994) mandated the management of species associated with old-growth forests within the range of the Northern Spotted Owl, including a number of lichens thought to be associated with riparian habitat. As "riparian reserves", riparian

zones were given a central role in the conservation of biodiversity under the President's Forest Plan. An important question is to what extent the "riparian lichens" listed in the ROD, as well as other rare species that may be associated with riparian zones, will persist if forests are converted from one forest type to another. Community studies contribute to our knowledge of the distribution and habitat requirements of individual species. Chapter 4 expands on Chapter 2 by further evaluating information on the habitat requirements and level of rarity of a number of species that have been considered rare and/or riparian, including ROD-listed species. Understanding the links between riparian canopy types and epiphytic macrolichen and bryophyte species composition and abundance will facilitate more effective monitoring of species potentially at risk (USDA and USDI 1994) and management of epiphytic lichen and bryophyte communities.

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Chapter 2

The Association of Epiphytic Macrolichens and Bryophytes with
Riparian Stand Types Along a Valley Continuum, Oregon Coast Range

Andrea M. Ruchty and Bruce McCune

Abstract

We surveyed epiphytic macrolichens and bryophytes in seven riparian stand types in the Oregon Coast Range, including stands dominated by *Alnus rubra*, *Fraxinus latifolia*, conifers and *Acer macrophyllum*, as well as stands characterized by the presence of wet meadows (that may have been created by beaver), waterfalls and agricultural corridors. The main purpose of this study was to understand the association of epiphytes with stand types and the corresponding potential of canopy conversions to affect epiphyte communities. Our study area encompassed the north central to south central Oregon Coast Range (N45° 22' to N43° 45'; W 123° 20' to W 123° 50'). We defined stands as areas relatively homogenous in history and environment. Epiphyte communities differed among stand types. Epiphyte communities changed along a valley continuum of riparian environments, from higher elevation, older, conifer-dominated stands located along constrained stream reaches bounded closely by slopes, to lower elevation, hardwood-dominated stands located on broad floodplains or bottomlands along unconstrained rivers or streams. Green-algal foliose lichens and overall macrolichen species richness were positively associated with hardwood-dominated stands along more unconstrained stream reaches (one end of the valley continuum), while the alectorioid (forage) lichen *Alectoria sarmentosa,* and the old-growth associated species *Lobaria oregana,* were associated with higher elevation, conifer-dominated stands along constrained stream reaches (the other end of the valley continuum). Epiphyte communities were also affected by another environmental factor that we

hypothesized to be bark pH. Cyanolichen and bryophyte species richness appeared

to be higher with the relatively high bark pH of *Fraxinus latifolia* and *Acer*

macrophyllum compared with conifer species and *Alnus rubra*. Results suggest

that riparian canopy conversions in the Oregon Coast Range have great potential to

affect epiphyte communities.

Introduction

Riparian zones are widely recognized for their high level of plant and

animal diversity and important ecosystem functions, including as refuges and

dispersal corridors for plant, bird and mammal populations. Riparian zones are

also rich habitats for epiphytic lichens and bryophytes and have been termed

"hotspots" of epiphytic lichen diversity, often harboring greater diversity and

abundance of nitrogen fixing lichen species (cyanolichens) and rare species than

surrounding upland forests (Neitlich and McCune 1997, Peterson 2000, Rosso

2000).

Tree and shrub species composition and canopy structure of forests affect

the epiphyte communities that reside there. Some lichens, such as the rare riparian

forage lichen *Ramalina thrausta*, are usually associated with large old conifers at

low elevations, but are unknown from alder stands. Conversely, some riparian

lichens such as *Menegazzia terebrata* and *Cetrelia cetrarioides* appear to thrive on

red alder but are infrequent on conifers. Other species, such as *Usnea longissima*,

appear relatively tolerant of a broad range of forest types, but may be limited by

their poor dispersal ability (Keon 2000). These are just a few local examples of epiphyte habitat specificity: many more exist for both lichens and bryophytes within and without the Pacific Northwest region (Adams and Risser 1971, Barkman 1958, Jonsson 1997, Kuusinen 1996, Palmer 1986, Peck 1997, Studlar 1982).

Over the past century or more, humans extensively modified the forests of western Oregon's riparian zones and wetlands. Logging and clearing riparian forests for timber and agriculture may have led to increases in young, hardwood-dominated riparian zones in the Oregon Coast Range (Harrington et al. 1994, Hibbs et al. 1994, Poage 1995, Nierenberg 1996,). Pollen records show that red alder, in particular, has increased in abundance during the twentieth century (Heusser 1964, Davis 1973). Shifts in canopy dominance have undoubtedly caused shifts in epiphytic lichen and bryophyte species composition and abundance.

Land managers will protect epiphytic riparian lichens and bryophytes to some degree, simply by virtue of their protecting other riparian ecosystem functions and services such as water quality and fish production. An important issue remaining, however, is to what extent the epiphytes, including the "riparian lichens" listed in the Northwest Forest Plan's Record of Decision (ROD) (USDA and USDI 1994), will persist if forests are converted from one type to another. To understand how changes in tree species composition in riparian zones may affect epiphytic macrolichen and bryophyte communities, we need to know how diversity and species composition of these epiphytes varies among riparian forests with different canopy dominants. Understanding the links between riparian canopy

types and epiphytic macrolichen and bryophyte species composition and abundance will facilitate more effective monitoring and management of potentially at-risk species (USDA and USDI 1994).

The goals of this study are: (1) characterization of the epiphytic macrolichen and bryophyte communities in seven different riparian stand types in the Oregon Coast Range, including stands dominated by red alder (*Alnus rubra)*, Oregon ash (*Fraxinus latifolia)*, mixed conifers, and bigleaf maple (*Acer macrophyllum*) as well as stands associated with wet/beaver meadows, waterfalls and agricultural corridors, (2) to increase understanding of the environmental factors that strongly influence the distribution of epiphytic macrolichens and bryophytes in riparian forests, and (3) to use the information gained through this study to suggest ways in which managers may address the habitat needs of lichens and bryophytes in riparian zones, including rare species and those listed in the ROD.

This study differs from previous work on epiphyte species – habitat relationships that has focused on the relationship of epiphyte communities to host or substrate characteristics (Bates and Brown 1981, Kenkel and Bradfield 1986, Kuusinen 1996, Peck 1997, Studlar 1982). In contrast to these studies, this study was designed specifically to evaluate epiphyte communities at the stand level, how they differ among riparian stand types, and thus to evaluate the potential for shifts in canopy composition to affect riparian epiphyte communities across the landscape.

Methods

Study area

This study was carried out in the Oregon Coast Range from June through September 1998-1999. Our overall study area extended from N45° 22' to N43° 45' and W 123° 20' to W 123° 50' (Figure 2.1). The study area was divided by equal increments of latitude into six sampling blocks, to control for geographical variation in the sampling design. One stand of each canopy type was located within each of the six geographical blocks, for a total of 42 stands. The wet meadow in block 2 (stand 2-5) was eliminated as an outlier during analysis of the data. The single exception to this design was for stand 6-2, which was located in block 5 because we did not locate a suitable Oregon ash stand in block 6 (Figure 2.1). Most stands were located on Bureau of Land Management lands. This study area was chosen to focus on riparian habitats in the Oregon Coast Range and foothills but to exclude the coastal Sitka spruce (*Picea sitchensis*) zone, which is floristically distinct. All stands were located within this area except where suitable plots within this area were not found. This occurred in three cases (stands 3-6, 3-7 and 6-7) where we sampled just outside the blocks (Figure 2.1).

The Oregon Coast Range is characterized by steep mountain slopes with main ridge summits from ~450 to 750 m and the highest peak in the range (Marys Peak) at 1,249 m. The Oregon Coast Range is bordered on the east by the Willamette Valley, a broad alluvial plain, and on the west by the Pacific Ocean. Western Oregon has a maritime climate, with mild, wet winters and warm dry
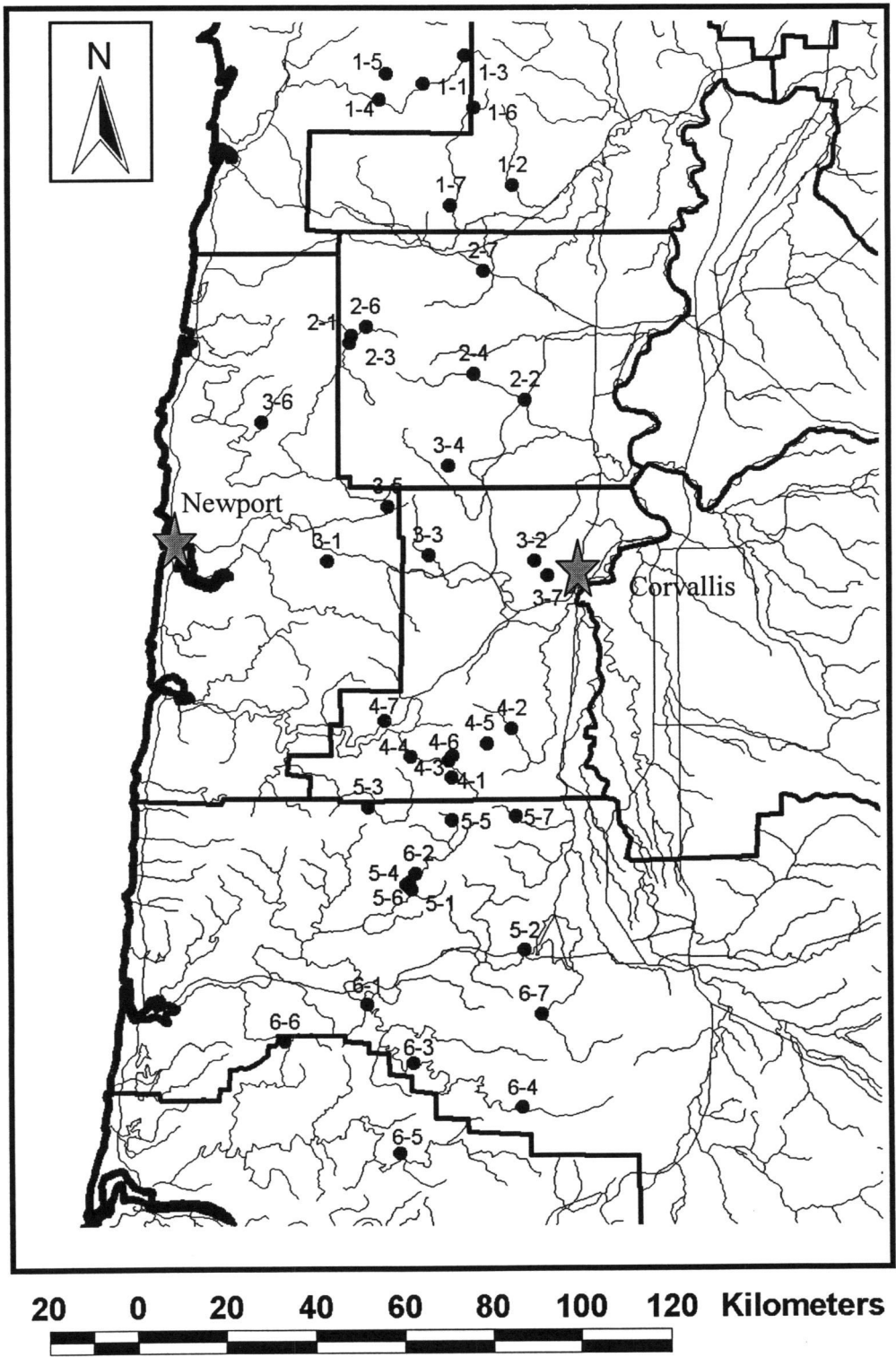
Figure 2.1. Map of riparian stands sampled from 1998-1999, Oregon Coast Range.

summers (Franklin and Dyrness 1973). Within our study area, average annual

precipitation ranges from 47 to 155 cm (Daly et al. 1994). Dominant tree species

include the large and long-lived conifers *Pseudotsuga menziesii* (Douglas-fir),

Tsuga heterophylla (western hemlock), *Thuja plicata* (western redcedar) and

coastal *Picea sitchensis* (Sitka spruce). Mature forests have lush understories of

ferns (especially *Polystichum munitum*), herbs, shrubs and cryptogams (Franklin

and Dyrness 1973). Hardwood tree species, including *Alnus rubra* (red alder), *Acer*

macrophyllum (bigleaf maple) and *Fraxinus latifolia* (Oregon ash) are generally

concentrated in riparian zones (Harris 1984).

Stand selection

We defined a stand as an area relatively homogenous in history and

environment. We sampled seven different riparian stand types for epiphytic lichen

and bryophyte communities. The seven stand types included four types defined by

canopy dominance, including *Alnus rubra* (red alder), *Fraxinus latifolia* (Oregon

ash), mixed conifer, and

Acer macrophyllum (bigleaf maple) stands. We defined canopy dominance

as meaning that the species or species group comprised greater than 50% of the

total stand basal area. We refer to the stand component with canopy dominance as

the "modal" cohort. Three additional stand types were defined by characteristics

unrelated to canopy dominance. The wet or beaver meadow type was the forested

area surrounding a wet meadow that, in many cases, was created by beavers

(*Castor canadensis*). The waterfall type included the riparian forest within the main and diffuse spray zones of a waterfall. The agricultural corridor type consisted of the narrow strip (relative to other stand types) of riparian vegetation along a stream or river, immediately bordered by agricultural fields.

The area of sampled stands was no less than 2000 m^2 and no greater than 4000 m^2. Stands within this size range are used in the Forest Health Monitoring Program (McCune et al. 1997). To limit our sampling to riparian zones, which are notoriously hard to define and delimit, we sampled within 91.4 m (300 ft.) of the stream (measured along the slope, perpendicular to the stream). This (or two site potential trees – whichever is greatest) is the riparian buffer width recommended for fish-bearing streams on federal land in the Oregon Coast Range (USDA and USDI 1994). Only riparian areas associated with fish-bearing streams were sampled. By focusing our sampling on these areas, we hope our results will apply to management under this buffer strip requirement. To increase the chance of sampling sites with well-developed epiphyte floras, the modal cohort of trees had to be estimated at 50 years or older. In most stands, cores were taken to confirm whether this criterion had been met. Stand choices were made without regard to present management regimes or previous human impacts.

Stand characterization

Stand basal area, separated by tree species, was determined using 4-6 wedge prism measurements taken at approximately equal spaced points within the stand.

Prisms with basal area factors of either 10 or 20 were used. We recorded the

presence, abundance and species composition of secondary woody cohorts,

including "understory" and "remnant" cohorts, in addition to the "modal cohort".

Abundance of woody species within cohorts was estimated using the following

scale: 1 = rare ($\leq$ 3 individuals in plot); 2 = uncommon (4-10 individuals in plot); 3

= common (> 10 but comprising less than half the total number of woody species

present); and 4 = abundant (comprising more than half the total number of woody

species present). The understory cohort consisted of trees and woody shrubs that

were conspicuously shorter than the modal, dominant cohort. The remnant cohort

was comprised of trees that were emergent above the modal canopy, and that were

presumed to be, on average, older than the modal canopy component. Additional

stand measurements included slope (in degrees), aspect (in degrees East of

magnetic North), the width of the primary floodplain or bottomland associated with

the riparian zone (determined through direct measurement or from topographic

maps), and the width of the stream channel, measured with a range-finder or

measuring tape. Stream constraint was subjectively scored using a continuous

scale from 0 (unconstrained streams with little to no bank and wide floodplains) to

10 (constrained streams with high banks bordered by steep slopes). We created a

variable called topographical shelter to characterize the riparian zone's

topographical sheltering from the sun and wind. This variable was scored in one of

three categories: (1) sheltered, (2) intermediate, or (3) open. Dominant

topographic position described the topographic position comprising the majority of

the stand, and was scored in one of four categories (1-4): primary floodplain or bottomland, lower slope, upper slope, or bench.

Stand age determination

Increment cores, along with tree diameter at breast height (dbh) (taken in cm) were collected from trees representing each canopy cohort (the understory, modal and remnant cohorts). Initially, tree cores were taken simply for confirmation that the stand age criterion had been met. Such a wealth of cores and measurements of dbh were collected, however, that we decided to use these data to examine relationships of stand age to macrolichen and bryophyte community structure. In most stands, both cores and dbh measurements were taken, though in some (located in public, exposed or privately owned sites) only dbh measurements were taken. In two stands, neither cores nor dbh data were taken.

Tree ages were determined from cores and dbh measurements. Cores were stored in plastic straws, then glued into grooved boards with the wood grain oriented perpendicular to the board. Cores were then sanded, and annual rings counted. Cores that did not contain the center were treated in one of two ways to approximate tree age. If enough curvature in the annual rings was present to indicate proximity to the tree center, an acetate sheet with concentric circles inscribed on it was placed over the core and matched to the annual ring pattern. This allowed estimation of distance to the tree center. Multiplying the growth rate (rings/cm), calculated as an average for the entire core, by the distance from the

tree center, estimated the number of missing annual rings. If no curvature was present on the core, the core length was subtracted from the tree radius to estimate missing core length. The length was then multiplied by the average growth rate to calculate tree age.

