Lichen Refugia Within Sub-Boreal Spruce Forests: The Role of Riparian Alder Swales.

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ABSTRACT

Wetland swales, corridors of willows and alders adjacent to streams and seepage areas, may play a role as refugia for lichen biodiversity because they likely escape stand replacement disturbance such as fire more often than adjacent upland forest, especially in moist to drier sub-boreal and boreal landscapes, and are also not disturbed by forest harvesting. Macrolichen communities in 75 alder-dominated wetland swales along an east (wet) to west (dry) gradient in the Sub-Boreal Spruce biogeoclimatic zone of central interior British Columbia were examined. Spatial analysis of wetland swales indicated an average size of 20.5 m wide by 854 m long (following patch contours). A total of 43 macrolichen species (and six other macrolichen genera) were found in the alder dominated sites, with a maximum of 30 taxa present in the richest site. The macrolichen diversity of alder swales included the old-growth associated lichens Lobaria scrobiculata, L. retigera, Nephroma isidiosum, and Sticta limbata. Canonical Correspondence Analysis identified mean annual temperature and abundance of large stems (dbh > 10 cm) as significant explanatory variables for chlorolichens and mean annual precipitation and age of adjacent conifer forest as significant explanatory variables for the majority of the cyanolichens. Regional precipitation gradients explained the exclusion of many lichen species from both the most westerly and most easterly swales, with drier summer conditions and heavy winter snowpack, respectively, being major limiting factors. Within sites, lichens preferentially occupied large leaning stems, which provided greater precipitation interception and long-lived substrates for many old-growth associated lichen species. Physiological analyses of six common cyanolichens indicated low contributions of cyanolichens to the nitrogen budgets of alder swales. However, adaptations and niches of each of these cyanolichens were revealed. Nephroma

ii

parile was the best adapted to the widest range of conditions, followed by *Lobaria pulmonaria*. *Pseudocyphellaria anomala* was adapted to warm, bright locations. *Lobaria hallii, L. scrobiculata,* and *Sticta fuliginosa* appeared to be well adapted to spring and autumn conditions, thereby maximizing the length of their growing seasons. We conclude that alder swales provide major refugia for old-growth dependent lichens and may represent valuable dispersal corridors between remnant old-growth coniferous forests in B.C.'s Sub-Boreal Spruce landscapes.

TABLE OF (CONTENTS
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.

Abstract		ii
Table of Contents		iv
List of Tables		v
List of Figures		vi
Acknowledgement		vii
Chapter One	Introduction	· 1
Chapter Two	Site Description and General Methods	4
Chapter Three	The role of alder swales in maintaining macrolichen Diversity in sub-boreal forests of B.C	9
Chapter Four	The importance of alder swales as lichen refugia within Sub-Boreal Spruce forests in British Columbia's central-interior plateau.	32
Chapter Five	Chapter Five. Physiology of six common cyanolichens in alder swales of central-interior British Columbia.	54
Chapter Six	Conclusion	. 68
Literature Cited		71

LIST OF TABLES

Table 3.1. Summary of alder-lady fern seepage site characteristics from GIS queries, mean \pm standard deviation.	16
Table 3.2. Location and average climate, based on modeled mean data from 1971 to 2000, in Climate B.C. version 3.2, in each of alder swales in each subzone of the Sub-Boreal Spruce (SBS) biogoclimatic zone.	17
Table 3.3. P-values between beta diversity and the most important site variables measured in each subzone of the Sub-Boreal Spruce (SBS) biogeoclimatic zone, as determined with Mantel tests.	20
Table 3.4. Mean densities of stems in each size strata and mean diameter of stems sampled in each climate subzone of the sub-boreal spruce, \pm SD.	20
Table 4.1. Average climate data for alder swales, by subzone of Sub-Boreal Spruce, based on modeled mean data from 1971 to 2000.	39
Table 4.2. Species list with abbreviations (Abbr.), functional groups (Func.) and percent occurrence in the plots of each subzone.	40
Table 4.3. Indicator species, and their indicator values (in bold), of epiphytic lichens in each subzone of the Sub-Boreal Spruce (SBS) biogeoclimatic zone.	42
Table 5.1. Average mass, \pm SD, of dominant cyanolichen species in each subzone (g/ha).	58
Table 5.2. Amount of nitrogen fixed annually $(g N_2/ha/yr)$ in each subzone of the Sub-Boreal Spruce (SBS) biogeoclimatic zone by the dominant cyanolichens.	58

.

LIST OF FIGURES

Figure 2.1. Map of the study region in British Columbia showing the locations of the sites in each biogeoclimatic subzone.	. 8
Figure 3.1. Illustration of the distribution of alder-lady fern seepage sites (alder swales) within the wet, cool (wk) and very wet, cool (vk). Sub-Boreal Spruce (SBS) subzone portions of Tree Farm License 30, (TFL 30) British Columbia.	_ 21
Figure 3.2. Boxplots representing α diversity in each subzone.	22
Figure 4.1. Canonical correspondence analysis of the relationship between alder swales in of the three subzones of the Sub-Boreal Spruce biogeoclimatic zone, and environmental variables.	43
Figure 4.2. Canonical correspondence analysis of the relationship between the abundance of lichen taxa and site characteristics in alder swales. The species abbreviations and functional groups are in Table 3.1.	44
Figure 4.3. Canonical correspondence analysis of the relationships between each of the lichen taxa and the stem characteristics in each of three subzones of the Sub-Boreal Spruce biogeoclimatic zone.	45
Figure 5.1. Effect of temperature on the photosynthetic rate of thalli of six cyanolichen species collected in mid October 2008.	60
Figure 5.2. Effect of temperature on the respiration rate of thalli of six Cyanolichen species collected in mid October 2008.	61
Figure 5.3. Rate of acetylene reduction in six cyanolichen species across a temperature gradient based on thalli collected in mid October 2008.	62
Figure 5.4. Rate of acetylene reduction in cyanlichen species across a temperature gradient, based on a second, independent collection made at the end of November 2008.	63

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Chapter One. Introduction.

Most studies on lichens and old-growth forests in British Columbia have focused on coniferous forest stands. In mountain environments this has led to the examination of areas such as wet toe-slope positions, where topography and groundwater flow reduce the incidence of stand-destroying fires. These old-growth regions support rich epiphyte communities that include rare species not found in other portions of the landscape. In contrast, forested landscapes in B.C.'s interior plateau are dominated by younger, often evenaged, coniferous forests, reflecting their past history of disturbance by forest harvesting, fires, and insect damage.

Plateau landscapes in B.C.'s interior, however, also include areas where the frequency of disturbance appears to be much lower. In particular, willow and alder swales along small first-order streams and in wet seepage areas may represent stable plant communities. In more mountainous regions, such as the very wet subzone of the Sub-Boreal Spruce biogeoclimatic zone, alder swales occupy entire slopes and carry runoff during parts of the year when ephemeral streams overflow their banks. Fires often skip over the wet depressions in which riparian alder swales are found and they are rarely targeted for forest harvesting, though they are sometimes disturbed by mechanical or herbicide treatments of adjacent coniferous stands. These riparian swales follow the branching network of streams extending across the Sub-Boreal Spruce landscape, resulting in the presence of hardwood-dominated swales across a range of environmental conditions.

Many researchers have found riparian areas to support rich epiphytic lichen communities, including many species that are otherwise restricted to old-growth coniferous

forests. Furthermore, hardwoods, both in riparian regions and upland forested gaps, have been found to support rich epiphyte communities, and so the term "hotspots" of lichen diversity has been applied to these regions. Because epiphytic lichen diversity of the interior of British Columbia has been predominantly investigated in conifer forests, and because research from the Pacific Northwest indicates that riparian hardwoods support rich epiphyte communities, research is needed into the ability of alder swales to support epiphytic lichen communities. Central B.C. provides an excellent location for this research because it extends across three subzones of the Sub-Boreal Spruce (SBS) biogeoclimatic zone, differing mainly in precipitation, thereby allowing for an examination of how the communities change along this climatic gradient and what, if any, impact that has upon lichen diversity in alder swales.

The goal of the study was to assess the lichenological importance of alder dominated deciduous wetland swales and their ability to function as refugia for macrolichen diversity along a longitudinal precipitation gradient in SBS forests of the Prince George Forest District. Specifically, the objectives, which will be addressed in separate chapters, were:

 to examine the covarying responses of lichen communities to interactions between substrate characteristics (physical and chemical) and regional climatic gradients.

2) to investigate how the individual species that make up the changing composition of epiphytic lichen communities on riparian alders in alder swales respond to climatic, bark, and site characteristics.

3) to examine the physiological responses (rates of acetylene reduction, photosynthesis, and respiration) of common cyanolichens as well as to determine their relative rates of acetylene reduction as related to their contributions to the nitrogen budget of the SBS biogeoclimatic zone.