To estimate tree age in stands with dbh data but no core data, core age (by tree species) was regressed on dbh using the no-intercept model (intercept is forced through the origin). For such regressions, r^2 measures the proportion of variability about the origin that is explained by the regression. This cannot be compared to r^2 values for models that include an intercept. In the two cases where no data were taken, field notes were used to roughly estimate stand age. Regression equations (SPSS 1998) by tree species are as follows: Douglas-fir: age = 1.738(dbh) (n = 15, r^2 = 0.90); bigleaf maple: age = 1.506(dbh) (n = 13, r^2 = 0.83); red alder: age = 1.379(dbh) (n = 27, r^2 = 0.89); Oregon ash: age = 1.398(dbh) (n = 12, r^2 = 0.91); western redcedar: age = 1.243(dbh) (n = 6, r^2=0.90).

For stands defined by canopy dominance, average stand age was calculated as the average age of the modal tree species. For other stand types, average stand age was the average age of all cores taken within the stand. We used the age of the oldest tree in each stand (which we derived from cores, or estimated from regression equations or field notes), to represent the remnant cohort.

As the correlation between dbh and tree age was weak, especially for bigleaf maple and Oregon ash, tree ages calculated using the regression equations

were used to estimate average stand age and the age of the remnant cohort only when no cores had been taken in a stand.

Epiphyte sampling

Epiphytic lichen and bryophyte surveys were time constrained to standardize the sampling effort across all stands. Lichens were sampled for 2 hrs or until 10 min had passed without finding a new species, but in this case, 1 hr 15 min was the minimum sampling time. This time-constraint protocol has been used with success in lichen community surveys by the Forest Health Monitoring program (McCune et al. 1997). Bryophytes were sampled for 1 hr. The sampling method had two parts that were performed simultaneously. (1) In each stand, species were identified or specimens were collected for identification, the collection representing the species diversity of epiphytic macrolichens and bryophytes in the plot as fully as possible. The population being sampled consisted of all macrolichens and bryophytes occurring on dead and living woody plants, excluding the 0.5m basal portions of trees, shrubs and stumps. Lichens and bryophytes on fallen branches and other litter were included; fallen branches provide a sample of the canopy lichens in areas of adequate size (McCune et al. 1997). (2) The abundance of each lichen species was estimated using a four-step scale: 1 = rare ($\leq$ 3 individuals in plot); 2 = uncommon (4-10 individuals in plot); 3 = common (> 10 but less than half of the boles and branches have that species present); and 4 = abundant (more than half of boles and branches in the plot have the subject species present).

Vouchers are housed at the Oregon State University herbarium. Nomenclature of

lichen species follows Esslinger and Egan (1995), Halonen et al. (1998) for *Usnea*,

Jørgensen and Tønsberg (1999) for *Leptogium*, Lindblom (1997) for *Xanthoria* and

McCune and Geiser (1997); nomenclature of mosses follows Anderson et al.

(1990) and Lawton (1971); nomenclature of liverworts follows Stotler and

Crandall-Stotler (1977) and Christy and Wagner (1996); nomenclature of vascular

plants follows Hitchcock and Cronquist (1973). Certain difficult taxonomic groups

were grouped under a single name: *Cladonia ochrochlora* and *Cladonia*

coniocraea were both called *C. ochrochlora*; no attempt was made to distinguish

Cladonia chlorophaea from *Cladonia asahinae* (a species less likely to be found

within our sampling area).

Species functional groups

For some analyses, epiphyte species were categorized into functional

groups. Cyanolichens contain cyanobacteria as a primary or secondary photobiont

and include species of *Lobaria*, *Nephroma* and *Peltigera*; cyanolichens tend to be

sensitive to air pollution (Richardson 1988) and are functionally related by their

ability to fix atmospheric nitrogen. Though it meets these criteria, *Lobaria*

oregana was excluded from this group and treated as its own functional group

because it typically does not group with other cyanolichens in ordinations (Neitlich

and McCune 1997, Peterson 2000). Green-algal foliose lichens included species of

Platismatia, *Parmelia*, *Hypogymnia* and non-pendulous species of the genus

Usnea. Alectorioid lichens included the pendulous species of the genera *Usnea*,

Bryoria, and *Alectoria*. Alectorioid lichens are also known as "forage" lichens, as

they are consumed and used in nest building by *Glaucomys sabrinus*, the flying

squirrel (Maser et al. 1986; Maser et al. 1985, Rosentreter and Eslick 1993) and are

eaten by both deer (Stevenson 1978) and caribou (Rominger and Oldemeyer 1989).

The bryophyte functional group included all mosses and liverworts.

Data Preparation

To focus the analyses on meaningful trends in the epiphyte community data,

all species present in less than 5% of the stands (less than three stands) were

excluded from all statistical analyses except Indicator Species Analysis. This

reduced the overall lichen species richness (number of species) from 108 to 76 and

the overall bryophyte species richness from 56 to 40 species.

Multivariate outlier analysis (McCune and Mefford 1999) calculated the

average distance (using Sørensen distance) from each stand to every other stand.

Stands with average distances greater than 2 standard deviations from the grand

mean of distances were considered outliers. Outlier analysis of the lichen and

bryophyte data together revealed stand 2-5 as an outlier, more than 4 standard

deviations from the grand mean of distances. This stand is an unusual, high

elevation peat bog, and due to its unusual characteristics and extreme outlier status,

it was eliminated from this study. In the lichen ordination, stands 4-4 and 5-1 were

revealed as outliers and in the bryophyte ordination, stands 2-3 and 3-7 were

outliers. However, inspection of ordinations showed that these stands occupied extreme positions along important gradients in species composition, and in effect, represented endpoints of these community gradients. In no other way were they unusual or atypical stands; therefore, they were retained in all data analyses.

Calculations of diversity

We used species richness as a measure of stand-level alpha diversity and total species richness across stands as a measure of gamma diversity. We defined beta diversity as the average change in species composition among sample units within a stand type. We calculated the average within-type Sørensen distance (D) and converted this to beta diversity measured in half changes (β_D) using the following equation:

$$\beta_D = \frac{\log\,(1\text{-}D)}{\log\,(0.5)}$$

One half change represents a species compositional change of 50%. Note that this method of calculating beta diversity accounts for differences among stands in both species presence and abundance.

Multi-Response Permutation Procedure

Multi-Response Permutation Procedure (MRPP) (McCune and Mefford 1999) is a non-parametric procedure that tests for multivariate differences between two or more groups. MRPP produces a test statistic (T), chance–corrected within-group agreement (A) and a p-value, where p = the probability of a smaller or equal

weighted mean within-group distance. A = 1 when all items are identical within groups, A = 0 when heterogeneity within groups equals expectation by chance and A < 0 when heterogeneity within groups is greater than that expected by chance. To test whether lichen and bryophyte communities differed among stand types, MRPP analysis was performed on the species abundance matrix using the Sørensen distance measure and stand type as the classifying variable.

Indicator Species Analysis

We used Indicator Species Analysis to test whether any species were strongly associated with, and thus "indicated" a particular stand type. Dufrêne and Legendre's (1997) Indicator Species Analysis (McCune and Mefford 1999) calculates a percent of perfect indication, based on comparing how often and with what abundance species are found in a given group of stands compared to how often and with what abundance that species is found in all stands. A Monte Carlo test of significance compares observed indicator values with values that would be expected by chance. The resulting p-value expresses the proportion of randomized trials with indicator values equal to or exceeding the observed indicator value.

Non-metric Multidimensional Scaling

In ecological studies we cannot know whether we have measured the environmental variables that are most important to plant communities. By measuring lichen and bryophyte species composition and abundance, we have

measured the integrated response of these communities to stand environment. This approach to analysis of communities is referred to as indirect gradient analysis. Non-metric Multidimensional Scaling (NMS) (Kruskal 1964) is an indirect gradient analysis ordination method that is unconstrained by the assumptions of normality and linearity that are inherent to many other ordination methods. Because NMS ordination is based on ranks, it lessens the 'zero-truncation problem' (Beals 1984) that is typically problematic in analyses of community data.

NMS ordinations were performed on lichen and bryophyte data separately. The NMS autopilot function was set to perform a maximum of 300 iterations with a 0.0001 instability criterion. In NMS ordinations of sample units (stands) in species space, the stands are placed along axes that represent gradients in species composition. By overlaying plots of measured environmental variables on ordinations of stands in species space and examining correlations between those variables and ordination axes, we generated hypotheses about which factors influenced species distributions.

Linear regression

To clarify relationships between species functional groups and specific environmental factors, we regressed species richness for functional groups on environmental variables using simple linear regression, (SPSS 1998).

Results

Differences in epiphyte communities among stand types

Epiphyte communities clearly differed among stand types. With combined lichen and bryophyte data, MRPP revealed that epiphyte communities differed among stand types more than would be expected by chance (T = -9.09, A = 0.15, p = <0.0005). With lichen data alone stand types differed in species composition (MRPP: T = -7.93, A = 0.13, p = < 0.0005), as they did when only the bryophyte data were used (MRPP: T = -8.18, A = 0.16, p = < 0.0005).

Stand types differed as epiphyte habitat (Table 2.1). Red alder stands hosted fewer lichen species by stand (species richness) and fewer total lichen species (gamma diversity), as well as fewer ROD-listed lichen species than any other stand type. No lichen species indicated red alder stands (Table 2.2), because species found in alder stands were also often found in other stand types. Red alder stands had moderate species richness of bryophytes but less compositional variability among stands than many other stand types (beta diversity) and comparatively low gamma diversity (Table 2.1). A single moss species, *Rhizomnium glabrescens*, indicated alder stands (Table 2.2).

Oregon ash stands were exceptionally rich in lichen species, averaging 35 species per stand, more than 25% of which comprised ROD-listed species. This stand type also had the highest lichen gamma diversity (Table 2.1). A number of species indicated Oregon ash stands, including the ROD listed species *Usnea longissima* (Table 2.2).

Table 2.1. Characteristics of lichen and bryophyte communities by stand type.
L = lichens B = bryophytes

stand type with number of stands sampled	mean species richness		beta diversity (average half changes)		gamma diversity		Number of indicator species		Percent ROD-listed lichens[1]
	L	B	L	B	L	B	L	B	
Alnus rubra (6)	21.5	18.0	1.1	0.6	58	31	0	1	17.2
Fraxinus latifolia (6)	35.2	16.7	0.8	0.7	70	32	4	3	25.6
mixed conifer (6)	29.5	19.5	1.1	0.8	67	36	4	2	25.4
Acer macrophyllum (6)	28.5	21.5	1.3	0.6	67	37	0	3	21.8
wet/beaver meadow (5)	31.4	16.0	1.0	0.8	65	32	2	1	20.4
waterfall (6)	28.5	18.7	1.2	0.7	63	32	0	0	25.4
agricultural (6) corridors	34.0	16.5	0.7	0.6	60	30	16	5	18.2
overall	29.8	18.1	1.2	0.8	108	56	26	15	19.4

[1] Only two ROD-listed bryophyte species were encountered, so a column quantifying their percent presence was not attempted. Percentages reflect average by stand type.

Agricultural corridors also supported a rich lichen flora, with nearly as many lichens per stand as found in Oregon ash stands, but with lower gamma diversity than most other stand types (Table 2.1). The canopy composition of agricultural corridors was similar to that of Oregon ash stands. In both stand types the most common tree species was Oregon ash (Oregon ash accounted for 62% and 40%, respectively, of the total basal area in Oregon ash stands and agricultural corridors). Across stand types, we found that Oregon ash basal area was correlated with cyanolichen species richness (simple linear regression, $r^2 = 0.23$). Other tree species present, (in both Oregon ash stands and agricultural corridors), in decreasing order, were red alder, bigleaf maple and conifers.

Table 2.2. Indicator species by stand type. Indicator species are organized in order of decreasing strength of indicator value. All p-values are from Monte Carlo tests of significance where p = the proportion of randomized trials with indicator value equal to or exceeding the observed indicator value.

Stand Type	Lichen indicators (p = ≤ .05)	Bryophyte indicators (p = ≤ .05)
Alnus rubra	none	*Rhizomnium glabrescens*
Fraxinus latifolia	*Evernia prunastri, Usnea longissima, Leptogium polycarpum, Physcia aipolia*	*Porella navicularis, Radula complanata, Homalothecium fulgescens*
Mixed conifer	*Lobaria oregana, Cladonia squamosa v. subsquamosa, Sphaerophorus globosus, Cavernularia hultenii*	*Scapania bolanderi, Hypnum circinale, Cephalozia lunulifolia*
Acer macrophyllum	none	*Hypnum subimponens, Rhytidiadelphus triquetrus*
Wet/beaver meadows	*Parmelia hygrophila, Pseudocyphellaria anthraspis*	*Orthotrichum laevigatum*
Waterfalls	none	none
Agricultural corridors	*Lobaria scrobiculata, Physcia tenella, Ramalina dilacerata, Xanthoria polycarpa, Physcia adscendens, Pseudocyphellaria anomala, Melanelia exasperatula, Lobaria pulmonaria, Sticta fuliginosa, Hypogymnia tubulosa, Ramalina menziesii, Physcia stellaris, Physconia perisidiosa, Usnea wirthii, Melanelia fuliginosa, Physconia americana*	*Metaneckera menziesii, Homalothecium nuttallii, Orthotrichum lyellii, Pterogonium gracile, Orthotrichum consimile, Zygodon viridissimus*

The comparatively low lichen beta diversity values of Oregon ash stands and agricultural corridors, relative to other stand types, show that the lichen species composition within these stand types was fairly consistent (Table 2.1). Neither ash stands nor agricultural corridors supported high bryophyte species richness or gamma diversity (Table 2.1), though a number of bryophyte species indicated these stand types, including two liverworts and one moss in Oregon ash stands, and six mosses in agricultural corridors (Table 2.2). The bryophyte community composition in Oregon ash stands was more variable across stands than in agricultural corridors, which had low bryophyte beta diversity compared to many other stand types (Table 2.1).

Wet meadows were also rich in lichen species, at both a stand and landscape level, and lichen beta diversity was moderate compared to most other stand types.

In contrast, wet meadows had the lowest bryophyte species richness of any stand type (Table 2.1). Landscape level bryophyte diversity was also low in comparison to other stand types, though bryophyte beta diversity was comparatively high. Two lichen species indicated wet meadows, including the ROD-listed species *Pseudocyphellaria anthraspis,* as did one bryophyte species (Table 2.2).

Bigleaf maple stands hosted the richest bryophyte flora of any stand type, both within and across stands (Table 2.1). In fact, bryophyte species richness was directly correlated with bigleaf maple basal area (r^2 = 0.25 from simple linear

regression across stand types). Two bryophyte species indicated bigleaf maple

stands (Table 2.2). In contrast, bigleaf maple stands were generally poor habitat for

lichens, hosting fewer lichen species than most other stand types, though they could

on occasion support rich lichen floras, as reflected in their high gamma diversity

(Table 2.1). For instance, one maple stand hosted 43 lichen species, one of the

highest species richness values measured for any stand, while another stand hosted

only 11 lichen species, the poorest lichen flora of any stand sampled during this

study. This variability among stands is reflected in the relatively high lichen beta

diversity for bigleaf maple stands (Table 2.1). No lichens indicated this stand type.

Conifer stands hosted rich and distinct lichen and bryophyte floras. Species

richness, beta diversity and gamma diversity of both lichens and bryophytes were

all relatively high in conifer stands (Table 2.1) and a number of species indicated

this stand type (Table 2.2), including the nitrogen-fixing, old-growth-associated

species *Lobaria oregana* (McCune 1993, Neitlich 1993, Neitlich and McCune

1997, Pike et al. 1975, Sillett et al. 2000). For a list of all lichen and bryophyte

species encountered by stand type, see Table 2.3.

Table 2.3. Complete list of epiphytic lichen and bryophyte species encountered
during surveys in Oregon Coast Range, 1998-1999. Presence is recorded as the
total number of stands of a given type in which the species was found. Total stands
surveyed per stand type = 6, except for wet meadows where total = 5. Stand types
are as follows: red alder, ash = *Fraxinus latifolia*, con. = mixed conifer, maple =
Acer macrophyllum, wet mead. = wet meadow, falls = waterfalls, ag corrs =
agricultural corridors. Species listed in the Record of Decision (USDA and USDI
1994) are recorded with survey strategy rank*; ranks for species listed as riparian
are bolded. Species listed by the Oregon Natural Heritage Program are recorded
with Oregon Natural Heritage Program rank**.