Chapter Two describes the climate of each of the three SBS subzones and the sampling methods used to investigate the macrolichen diversity of randomly selected riparian alder swales along the precipitation gradient. Chapter Three describes the influence of site and climatic characteristics on macrolichen diversity in each of the three subzones. Chapter Four investigates the response of the macrolichen species to site and stem characteristics. Chapter Five describes the physiology of six common cyanolichen species and relates these data to the ecology of these lichens. Chapter Six provides a summary of the thesis.

Chapter Two. Site Description and General Methods.

The study sites were located between 53.9° N and 54.5° N and 121.5° W and 123° W. This region falls within three biogeoclimatic units of the Sub-Boreal Spruce (SBS) biogeoclimatic zone (Figure 2.1). From east to west, wettest to driest respectively, these units are the very wet and cool subzone (SBSvk), the Willow variant of the wet and cool subzone (SBSwk1, hereafter referred to as SBSwk), and the Mossvale variant of the moist and cool subzone (SBSmk1, hereafter referred to as SBSmk). Subzone boundaries used followed the boundaries published by B.C. Ministry of Forests and Range (Victoria, B.C) (ftp://ftp.gov.bc.ca/HRE/external/!publish/becmaps; accessed 6 May 2008).

Average annual precipitation in the SBSmk, SBSwk, and SBSvk are 724 mm, 931 mm, and 1 247 mm respectively (DeLong et al. 1993; DeLong 2003). Mean annual temperature in these three subzones is 1.5 °C in SBSmk (DeLong et al. 1993) and 2.6 °C in both the SBSwk and SBSvk (DeLong 2003).

All the sampled alder swales were in wet depressions along streams and so the vascular vegetation of the sites varied little between subzones. Mountain alder (*Alnus incana* ssp. tenuifolia(Nutt.) Breitung) was the predominant species of alder observed in the sites. Green alder (*Alnus crispa* ssp. crispa (Aiton) Turrill) was present in four of the sites in the SBSvk and in one site in the SBSmk. Differences existed primarily in the abundance of each taxon. Willows (*Salix* spp.), devil's club (*Oplopanax horridus* (Sm.) Miq.), and red-osier dogwood (*Cornus sericea* L.) were also present in some sites. The main herbs observed included lady fern (*Athyrium filix-femina* Roth), spiny wood fern (*Dryopteris expansa* (C. Presl) Fraser-Jenk. & Jermy), oak fern (*Gymnocarpium dryopteris* (L.) Newman), skunk

cabbage (*Lysichiton americanus* Hulten & H. St.John), and horsetails (*Equisetum* spp). Mosses such as *Mnium* spp, *Dicranum* spp, and *Pleurozium schreberi* (Brid.) Mitt. were present in some of the sampled sites. Mountain alders ranged in height from two meters to five metres. The height of the trees in the adjacent, mature forest was upwards of 15 meters.

Within each biogeoclimatic subzone, 25 points of latitude and longitude coordinates were generated randomly. The nearest first or second order stream with adjacent alder swale was subsequently sampled. Eligible sites were further restricted to those within 1 km of road access points. Taken together these three sets of 25 sites constitute our longitudinal gradient across the Sub-Boreal Spruce zone in this region (Figure 2.1). At each site, a 100 meter long lichen sampling transect was subsequently established parallel to each stream following elevation contours. Each transect was established halfway between the stream bank and the edge of the alder swale, typically between three and five meters from the stream edge. Transects were placed a minimum of 50 m from the nearest road. At 10 meter intervals along each transect, the nearest mountain alder stem in each of the following six categories was sampled: 1) live stems with diameter at breast height (dbh) less than 10 cm; 2) dead stems with dbh less than 10 cm; 3) live stems with dbh between 10 and 15 cm; 4) dead stems with dbh between 10 and 15 cm; 5) live stems with dbh greater than 15 cm; 6) dead stems with dbh greater than 15 cm. Alder stems in each of the six categories were not present in all the sites sampled. This resulted in between 10 and 47 stems being sampled in each site.

The sampled region on each stem began 0.5 meters above the ground and extended for two metres along the stem. Within this region all macrolichens were identified to species with the exception of *Bryoria*, *Usnea*, *Physcia*, *Cladonia*, *Xanthoria*, and *Melanelia*, which were recorded at the genus level. Each macrolichen species (or genus) present was assigned

an abundance rating between 0 and 5 (0: absent, 1: \leq 3 thalli present, 2: > 3 to \leq 6 thalli present, 3: \leq 20% cover, 4: \leq 50% cover, 5: >50% cover) (Goward and Arsenault 1997). Macrolichen taxonomy follows Goward et al. (1994) and Goward (1999) with the exception of the genera *Tuckermannopsis* and *Kaerenfeltia*, which are recognized here as distinct from *Cetraria*. Presence/absence binary data was also collected for the species (and genera) on the entire stem of each sampled stem.

For each stem sampled, dbh, average angle of lean, and average direction of lean were measured. The percent bark cover, percent total crust lichen cover, and percent total macrolichen cover were estimated visually to the nearest 10 percent on the top and bottom sides of each stem sampled. The two estimated values were averaged to give the percent cover of bark, crust lichens, and macrolichen cover on each stem sampled. Crust lichens were not identified. Within each site, the average height of thalli of *Parmelia sulcata* and *Hypogymnia physodes*, greater than 2 cm in diameter, above the ground was recorded to give the average depth of the winter snowpack (Sonesson et al. 1994).

At each 10 meter point along the lichen sampling transect canopy cover was measured with a spherical densiometer (Model A, Forest Densiometers, Bartlesville OK), and averaged for each alder swale. At each 10 meter point, the number of buried organic horizons in the top 20 cm of the soil profile were counted, to estimate the frequency of flooding in each site. In each site, the five largest living alder stems were cored to determine their ages. The three largest conifers adjacent to the swale were cored to estimate conifer stand age. The average width of each sampled stream was also recorded.

Elevation-corrected ClimateBC data (Version 3.2, University of British Columbia, Vancouver), using modeled mean data from 1971 to 2000 (Wang et al. 2006), were obtained

for each of the sampled sites.

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Figure 2.1. Map of the study region in British Columbia showing the locations of the sites in each biogeoclimatic subzone. Subzone boundaries follow those published by B.C. Ministry of Forests and Range (ftp://ftp.gov.bc.ca/HRE/external/!publish/becmaps; accessed 6 May 2008).

Chapter Three. The role of alder swales in maintaining macrolichen diversity in subboreal forests of B.C.

Introduction

The central-interior of British Columbia is dominated by coniferous forests. Historically, these forests consisted of a complex mosaic of different-aged stands, reflecting past disturbance processes, such as fires and insect outbreaks. For canopy lichens, this disturbance history poses major constraints to dispersal and colonization within regional landscapes. Radies and Coxson (2004), for instance, found that many canopy lichen species that were present in old-growth stands were absent from adjacent 120- to 140-year-old stands.

Wetland swales, typically alder and willow communities associated with the wet banks of streams and moist depressions, in contrast, may represent a more stable or persistent ecological element within regional landscapes. Alder swales may be more resistant to fire as they are found in topographic positions that are depressed and generally wetter than the surrounding landscape. Bergeron (1991) indicated that disturbance due to fire is dependent upon local conditions and topographic placement, often resulting in riparian areas being less affected by fire than adjacent forests. This observation has also been noted by Suffling et al. (1982) and Denneler et al. (1999). The linear nature of alder swales may also be important within regional landscapes. Alder swales may provide corridors between what would otherwise be isolated patches of habitat (Opdam et al. 1995; Burel 1996) thereby allowing for the rapid dispersal of many species (DeFerrari and Naiman 1994; Forman 1995).

Hardwood and shrub patches can persevere for long periods of time in regional landscapes (Egler 1950; Pound and Egler 1953; Bramble and Byrnes 1972; Nierig et al.

1986). Lertzman et al. (1994) suggested that they may represent stable patches within what are otherwise heterogeneous, conifer dominated landscapes. These persistent hardwood patches enhance site fertility through the decomposition of their leaves and enhance crown development in adjacent conifers by providing gaps in the canopy of coniferous forests (Wardman and Schmidt 1998; Tasche and Schmidt 2001).

Rich cyanolichen communities have been previously found on hardwoods, in both riparian zones (McCune et al. 2002; Peterson and McCune 2003) and upland regions (Neitlich and McCune 1997). Peterson and McCune (2003) hypothesized that deciduous hardwoods are able to act as hotspots for epiphytic lichen diversity. This may result from greater interception of water and light during winter months while providing a sheltered, high-humidity environment protected from higher light intensities during summer months (Peterson and McCune 2003). Alder swales may have particularly significant ecological value for canopy lichens due to the importance of alder as a substrate for epiphytic lichen communities because Goward and Arsenault (2000*a*) found that alder had the greatest diversity of cyanolichens among 10 hardwood genera investigated.