* ROD = Record of Decision, Forest Service and Bureau of Land Management forest management within the range of the Northern Spotted Owl. Survey strategies:

1 = manage known sites

2 = survey prior to activities and manage sites

3 = conduct extensive surveys and manage sites

4 = conduct general regional surveys

** ONHP = Oregon Natural Heritage Program:

1 = threatened with extinction or presumed to be extinct throughout their range

2 = threatened with extirpation or presumed to be extirpated from the state of Oregon

3 = may be threatened or endangered in Oregon or throughout their range, but more information is needed

4=status of concern, but not currently endangered or threatened, including very rare taxa that are currently secure

LICHENS	ROD	red alder	ash	con.	maple	wet mead.	falls	ag. corrs
Alectoria sarmentosa		0	2	4	0	0	1	1
Bryoria sp.		1	0	1	0	0	2	0
Bryoria capillaris		0	0	0	0	0	0	1
Bryoria friabilis		0	1	2	2	0	0	0
Bryoria fuscescens		0	0	1	0	0	0	0
Bryoria pseudofuscescens		0	1	2	1	1	1	0
Bryoria trichodes		0	0	1	0	0	0	0
Candelaria concolor		0	0	0	0	0	0	1
Cavernularia hultenii		0	0	3	1	0	0	0
Cavernularia lophyrea		1	0	0	1	1	0	0
Cetraria chlorophylla		0	1	1	2	2	1	3
Cetraria orbata		4	3	5	5	5	4	4
Cetrelia cetrarioides	4	2	1	0	1	1	0	0
Cladonia albonigra		1	0	0	1	0	0	0
Cladonia bellidiflora (squamatic acid chemotype)		0	0	2	0	0	1	0
Cladonia fimbriata		5	5	3	3	4	5	5
Cladonia furcata		0	1	0	0	0	0	0
Cladonia ochrochlora		6	2	4	6	5	6	2
Cladonia squamosa v. subsquamosa		0	5	3	1	3	0	0
Cladonia transcendens as interpreted by McCune and Geiser (1994)		2	1	4	3	1	1	0

Table 2.3 continued

LICHENS	ROD	red alder	ash	con.	maple	wet mead.	falls	ag. corrs
Cladonia verruculosa		2	1	1	0	0	1	0
Evernia prunastri		2	6	2	3	4	3	5
Hypogymnia apinnata		2	2	4	3	2	2	1
Hypogymnia enteromorpha		6	4	6	5	5	6	5
Hypogymnia imshaugii		0	2	0	1	1	2	4
Hypogymnia inactiva		1	1	3	3	2	3	4
Hypogymnia occidentalis		3	0	1	4	2	3	2
Hypogymnia physodes		1	5	4	2	3	3	5
Hypogymnia tubulosa		1	6	3	2	4	3	6
Hypotrachyna sinuosa		4	6	4	3	5	3	4
Leptogium corniculatum		3	6	4	5	1	4	5
Leptogium cyanescens	**4**	0	1	0	0	0	0	0
Leptogium polycarpum		1	6	1	5	1	4	2
Leptogium teretiusculum		0	0	0	0	0	0	1
Lobaria oregana	4	3	0	5	2	1	4	0
Lobaria pulmonaria	4	2	6	3	3	4	3	6
Lobaria scrobiculata	4	1	5	0	0	1	0	6
Loxosporopsis corallifera		0	0	1	0	0	1	0
Melanelia sp.		0	0	0	0	1	0	0
Melanelia elegantula		0	1	0	0	0	1	0
Melanelia exasperatula		0	1	0	0	0	0	4
Melanelia fuliginosa		1	6	1	4	4	1	5
Melanelia subelegantula		0	0	0	0	0	0	1
Menegazzia terebrata		5	4	3	3	4	3	2
Nephroma bellum	4	1	0	1	0	0	0	0
Nephroma helveticum	4	0	3	3	1	1	4	0
Nephroma laevigatum	4	1	3	4	4	4	6	0
Nephroma resupinatum	4	1	5	2	4	1	5	2
Nodobryoria oregana		0	0	0	0	0	1	0
Normandina pulchella		1	4	0	3	2	3	5
Pannaria sp.		0	0	0	1	1	0	0
Pannaria leucostictoides	4	0	0	0	1	0	0	0
Pannaria saubinetii	4	1	1	1	1	0	2	0
Parmelia hygrophila		0	1	1	1	4	1	3
Parmelia pseudosulcata		0	0	1	1	1	0	0
Parmelia saxatilis		1	1	0	0	1	1	2
Parmelia sulcata		6	6	6	5	4	6	6
Parmeliella parvula		0	0	1	0	0	0	0
Parmeliopsis hyperopta		1	0	0	0	0	0	0
Parmotrema arnoldii		0	0	0	1	1	0	0

Table 2.3 continued

LICHENS	ROD	red alder	ash	con.	maple	wet mead.	falls	ag. corrs
Parmotrema chinense		1	1	0	0	1	0	3
Peltigera britannica		0	0	0	0	0	1	0
Peltigera collina	4	4	6	5	5	5	6	6
Peltigera membranacea		1	2	1	3	1	3	0
Peltigera neopolydactyla		1	1	1	0	0	0	0
Peltigera pacifica	4	0	0	1	1	0	0	0
Peltigera praetextata		0	1	0	0	0	0	0
Physcia adscendens		0	5	0	0	1	0	6
Physcia aipolia		1	5	1	2	1	1	3
Physcia stellaris		0	2	0	1	1	0	4
Physcia tenella		1	5	0	2	0	0	6
Physconia americana		0	2	0	0	0	0	3
Physconia perisidiosa		0	1	0	0	0	0	3
Platismatia glauca		3	5	5	3	4	4	5
Platismatia herrei		1	0	5	4	4	2	3
Platismatia lacunosa	**4**	2	1	2	2	2	1	0
Platismatia norvegica		0	0	1	0	1	0	0
Platismatia stenophylla		1	1	2	1	1	2	0
Polychidium contortum		0	0	1	0	0	0	0
Pseudocyphellaria anomala	4	0	5	2	2	1	2	6
Pseudocyphellaria anthraspis	4	0	1	3	1	4	2	0
Pseudocyphellaria crocata	4	2	4	3	1	2	3	1
Ramalina dilacerata		4	6	0	3	4	2	6
Ramalina farinacea		5	6	4	5	5	4	5
Ramalina menziesii		0	3	0	0	0	0	4
Ramalina roesleri		0	0	0	0	1	0	1
Ramalina thrausta	**4**	0	0	2	1	0	1	0
Sphaerophorus globosus		4	1	6	4	4	5	1
Sticta fuliginosa	4	0	6	2	3	2	2	6
Sticta limbata	4	1	4	2	3	2	3	3
Usnea sp.		0	1	0	0	0	0	1
Usnea cornuta		3	2	3	3	2	2	1
Usnea diplotypus		0	0	0	0	0	1	0
Usnea esperantiana		0	1	0	0	1	0	1
Usnea filipendula		5	5	5	5	4	5	6
Usnea fragilescens v. mollis		2	0	0	1	2	1	0
Usnea glabrata		0	4	3	3	2	2	2
Usnea glabrescens		1	0	0	0	0	0	0
Usnea lapponica		2	0	1	3	1	0	0
Usnea longissima	**4**	1	5	2	1	3	1	1

Table 2.3 continued

LICHENS	ROD	red alder	ash	con.	maple	wet mead.	falls	ag. corrs
Usnea madeirensis		1	0	1	0	0	0	0
Usnea scabrata		1	0	0	0	0	2	0
Usnea subfloridana		3	0	3	1	4	2	1
Usnea substerilis		0	0	1	0	0	0	0
Usnea wirthii		4	5	5	6	5	6	6
Xanthoria candelaria		0	0	0	1	0	0	1
Xanthoria fulva		0	1	0	0	0	0	1
Xanthoria polycarpa		0	2	0	0	0	0	5

BRYOPHYTES	ROD/ ONHP	red alder	ash	con.	maple	wet mead.	falls	ag. corrs
Antitrichia curtipendula	4	6	4	6	5	5	6	4
Aulacomnium androgynum		0	0	0	0	1	0	0
Blepharostoma trichophyllum		0	0	1	0	0	0	0
Calopogeia trichomanis		0	0	1	0	0	0	0
Cephalozia lunulifolia		0	0	3	1	0	0	0
Ceratodon purpureus		0	0	0	0	1	0	0
Claopodium crispifolium		6	2	4	6	2	5	1
Dendroalsia abietina		0	3	1	0	0	1	3
Dicranum fuscescens		2	1	5	4	2	5	1
Dicranum scoparium		4	1	3	4	3	2	0
Dicranum tauricum		1	0	0	1	1	2	0
Douinia ovata	4	0	0	2	0	0	0	0
Drepanocladus uncinatus		0	1	0	0	0	0	1
Eurhynchium oreganum		4	1	3	4	1	3	0
Eurhynchium praelongum		0	0	1	0	0	0	0
Frullania bolanderi		0	3	0	0	0	1	3
Frullania nisquallensis		6	4	6	6	5	6	5
Heterocladium macounii		1	0	0	0	0	0	0
Homalothecium fulgescens		2	6	2	5	4	2	4
Homalothecium nuttallii		6	5	5	6	3	5	6
Hypnum circinale		3	0	6	3	1	5	0
Hypnum subimponens		5	4	5	6	2	5	5
Isothecium myosuroides		6	6	6	6	5	6	6
Lepidozia reptans		0	0	3	2	0	0	0
Leucolepis acanthoneuron		6	1	5	5	2	5	1
Metaneckera menziesii		0	5	4	6	2	4	6
Metzgeria conjugata		1	0	1	1	0	1	0
Neckera douglasii		6	5	6	6	5	6	5

Table 2.3 continued

BRYOPHYTES	ROD/ ONHP	red alder	ash	con.	maple	wet mead.	falls	ag. corrs
Orthotrichum sp.		1	0	0	1	0	0	1
Orthotrichum consimile		4	4	2	5	3	3	6
Orthotrichum laevigatum		0	0	0	0	2	0	0
Orthotrichum lyellii		4	6	4	4	4	4	6
Orthotrichum pulchellum		1	3	2	3	3	2	2
Orthotrichum speciosum		0	1	0	0	1	0	1
Orthotrichum rivulare		0	0	0	0	0	0	1
Plagiomnium venustum		2	4	0	4	4	2	4
Plagiothecium undulatum		0	0	1	0	1	0	0
Porella cordaena		0	1	1	2	1	0	2
Porella navicularis		6	6	6	6	5	6	6
Porella roellii		0	1	1	3	0	3	0
Porothamnium bigelovii		0	0	0	0	0	2	0
Pterogonium gracile		0	4	0	1	0	0	5
Ptilidium californicum	1/2	0	0	2	0	0	0	0
Racomitrium aciculare		1	0	0	0	0	0	0
Radula bolanderi		5	3	4	1	3	3	1
Radula complanata		2	6	2	5	3	1	5
Rhizomnium glabrescens		6	0	3	3	1	4	0
Rhytidiadelphis loreus		4	1	3	2	1	3	1
Rhytidadelphus triquetrus		1	2	0	4	1	0	0
Riccardia latifrons		0	0	0	1	0	0	0
Scapania bolanderi		1	0	6	3	0	4	0
Scleropodium cespitans		1	0	0	1	0	0	1
Tetraphis pellucida		0	0	0	2	0	0	0
Tortula princeps		0	1	0	0	0	0	2
Ulota obtusiuscula		4	2	2	0	2	4	0
Zygodon viridissimus		0	3	0	1	0	1	4

Environmental gradients affecting lichen community composition

NMS ordination of the lichen data produced a 3-dimensional ordination that

accounted for 88% of the variation in the data (Figure 2.2). In our NMS ordination

of stands in lichen species space, the 1st ordination axis expressed the strongest

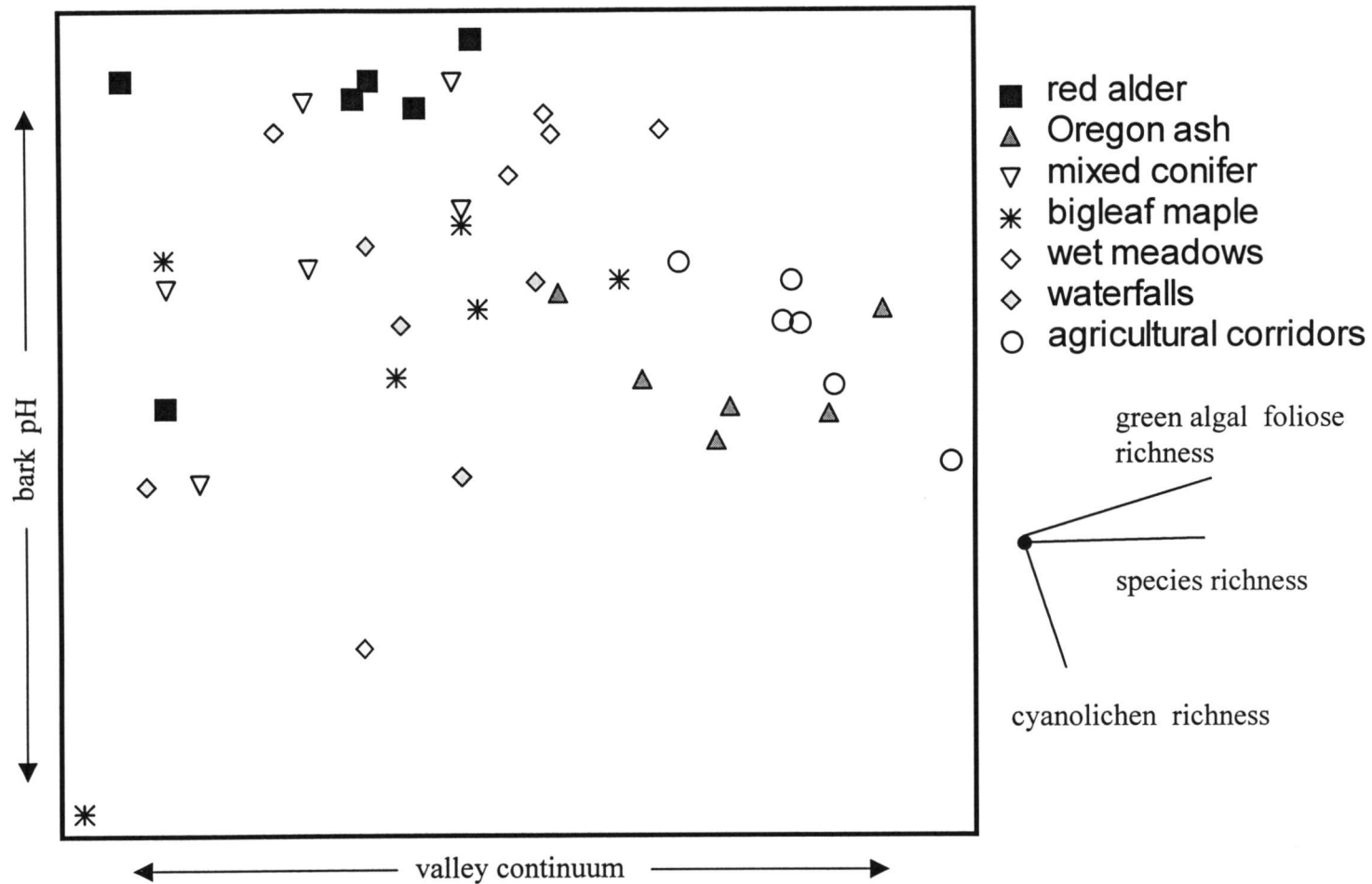gradient in lichen community composition, accounting for 54% of the variation in

Figure 2.2. NMS ordination of stands in lichen species space, rotated to maximize correlation of valley continuum with horizontal axis. Correlation coefficient for individual variables associated with each axis listed in Table 2.4.

the data. Axis 3 expressed the second strongest gradient in lichen species composition, accounting for 21% of the variation in the data. Axis 2 accounted for only 13% of the variation in the data, and will not be discussed further. We interpret axis 1 of the ordination as representing the valley continuum: a gradient in epiphyte community composition from higher elevation, conifer-dominated riparian zones with greater basal area located along more constrained streams bounded closely by slopes (narrow, enclosed valleys) to lower elevation, hardwood-dominated riparian zones located on wide floodplains along unconstrained river/stream reaches (broad, low valleys) (Figure 2.3, Table 2.4). Within the study area, narrow, enclosed valleys tended to be located in areas that typically receive more precipitation (Daly et al. 1994). It is clear that both biotic factors (tree and shrub species composition) and abiotic factors (elevation, precipitation, topographic position, etc.) vary along this gradient (Figure 2.4, Table 2.4). Overall lichen species richness is strongly positively associated with axis 1 and broad, low valley environments ($r^2 = 0.42$); many of the species driving this richness gradient are green-algal foliose lichens ($r^2 = 0.43$). As a group, alectorioid lichens show a bimodal distribution along the valley continuum (Figure 2.4), but appeared to be more abundant in stands with older average tree age (p = 0.04, $r^2 = 0.12$) or stands with older trees (p = 0.03, $r^2 = 0.12$) (both from simple linear regression).