We examined canopy lichens in alder dominated riparian swales in the Sub-Boreal Spruce (SBS) biogeoclimatic zone in central interior British Columbia. The study area spans a 200 km long climatic gradient, from upslope alder swales in a wet climatic region in the eastern part of the region (adjacent to the Rocky Mountains), to alder swales in a drier climatic region in the west (in the central-interior plateau). The placement of study plots along this gradient allowed us to examine the covariate responses of lichen communities to interactions between substrate characteristics (physical and chemical) and regional climatic gradients in alder swales.

Methods

Landscape Metrics

The distribution and abundance of alder swales were examined in two areas along the regional climate gradient, using ArcView software (ESRI, Redlands, USA) to query Terrestrial Ecosystem Mapping databases for the Aleza Lake Research Forest (ALRF) (ALRF Society 2008) and Tree Farm License 30 (TFL 30) (BC Ministry of Forests 2002) (see Figure 1 for location) for occurrence of alder-lady fern seepage site complexes which provide a proxy for alder swales in this region (DeLong 2003). The ALRF is found in the SBSwk, while TFL 30 includes portions of both the SBSwk and SBSvk. No part of the SBSmk was included in the GIS analyses. Among the summary statistics calculated from map queries were mean swale area, mean shortest swale axis length, mean longest swale axis length, and total linear distance of swale features. The longest axis length was the longest straight line distance through the site. Linear distance was the length of the site following all of its contours.

Bark pH

Bark samples for the pH analysis were collected from six randomly selected sites in each subzone. Within these sites, bark was collected from the same stems as the lichen assessments were conducted on and was collected from the portion of the upper surface of the stems that contained the fewest epiphytes at a distance of 1.3 meters, \pm 5 cm, along the stem. This removed any influence of modification of the bark chemistry by the epiphytes (Lang et al. 1976). Further cleaning was done in the lab. Pieces of bark 1 cm² were placed in

10 mL of 25mM KCl overnight (Farmer et al. 1990) and the pH measured with a glass electrode.

Analyses

The number of species within a community, α diversity (Whittaker 1972), was calculated based on individual stems and transects. α diversity was scaled by diameter, by dividing by dbh, to account for larger stems having more species simply due to their larger area. The number of species within a larger region, γ diversity (Whittaker 1972), was calculated for each subzone and across all sites sampled in the SBS biogeoclimatic zone. Intercommunity diversity was calculated pair wise using β_t (Wilson & Schmida 1984) between the sites in each subzone. The correlation between each of these pairwise β_t matrices and the pairwise matrices formed from the collected site data was investigated through Mantel tests with the strength of the relation between the distance matrices evaluated with Pearson correlation coefficients (Mantel 1967). Unique pairwise distance matrices based on the site data were calculated for each site variable by taking the absolute value of the difference between the values of the site variable in the two sites (McCune & Allen 1985). Diversity indices were calculated in R (R Development Core Team 2006). The Mantel tests were performed in PC-Ord v. 5 (McCune & Mefford 1999) using a randomization test with 9 999 permutations. Examining diversity at several levels can lead to a greater understanding of the patterns of diversity and the forces that affect it (Loreau 2000).

Results

Based on data generated from ClimateBC the SBSmk sites had the lowest mean annual temperature and lowest mean July temperature of the three subzones while the SBSvk sites had the highest mean January temperature (Table 3.2). Average snowfall did not differ between the sites of the SBSmk and SBSwk and was greatest in the SBSvk (Table 3.2). Mean annual precipitation increased from an average of 755 mm in the SBSmk sites to 819 mm in the SBSwk sites to 953 mm in the SBSvk sites. The average elevation was greatest in the sites of the SBSvk a result of alder swales being located on slopes as well as valley bottoms as compared to the other subzones where sites were all from sites on plateaus.

The GIS queries showed that the portion of the SBSwk queried had greater densities (i.e. number of discrete patches) of alder-lady fern sites than did the SBSvk portion. The mean area (Welch's t-test; d.f. = 2; p=0.03) and mean width of the seepage sites were greatest in the SBSvk portion of TFL 30 (Table 3.1). Alder-lady fern seepage sites in the SBSwk had the greatest average length.

The values for bark pH in the SBSmk sites ranged from 4.59 to 5.94 with an average and standard deviation of 5.48 ± 0.29 . In the SBSwk sites, bark pH ranged between 4.15 and 6.18 with an average and standard deviation of 5.37 ± 0.31 . In SBSvk sites, bark pH ranged between 4.9 and 6.4 with an average and standard deviation of 5.4 ± 0.23 . The values of pH were not correlated with stem diameter, angle of lean, direction of lean, percent lichen cover, percent moss cover, or estimated mean annual precipitation in the site and none of the differences between subzones were significant. The sites of the SBSwk had the greatest number of buried organic horizons at 7.9 per site while the sites of the SBSmk and SBSvk had an average of 6.2 buried organic horizons per site. At least one buried organic horizon

was present in 61 of the 75 sites. The average height of the snowpack lichen line, as estimated from *Parmelia sulcata* and *Hypogymnia physodes*, was 1.6 meters in the SBSmk sites, 1.4 meters in the SBSwk sites, and 2.2 meters in the SBSvk sites. In the SBSvk sites, this was significantly higher than in the other two subzones (Wilcoxon rank sum test, p<0.01).

Overall, there were 43 species and six additional genera of lichens observed in the 75 sites sampled. There were 37 taxa observed in the SBSmk, 43 in the SBSwk, and 40 in the SBSvk. Stem level alpha diversity was not found to significantly vary with diameter class in any of the three subzones. However, larger stems generally tended to support richer lichen communities and stems smaller than 10 cm dbh generally supported communities of consistently low diversity, in all three subzones (Figure 3.2 A-C). Live and dead alder stems did not significantly differ in either the number of species present or the composition of the communities present.

The SBSwk sites had significantly more species per site than the sites in either of the other two subzones (p<0.01). The SBSmk sites had the lowest variation in the number of species and had the lowest maximum number of species in a site (Figure 3.2 D). The SBSwk sites had the highest average number of species in a site, the highest maximum number of species in a site, and the highest minimum number of species in a site. The SBSvk sites had the lowest average number of species in a site and the lowest minimum number of species in a site. The SBSvk sites had the lowest average number of species in a site and the lowest minimum number of species in a site. The SBSvk sites had

A consistent linear relation between diameter and age in alders was found ($r^2 = 0.86$ based on an n of 440; age = 2.7*diameter). The SBSwk sites had the largest stems (student's t-test; d.f. = 48; p<0.01), with an average sampled stem dbh of 8.3 cm corresponding to an

age of 23 years. Sites in the SBSwk had the greatest densities of stems over 10 cm dbh (student's t-test; d.f. = 48; p<0.025). Sites in the SBSvk had the greatest average density of stems smaller than 10 cm dbh (Table 3.4; student's t-test; d.f. = 48; p<0.05). The maximum alder age in the SBSmk, SBSwk, and SBSvk were 71, 64, and 53 years, respectively.

At the site level, the number of buried organic horizons, distance between sites and mean annual precipitation were each significantly correlated with β_t between sites of the SBSwk (Table 3.3). For the SBSvk sites the abundance of stems with dbh greater than 10 cm, distance between sites, and mean July temperature were significantly correlated with β_t (Table 3.3).

subzones of the Sub-Boreal Sp	oruce (SBS) bio	geolimatic zone.				
	area of	density of				
SBS subzone and portion of	subzone	seepage sites	shortest	longest axis	area of seepage	mean linear distance
region queried	inquiried (ha)	(sites/ha)	axis (m)	(m)	sites (ha)	of seepage sites (m)
wet (wk) TFL 30 ¹ , ALRF ²	59294	0.027	16.9 ± 8.7	414.7 ± 229.0	5.0 ± 7.0	862 ± 825
very wet (vk): TFL 30 ¹	62162	0.025	22.0 ± 32.0	364.4 ± 207.4	6.0 ± 9.1	850 ± 945
¹ Tree Farm License 30						
² Aleza Lake Research Forest						

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Tablı	subz

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					mean annual	mean January	mean July	mean annual	mean annual
		Latitude	Longitude	Elevation	temperature	temperature	temperature	precipitation	snowfall
subzone	site no.	(N∘)	(M₀)	(m asl)	(°C)	(°C)	(°C)	(mm)	(mm)
SBS mk	-	54.1859	122.6561	727	2.7	-11.7	14.6	679	280
SBS mk	2	54.21924	122.70812	722	2.6	-11.8	14.5	682	283
SBS mk	ო	54.2394	122.76479	686	2.8	-11.6	14.5	667	274
SBS mk	4	54.22506	122.65763	728	2.5	-12.2	14.3	669	291
SBS mk	വ	54.1711	122.66563	711	2.9	-11.5	14.8	663	272
SBS mk	9	54.22849	122.69439	742	2.5	-12	14.3	701	293
SBS mk	7	54.27801	122.79908	752	2.5	-11.4	14.3	671	281
SBS mk	8	54.26805	122.83695	707	2.7	-11.3	14.6	657	272
SBS mk	ი	54.26041	122.77349	728	2.6	-11.6	14.4	673	280
SBS mk	10	54.31443	122.65337	712	2.3	-12.3	13.9	747	319
SBS mk	1	54.32883	122.65741	716	2.2	-12	13.8	752	321
SBS mk	12	54.32445	122.66867	724	2.2	-11.9	13.7	753	322
SBS mk	13	54.30842	122.68071	209	2.3	-11.9	13.9	754	319
SBS mk	14	54.30837	122.72954	737	2.4	-1	13.8	764	321
SBS mk	15	54.32153	122.76935	761	2.5	-10.6	13.9	736	307
SBS mk	16	54.33748	122.82087	780	2.1	-10.5	13.3	749	326
SBS mk	17	54.36741	122.85246	792	2.6	-9.6	13.7	861	354
SBS mk	18	54.39559	122.8613	864	2.3	-9.6	13.3	862	365
SBS mk	19	54.41131	122.67717	788	2.3	-10.8	13.6	807	346
SBS mk	20	54.39289	122.69786	818	2.8	-10.2	14	887	361
SBS mk	21	54.3579	122.718	859	2.7	-10.1	13.8	889	360
SBS mk	22	54.36707	122.75123	861	2.3	-9.8	13.2	814	344
SBS mk	23	54.44177	122.68716	726	2.5	-10.9	14	789	334
SBS mk	24	54.43978	122.73636	768	2.4	-10.4	13.8	790	336
SBS mk	25	54.42254	122.72885	795	2.5	-10.1	13.7	. 829	350
SBS mk	average			757	2.5	-11.1	14	755	316

Table 3.2. Location and average climate, based on modeled mean data from 1971 to 2000 in Climate B.C. version 3.2, in each of the alder swales in each subzone of the Sub-Boreal Spruce (SBS) hinderchimatic and

mean annual	snowfall	(mm)	352	352	352	353	335	347	347	346	340	292	295	298	306	291	279	319	324	331	312	311	270	282	283	271	317
mean annual	precipitation	(mm)	886	885	884	885	857	881	884	874	859	787	798	811	797	763	734	824	822	839	806	809	717	736	734	726	819
mean July	temperature	(°C)	15.1	15	15	15	15	15.1	15.2	15	14.9	14.8	14.8	15.1	15.1	15	15	15	14.9	14.9	15	15.2	15.2	14.8	14.2	15	15
mean January	temperature	(°C)	-12.2	-12.3	-12.3	-12.3	-11.3	-12	-12.1	-11.9	-11.8	-9.7	-9.7	6.6-	-10.9	-10.9	-10.9	-11.1	-11.5	-11.7	-11.2	-11.4	-11.1	-10.6	-8.8	-10.4	-11.2
mean annual	temperature	(°C)	e	2.9	2.9	2.9	ო	ო	3.1	2.9	2.9	3.2	3.3	3.4	3.1	3.1	3.1	3.1	2.9	2.9	ო	3.2	3.3	ო	ო	3.2	3.1
	Elevation	(m asl)	684	693	700	707	698	669	651	701	712	680	689	696	700	713	730	689	692	707	664	624	667	718	707	655	687
	Longitude	(∧ ₀)	122.07459	122.06738	122.06303	122.06922	122.13383	122.12757	122.10118	122.13335	122.00732	122.04841	122.07291	122.12488	122.1819	122.22363	122.26324	122.16627	121.93089	121.96153	121.86128	121.8645	122.30334	121.7933	121.78919	121.74778	
	Latitude	(N∘)	54.09734	54.09694	54.09516	54.09368	54.0328	54.09297	54.09171	54.08	54.06652	53.92176	53.93038	53.94145	53.9986	53.99932	54.00681	54.01734	54.0657	54.06994	54.05635	54.07285	54.04337	53.92723	53.94137	53.91691	
		site no.	2	ო	4	S	9	7	8	6	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	average
		subzone	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk	SBS wk											

Table 3.2 continued.

mean annual snowfall (mm)	331	327	344	346	350	462	397	405	342	345	349	360	359	379	393	374	378	372	414	409	393	435	404	378	385	377
mean annual precipitation (mm)	848	845	879	884	896	1135	1057	1013	870	877	886	006	894	958	982	958	970	964	1055	1046	959	1128	984	913	917	953
mean July temperature (°C)	15.1	15.2	14.8	14.8	14.8	14.5	15	14.1	15.1	15.2	15.1	14.8	14.8	15.1	14.7	15.1	14.9	15.3	14.5	14.5	14.5	15.1	14.4	14.4	14.2	14.8
mean January temperature (°C)	-11.1	-10.8	-10.7	-10.7	-10.5	-9.1	-8.9	-9.2	-11.3	-11.2	-10.9	-10.7	-10.9	-10	-9.8	6.6-	-10.9	6.9-	-9.5	9.6-	-10.3	-9.4	-10	-10	-10,1	10.2
mean annual temperature (°C)	3.1	3.2	ო	ო	ო	3.1	3.5	2.8	3.1	3.1	3.1	2.9	2.9	3.2	ო	3.3	3.3	3.4	2.9	2.9	2.7	3.4	2.7	2.6	2.5	ო
Elevation (m asl)	688	660	751	752	760	817	770	865	673	633	636	716	716	710	808	679	698	662	931	923	797	830	819	804	840	758
Longitude /ºW)	121.79346	121.7897	121.75231	121.74831	121.73892	121.52136	121.66524	121.59678	121.81773	121.89733	121.87384	121.90965	121.95125	121.91503	121.85093	121.8583	121.8338	121.82125	121.72165	121.73708	122.02358	122.07269	122.04839	122.07265	122.027	
Latitude	54.09554	54.08939	54.10229	54.10511	54.10547	54.09428	54.16078	54.11462	54.16047	54.23277	54.248	54.2766	54.29438	54.31158	54.30304	54.29498	54.28451	54.27206	54.27696	54.2696	54.30193	54.30334	54.31734	54.36619	54.35423	
site no	-	2	e	4	S	9	7	8	6	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	average
edozdius	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk	SBS vk

Table 3.2 continued.

Table 3.3. P-v	alues be	tween $\beta_t d$	liversity a	nd the site	variables me	asured in	each subzone o	of the Sub-E	soreal Spruc	61
biogeoclimatic	s zone, a:	s evaluate	d with Pe	arson corre	slation coeffici	ients fron	ิ Mantel tests. ไ	The sign of t	the correlatic	n is
indicated in pe	arenthese	es followin	g p-value	s <0.1.						
		mean	mean	# buried	abundance					mean
	stream	conifer	canopy	organic	of stems	stern	distance	mean Jan	mean July	annual
subzone	width	age	cover	horizons	>10 cm dbh	density	between sites	temp	temp	precip
moist (mk)	0.51	0.07 (+)	0.11	0.43	0.14	0.37	0.43	0.29	0.09 (+)	0.09(-)
wet (wk)	0.57	0.11	0.49	0.02 (+)	0.09 (+)	0.4	0.01 (+)	0.34	0.13	0.04 (+)
very wet (vk)	0.36	0.29	0.34	0.16	0.03 (+)	0.17	0.0001 (+)	0.34	0.007 (+)	0.07 (-)
1 moon conifor			0101 0010	the the the	three lorgest	ooniforo.	Jooo of to ool	the contract	o lod oldor o	

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mean coniter age is based on cores taken from the three largest coniters adjacent to each of the sampled alder swales.

ampled in each	!
liameter of stems s	andard deviation.
strata and mean d	oclimatic zone, ± st
s in each size	(SBS) bioged
of stem	I Spruce
Mean densities	the Sub-Borea
Table 3.4.	subzone of

	Poiodi opidoo (000)			
	stems < 10 cm dbh ¹	stems between 10 and 15	stems ≥ 15 cm dbh ¹	dbh ¹ of stems
SBS subzone	(stems/ha)	cm dbh ¹ (stems/ha)	(stems/ha)	sampled
moist (mk)	25.6 ± 19.7	1.8 ± 2.2	1.1 ± 2.3	7.5 ± 4.3
wet (wk)	22.8 ± 36.4	3.9 ± 4.9	1.1 ± 0.9	8.3 ± 4.2
very wet (vk)	35.9 ± 17.4	2.2 ± 3.9	0.5 ± 2.5	7.1 ± 4.2
¹ diameter at breast	height			



Figure 3.1. Illustration of the distribution of alder-lady fern seepage sites (alder swales) within the wet, cool (wk1) and very wet, cool (vk) Sub-Boreal Spruce (SBS) subzone portions of Tree Farm License 30 (TFL 30), British Columbia.