Species strongly positively correlated with axis 1 and broad, low, hardwood dominated valleys include *Evernia prunastri* ($r^2 = 0.73$), *Hypogymnia tubulosa* (r^2

- More old-growth associated species
- More *Alectoria sarmentosa*, an alectorioid lichen

- Greater lichen species richness
- More green-algal foliose lichen species
- More cyanolichen species

Epiphyte community patterns

- Higher elevations
- Narrow floodplains
- Streams with close, constraining slopes
- Greater basal area
- Dominated by conifers such as Douglas-fir, western redcedar and western hemlock
- Older stand ages

- Lower elevations
- Broad floodplains
- Unconstrained streams
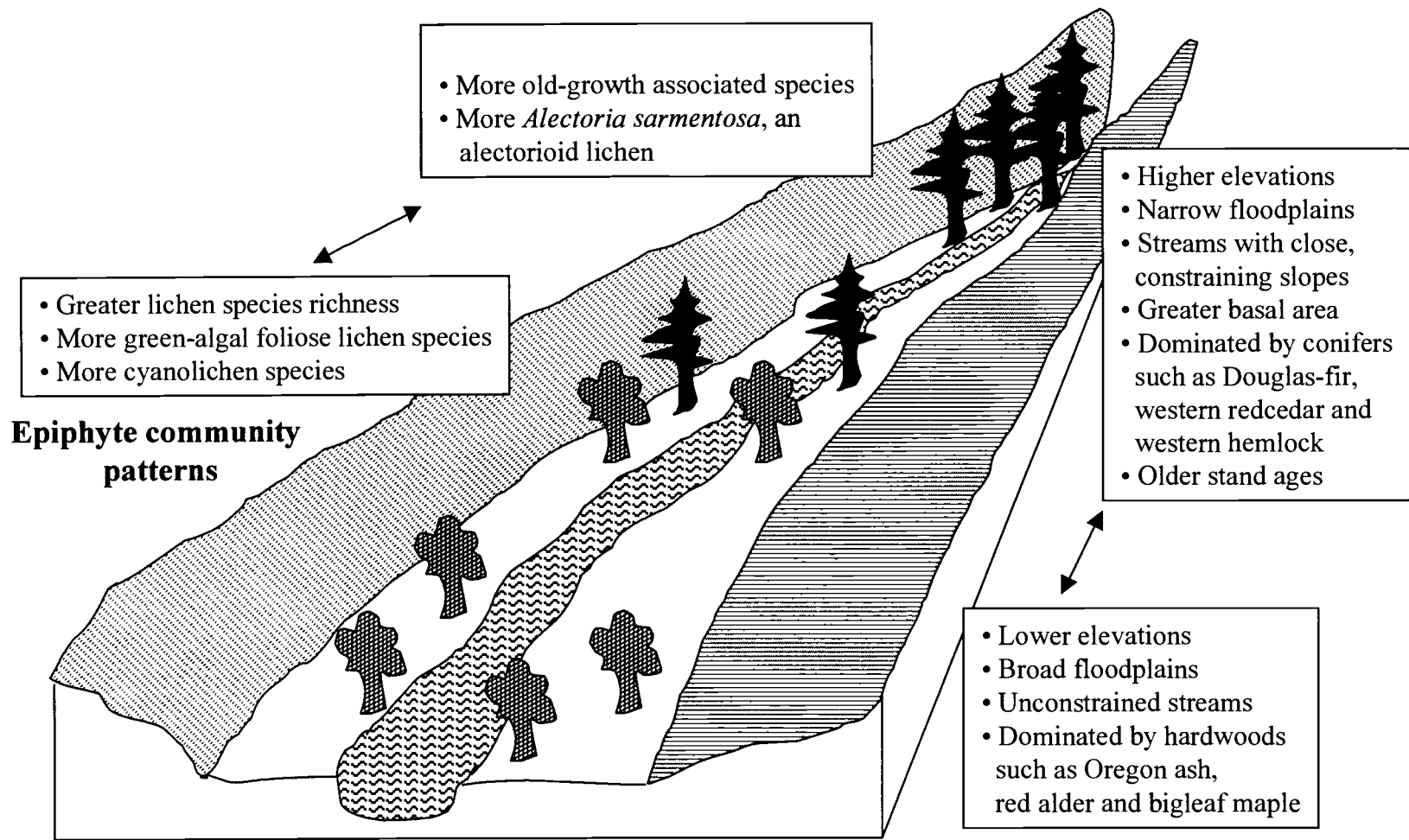- Dominated by hardwoods such as Oregon ash, red alder and bigleaf maple

Figure 2.3. The Oregon Coast Range valley continuum.   **Riparian zone characteristics**

Table 2.4. Correlation coefficients (Pearson's r) for variables strongly associated ($|r| > 0.5$) with one or more lichen ordination axes. All correlations > 0.5 are bolded. Note that r values are presented in this table (rather than r^2) in order to show the positive or negative association of variables with ordination axes.

	Axis 1	Axis 2	Axis 3
% variation explained	54%	13%	21%
valley continuum abiotic variables:			
reach constraint *(scored using a continuous scale from 0 = unconstrained to 10 = very constrained)*	**-0.68**	0.00	-0.05
dominant topography *(1 = flood plain, 2 = lower slope, 3 = upper slope, 4 = bench)*	**-0.63**	0.13	0.00
topographical shelter *(1 = sheltered, 2 = intermediate, 3 = open and unsheltered)*	**0.70**	-0.01	0.00
bottomland width	**0.51**	0.03	-0.18
longitude	**-0.67**	0.43	0.08
precipitation	**-0.53**	0.18	0.24
canopy variables			
percentage of stand basal area in Oregon ash	**0.70**	-0.14	-0.29
abundance of modal Oregon ash	**0.77**	-0.14	-0.27
percentage of stand basal area in red alder	-0.15	0.44	**0.53**
percentage of stand basal area in conifers	**-0.51**	-0.46	0.01
stand basal area	**-0.58**	-0.08	0.04
abundance of understory salmonberry (*Rubus spectabilis*)	**-0.57**	0.38	0.12
abundance of understory vine maple (*Acer circinatum*)	**-0.51**	0.33	-0.08
richness variables			
lichen species richness	**0.65**	**-0.53**	0.09
green algal foliose species richness	**0.66**	-0.37	0.37
cyanolichen richness	0.32	-0.37	**-0.54**
lichen species			
Cladonia ochrochlora	**-0.68**	0.48	0.15
Cladonia squamosa v. subsquamosa	**-0.51**	-0.09	-0.17
Evernia prunastri	**0.85**	-0.41	-0.08
Hypogymnia enteromorpha	-0.29	-0.05	**0.54**
H. inactiva	0.05	**-0.64**	0.06
H. physodes	**0.69**	-0.60	0.03
H. tubulosa	**0.84**	-0.34	-0.06
Hypotrachyna sinuosa	**0.52**	0.04	0.37
Leptogium corniculatum	0.21	-0.07	**-0.66**
Lobaria pulmonaria	**0.84**	-0.33	-0.17
Lobaria scrobiculata	**0.73**	-0.24	-0.27
Melanelia exasperatula	**0.53**	-0.24	-0.08

Table 2.4, continued

% variation explained	Axis 1 54%	Axis 2 13%	Axis 3 21%
M. fuliginosa	**0.78**	-0.21	-0.08
Menegazzia terebrata	-0.09	0.34	**0.56**
Parmelia sulcata	**0.67**	-0.20	**0.50**
Peltigera collina	**0.53**	-0.44	-0.47
Physcia adscendens	**0.72**	-0.20	-0.17
P. aipolia	**0.56**	-0.23	-0.15
P. stellaris	**0.57**	-0.07	-0.18
P. tenella	**0.74**	-0.20	-0.22
Platismatia glauca	0.38	**-0.68**	0.34
Platismatia herrei	0.11	**-0.55**	0.23
Pseudocyphellaria anomala	**0.58**	-0.23	-0.37
Ramalina dilacerata	**0.78**	-0.08	-0.10
Ramalina farinacea	**0.62**	-0.15	0.37
Ramalina menziesii	**0.66**	-0.14	-0.21
Sticta fuliginosa	**0.59**	-0.23	-0.39
Usnea subfloridana	0.09	-0.20	**0.52**
Xanthoria polycarpa	**0.64**	-0.21	-0.21

= 0.71), *Lobaria pulmonaria* (r^2 = 0.70), *Melanelia fuliginosa* (r^2 = 0.60), and

Ramalina dilacerata (r^2 = 0.61). In contrast, *Cladonia ochrochlora* (r^2 = 0.47),

Cladonia squamosa v. subsquamosa (r^2 = 0.26), and *Lobaria oregana* (r^2 = 0.23)

are negatively correlated with axis 1 and associated with higher elevation, narrow,

conifer-dominated valleys. The distribution of many species was most strongly

related to the valley continuum, while a smaller number of species were most

strongly related to factors represented by axis 3, the second strongest gradient in

lichen composition.

Factors driving the distribution of lichen communities along axis 3 are more

obscure: few of the environmental variables we measured are strongly associated

with this axis (Figure 2.2, Table 2.4). By examining the pattern of stand types and
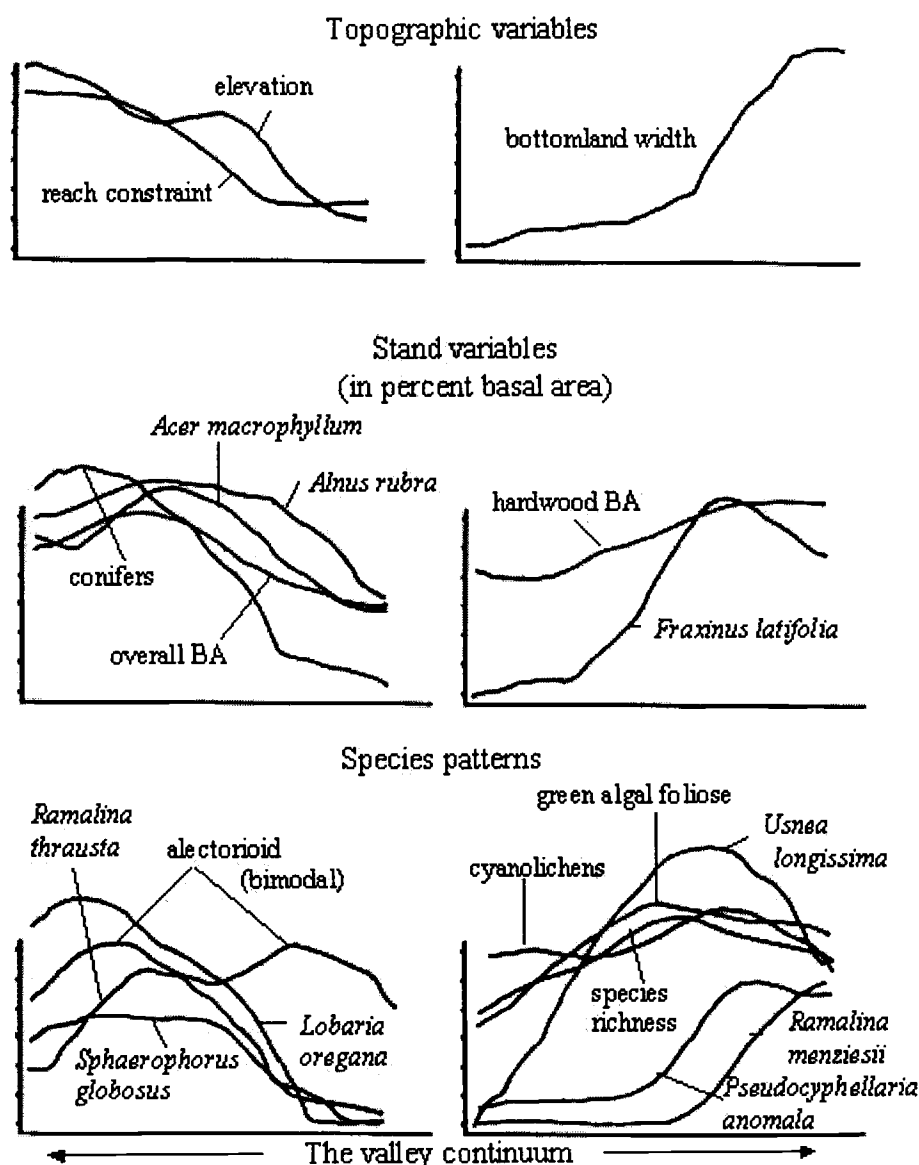
Figure 2.4. Patterns of environmental factors and lichen species distributions along a valley continuum, Oregon Coast Range. Most curves are fitted to scatterplots showing the approximate upper bound of the variable with respect to the ordination axis. The curves for % hardwood BA, reach constraint, *Sphaerophorus globosus* and *Ramalina menziesii*, show a moving average, which was used in cases where envelope lines extended beyond the range of the points in the scatterplot.

lichen species along axis 3, we hypothesized underlying factors. As a group, cyanolichens were negatively correlated with axis 3 ($r^2 = 0.29$); the cyanolichen species *Leptogium corniculatum* ($r^2 = 0.44$) and *Peltigera collina* ($r^2 = 0.22$) were strongly negatively associated with this axis and largely unrelated to the valley continuum. Green algal foliose lichens were weakly positively correlated with this axis ($r^2 = 0.12$). *Menegazzia terebrata* ($r^2 = 0.31$), *Sphaerophorus globosus* ($r^2 = 0.23$) and *Usnea subfloridana* ($r^2 = 0.27$) all showed positive correlations with axis 3 and were largely unrelated to the valley continuum (Table 2.4). Particular stand types also distributed differentially along these primary axes. Conifer and red alder stands are clumped together in upper half of the ordination (the top half of axis 3), while wet/beaver meadows, waterfalls, and bigleaf maple stands, to a lesser extent, are more spread out along this axis. Oregon ash stands and agricultural corridors are clumped towards the center of axis 3, and at the right side of the ordination (Figure 2.2). Red alder and conifer stands are the purest stands in the sense of tree dominance (red alder stands contain an average of 81% of total stand basal area in red alder, and conifer stands contain an average of 76% conifer basal area), whereas bigleaf maple stands, wet/beaver meadows and waterfalls tend to have more mixed tree species compositions: maple stands contain, on average, 59% bigleaf maple, 14% alder and 15% conifer basal area; beaver meadows contain 60% alder, 11% conifer, 9% maple and 8% ash basal area; waterfalls contain, on average, 26% alder, 1% ash, 43% conifer and 13% maple. The pattern that emerges is this: stands that are more compositionally homogenous in tree species

are more clumped along axis 3, while heterogeneous stands are more spread out along this axis. This pattern suggests that the factor (or factors) driving the distribution of epiphytes along axis 3 could be linked to tree composition. We hypothesize that alder and conifer stands clump together higher along ordination axis 3 than bigleaf maple and Oregon ash, because of their comparatively low bark pH (average bark pH values for these species were ordered as follows: Douglas-fir < red alder <Oregon ash < bigleaf maple, from S. Jovan, unpublished data). Furthermore, we hypothesize that this pH gradient is expressed as higher cyanolichen richness at the lower (negative) end of axis 3 (where stand types with trees with higher bark pH have, to some extent, clumped) (Figure 2.5).

Environmental gradients affecting bryophyte species composition

Ordination of the bryophyte data produced a 2-dimensional solution that explained 81% of the variation in the data. Two separate environmental gradients strongly influenced bryophyte communities (Table 2.5; Figure 2.6). The first axis expresses the strongest gradient, accounting for 59% of the variation in the data, while the second axis accounted for an additional 23%. As in the lichen ordination, the valley continuum is the strongest gradient in bryophyte community composition (Table 2.5).

Species positively correlated with axis 1 and broad, hardwood-dominated valleys include *Pterogonium gracile* ($r^2 = 0.57$), *Orthotrichum consimile* ($r^2 =$
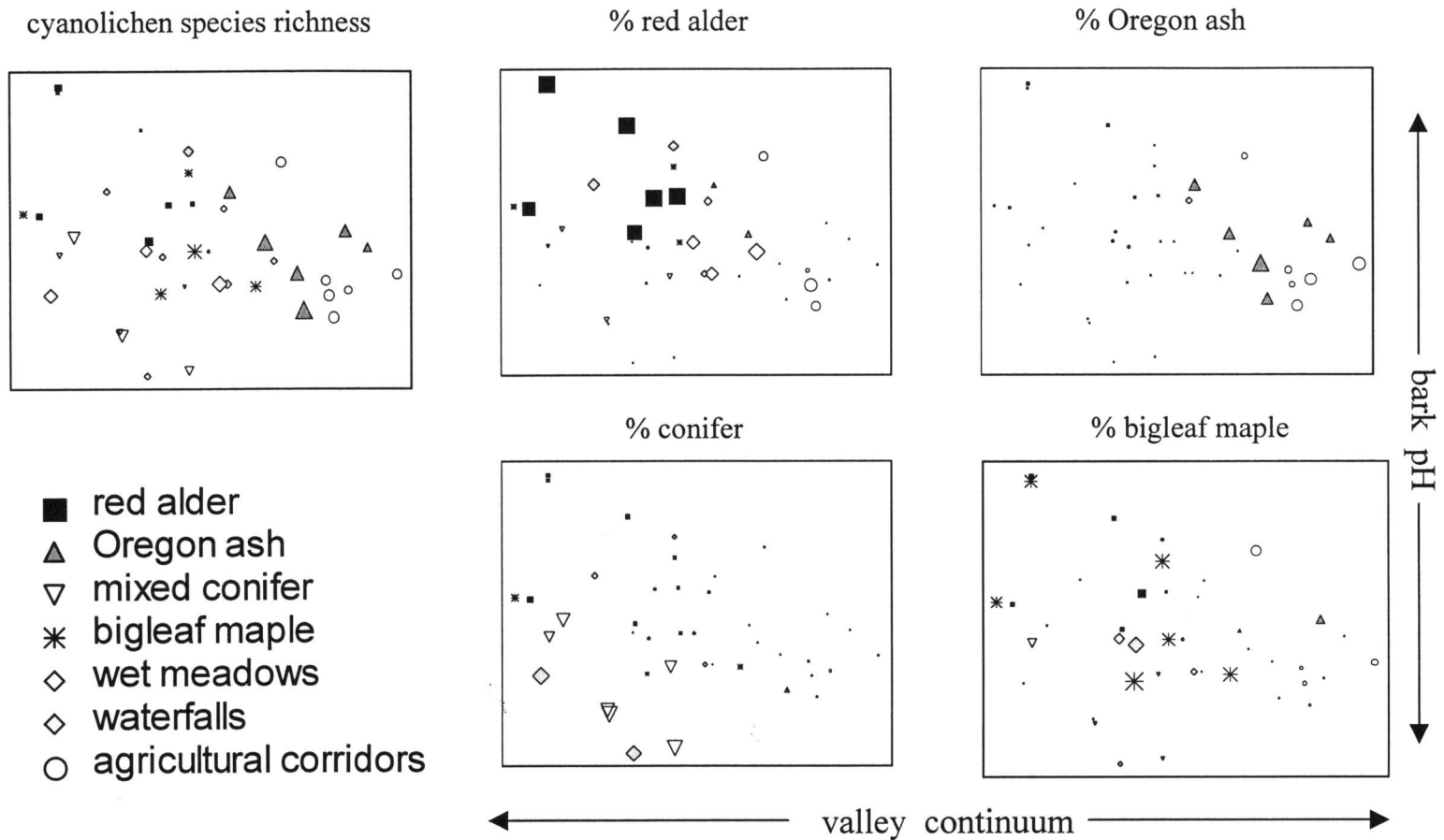
Figure 2.5. NMS ordination of stands in lichen species space with stand canopy composition and cyanolichen species richness overlaid. Larger symbols denote greater % basal area in given canopy species, and greater cyanolichen species richness, respectively.

Table 2.5. Correlation coefficients (Pearson's r) for variables strongly associated ($|r|>.5$) with one or more bryophyte ordination axes. Strongest correlations are in bold face.

| % variation explained	Axis 1 50%	Axis 2 23%
valley continuum abiotic variables		
reach constraint *(scored using a continuous scale from 0 = unconstrained to 10 = very constrained)*	**-0.68**	-0.34
topographical shelter *(1 = sheltered, 2 = intermediate, 3 = open and unsheltered)*	**0.65**	0.33
precipitation	**-0.57**	0.33
longitude	**-0.64**	0.01
canopy variables		
stand basal area	**-0.51**	-0.24
percentage of stand basal area in hardwoods	**0.62**	0.23
percentage of stand basal area in red alder	-0.16	**0.65**
percentage of stand basal area in Oregon ash	**0.72**	0.07
percentage of stand basal area in conifers	**-0.63**	-0.22
percentage of stand basal area in bigleaf maple	-0.06	**-0.60**
abundance of understory western hemlock (*Tsuga heterophylla*)	**-0.58**	0.02
abundance of understory willow (*Salix spp.*)	**0.51**	0.07
abundance of modal Oregon ash	**0.75**	0.11
richness variables		
bryophyte richness	-0.19	**-0.52**
bryophyte species		
Claeopodium crispifolium	-0.49	**-0.55**
Dendroalsia abietina	**0.56**	-0.11
Frullania nisquallensis	**-0.57**	0.10
Homalothecium fulgescens	**0.55**	-0.28
Hypnum circinale	**-0.63**	-0.35
Isothecium myosuroides	**-0.65**	0.02
Leucolepis acanthoneuron	**-0.52**	-0.47
Metaneckera menziesii	0.41	**-0.63**
Orthotrichum consimile	**0.67**	0.40
Orthotrichum lyellii	**0.63**	0.40
Pterogonium gracile	**0.75**	-0.10
Radula bolanderi	-0.10	**0.58**
Rhizomnium glabrescens	**-0.65**	-0.02
Scapania bolanderi	**-0.64**	-0.30
Ulota obtusiuscula	-0.37	**0.64**
Zygodon viridissimus	**0.56**	-0.21
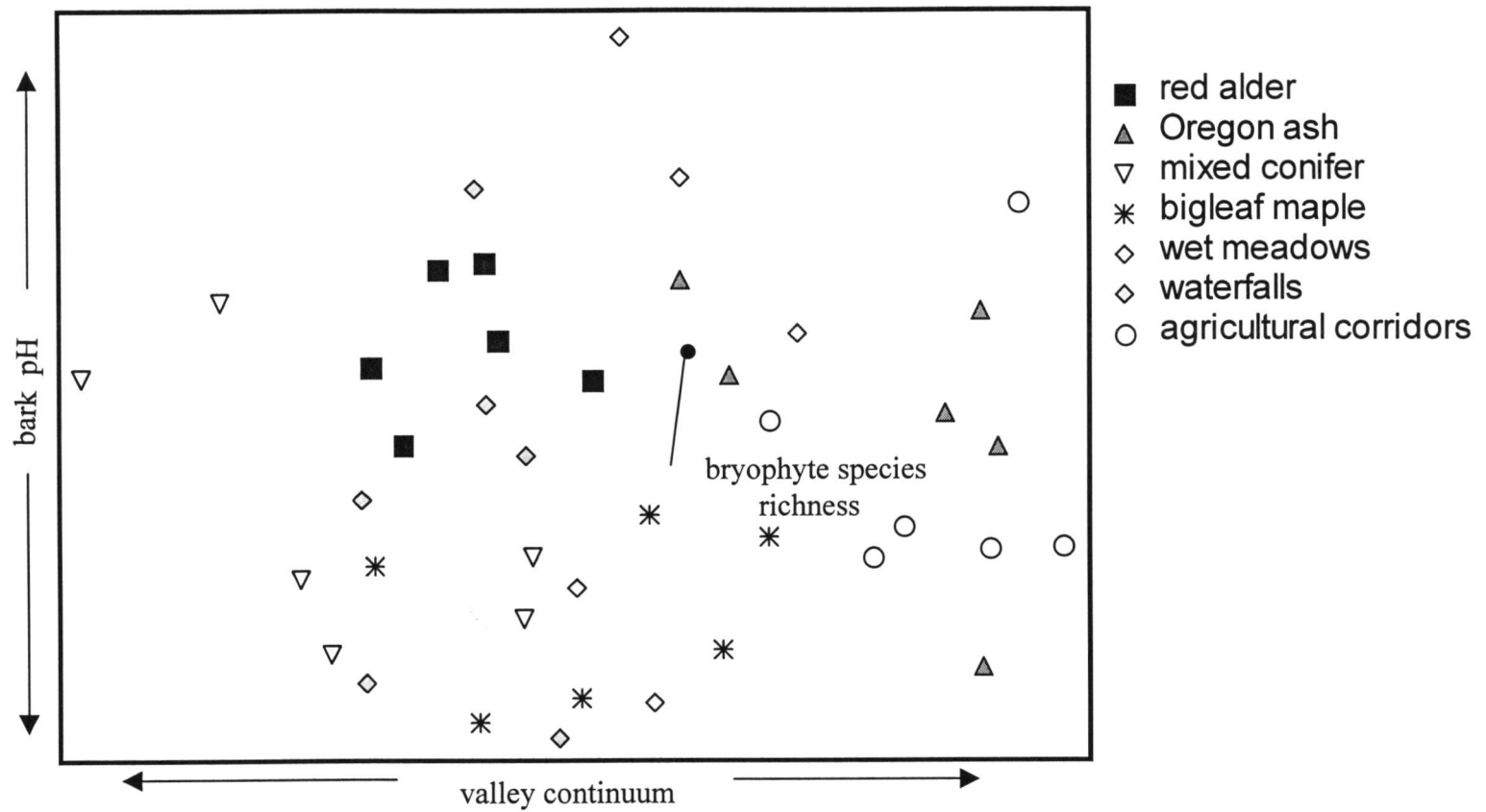
Figure 2.6. NMS ordination of stands in bryophyte species space, rotated to maximize correlation of valley continuum with horizontal axis. Correlation coefficient for individual variables associated with each axis listed in Table 2.5.

bryophyte species richness

% red alder

% Oregon ash

% conifer

% bigleaf maple

bark pH

■ red alder
▲ Oregon ash
▽ mixed conifer
✳ bigleaf maple
◇ wet meadows
◇ waterfalls
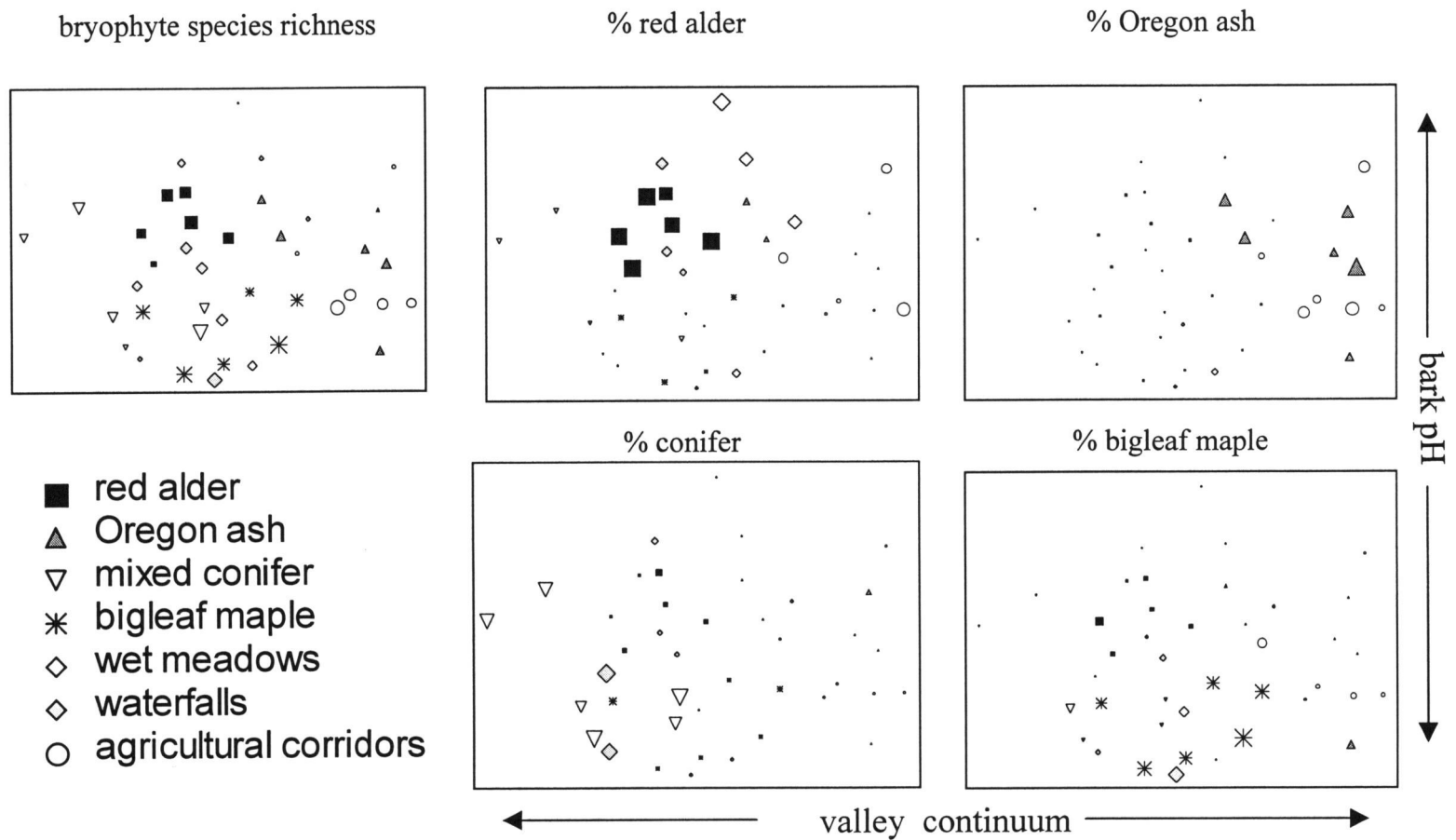○ agricultural corridors

valley continuum

Figure 2.7. NMS ordination of stands in bryophyte species space with stand canopy composition and bryophyte species richness overlaid. Larger symbols denote greater % basal area in given canopy species, and greater bryophyte species richness, respectively.

0.45), *Orthotrichum lyellii* ($r^2 = 0.39$), and *Dendroalsia abietina* ($r^2 = 0.31$).

Species associated with narrow, conifer dominated valleys (and negatively

associated with axis 1) include *Frullania nisquallensis* ($r^2 = 0.33$), *Hypnum*

circinale ($r^2 = 0.39$), *Isothecium myosuroides* ($r^2 = 0.42$), *Rhizomnium glabrescens*

($r^2 = 0.42$) and *Scapania bolanderi* ($r^2 = 0.41$). The distribution of stand types

along axis 2 in the bryophyte ordination is less consistent with the pH gradient

hypothesized to explain variation along the vertical axis in the lichen ordination. In

the bryophyte ordination, stands with greater conifer basal area clump in the lower

half of the ordination, along with bigleaf maple and Oregon ash, while red alder

stands, with bark more similar in pH to that of conifers, clump high along the

vertical ordination axis. Excepting the conifer stand type, all other stand types

show a pattern of distribution in the bryophyte ordination that is similar to that seen

in the lichen ordination. It is possible that bark pH may also affect bryophyte

communities (Figure 2.7); bryophytes growing on conifers, however, may respond

more strongly to other unknown factors. Unlike lichen species richness, bryophyte

species richness is more strongly associated with the 2nd axis than with the valley

continuum (Figure 2.6). Bryophyte species richness is negatively correlated with

axis 2 ($r^2 = 0.28$), and rises with increasing dominance by bigleaf maple ($r^2 = 0.25$, p

= 0.001, from simple linear regression). In contrast, the percentage basal area in

red alder is positively correlated with axis 2 ($r^2 = 0.41$). Bryophyte species

richness, like cyanolichen richness, appears to be positively associated with higher

bark pH.

Discussion

The valley continuum

Species composition and abundance of epiphytic lichens and bryophytes differed among the seven riparian stand types. The factors hypothesized to underlie these differences included bark pH and the distribution of stand types along a valley continuum: as elevation and precipitation decreased, bottomland width expanded, stream reaches became less constrained, and riparian stands became more hardwood-dominated (primarily due to increase in basal area in Oregon ash) (Figures 2.3 and 2.4). Along this continuum, overall lichen species richness increased, including green-algal foliose lichen and cyanolichen richness. The abundance of *Lobaria oregana*, an old-growth associated lichen (McCune and Geiser 1997, Sillett et al. 2000) decreased along this continuum. According to the river continuum concept (Vannote et al. 1980), from stream headwater to mouth, species respond, by their occurrences and relative abundances, to the physical gradients present; these species have functional relationships corresponding to their position along this continuum. The valley continuum observed for epiphytes rests on the same conceptual framework as the river continuum concept, though no functional component is inferred in this case.

Bark pH

Both bryophyte species richness and cyanolichen richness were more strongly associated with the vertical ordination axis, the axis representing our hypothesized

pH gradient (axis 3 in the lichen ordination and axis 2 in the bryophyte ordination), than with axis 1 (the valley continuum). We hypothesize that bark pH influenced epiphyte community composition, limiting cyanolichens and many bryophytes to bark environments with relatively high pH. This hypothesis is based on observed trends in our data combined with the findings of other authors. Conifers and alder tend to have the most acidic bark of the tree species sampled within this study (S. Jovan, unpublished data) and these stand types were negatively associated with cyanolichen richness in our study. Other hardwood species, specifically bigleaf maple and Oregon ash, tend to have higher bark pH than conifers and some other hardwood species, such as red alder (Barkman 1958, Kenkel & Bradfield 1986, S. Jovan, unpublished data) and were positively associated with overall bryophyte species richness and cyanolichen richness. A number of studies have demonstrated epiphyte habitat specificity and observationally linked such specificity to bark characteristics, including bark pH. Barkman (1958) reported that pH can be an important determinant of which lichen species can colonize a bark surface. Kenkel and Bradfield (1976) recognized that bark pH is probably an important factor in differentiating epiphytic bryophyte communities on *Acer macrophyllum* from those on coniferous species. Recent work by Goward and Arsenault (2000) linked the presence of cyanolichens in a primarily coniferous forest to the presence of a hardwood tree (*Populus*). They hypothesized that leachates from *Populus* create a "dripzone effect", raising the pH of subtending conifer branches and creating an environment more suitable for cyanolichens. Studlar (1982) and Palmer (1986)

attributed differences in bryophyte community composition among tree species to pH.

The effect of bark pH on epiphyte communities may be more apparent in riparian zones, where there is greater tree species diversity, more hardwood species (Harris 1984) and presumably a greater range in bark pH, than in upland forests. The tendency of riparian forests to host more cyanolichen species, which are often restricted to bark with a relatively high pH (Gauslaa 1985) enhances the visibility of the pH effect. Why do Oregon ash and bigleaf maple, both with comparatively high bark pH, appear to differ so in their capacity to host cyanolichens at a stand level? Though maple stands had lower mean lichen species richness than Oregon ash stands, it is important to note that maple stands are *sometimes* good lichen habitat, and the rich lichen communities there may rival the luxurious lichen floras of Oregon ash forests. The difference in these two species as lichen habitat probably lies not in the nature of the substrate, but with some other environmental variable that may affect microclimate or competition dynamics. For instance, in dark, moist stands, are bryophytes able to out-compete lichens? Are ash canopies thinner, transmitting more light than maple canopies? These questions need further study. It is important to note that, though we hypothesize that bark pH plays a role in the distribution of epiphyte species within the stands sampled for this study, the evidence we have provided to support this hypothesis is limited, and we are unable to either support or eliminate alternate hypotheses that may account for the observed patterns.