Figure 3.2. Boxplots representing α diversity in each subzone. A-C: stem level α diversity scaled by diameter in all sites (A: stems less than 10 cm dbh; B: stems between 10 and 15 cm dbh; C: stems larger than 15 cm dbh), D: α diversity with in each site. The dashed lines indicate the average diversity. The box shows the 25, 50, and 75 percentiles with the whiskers indicating the 10 and 90 percentiles; * indicates observations plotting beyond the whiskers. Diameter scaling was accomplished by dividing α diversity by stem diameter.

Discussion

In boreal and montane environments, alder swales represent islands of deciduous tree cover within landscapes that are otherwise dominated by coniferous trees. The landscape metrics indicated that the size and shape of the alder-lady fern seepage sites vary considerably both within and between the queried portions of the SBSwk and SBSvk. Seepage site dimensions were found to vary a great deal from site to site. These seepage sites often exist as discontinuous patches along many streams and occupy entire slopes at higher elevations. The GIS analyses included many of these latter seepage slopes, in the SBSvk, where the whole slope carries water though ephemeral streams may still be present. These sites led to the higher standard deviation of the shortest axis in the alder-lady fern sites of the SBSvk. We found that patch density of alder-lady fern seepage sites was greater in the SBSwk than in the SBSvk and that smaller areas of alder-lady fern sites were present in the SBSwk as compared to the SBSvk. Our GIS results also indicated that the alder-lady fern sites of the SBSvk were shorter, on average, than the sites of the SBSvk, suggesting that although the patches of the SBSvk were more discontinuous, more patches were found in the SBSwk. The frequency of flood events may contribute to the higher density of alder-lady fern sites in the SBSwk than in the wetter SBSvk. Flood events can cause higher mortality in developing alder seedlings in newly colonized sites, reducing the frequency with which alder swales are established. Similar suggestions have been made regarding hardwood establishment in other riparian systems (Wilson 1970; Stromberg et al. 1991). At a larger scale, Meddens et al. (2008) spatially analyzed landscape patches across North America, using roads, timber harvested areas, agricultural land, and urbanization to define edges of

forested patches. They found greater density of forested patches in the landscape and lower patch area in drier regions as compared to wetter regions.

Patch density may also play an important role in facilitating connectivity between dispersed alder swales in regional landscapes. We would expect lichen propagule dispersal to occur much more easily and quickly between adjacent patches (Sillett et al. 2000). This hypothesis was confirmed by our observation that alder swales located in closer proximity to one another (in both SBSwk and SBSvk) supported more similar lichen communities than did sites farther removed from one another. This suggests that clusters of alder swales in the landscape act as metapopulations for arboreal lichens. This ability of alder swales to support lichen metapopulations is particularly significant in the SBSvk where mountainous topography can result in a high degree of isolation between alder swales.

The rich epiphytic communities supported by deciduous patches within conifer dominated landscapes may result from differences between coniferous and deciduous trees. Some properties of hardwoods, such as branch arrangement and bark chemistry, differ from conifers, while other properties, such as bark thickness, change as hardwood stems age. Hardwoods, in general, produce branches which curve upwards, drawing rainwater to the bole, while conifers have drooping branches which lead water towards the ends of the branches (Barkman 1969). On hardwoods this can result in high canopy humidity during summer months when the trees are foliated (Geiger 1965), a feature that is beneficial to the development of diverse lichen communities in alder swales. These properties of hardwoods may further enhance the quality of habitat of riparian alder swales for old-growth associated cyanolichens such as *Lobaria scrobiculata* and *Nephroma parile*, which were present in all three SBS subzones.

Another major difference between hardwood and coniferous substrates is that of bark pH. Conifer bark is generally acidic with pH values less than 5.0 (Gauslaa 1985; Kuusinen 1996a) and as low as 2.0 (Grodzinska 1977; Gustafsson and Eriksson 1995). Conversely, hardwood bark has higher pH in the range of 4.0 to 6.5 (Grodzinska 1977; Boudreault et al. 2008). Boudreault et al. (2008) found that pH was negatively correlated with species richness of mosses and lichens and positively correlated with bark roughness but not correlated with diameter. Similarly, our bark pH values showed no significant differences between diameter size classes. Although they fell within the range of values expected for hardwood bark, they were higher than previous measurements of bark pH in *A. incana* (Grodzinska 1977). Overall, bark pH was weakly (and negatively) correlated with mean annual precipitation, possibly reflecting the greater dilution of bark exudates of alder swales growing in high precipitation subzones.

Soil chemistry can also play a major role in influencing bark chemistry, with cation composition of the bark often similar to that of the underlying soils (Gauslaa and Holien 1998; Campbell and Fredeen 2007). By growing along streams, alders may have access to additional nutrients transported from upstream areas, especially during flood events. The number of buried organic horizons, related to flooding cycles, within the sampled alder swales may indicate how geomorphically active sites were and may also contribute to lichen diversity by regularly adding fine textured horizons. Campbell and Fredeen (2007) found higher abundances of cyanolichens on trees growing in fine textured soils. They attributed this difference to the higher clay content, higher cation exchange capacity, and higher concentrations of cations in the fine textured soils. We found greater diversity in sites of the SBSwk that were more geomorphically active, though coarse textured horizons were

frequently observed. This greater diversity may result from greater mean annual precipitation, which also was positively correlated with diversity in swales of the SBSwk and which could lead to greater frequencies of floods.

Forest age and the presence of old remnant trees within a stand are known to have a major influence on epiphytic communities. Old-growth forests are often able to support greater diversity than are young even-aged stands (Berryman and McCune 2006), both as a result of their intercepting more propagules of slow dispersing species over time (Sillett et al. 2000) and from the more favorable conditions that old-growth forests may provide for establishment and growth (Tibell 1992; McCune et al. 2000). Lichen diversity in our alder swales was positively correlated with the age of adjacent coniferous forest stands, especially in the SBSmk alder swales. This is not surprising, given that most points within alder swales would be within dispersal range of lichen propagules from surrounding forest. However, the continued presence of a core suite of old-growth associate lichens across most swales, including those adjacent to our youngest sampled coniferous forests (37 years old) suggest that the topographic position and microclimate of most swales, typically in wet depressions or small drainages, may confer some protection from edge effects induced by changes in the composition of surrounding stands. In our swales of the SBSmk, where the youngest coniferous forests, adjacent to the sampled alder swales, were found, as determined through tree cores, forest age was most strongly, and positively, correlated with diversity.

Within alder swales, we speculate that large stems act in a manner similar to that of old remnant trees in supporting epiphyte diversity. These stems provide a greater range of microclimatic conditions than are otherwise available in the sites (Hazell and Gustafsson 1999; Sillett and Goslin 1999). Generally larger alder stems in our swales supported richer

communities of canopy macrolichens and, in the SBSwk and SBSvk, macrolichen diversity was positively correlated with the abundance of alder stems larger than 10 cm dbh. The species that tended to grow on larger than average alder stems included the cyanolichens *Lobaria retigera* and *Collema subulatum* as well as the chlorolichens *Hypogymnia austeroides*, *Ramalina thrausta*, and *Parmelia hygrophila*.

The development of large alder stems reflects both constraints on germination and site growing conditions (Tallantire 1974). McVean (1953, 1955) found that germinating alder seeds had reduced life expectancy in locations with frequent spring frosts when compared to locations with no spring frosts. This observation is significant for our alder swales where topography favors cold-air ponding along small depressions and valleys where they are located. We would also expect that our higher elevation SBSvk alder swales would experience frequent spring frost events. This is supported by our observation that alder stems in higher elevation sites of the SBSvk were younger than those in the lower elevation sites, notwithstanding the generally older age of the surrounding coniferous forest.

Furthermore, increasing winter precipitation, in the form of snow, may also shorten the life of individual stems and prevent the growth of large stems. Zhu et al. (2006) observed that *Betula* tended to bend and uproot more frequently under snow than other species as a result of having a flexible stem, like alder. Stem breakage was also a major type of snow damage in *Betula* (Zhu et al. 2006). The amount of snow and the depth of the winter snowpack in the alder swales of the SBSvk may have led to the alder stems in many of the sampled sites having a tendency to be flattened and either break, grow horizontally, or be uprooted as they age. Peltola et al. (1997) found that moderate winds can break trees with a heavy snow accumulation.

Individual alder stems in the region we studied did not reach ages greater than 50 years, regardless of climate. However, through vegetative reproduction, alder swales may persist in the landscape for long periods of time. Kullman (1992) observed that grey alder stems came largely from pre-existing root systems and frequently suckers were produced at a distance of up to 15 meters from the parent stem. Kullman concluded that these stems originated from root systems that were much older than the oldest living stem. Tallantire (1974) made similar observations on the perseverance of alder root systems, noting that some will continue regenerating shoots for upwards of 200 years. Personal observations indicated that vegetative reproduction of alders is common in alder swales.