Differences in epiphyte communities among stand types

Riparian forests dominated by Oregon ash were exceptional lichen habitat, with the highest species richness of any stand type and the highest proportion of ROD-listed species and cyanolichens (Table 2.1). Cyanolichens can contribute significant amounts of nitrogen to forest ecosystems (Denison 1979, McCune 1993, Pike et al. 1972,), an important function in the generally nitrogen limited forests of the Pacific Northwest (Harris 1984). Oregon ash stands hosted a number of indicator lichen and bryophyte species (Table 2.2), including the ROD–listed lichen species *Usnea longissima*, a species that may be dispersal-limited (McCune and Geiser 1997, Keon 2000). Because of their association with wide bottomlands (often rich agricultural areas) and proximity to the Willamette Valley, Oregon ash stands are often at risk from land development and air pollution. The value of Oregon ash stands as habitat for rare lichens and species sensitive to air pollution (including cyanolichens) combined with their relative rarity in the Coast Range, suggest a need to carefully manage this habitat.

Riparian conifer stands host distinctive lichen and bryophyte floras that include a number of indicator species. Among the lichen indicators is the old-growth-associated, dispersal-limited species *Lobaria oregana* (McCune and Geiser 1997, Sillett et al. 2000, Shirazi et al. 1996). Conifer-dominated riparian zones may provide important refugia and dispersal sources for this species on the landscape.

Stands dominated by bigleaf maple are hotspots for bryophyte species richness in riparian zones. Wet meadows and waterfalls also host distinctive epiphyte floras; some rare species were found only in these stand types (Ruchty and McCune 2000c).

Red alder is one of the first species to colonize a site after disturbances such as fire or logging (Hibbs et al. 1994). Red alder stands are probably the fastest expanding stand type in riparian zones on the Oregon Coast Range landscape; pollen records show that alder has become more common in the twentieth century than it has been during several previous centuries (Heusser 1964, Davis 1973). Red alder may exclude other species, especially the shade-intolerant, slower-growing species of conifers, from colonizing riparian zones (Hibbs et al. 1994). Though lichen species richness was low in red alder stands, and bryophyte species richness was only moderate, a number of species were found most often in this stand type (Table 2.3). These species include the ROD-listed lichen species *Cetrelia cetrarioides*. In addition, Peck (1997) found that mature red alder hosts large quantities of harvestable, mat-forming bryophytes.

The unusually high number of both lichens and bryophytes indicating agricultural corridors is in part probably attributable to the proximity of some of the sampled agricultural corridors to human population centers, such as Corvallis, Oregon. Pollutants such as agricultural fertilizers and fossil fuel combustion products may contribute to the presence of such nitrophilous lichen taxa as *Melanelia*, *Physcia*, *Physconia*, and *Xanthoria* among the indicator species. In

addition, agricultural corridors tended to be near the Willamette Valley, resulting in the presence of species common to the Willamette Valley (but uncommon in the Coast Range). This pattern is especially evident among the bryophyte indicators, where we see *Pterogonium gracile* and *Zygodon viridissimus*, both species infrequent in the Coast Range, but common in the Willamette Valley.

On a landscape level, riparian zones have undergone many changes as a result of land management activities. Forests have generally decreased in age and the proportion of forest occupied by early successional species, such as red alder and Douglas-fir, has increased. Oregon ash and bigleaf maple forests are not widely recognized for their ecological value, though the land they occupy is often recognized for its timber production or development potential, and ash stands on private land are at risk of conversion to agriculture, pastures, or conifer plantations. For epiphytes, these trends are likely to mean less landscape-level epiphyte diversity. In particular, there would be fewer nitrogen-fixing cyanolichen species, alectorioid (forage) lichens, and many ROD-listed species. If the Coast Range landscape becomes more fragmented, refuges and forests important as dispersal centers for lichen and bryophyte species will become smaller and farther apart. What does this mean for riparian areas and the epiphytes that live there? Laws protecting riparian areas in a landscape of young forests may mean that riparian forests are more important than ever before, as hotspots of epiphytic lichen and bryophyte diversity and potential dispersal centers. Riparian zones may well prove to be important refuges for epiphytes with important functions in forested

ecosystems, including alectorioid or forage lichens that are food for deer (Stevenson 1978), and food and nest building material for flying squirrels (Maser et al. 1985, Maser et al. 1986, Rosentreter and Eslick 1993) as well as a variety of epiphytes that are shelter and food for insects (Pettersson et al. 1995, Seaward 1977), nest building materials and sources of insect prey for birds (Richardson and Young 1977, Pettersson et al. 1995), and nitrogen sources in a nitrogen-limited forest ecosystem (Denison 1979, Pike et al. 1972, McCune 1993). Under the President's Forest Plan (USDA and USDI 1994) "riparian reserves" play a key role in the preservation of biodiversity in Pacific Northwest forests. Management actions that affect the canopy composition of riparian zones should be carefully reviewed to assess potential impacts to epiphyte communities.

Though all stand types contribute to landscape-level epiphyte diversity, stand types clearly differ in their potential as epiphyte habitat. By preserving or enhancing certain stand types on the riparian landscape, managers can also help to preserve and promote epiphyte diversity. It is also clear that protecting or promoting specific habitats may not protect all species. Certain rare and sensitive species will require species-centered evaluation and protection efforts in addition to broader scale habitat protection (Noss 1990). For example, *Ramalina thrausta*, a ROD-listed riparian species, was found very infrequently (in only four stands) during this study. *Leptogium cyanescens* (also a ROD-listed riparian species) was encountered only once in an Oregon ash stand; another ROD-listed species, *Pannaria leucostictoides,* was only found once in a bigleaf maple stand. *Douinia*

ovata, and *Ptilidium californicum*, both ROD-listed liverworts, were encountered only twice, both times in conifer stands. These species may be more rare within the Oregon Coast Range than has been previously recognized. We do not know enough about many of these and other species to judge whether they are at risk in the Oregon Coast Range, whether they are dependant upon riparian habitat and if so whether their risk is increasing or decreasing (Ruchty and McCune 2000c). Basic ecological research is needed to improve our understanding of the life history traits and habitat needs of these epiphytes.

Acknowledgements

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Chapter 3

Is Lichen Growth Linked to Canopy Composition?: A Transplant Experiment

Andrea M. Ruchty and Bruce McCune

Abstract

We compared the growth of epiphytic macrolichens (*Cetrelia cetrarioides*, *Hypogymnia inactiva*, *Lobaria oregana* and *Lobaria pulmonaria)* under three forest canopy types: *Alnus rubra* (red alder*)*, *Acer macrophyllum* (bigleaf maple), and *Pseudotsuga menziesii* (Douglas-fir*)*. Six to ten transplants of each species were placed under each canopy type in each of five riparian stands (treated as blocks) located in the Oregon Coast Range, Pacific Northwest of North America. Transplants were placed in the field for one year. Transplants were made by attaching nylon loops to lichen thallus fragments with dabs of silicone, and attaching this apparatus to pony-tail holders or plastic zip-ties. Growth was calculated using the methodology developed by McCune et al. (1996). We predicted that if canopy microclimate is important in determining the transplant species' distributions, then the transplants should show distinct growth response patterns under the different canopy treatments, corresponding to their known habitat specificities. The growth, health, and survival of the four individual lichen transplant species were not differentially affected by canopy treatment. As a group, however, lichen transplants were less healthy and died more frequently under bigleaf maple than under other canopies ($p = 0.003$ for lichen health and $p = 0.005$ for survival). *Hypogymnia inactiva* grew less well and was less healthy than the other three lichen species, though its survival rate was similar to that of the other transplant species.

Introduction

While in the field, lichenologists often note and wonder at interesting patterns of epiphytic lichen habitat specificity. Such patterns have been observed for many lichen species found in the Pacific Northwest of North America. For example, *Ramalina thrausta* and *Cetrelia cetrarioides* are both most often found in riparian zones, where *Ramalina thrausta* is associated with old-growth conifers (USDA and USDI 1994, McCune and Geiser 1997), and in the Pacific Northwest, *Cetrelia cetrarioides* is almost exclusively found on *Alnus rubra* (red alder*)* (Culberson and Culberson 1968). *Lobaria oregana* and *Pseudocyphellaria rainierensis* are both Pacific Northwest old-growth conifer associates (Sillett 1995, Sillett 1998); recent research demonstrated that the old-growth association of *Lobaria oregana* is due to dispersal limitations (Sillett et al. 2000). *Usnea longissima* has been considered a strong riparian associate (USDA and USDI 1994); this widely held belief has only recently been called into question (Keon 2000). Though observational and anecdotal reports of lichen habitat specificity abound in the literature (Amadjian and Hale 1973, Barkman 1958, Seaward 1977, etc.) the mechanisms driving lichen habitat specificity have rarely been tested using an experimental approach.

Why might epiphytic lichens show habitat specificity? There are a number of possible reasons. To colonize new substrate, epiphytic lichens must first disperse from elsewhere and then establish propagules (such as isidia, soredia, fragments or spores) on suitable habitat. The substrate that the bark provides may

have features necessary for an epiphyte's successful colonization and growth, such as a specific texture, water holding capacity or chemical attributes (Barkman 1958). Successful establishment and growth also depend upon a species' competitive ability. The microclimate (including factors such as light, moisture and temperature) created by tree structure and canopy environment may also provide necessary resources or environmental conditions.

It is possible to explore mechanisms driving habitat specificity by using lichen transplants. The use of pendant transplants allows manipulation of dispersal and establishment and eliminates competitive interactions. As a result, it is possible to focus on the effects of canopy microclimate. Lichen transplant experiments have great potential to add to our knowledge of the mechanisms driving lichen habitat specificity by measuring lichen performance in various habitats.

We tested whether canopy microclimate in riparian zones appears to influence epiphytic macrolichen habitat specificity by measuring the growth responses of four macrolichen species under three different canopy types: *Alnus rubra* (red alder), *Acer macrophyllum* (bigleaf maple), and *Pseudotsuga menziesii* (Douglas-fir). The lichen transplant species vary in habitat specificity. *Cetrelia cetrarioides* is a green-algal foliose lichen found, in the Pacific Northwest, almost exclusively on red alder in riparian areas (Culberson and Culberson 1968). *Cetrelia cetrarioides* is probably the most specialized of the four lichen species used in this experiment. In contrast, *Hypogymnia inactiva* is a green-algal foliose

lichen found on a wide variety of substrates in a wide variety of habitats (including both riparian and upland sites). *Lobaria oregana* is an old-growth associate endemic to the Pacific Northwest (Jordan 1973) and is most often found in montane, coniferous forests. In a comparison of lichen species composition across a variety of Oregon Coast Range riparian forests, Ruchty and McCune (2000a) found that *Lobaria oregana* indicated mixed conifer riparian stands. *Lobaria pulmonaria* has a circumboreal distribution and, in Oregon, is found in greatest abundance on hardwoods in Willamette Valley and Coast Range riparian areas, though it is not limited to these habitats. Ruchty and McCune (2000a) found that, in the Oregon Coast Range, this species indicates agricultural corridors; agricultural corridors are riparian zones (often dominated by hardwoods) bordered by agricultural fields. The lichen species *Cetrelia cetrarioides, Lobaria oregana,* and *Lobaria pulmonaria* were determined by the Forest Ecosystem Management Assessment Team (FEMAT) to be species of special concern within the range of the Northern Spotted Owl and are listed in the President's Forest Plan as survey and manage species (USDA and USDI 1994).

If canopy microclimate has important influences on growth of these four lichen species, we would predict that the more habitat-restricted lichens, *Cetrelia cetrarioides* and *Lobaria oregana,* should grow best under the canopies where they are most often found: red alder and Douglas-fir, respectively. *Lobaria pulmonaria,* less of a habitat specialist, might do best under either hardwood

canopy, while the growth of the generalist *Hypogymnia inactiva* should not differ

under the different canopy types.

In light of the recognized importance of riparian habitats to epiphytic lichen

diversity (Neitlich and McCune 1997, Peterson 2000, Rosso 2000, Ruchty and

McCune, 2000a) and the central role of "riparian reserves" in preserving

biodiversity under the present forest management regime in the Pacific Northwest

(USDA and USDI 1994) the question of lichen habitat specificity in riparian zones

is important and timely.

Methods

Site selection

In early October of 1998, five riparian stands in the Oregon Coast Range

were chosen arbitrarily but without preconceived bias as lichen transplant sites (see

Table 3.1 for site coordinates and descriptions). We defined a stand as a forested

area relatively homogeneous in age and canopy structure. Each stand contained a

mixture of bigleaf maple, red alder, and Douglas-fir as overstory canopy

components.

Table 3.1. Transplant site coordinates and descriptions.

Stand	Latitude/Longitude	Site Descriptions
Marys Peak	N44° 32' W123° 33'	A wetland with large red alder and a few bigleaf maple, surrounded by large Douglas-fir.
Salmon Creek	N44° 36' W123° 35'	A mixture of small Douglas-fir and large bigleaf maple at the edge of a

Table 3.1, continued

Stand	Latitude/Longitude	Site Descriptions
		short bench, above Salmon Creek, with red alder at the margin of Salmon Creek.
Peak Creek	N44° 20' W123° 30'	A mixture of both small and large Douglas-fir, large bigleaf maple, and large red alder, near Green Peak Falls
Oak Creek	N44° 36' W123° 20'	In the foothills of the Coast Range at the edge of the Willamette Valley. A mixture of small and large hardwoods, including red alder, bigleaf maple, and Oregon ash as well as immature Douglas-fir.
Tobe Creek	N44° 20' W123° 35'	Steep slope dominated by conifers, with large, open-grown bigleaf maple and small red alder.

Lichen transplants

In each of the five riparian stands, transplants of four lichen species

(*Cetrelia cetrarioides*, *Hypogymnia inactiva*, *Lobaria oregana* and *Lobaria*

pulmonaria) were placed under bigleaf maple, red alder, and Douglas-fir canopies.

Transplants were placed under canopies where a minimum of two same-species

trees were located relatively close together (within ~5 m) forming a monospecies

canopy over the transplants. Although two trees were the minimum required to

form a canopy, most of the time the canopy consisted of more than two trees.

Transplants were prepared by attaching a nylon monofilament loop to lobes of

lichen thalli with silicone sealer (McCune et al. 1996). Transplants were hung on

wooden dowels suspended horizontally between branches and boles of trees in such

a way that transplants were located beneath the canopy at approximately 2.5 – 4.5

m above the ground. *Cetrelia cetrarioides* transplants were attached to dowels

using plastic zip-ties while all other transplants were attached to dowels using hair

bands (McCune et al. 1996). Ten transplants each of *Cetrelia cetrarioides* and

Lobaria pulmonaria, 8-9 transplants of *Hypogymnia inactiva,* and 6 transplants of

Lobaria oregana were hung from dowels under each canopy type at each site. All

Cetrelia transplants were constructed from thalli collected at a single site (a

recently felled tree in a riparian zone) in northwestern Oregon. *Cetrelia* transplants

ranged in size from ~1.5 cm^2 to 3 cm^2. All other transplants had been made

previously and stored at H.J. Andrews Experimental Forest (in the Oregon Cascade

Mountains) for a year previous to use in this study. *Lobaria* transplants ranged in

size from ~3 cm^2 to 10 cm^2, while *Hypogymnia* transplants were from ~2 cm^2 to 4

cm^2. Transplants were installed in early October 1998 and were collected and

weighed in late September 1999.

Growth response calculations

After nearly a year in the field, lichen transplants were retrieved, air dried in

the laboratory and weighed to the nearest 10^{-4} gram. Lichen transplant growth rates

were adjusted for moisture content using the sacrificial method (McCune et al.

1996). Growth in grams was converted to percent growth of lichen thalli. Four

lichen growth response measures were calculated using the percent growth data.

Mean and median percent growth were calculated using data from thalli whose

growth rates were positive. All thalli that lost mass were eliminated from these calculations because it was impossible to determine whether losses were due to poor growth performance or chance events that may have broken or removed portions of thalli or whole thalli. Lichen health was calculated as the number of transplants with positive growth divided by the number of transplants with any thallus remaining. Lichen survival was calculated as the number of lichen transplants with thalli remaining divided by the total number of transplants (including those with thalli missing entirely). Average growth responses were calculated for each species for each of the three canopy treatments for each stand.

Transplants that could not be identified (due to loss of thalli and label) were excluded from analyses. Transplants with inexplicably high growth rates extremely divergent from the mean were eliminated as outliers. The three eliminated outliers included two *Cetrelia cetrarioides* transplants with 92% and 252% growth and one *Hypogymnia inactiva* transplant with 166% growth.

Statistical analyses

Three-factor blocked ANOVA's (SPSS 1998) with lichen species and canopy treatment as fixed factors and block as a random factor were performed for each growth response separately. Sheffé Multiple Comparison Procedures contrasted growth responses among species and among treatments.

Results

Lichen species were not differentially affected by canopy treatment; in other words, there were no species × treatment interactions. This was true for all response measures: mean lichen growth (Table 3.2), median lichen growth (Table 3.3), lichen health (Table 3.4), and lichen survival (Table 3.5).

Overall, lichens experienced inferior health and survival under bigleaf maple canopies (p = 0.003 for lichen health and p = 0 .005 for survival, respectively; Figure 3.1, Table 3.6).

Table 3.2. Three-way Analysis of Variance. Lichen transplant mean growth is the dependent variable, Treatment = canopy type, and Species = lichen species.

	Sum of Squares	Degrees of Freedom	Mean Square	F	p
Blocks	257	4	64	1.16	0.346
Main Effects:					
Treatment	312	2	156	2.81	0.073
Species	1950	3	650	11.69	0.000
Interactions:					
Treatment*Specie	179	6	30	0.54	0.778
Residual	2113	38	56		

Table 3.3. Three-way Analysis of Variance. Lichen transplant median growth is the dependent variable, Treatment = canopy type, and Species = lichen species.

	Sum of Squares	Degrees of Freedom	Mean Square	F	p
Blocks	231	4	58	0.70	0.595
Main Effects:					
Treatment	305	2	152	1.85	0.171
Species	1903	3	634	7.71	0.000

Table 3.3, continued

	Sum of Squares	Degrees of Freedom	Mean Square	F	p
Interactions:					
Treatment*Species	512	6	85	1.04	0.417
Residual	3126	38	82		

Table 3.4. Three-way Analysis of Variance. Lichen transplant health is the dependent variable, Treatment = canopy type, and Species = lichen species.

	Sum of Squares	Degrees of Freedom	Mean Square	F	p
Blocks	7169	4	1792	2.67	0.045
Main Effects:					
Treatment	9101	2	4551	6.77	0.003
Species	23324	3	7775	11.57	0.000
Interactions:					
Treatment*Specie	2564	6	427	0.64	0.701
Residual	29569	44	669		

Table 3.5. Three-way Analysis of Variance. Lichen transplant survival is the dependent variable, Treatment = canopy type, and Species = lichen species.

	Sum of Squares	Degrees of Freedom	Mean Square	F	p
Blocks	6544	4	1636	3.68	0.011
Main Effects:					
Treatment	5368	2	2684	6.03	0.005
Species	2288	3	763	1.72	0.178
Interactions:					
Treatment*Specie	1807	6	301	0.667	0.669
Residual	19573	44	445		

Table 3.6. Between treatment comparisons of lichen transplant health and survival. Treatments include transplant placement under red alder (ALRU), bigleaf maple (ACMA), and Douglas-fir (PSME). Mean differences in health and survival between canopy treatments are across all lichen species and stands.

Growth Measure	Treat-ment 1	Treat-ment 2	Mean Difference (Treat. 1 – Treat. 2)	Standard Error of the difference	p	95% Confidence Interval for difference	
						lower bound	upper bound
Health	ALRU	ACMA	26.0	8.2	0.011	5	47
Health	ALRU	PSME	-.35	8.2	0.999	-21	20
Health	ACMA	PSME	-26.3	8.2	0.010	-47	-6
Survival	ALRU	ACMA	21.9	6.7	0.008	5	39
Survival	ALRU	PSME	4.4	6.7	0.805	-13	21
Survival	ACMA	PSME	-17.5	6.7	0.041	-34	-0.60

Mean growth, median growth, and health (all $p < 0.000$) but not survival ($p = 0.18$) differed among the four lichen species. Most of the variation among the species was attributable to *Hypogymnia inactiva,* which grew more slowly and was less healthy than the other three species (Figure 3.1; Table 3.7).

Table 3.7. Comparisons of growth responses (with standard deviation) among lichen transplant species. Data are across all sites and treatments.

| transplant lichen species	Mean Growth		Median Growth	
	mean ± s.d.	75th percentile	mean ± s.d.	75th percentile
Cetrelia cetrarioides	15.4 ± 10.8	21.6	17.2 ± 14.9	22.4
Hypogymnia inactiva	4.7 ± 2.8	7.7	4.2 ± 2.9	6.1
Lobaria oregana	19.5 ± 6.8	22.4	19.2 ± 6.8	22.0
Lobaria pulmonaria	20.5 ± 7.3	25.5	18.5 ± 6.9	21.2
	Health		Survival	
	mean ± s.d.	75th percentile	mean ± s.d.	75th percentile
Cetrelia cetrarioides	75.1 ± 26.0	100.0	61.8 ± 19.2	80.0
Hypogymnia inactiva	34.9 ± 16.3	50.0	74.1 ± 18.4	88.0
Lobaria oregana	85.0 ± 32.7	100.0	59.3 ± 22.9	75.0
Lobaria pulmonaria	78.9 ± 32.5	100.0	71.1 ± 29.7	90.0
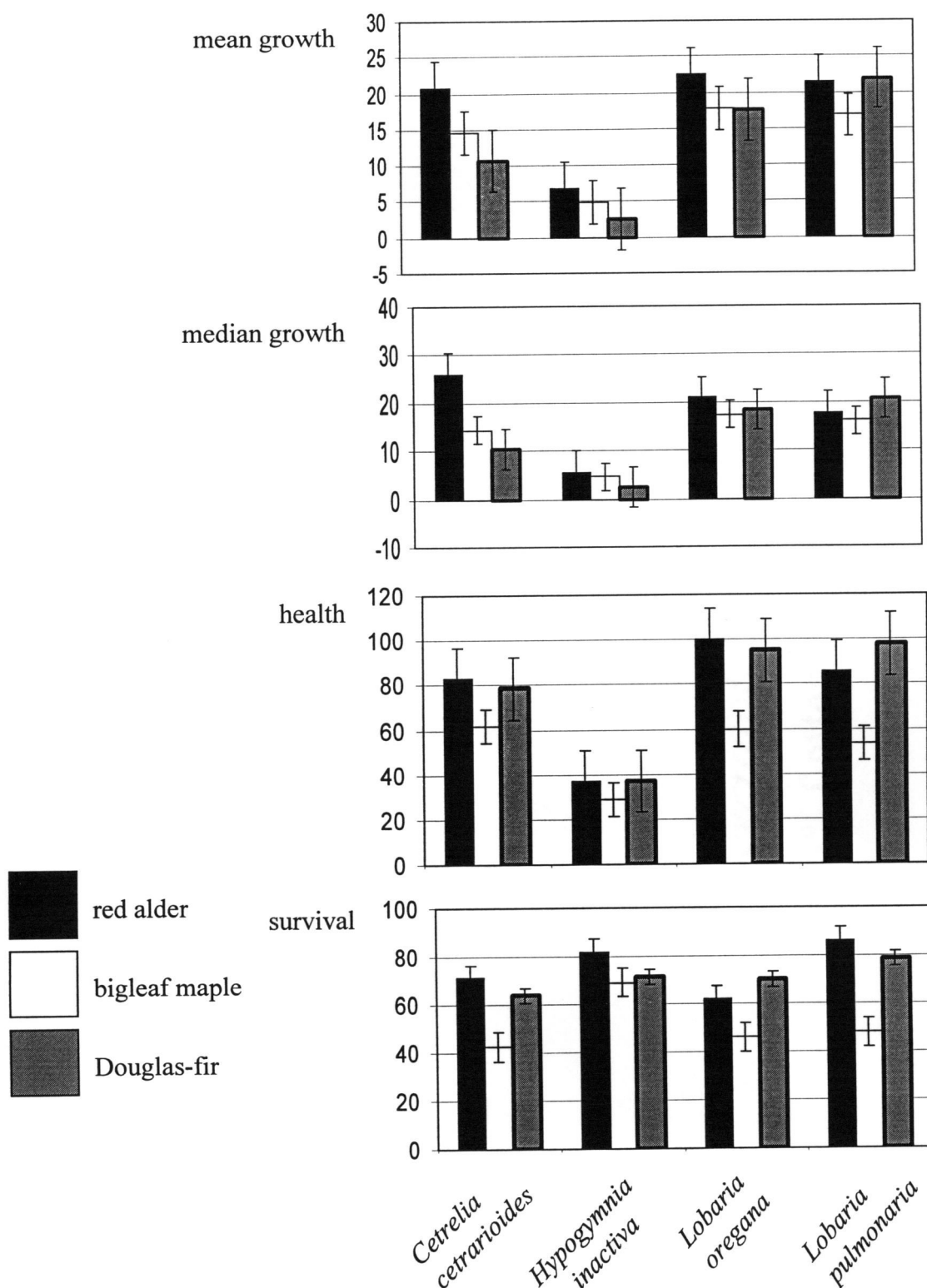
Figure 3.1. Growth, health and survival of four lichen species grown as transplants under three canopy types.

Reasoning that the distinct growth response of *Hypogymnia inactiva* (compared to the other transplant species) may have obscured statistical indications of more subtle differences in growth responses among *Cetrelia cetrarioides*, *Lobaria oregana* and *Lobaria pulmonaria*, and that the overall negative growth responses of all transplant species to bigleaf maple canopies (Figure 3.1) may have obscured more subtle differences in growth responses between red alder and Douglas-fir canopy treatments, we excluded *Hypogymnia inactiva* and bigleaf maple from additional analyses. Three-way ANOVAs (the three factors being species, treatment and block) showed that mean growth and median growth of lichens did not significantly differ, though there still appeared to be a difference of marginal significance in health among the three lichen species (p = 0.057). This resulted from poorer health of *Cetrelia cetrarioides* compared to *Lobaria oregana* in the two canopy treatments across all stands (p = 0.060).

Lichen health and survival differed among blocks across all species and canopy types (p = 0.045 for health and p = 0.011 for survival). Lichen survival ranged from 55% at Marys Peak to 80% at Tobe Creek and lichen health ranged from 50% at Peak Creek to 78% at Salmon Creek.

Though differences in growth responses among canopy treatments were not statistically significant (possibly through lack of statistical power), it is interesting to note the patterns of lichen growth responses expressed by graphs of the four lichen transplant species under the three canopy types (Figure 3.1). The green algal foliose lichens *Cetrelia cetrarioides* and *Hypogymnia inactiva* tended to grow

faster under red alder and bigleaf maple canopies than under Douglas-fir, whereas

the cyanolichens *Lobaria pulmonaria* and *Lobaria oregana* grew faster under red

alder and Douglas-fir canopies than under bigleaf maple. These patterns did not

hold true using lichen health and survival as growth responses. In these cases, all

lichen species showed superior performance under red alder and Douglas-fir

canopies.

Discussion

In this experiment, if particular lichen transplant species showed differences

in growth responses among canopy types (a significant species × canopy treatment

interaction) this would suggest that species-specific responses to canopy

microclimate are important determinants of the distribution of that lichen species.

We predicted that, if local canopy microclimate is an important factor influencing

the growth responses of our four lichen transplant species, the more habitat-

restricted lichens *Cetrelia cetrarioides* and *Lobaria oregana* would grow best in the

canopy microclimate where they are most often found (under red alder and

Douglas-fir, respectively). *Lobaria pulmonaria*, less of a habitat specialist, might

do best under either hardwood canopy, while the generalist *Hypogymnia inactiva*

should respond similarly to each canopy type. We found that the growth responses

of transplant species did not conform to these predictions. The growth, health and

survival of individual lichen species were not differentially affected by canopy

treatment, though, as a group, lichen transplants were less healthy and survived less

often under bigleaf maple canopies. This result does not exclude the possibility that these species differ in response to microclimate. It does strongly suggest, however, that local canopy microclimate is a subordinate factor in determining the distribution of the four lichen species used as transplants in this study.

Our findings add to a growing body of data suggesting that microclimate may not be as influential in determining lichen distribution as has been popularly thought. In the Sillett et al. (2000) and Sillett and McCune (1998) transplant studies, growth responses of old-growth associated lichens were contrasted between young and old-growth coniferous forests. Sillett and McCune (1998) found that transplants of two Pacific Northwest old-growth associated species (*Lobaria oregana* and *Pseudocyphellaria rainierensis*) grew at least as well in young forests as they did in old-growth, and Sillett et al. (2000) demonstrated that dispersal may be the most important factor limiting the distribution of *Lobaria oregana*. *Lobaria pulmonaria* and *Hypogymnia inactiva* have also been shown to achieve similar growth rates in young vs. old-growth forests (Sillett et al. 2000).

In our study, we tested the growth responses of species with very different habitat preferences, including *Cetrelia cetrarioides*, an infrequent species usually found on red alder, an early successional, rapidly growing tree species common in riparian zones of the Oregon Coast Range (Hibbs et al. 1994). Because this host is common, it is unlikely that a dispersal bottleneck explains the habitat specificity of *Cetrelia cetrarioides*. Future experiments with *Cetrelia cetrarioides* could reveal mechanisms behind its habitat specificity. Some possibilities are bark pH, bark

texture or propagule establishment. Since *Cetrelia cetrarioides* is uncommon, listed as a survey and manage species under the President's Forest Plan (USDA and USDI 1994), and found almost exclusively in riparian zones, care should be taken in its collection and use in transplant studies. In our study, we used small lobes (approximately $1.5 - 3.0$ cm^2 as transplants in an attempt to minimize our need for transplant material (and corresponding collection impact).

Transplants under red alder and Douglas-fir canopies were 26 percent healthier than those under bigleaf maple canopies ($p = 0.011$ and 0.010, respectively). This finding supports a wealth of casual observation accumulated by acquisitive lichenologists who have recognized that mature bigleaf maple trees are usually not very good places to collect macrolichens.

Hypogymnia inactiva grew more slowly and was less healthy than all the other lichen species used in this transplant study, a result that has been observed in other studies transplanting this species (Sillett et al. 2000, B. McCune, unpublished data). Interestingly, the survival of *Hypogymnia inactiva* did not differ significantly from any other lichen species. So, although *Hypogymnia inactiva* thalli were just as likely to remain intact on the transplant apparatus (survive) as the thalli of the other lichen species, this species was more likely to maintain or lose mass than to gain mass (which it did in only 35% of individuals). Why *Hypogymnia inactiva* transplants grow more slowly than the other lichen species is unknown. It is surprising in light of the fact that it is a common and relatively aggressive colonist of young trees and shrubs (Ruchty et al., 2000). The cause of

this discrepancy may be how the transplants are created and hung. *Hypogymnia inactiva* most often grows ascending from its substrate, whereas *Lobaria* often grows somewhat pendant. When transplants were created, a nylon monofilament was attached to the lower cortex of the lichen thallus with a dab of silicone. When placed in the field, the transplants were hung pendant from dowels or branches. Thus, the orientation of *Hypogymnia inactiva* transplants may end up being upside down or sideways (rather that ascending from the substrate), with the upper cortex and photosynthetic algal layer pointing toward the ground or to the side. This positioning may inhibit *Hypogymnia inactiva* from photosynthesizing. In contrast, pendant transplants of *Lobaria* species have an orientation similar to what they experience when growing on a tree bole or side of a tree branch. In future transplant experiments using *Hypogymnia inactiva*, we advise using an attachment apparatus (such as a zip-tie) that allows transplants to be tightened to the branch or dowel in an upright position, rather than hung pendant.

   Cetrelia cetrarioides performed well in its first reported use in a transplant study. Its growth and survival approximated that of *Lobaria pulmonaria* and *Lobaria oregana*, both proven transplant subjects (Denison 1979, Muir et al. 1997, Sillett and McCune 1998, Sillett et al. 2000, Shirazi et al. 1996). The health of *Cetrelia cetrarioides* was slightly inferior to that of *Lobaria oregana* (p = 0.060) a mild pattern that only became clear after the exclusion of *Hypogymnia inactiva* and bigleaf maple from the analysis. This result shows that *Cetrelia cetrarioides* has a slightly greater tendency to lose or maintain weight than *Lobaria oregana*.

However, when *Cetrelia cetrarioides* did gain mass, its growth rate did not differ from that of *Lobaria oregana*. As there was no difference in survival among the species, these facts suggest that *Cetrelia cetrarioides* may tend to fragment more easily or that it may be more prone to herbivory. Its thinner and, presumably, more fragile thallus and smaller size might cause this species to be more susceptible to these risks or more seriously affected by them.

Acknowledgements

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Chapter 4

Rare Lichen and Bryophyte Species in Riparian Forests of the Coast Range of
Oregon

Andrea M. Ruchty and Bruce McCune

Abstract

In this paper, we describe where and with what abundance potentially at-risk epiphyte species were found during a study of epiphytic lichen and bryophyte communities in riparian zones of the Oregon Coast Range (Ruchty and McCune 2000a). Species we considered potentially at risk included: (1) epiphyte species listed in the ROD (USDA and USDI 1994), (2) species we found to be rare and (3) species that were expected but absent. Of the nine species listed as "riparian" in the ROD, we encountered five. There were 16 additional ROD-listed lichen species and 2 ROD-listed bryophyte species encountered during epiphyte surveys. Many epiphyte species we found to be rare are more common on other substrates or in other habitats. Two lichen species that we found, *Nephroma bellum* and *Leptogium cyanescens*, may be more rare than has been previously recognized within the Oregon Coast Range. The information reported here is meant both to improve our understanding of the habitat requirements of epiphytic lichen and bryophyte species and to allow us to re-evaluate our assessments of their rarity within the Oregon Coast Range.