Although the availability of light and moisture are considered to be primary limiting factors for lichen growth (Kershaw 1985; Kenkel and Bradfield 1986), the nature and duration of snow cover in alder swales may be an important covariate factor. Prolonged periods of snow cover in alder swales reduce already limited light availability while prolonging the duration of thallus hydration. Prolonged periods of hydration under snow cover were implicated by Gannutz (1970) and Kappen et al. (1995) as an important factor in the carbon balance of lichens. Coxson and Stevenson (2007) suggested that canopy lichen growth rates are minimal during winter months due to winter snow cover and light conditions. In the SBSvk, where winter snowpacks are typically greatest, several species showed much lower abundance and frequency, including species of *Hypogymnia*, *Platismatia*, *Parmelia*, and *Tuckermannopsis*. This suggests that these species may be intolerant of submersion under snowpack, given that these species were otherwise common on all diameters in the drier subzones. Snow cover on lower stems within alder swales, especially in the SBSvk, can persist for over five months each year, exceeding thresholds that
Sonesson et al. (1994) hypothesized would kill many lichen species. We would hypothesize that during periods of low annual snowfall, more lichens will become established on lower portions of stems while during periods of high annual snowfall widespread dieback may occur, thereby reducing macrolichen diversity and cover.

Similar observations to ours of the height of the snowpack line were made by Sonesson et al. (1994) who noted that *Parmelia olivacea* Howe, *P. sulcata*, and *H. physodes* (L.) Nyl. tended to be found above the snow and the lowest occurrence of these species on trees was positively correlated with snow depth. Both mechanical damage and an inability to compensate for respiratory carbon loss under snowpack have been suggested as possible explanations for the vertical distributions of these species (Sonesson 1989). Our finding of a lack of significant differences in the height of the snowpack line between the sites in the SBSmk and SBSwk is not surprising given the similar average snowfall in these sites. The SBSvk sites received, on average, more snowfall than did the other sites and this likely resulted in the significantly higher average height of the lowest occurring thalli of *Parmelia sulcata* and *Hypogymnia physodes*.

Though precipitation as snow can be a negative factor for many lichens, summer precipitation remains an important positive predictor for lichen growth rates (Coxson and Stevenson 2007). Giordani (2006) observed that species richness of lichens was positively correlated with increasing summer precipitation while McCune and Antos (1982), Jovan and McCune (2004), and Radies (2008) observed that epiphytic lichens increased in diversity as site humidity and precipitation increased. From our correlations between β_t diversity and mean annual precipitation, we found that diversity showed a strong positive correlation with precipitation in the SBSwk. We were surprised that precipitation was not a strong positive

correlate for lichen diversity in all three subzones, however we would speculate that temperature and snowcover may be overriding influences, especially in the SBSvk.

Temperature has often been identified as an important variable in influencing lichen diversity (Pirintsos et al. 1993; McCune et al. 1997; Glavich et al. 2005; Giordani 2006). Jovan and McCune (2004) found the greatest cyanolichen diversity in warmer, wetter sites, with maximum nitrophile diversity in warmer, drier sites. However, along our climate gradient, temperature and precipitation are negatively correlated. Sites with warmer temperatures tended to be drier, while cooler sites were generally wetter. Goward (1994) found that lichen diversity in north-central British Columbia decreased with increasing elevation, suggesting a dominant role for temperature as a controlling variable. Berryman and McCune (2006) and Radies (2008) have also identified elevation as a significant factor in determining epiphyte diversity, due to the preferential colonization of low elevation forests (Peck and McCune 1997; Peterson and McCune 2001) due to the accumulation of soil moisture resulting in higher humidity environments (Radies 2008). However, humidity was not a limiting factor in our riparian alder sites. These opposing trends in temperature and precipitation along our longitudinal climate transect reduce lichen diversity at both ends of our gradient, in our coolest (eastern) sites, and in our driest (western) sites. As a result, alder swales in the SBSwk, having intermediate climatic conditions, showed the greatest absolute lichen diversity. The interaction between temperature and precipitation is also pronounced within each subzone. In both the SBSmk and SBSvk, where the greatest variation in topography exists and therefore the greatest variation in precipitation as snow, greater diversity was found in warmer, drier sites, i.e. lower elevations where less snow is received.

In the SBSwk with the least variation in topography, no interaction between temperature and precipitation was found and greater diversity was found in wetter portions of the landscape.

Wetland swales have been previously overlooked for their conservation importance (DeLong and Sanborn 2000). However, our analysis from sites placed along a longitudinal climate gradient in SBS forests of central-interior B.C. suggests that alder swales play a major role in the support of regional lichen assemblages. Given the rapid conversion of surrounding coniferous forests to early seral stages, both from forest harvesting and more recently from the outbreak of the mountain pine beetle (Aukema et al. 2006), lichen biodiversity contained within alder swales represents a significant conservation biology resource that merits specific recognition in landscape management objectives. Chapter Four. The importance of alder swales as lichen refugia within Sub-Boreal Spruce forests in British Columbia's central interior plateau.

Introduction

Riparian forest swales are often characterized as biodiversity hotspots (Naiman et al. 1993; Bratton et al. 1994; Rykken et al. 2007), which provide important dispersal corridors for many organisms (DeFerrari and Naiman 1994). In boreal and sub-boreal forests, riparian swales and adjacent wetlands can provide significant refugia from disturbance events such as forest fires, which can skip over or have reduced severity in wet microsites (Bergeron 1991). In central-interior British Columbia, small first and second order streams typically support narrow riparian forest swales of green alder and mountain alder. Although individual alder stems in these patches may not be very long-lived, senescing alder stems often produce new shoots that maintain the continuity of individual alders (Bramble and Byrnes 1983; Meilleur et al. 1994). In these ways alder communities can persist for decades (Egler 1950; Pound and Egler 1953; Bramble and Byrnes 1972) or longer (Nierig et al. 1986).

This raises the question as to whether or not alder riparian forest swales in centralinterior British Columbia function as refugia for old-growth associated canopy lichens. Previous studies have demonstrated that old-growth coniferous forest stands in these landscapes can support rich canopy lichen communities (Campbell and Fredeen 2004; Radies and Coxson 2004). Little is known about the development of canopy lichen communities within riparian forest swales in these landscapes. However, previous studies in the northwestern United States have shown that hardwoods can support diverse epiphyte

communities (Neitlich and McCune 1997; Peterson and McCune 2003), particularly in areas adjacent to streams and rivers (McCune et al. 2002).

This question about the ability of riparian forest swales to support old-growth associated canopy lichens is particularly important given the conservation biology status of British Columbia's sub-boreal spruce forests. The Sub-Boreal Spruce (SBS) biogeoclimatic zone is a major forested ecosystem in British Columbia, occurring from north 52° to 57° latitude, and from west 122° to 128° longitude (Meidinger and Pojar 1991). Although the wetter climatic portions of this landscape were historically dominated by old-growth coniferous forests, this area has been heavily impacted by both human-caused (logging) and natural disturbance (mountain pine beetle and fire) events in recent years. This has raised serious concerns about the conservation biology of old-growth forest associated lichens (Goward and Arsenault 2000a).

We have addressed this question by investigating the composition and abundance of macrolichen communities on riparian alders within SBS swales in central-interior British Columbia. We were particularly interested in the response of lichen communities to regional climate gradients, from SBSvk sites in the east, to warmer and drier SBSmk sites in the west. We have also investigated covariate changes in the nature and type of substrates available for lichen colonization within alder swales along this climate gradient and related changes in canopy structure and/or openness. We would hypothesize that riparian alder dominated swales in the SBS biogeoclimatic zone may serve as refugia for old-growth forest associated canopy macrolichens. If this is the case, these swales may provide valuable connectivity between remnant old-growth coniferous forest stands in surrounding SBS landscapes. They

may also provide an important source population for recolonization of lichens in adjacent second-growth forest stands.

Methods

The average abundance of each macrolichen taxon in each site was calculated and these values were used in canonical correspondence analysis (CCA), in the program. CANOCO v. 4.5 (ter Braak & Smilauer 2002). The ordination axes in CCA are constrained to be linear combinations of the environmental variables thereby allowing for the species distributions to be directly related to the environment (ter Braak 1986). The environmental vectors extend in the direction indicating its correlation with each axis. Species that plot closer to the head of each environmental vector are indicative of greater abundances in sites that have higher than average characteristics of that vector. Species plotted near the origin were, on average, found in sites that were average for all the vectors in the plot. Both intersite and interspecies plots were created using these average abundances. Interspecies differences within each of the three subzones were also investigated using the abundance of each macrolichen taxon on each stem. Biplot scaling and downweighting of rare species were used in all canonical correspondence analyses. Variables were included in the plot if they were significant at $p \le 0.05$ as determined through forward selection with Bonferonni adjustments. This ensured that only those variables which likely were related to the species distributions were used in the CCA (Mundfrom et al. 2006). The total set of variables used in the site level analyses were stream width, slope perpendicular to stream, average age of oldest adjacent conifers, average canopy cover, number of buried organic horizons, abundance of stems with dbh > 10 cm, stem density, mean annual precipitation, and mean annual temperature. The

total set of variables used in the stem level analyses were stem diameter, angle of lean, direction of lean, percent bark cover, and percent moss cover.