Introduction

Until relatively recently, knowledge of the species diversity and ecology of epiphytic lichens and bryophytes living in the forests of the Pacific Northwest was confined to a few researchers and academics that took a special interest in these groups. With increasing recognition of the roles that these epiphytes play in

ecosystems (Maser 1985, Maser 1986, McCune 1993, Nadkarni 1981, Pettersson et al.1995, Pike et al. 1972, Richardson and Young 1977, Rosentreter and Eslick 1993 and others), greater focus has been placed on these little known groups of organisms. In the President's Forest Plan (USDA and USDI 1994), certain epiphyte species were singled out as "survey and manage" species, due to concerns over their ability to persist under the current land management regimes within the range of the Northern Spotted Owl. These species were roughly classified according to habitat (riparian, oceanic-influenced etc.) and ranked according to their level of risk or sensitivity across the Pacific Northwest landscape. Since that time, researchers have striven to learn more about these species, and to increase understanding of their rarity and level of risk.

Plant community studies can provide important information on the distribution and habitat requirements of individual species. Ruchty and McCune (2000a) describes an observational study that looked at epiphytic lichen and bryophyte communities in riparian forests of the Oregon Coast Range; it is the first study focusing exclusively on epiphytes within riparian zones in the Pacific Northwest. As such, it provides an excellent opportunity to review what we know of ROD-listed "riparian" species (USDA and USDI 1994) as well as other rare and ROD-listed species.

This paper (Ruchty and McCune 2000c) supplements data presented in Ruchty and McCune (2000a) by: (1) describing where and with what abundance ROD-listed epiphyte species were found, (2) reporting species we found to be rare,

and (3) reporting species that were absent, but that we had expected to find. This information improves our understanding of the habitat requirements of these species and allows us to assess their rarity within the Oregon Coast Range.

Methods

We surveyed epiphytic macrolichens and bryophytes in seven riparian stand types in the Oregon Coast Range, including stands dominated by *Alnus rubra*, *Fraxinus latifolia*, conifers and *Acer macrophyllum*, as well as stands characterized by the presence of wet meadows (that may have been created by beaver), waterfalls and agricultural corridors. We defined "stands" as areas relatively homogenous in history and environment, and defined "rare" species as those species present in less than 5% of the stands sampled (two or fewer stands). Epiphytes were surveyed using time-constrained sampling. Epiphytic macrolichens were surveyed for a maximum of 2 hrs or until 10 min had passed without finding a new species (1 hr 15 min was the minimum sampling time). Epiphytic bryophytes were sampled for 1 hour. For a complete description of site selection criteria and sampling methodology see Ruchty and McCune (2000a).

Basic distributional information for lichens is from McCune and Geiser (1997) and Jørgensen and Tønsberg (1999), for mosses from Lawton (1971), and for liverworts from Christy and Wagner (1996). For some liverworts we reviewed collections in the Oregon State University herbarium.

Results and Discussion

ROD-listed species

Nine lichen species were classified as "riparian" in the ROD (USDA and

USDI 1994). These were *Cetrelia cetrarioides, Collema nigrescens, Leptogium*

burnetiae var. *hirsutum, Leptogium cyanescens, L. saturninum, L. teretiusculum,*

Platismatia lacunosa, Ramalina thrausta, and *Usnea longissima.* Of these, five

were encountered in our plots (Table 4.1). None of the ROD-listed riparian species

that were encountered more than once were restricted to a specific stand type.

Table 4.1. ROD-listed riparian species encountered during surveys – observations
on their habitat and abundance.

Lichen species	Distribution and Abundance
Cetrelia cetrarioides	Found in one-third of sampled red alder stands, but also found in Oregon ash stands, bigleaf maple stands and wet meadows on red alder and occasionally on other species.
Leptogium cyanescens	Only found once in an Oregon ash stand, on the bark of Oregon ash.
Platismatia lacunosa	Found in 40% of all wet meadows, where it was most common, but nearly as common in alder, ash and conifer stands. Most abundant in wet meadows and ash stands.
Ramalina thrausta	Most common and abundant in conifer stands; it was present in one-third of such stands. Also found in one bigleaf maple stand and near one waterfall.
Usnea longissima	Found in 83% of all Oregon ash stands and an indicator of this stand type.

Table 4.1, continued

Lichen species	Distribution and Abundance
	Also found in 60% of wet meadows and one-third of all conifer stands sampled. Though most common in these stand types, *Usnea longissima* was found in every riparian stand type. Within stands, this species had a clumped distribution.

There were 16 additional ROD-listed lichen and 2 ROD-listed bryophyte species encountered during riparian epiphyte surveys (Table 4.2).

Table 4.2. Additional ROD-listed epiphytic lichens and bryophytes encountered in this study. Table includes a description of their distribution and abundance in riparian forests, Oregon Coast Range. Rare species (those present in < 5% of stands) are in bold face. Frequency is the percentage of stands of a particular type where a particular species was found. Remarks on species abundances are rough estimates derived from field notes and average specimen abundance values. Specimen abundance values were determined using four abundance categories: 1 = rare ($\leq$ 3 individuals in plot); 2 = uncommon (4-10 individuals in plot); 3 = common (> 10 but less than half of the boles and branches have that species present); and 4 = abundant (more than half of boles and branches in the plot have the subject species present). Distributional information from Ruchty and McCune (2000$_a$) unless otherwise noted.

Lichens	Distribution and abundance
Lobaria oregana	Most frequent and abundant in conifer forests (in 83% of stands); also found near waterfalls, in red alder stands, bigleaf maple stands, and wet meadows.
Lobaria pulmonaria	Abundant in all Oregon ash stands and agricultural corridors; also found in every other stand type (occurred in 80% of wet meadows).
Lobaria scrobiculata	Found in all agricultural corridors in moderate abundance, but also common in Oregon ash stands (83% frequency). Not found in conifer, bigleaf maple, or waterfall stands.

Table 4.2, continued

Lichens	Distribution and abundance
Nephroma bellum	Found only twice, once in a red alder stand on western hemlock and once in a conifer stand, as litter.
Nephroma helveticum	Most frequent (67%) in waterfall stands; also in ash and conifer stands (50% frequency) with greater abundance in ash stands. Found in all stand types except red alder and agricultural corridors, but never in great abundance.
Nephroma laevigatum	Present in all waterfall stands; also commonly found in wet meadows (80% frequency), conifer and bigleaf maple stands (67% frequency), all in low to moderate abundance; never found in agricultural corridors.
Nephroma resupinatum	Found most often in Oregon ash and waterfall stands (83% frequency), also frequent in bigleaf maple (67%), but found in every stand type, always in low to moderate abundance.
Pannaria leucostictoides	Encountered only once, in a bigleaf maple stand. More common in upland *Quercus* savanna (B. McCune, personal communication).
Pannaria saubinetii	Found in all stand types except for wet meadows and agricultural corridors, never with more than 33% frequency and always with low abundance.
Peltigera collina	Nearly ubiquitous and abundant; found least often (66% frequency) and in low abundance in red alder stands.
Peltigera pacifica	Encountered once as an epiphyte in both a conifer and a bigleaf maple stand. More common on rotten logs (McCune and Geiser 1997).
Platismatia lacunosa	Most frequent (40%) in wet meadows. Less frequent, in low to moderate abundance in all stand types except for agricultural corridors.
Pseudocyphellaria anomala	In all stand types except red alder; most frequent and moderately abundant in agricultural corridors (100%) and Oregon ash stands (83%).
Pseudocyphellaria anthraspis	Most frequent in wet meadows (80%) and conifer stands (50%) in low to moderate abundance; but found in all stand

Table 4.2, continued

Lichens	Distribution and abundance
	types except for red alder and agricultural corridors.
Pseudocyphellaria crocata	In all stand types (with low abundance), but with greatest frequency in Oregon ash and waterfall stands.
Sticta fuliginosa	Moderately abundant in all Oregon ash stands and agricultural corridors; found in all other stand types except for red alder, with low to moderate frequency and abundance.
Sticta limbata	Most frequent in Oregon ash stands (67%), but with low abundance; moderately frequent but in low abundance in all stand types.

Bryophytes	Distribution and abundance
Antitrichia curtipendula	Moderate to high abundance in all red alder stands, wet meadows, waterfalls and conifer stands. Also often found in all other stand types.
Douinia ovata	Found only twice, both times in conifer stands, on conifer litter.
Ptilidium californicum	Found only once in a conifer stand on the bark of western hemlock.

Rare species

Rarity can be quantified in a number of ways. One way is simply by considering rarity within the sample (in this study defined as species found in fewer than 5% of the sampled stands). Rarity, measured in this sense, is not the same as landscape-level rarity. For example, epiphytic species that are rare in the riparian zone may be more common on other parts of the landscape. Finding these species in riparian zones helps us build on our knowledge of their environmental

tolerances. Species we found to be rare, but that are more common in upland sites, include *Bryoria* spp., *Nodobryoria oregana, Melanelia* spp., *Leptogium teretiusculum, Loxosporopsis corallifera, Polychidium contortum, Parmeliopsis hyperopta, Pannaria leucostictoides* and *Ceratodon purpureus*. Species common in nitrogen-rich habitats include *Candelaria concolor, Melanelia* spp., and *Xanthoria* spp. (McCune and Geiser 1997). Other species are common on substrates such as soil and rotten logs, but were probably able to occasionally grow as epiphytes in riparian zones because of the high relative humidity there (e.g. *Peltigera membranacea, P. pacifica, Cladonia* spp., *Aulacomnium androgynum, Blepharostoma trichophyllum, Calopogeia trichomanis, Drepanocladus uncinatus, Eurhynchium praelongum, Heterocladium macounii, Orthotrichum rivulare, Plagiothecium undulatum, Porothamnium bigelovii, Racomitrium aciculare, Riccardia latifrons,* and *Tetraphis pellucida).* Other species are common on the immediate coast but rarely found inland (*Parmotrema arnoldii, Ramalina roesleri*). As none of the aforementioned species are rare across the Coast Range landscape, they are not discussed further.

Conversely, rarity in the riparian zone may reflect rarity across the landscape. For certain species, including *Leptogium cyanescens* and *Nephroma bellum*, our study area seemed to encompass suitable habitat to support healthy populations. The fact that these ROD-listed species (USDA and USDI 1994) were rarely found in our study suggests that these species may be more rare in the Coast Range than has been previously recognized. Table 4.3 describes the reported

distribution of rare species, with a short synopsis of where rare species were found during this study.

Rare species described in Table 4.3 are separated into: (1) species present and apparently rare in the Coast Range, and for which riparian zones seem to encompass good habitat, (2) species absent from our riparian samples, and not known from the Coast Range, but with potential to occur there and, (3) species absent from and no longer expected in the Oregon Coast Range (these are cases where our expectations of their presence were erroneous, i.e. Oregon Coast Range riparian sites are not within the range of environmental tolerance for these species). Species classified in groups 1 and 2 are probably more rare than has been previously recognized.

Table 4.3. Rare and absent epiphytic lichen and bryophyte species in riparian areas of the central Oregon Coast Range.

Epiphyte species	Stand types where species were found during this study	Distribution: information from McCune and Geiser (1997) unless otherwise noted.
Present and apparently rare in the Coast Range		
Collema nigrescens	absent	On hardwood boles in low-elevation hardwood forests, often riparian.
Douinia ovata	conifer	Widespread in western North America on tree trunks, large branches or wet rocks. Seems to be an old-growth forest associate.
Leptogium cyanescens	Oregon ash	Listed in the ROD as riparian; rare on bark, rotten logs and rocks in the Pacific Northwest.
Leptogium saturninum	absent	Widespread, on hardwood trees and shrubs; most frequent in low elevation

Table 4.3, continued

Epiphyte species	Stand types where species were found during this study	Distribution: information from McCune and Geiser (1997) unless otherwise noted.
Lobaria hallii	absent	riparian forests east of the Cascades, less frequent from west of the Cascades, in riparian sites in foothills bordering the Willamette Valley. ROD-listed species (not as a "riparian" species); found in low elevation valley fringe riparian environments, usually on hardwoods.
Lobaria linita	absent	Found, in western Oregon, mostly as an epiphyte in moist habitats with coastal influence.
Ptilidium californicum	mixed conifer	From the west coast of North America, common from Lane Country.
Sulcaria badia	absent	On bark and wood of hardwoods (mainly *Quercus garryana*) and less often on conifers, in valley fringe environments; very rare. Also on hypermaritime dune forests of *Pinus contorta* var. *contorta*. Observed once at the edge of *Fraxinus* stand near Marys River in Coast Range, near Kings Valley; also at edge of Coast Range near Jackson Creek (Peterson et al. 1998, B. McCune, personal communication).

Absent and not known from the Coast Range, but with potential to occur

Hypotrachyna riparia	absent	Recently described (McCune 1998). On deciduous hardwoods in riparian habitats in Cascade foothills; as yet unknown from Coast Range.
Pannaria rubiginosa	absent	Found on hardwoods in riparian areas and wetlands, often near the Oregon coast.

Table 4.3, continued

Epiphyte species	Stand types where species were found during this study	Distribution: information from McCune and Geiser (1997) unless otherwise noted.
Absent and no longer expected in the Oregon Coast Range		
Leptogium burnetiae v. hirsutum	absent	A primarily boreal species that has never been found in Oregon.

Summary

Epiphyte community studies have the potential to contribute to our understanding of individual epiphyte species by providing information on the distribution and relative abundance of species of interest. We used distributional information gained during a study of epiphytic macrolichens and bryophytes in Oregon Coast Range riparian forests (Ruchty and McCune 2000a) to assess the rarity of species that are thought to be at-risk (USDA and USDI 1994) within our study area. In addition, we summarized known distributional information on species that were rare within our study area. We found that many epiphytes that were rarely encountered within our study area are more common in other areas or on other substrates. This study added to our growing knowledge of the environmental tolerances and affinities of these species. We also learned that some epiphyte species may be more rare within the Coast Range than has been previously recognized. These species include some we found to be rare and others that were absent. Additional study of the distributional patterns of these species

within the Oregon Coast Range is needed in order to evaluate their level of risk

under current land management regimes.

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Chapter 5. Conclusions

Epiphytic macrolichen and bryophyte communities differed among riparian stand types in the Oregon Coast Range. Community composition changed along a valley continuum of riparian environments, from higher elevation, conifer-dominated stands along constrained stream reaches, to lower elevation, hardwood-dominated stands along more unconstrained stream reaches on broad bottomlands. Along this continuum, overall lichen species richness and green-algal foliose lichen richness increased, while the frequency and abundance of some alectorioid (forage) lichens (particularly *Alectoria sarmentosa*) decreased, as did the frequency and abundance of the old-growth associated lichen, *Lobaria oregana*.

Bark pH is another factor that may influence epiphyte communities. We hypothesized that a stand-level pH gradient associated with canopy composition affected epiphyte communities, causing cyanolichen and bryophyte species richness to be greatest in stands dominated by trees with relatively high bark pH (Oregon ash and bigleaf maple) compared with stands dominated by trees with relatively high bark pH (Douglas-fir and red alder).

Oregon ash stands and bigleaf maple stands supported the greatest lichen and bryophyte species richness, respectively, at both the stand-level and the landscape level. Lichen species richness at the stand and landscape level was lowest in red alder stands. Agricultural corridors, often dominated by Oregon ash trees, were second only to Oregon ash stands in stand level lichen species richness,

but agricultural corridors hosted the second lowest (for lichens) and lowest (for bryophytes) landscape-level species richness of all the stand types.

Although epiphyte communities clearly differed among stand types, transplant experiments involving the lichen species *Cetrelia cetrarioides*, *Hypogymnia inactiva*, *Lobaria oregana* and *Lobaria pulmonaria*, suggested that habitat specificity does not result from species specific responses to canopy composition. Though lichen transplant species were not differentially affected by canopy microclimate, as a group, lichen transplants did not grow as well or survive as often in bigleaf maple stands. Other possible reasons for habitat specificity include dispersal and establishment limitations and interspecific competition. Our findings, linking bark pH with cyanolichen and bryophyte species richness, suggest that pH may play a role in restricting the habitat of certain species.

The canopy composition of Oregon Coast Range riparian forests have probably changed considerably as a result of historical land management practices, including logging and agriculture. In the Oregon Coast Range, red alder (and other hardwood) dominated riparian stands may be more common presently than they were historically. Today, older, intact Oregon ash and bigleaf maple forests are not widely recognized for their ecological value, though the land they occupy is often recognized for its timber production or development potential. Oregon ash stands on private land risk conversion to agriculture, pastures or young conifer plantations. For epiphytic macrolichens and bryophytes, loss of older, conifer-dominated riparian forests, and forests dominated by Oregon ash and bigleaf maple, will likely

cause a decrease in landscape level diversity, a decrease in species richness of nitrogen-fixing cyanolichens, alectorioid (forage) lichens and many ROD-listed species.

Stands differ in their potential as epiphyte habitat. Forest management that works to preserve or enhance certain stand types in the Oregon Coast Range will help conserve epiphyte diversity, including species that play important roles in Pacific Northwest forests, such as cyanolichens that fix atmospheric nitrogen, and alectorioid (forage) lichens that provide food for flying squirrels and deer. For certain rare or less well-known epiphyte species, conservation efforts will require species centered research and conservation efforts.

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