The ability of the species within each subzone to act as indicators of that subzone was investigated with indicator species analysis (Dufrêne and Legendre 1997) and Monte Carlo tests of significance in PC-ORD version 5.01 (McCune and Mefford 1999). The indicator value of each species in each subzone was calculated as the product of 100, mean abundance of the species in the subzone, and the relative frequency of occurrence of the species in the subzone. Indicator values can range from 0 when there is no indication to 100 when the species is present in all the plots of a single group and absent from all other plots. The maximum indicator value from the three subzones of each species was interpreted as the indicator value of that species. The significance of this indicator value was then tested with 10 000 permutations of Monte Carlo tests. A significance level of 0.05 was used to identify species indicative of each of the subzones.

Results

The average temperature in sampled alder swales was lowest in the SBSmk, at the western end of our longitudinal transect (Table 4.1). A marked east to west precipitation gradient was calculated, with the easternmost sites having both greatest annual precipitation and greatest winter snowfall accumulation.

Average alder canopy cover ranged from 87% in the SBSmk, to 82% in the SBSwk, and 85% in the SBSvk. These differences were not statistically significant. Overall, canopy cover estimates ranged from 37 to 96%. The average age of the oldest alders in each site

were fairly consistent across the three subzones, 33 years in the SBSwk, 32 years in the SBSmk, and 29 years in the SBSvk.

Alder swales in the SBSmk were associated with lower mean annual precipitation and lower mean annual temperatures than were the sites of the other two subzones (Figure 4.1). Alder swales in the SBSwk were associated with a greater abundance of large stems, compared to sites in the SBSvk (Figure 4.1).

Nine species of lichen forming fungi were found in only one subzone with an additional nine species not observed in one of the three subzones. One species, Tuckermannopsis platyphylla (Tuck.) Hale, was found only in the SBSvk. Five species, Collema subflaccidum Degel., Hypogymnia bitteri Lynge) Ahti, Leptogium burnetiae C. W. Dodge, Lobaria retigera (Bory) Trevisan, and Peltigera collina (Ach.) Schrader, were found only in the SBSwk. Three species, Collema furfuraceum (Arnold) Du Rietz, Kaerenfeltia merrillii (Du Rietz) Thell and Goward, and Nodobryoria oregana (Tuck.) Common and Brodo, were unique to the sites of the SBSmk. The species that were not observed in the SBSmk were Nephroma helveticum Ach., Pseudocyphellaria anomala Brodo and Ahti, Hyopgymnia austeroides (L.) Nyl., and Sticta limbata (Sm.) Ach.. Ramalina obtusata (Arnold) Bitter and *Xanthoria* spp. were not observed in the sites of the SBSwk. *Tuckermannopsis orbata* (Nyl.) M. J. Lai and *Hypogymnia metaphysodes* (Asahina) Rass. were not observed in the SBSvk sites (Table 4.2). Indicator species analysis suggested the presence of three indicator species for the SBSmk, nine for the SBSwk, and one for the SBSvk (Table 4.3).

The ordination based on the average abundances of each of the macrolichen taxa in the sites indicated that the significant environmental vectors identified through forward

selection were mean annual temperature, mean annual precipitation, age of adjacent conifer forest, and the abundance of stems with dbh greater than 10 cm in a site (Figures 4.2, 4.3). These four vectors explain 84% of the variation in the weighted averages of species with respect to the environmental data. The first two eigenvalues were 0.08 and 0.052. The age of the conifer forest (r^2 =0.49) and mean annual precipitation (r^2 =0.66) were both correlated with the first canonical axis. The abundance of stems larger than 10 cm dbh (r^2 =0.43) and mean annual temperature (r^2 =0.85) were correlated with the second canonical axis.

All the observed cyanolichens, with the exception of four species, were associated with increased mean annual precipitation as a major environment trend (Figure 4.2). These four exceptions were *Collema sublflaccidum*, *Leptogium burnetiae*, *Lobaria retigera* (Bory) Trevisan, and *Collema furfuraceum*. There was also a general trend of increasing diversity with increasing abundances of large alder stems, especially for rare species including *Hypogymnia metaphysodes*, *Hypogymnia austeroides*, *Collema subflaccidum*, and *Ramalina obtusata* (Figure 4.2).

The ordinations within individual subzones, based on the stem level abundances of the macrolichen taxa, identified stem diameter, percent moss cover, and angle of lean as the most significant variables for determining species abundances on individual stems (Figure 4.3). The cyanolichens responded most strongly to stem diameter and percent moss cover in all three subzones (Figure 4.3).

In the ordination based on the sampled stems of the SBSmk, the first two eigenvalues were 0.049 and 0.023 with the three variables explaining 67% of the species environment variation (Figure 4.3A). In the ordination based on the sampled stems of the SBSwk, the first two eigenvalues were 0.077 and 0.024 with the three environmental vectors explaining 74%

of the species-environment variation (Figure 4.3B). In the ordination based on the sampled stems of the SBSvk, the first two eigenvalues were 0.081 and 0.046 with the three environmental vectors explaining 75% of the species-environment variation (Figure 4.3C).

Table 4.1. Average climate data for alder swales, by subzone of Sub-Boreal Spruce (SBS), based on modeled mean data from 1971 to 2000 obtained from Climate B.C. v 3.2.

	Te	mperature (°	C)		
SBS subzone	Mean Annual	Mean January	Mean July	Mean Annual Precipitation (mm)	Mean Annual Snowfall (mm)
Moist (mk1)	2.7	-10.7	14.1	734	287
Wet (wk1)	3.3	-10.9	12.4	791	292
Very-wet (vk)	3.3	-9.7	14.9	918	340

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Table 4.2. Species list with abbreviation (Abbr.), functional groups (Func.) and percent occurrence in the plots of each Sub-Boreal Spruce (SBS) subzone. The functional groups are alectorioid (A), cyanolichen (C) and matrix (foliose macrolichens with a green-algal biont) lichen (M). n=25 in each subzone.

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			% O	ccurrenc	e
			by SBS	Subzon	e
		-	, .		
					Very-
			Moist	Wet	wet
Species	Abbr.	Func.	(mk1)	(wk1)	(vk)
Alectoria sarmentosa (Ach.) Ach.	alec sar	A	96	100	100
Bryoria spp. Brodo & D. Hawk1sw.	bryo spp	А	100	96	96
Cladonia spp. P. Browne	clad spp	Μ	4	32	16
Collema furfuraceum (Arnold) Du Rietz	coll fur	С	4	0	0
Collema subflaccidum Degel.	coll sub	С	0	4	0
Hypogymnia austeroides (Nyl.) Räsänen	hypo aus	Μ	0	12	4
Hypogymnia bitteri (Lynge) Ahti	hypo bit	Μ	0	4	0
Hypogymnia enteromorpha (Ach.) Nyl.	hypo ent	Μ	56	52	28
Hypogymnia metaphysodes (Asahina) Rass.	hypo met	Μ	8.	20	4
Hypogymnia occidentalis L. Pike	hypo occ	Μ	56	48	12
Hypogymnia physodes (L.) Nyl.	hypo phy	Μ	92	96	64
Hypogymnia rugosa (G. Merr.) L. Pike	hyo rug	Μ	20	20 [·]	8
Hypogymnia tubulosa (Schaerer) Hav.	hypo tub	Μ	80	72	40
Hypogymnia vittata (Ach.) Parrique	hypo vit	Μ	40	32	20
Kaerenfeltia merrillii (Du Rietz) Thell &					
Goward	kaer mer	Μ	4	0	0
Leptogium burnetiae C. W. Dodge	lepr bur	С	0	4	0
Leptogium saturninum (Dickson) Nyl.	lept sat	С	8	36	12
Lobaria halii (Tuck.) Zahlbr.	loba hal	С	0	52	28
Lobaria pulmonaria (L.) Hoffm.	loba pul	С	24	72	52
Lobaria retigera (Bory) Trevisan	loba ret	С	0	8	0
Lobaria scrobiculata (Scop.) DC.	loba scr	С	12	56	48
Melanelia spp. Essl.	mela spp	Μ	92	96	64
Nephroma bellum (Sprengel) Tuck.	neph bel	С	16	44	16
Nephroma helveticum Ach.	neph hel	С	0.	40	16
Nephroma isidiosum (Nyl.) Gyelnik	neph isi	С	12	44	16
Nephroma parile (Ach.) Ach.	neph par	С	20	76	80
Nephroma resupinatum (L.) Ach.	neph res	С	16	56	36
Nodobryoria oregana (Tuck.) Common &	•				
Brodo	nodo ore	А	12	0	0
Parmelia hygrophila Goward & Ahti	parm hyg	Μ	44	68	40
Parmelia sulcata Taylor	parm sul	Μ	100	100	88

Table 4.2 continued.

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Parmeliopsis ambigua (Wulfen) Nyl.	parm amb	М	100	68	64
Parmeliopsis hypteropta (Ach.) Arnold	parm hyp	Μ	72	36	56
Peltigera collina (Ach.) Schrader	pelt col	С	0	12	0
Physcia spp. (Schreber) Michaux	phys spp	Μ	48	56	32
Platismatia glauca (L.) Culb. & C. Culb.	plat gla	М	80	84	48
Platismatia norwegica (Lynge) Culb. & C.					
Culb.	plat nor	Μ	8	48	20
Pseudocyphellaria anomala Brodo & Ahti	pseu ano	С	0	52	36
Ramalina dilacerata (Hoffm.) Hoffm.	rama dil	Μ	84	80	28
Ramalina farinaceae (L.) Ach.	rama far	М	4.	8	4
Ramalina obtusata (Arnold) Bitter	rama obt	Μ	4	0	4
Ramalina thrausta (Ach.) Nyl.	rama thr	А	4	8	12
Sticta fuliginosa (Hoffm.) Ach.	stic ful	С	0	32 [·]	12
Sticta limbata (Sm.) Ach.	stic lim	С	0	4	4
Tuckermannopsis chlorophyla (Willd.)					
Hale	tuck chl	Μ	84	88	72
Tuckermannopsis orbata (Nyl.) M. J. Lai	tuck orb	Μ	24	4	0
Tuckermannopsis platyphyla (Tuck.) Hale					
Syn	tuck pla	Μ	0	0	8
Usnea spp. Dill. ex Adans.	usne spp	А	92	96	84
Vulpicida pinastri (Scop.) Mattsson & M. J.					
Lai	vulp pin	М	92	60	76
Xanthoria spp. (Fr.) Th. Fr.	xant spp	Μ	12	0	4

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species	Moist (SBSmk)	Wet (SBSwk)	Very-wet (SBSvk)	р
Parmeliopsis ambigua	62	11	15	0.0001
Tuckermannopsis orbata	23	0	0	0.0022
Vulpicida pinastri	41	13	26	0.0421
Leptogium saturninum	0	32	1	0.0047
Lobaria hallii	0	40	7	0.0004
Lobaria pulmonaria	2	41	19	0.0044
Nephroma resupinatum	2	28	14	0.0408
Parmelia hygrophila	8	38	11	0.0145
Platismatia glauca	21	45	10	0.0058
Platismatia norvegica	1	35	4 ·	0.0011
Sticta fuliginosa	0	28	2	0.0061
Tuckermannopsis chlorophylla	30	41	12	0.0199
Nephroma parile	1	33	43	0.0029

Table 4.3 Indicator species, and their indicator values (in bold), of epiphytic lichens in each subzone of the Sub-Boreal Spruce (SBS) biogeoclimatic zone. P-values are from Monte Carlo tests.



ure 4.1. Canonical correspondence analysis of the relationship between alder swales in each of the three subzones of the Sub-Boreal Spruce biogeoclimatic zone, and environmental variables, based on abundance data of macrolichen species in each swale. The inset shows the environmental vectors where the direction of the arrows indicates the correlation with the first two canonical axes and the length of the arrows represents the strength of the correlations.



Figure 4.2. Canonical correspondence analysis of the relationship between the abundance of each of 49 lichen taxa and site characteristics in 75 alder swales. The species abbreviations and functional groups are in Table 4.2. The inset shows the environmental vectors where the direction of the arrows indicates the correlation with the first two canonical axes and the length of the arrows represents the strength of the correlations.



Figure 4.3. Canonical correspondence analysis of the relationships between each of the lichen taxa and the stem characteristics in each of three subzones of the Sub-Boreal Spruce (SBS) biogeoclimatic zone. A: moist (SBSmk), B: wet (SBSwk), C: very-wet (SBSvk). Environmental vectors are shown to the right of each plot. Vector 1: diameter; 2: angle of lean; 3: percent moss cover.

Discussion

An overlooked part of the conservation biology story of central-interior British Columbia is the role that riparian alder forest swales may play in conserving lichen biodiversity. Alder swales constitute only a small proportion of regional landscapes, less than 1% in our 122,000 ha study area. However, their significance may extend far beyond their actual area, given that they occur as linear corridors adjacent to streams across the landscape, thus providing a high degree of connectivity in regional landscapes. Further the same disturbance processes that have drastically reduced the amount of old-growth coniferous forests in SBS landscapes may operate with far less frequency in wet alder swales, both due to their topographic position in wet depressions typically skipped over by fires (Bergeron 1991), and their general lack of timber-harvesting values. Although some alder dominated sites on wet seepage slopes in the very-wet climate subzone have been treated by herbicide or mechanical treatments as a deliberate policy to reforest greater land cover (C. DeLong personal communication, 2008), fortunately, this practice has been decreasing due to changes in policy and the high cost of conducting these conversions.

Against this backdrop, our finding that many of the lichens growing within our alder swales have been described previously as old-growth associated lichens assumes considerable interest. If we look, for instance, at the list of old growth-dependent canopy lichens developed by Campbell and Fredeen (2004), we see that the chlorolichens *Hypogymnia vittata* (Ach.) Parrique and *Platismatia norvegica* (Lynge) Culb. are common in alder swales in all of the three sampled subzones. The comparison is even more dramatic when we consider old-growth cyanolichens listed by Campbell and Fredeen, with *Lobaria pulmonaria* (L.) Hoffm., *L. hallii* (Tuck.) Zahlbr., *L. scrobiculata* (Scop.) DC., *Nephroma helveticum* Ach., *N. isidiosum* (Nyl.) Gyelnik, *N. parile* (Ach.) Ach., *Pseudocyphellaria*

anomala Brodo and Ahti, and *Sticta fuliginosa* (Hoffm.) Ach. all present in our SBSwk and SBSvk alder swales. This would suggest that alder swales represent important refugia for old growth-dependent lichens in SBS landscapes. McCune et al. (2002) similarly found that deciduous forests growing adjacent to montane streams in western Oregon were an important refugium for canopy cyanolichens, although their study indicated that rare species were more common along large streams rather than along smaller upland streams.

Clearly one of the factors that promotes lichen diversity in alder swales must be their persistence over time, which allows for the gradual accumulation of old-growth forest species. The widespread presence of *Ramalina dilacerata* (Hoffm.) Hoffm. in our alder swales is instructive in this regard. Its presence has previously been associated with fire-free refugia that have long site continuity (Karström 1992). Although individual alder stems do not appear to achieve great longevity, their continuing ability to send up new sprouts has the potential to provide substrate for lichen colonization in alder swales over very long time periods, similar to that demonstrated by Ruchty et al. (2001) for persistent patches of the shrub *Acer circinatum* Pursh in Oregon. Both Snall et al. (2005) and Kuusinen (1994a, 1994b) showed the importance of deciduous stand elements for retention of epiphytic lichens in Scandinavian boreal forests. However, Snall et al.'s modeling of host availability assumed a dispersed availability of willows in a landscape where all components were equally susceptible to fire, unlike the apparent situation of our alder swales, which may function as refugia through multiple disturbance events.

When considering the accumulation of old-forest associated lichens in alder swales, we must look at both the suitability of available habitat and dispersal limitations from source populations (Ockinger et al. 2005). Sillett et al. (2000) hypothesized that dispersal limitations were a primary constraint on the accumulation of rare cyanolichens in old-growth forests of

the U.S. Pacific Northwest. Similar limitations may exist in our riparian forest swales, where old-growth associated cyanolichens such as *Lobaria retigera* and *Sticta limbata*, which may be representative of bipartite cyanolichens, were often absent from seemingly suitable habitat.

A common constraint on the establishment and survival of canopy epiphytes is nutrient availability and the pH of stemflow precipitation (Hauck et al. 2002). The position of alder swales in groundwater receiving topographic position should enhance nutrient availability for canopy epiphytes, especially when compared to surrounding coniferous forests. Goward and Spribille (2005) noted the importance of wet nutrient-receiving sites in supporting the diversity of calicioid lichens and foliose cyanolichens in B.C.'s inland mountain ranges. However, the profusion of cyanolichens on both deciduous (Goward and Arsenault 2000a) and coniferous substrates in the SBSwk and SBSvk (Goward and Arsenault 2000c; Goward and Spribille 2005), suggests that substrate pH may not be a limiting factor in this region.

Other important environmental variables that influence lichen communities in alder swales are regional temperature and precipitation gradients. These have previously been identified as major variables in landscape-level studies examining the distribution and abundance of epiphytic lichen communities (McCune et al. 1997; Jovan and McCune 2004; Giodani 2006; Gauslaa et al. 2007). Climate B.C. model results predicted greatest precipitation at the easternmost end of our longitudinal transect, in the SBSvk, declining in the alder swales of more western (SBSmk) transect locations.

Our indicator species of the SBSmk, *Parmeliopsis ambigua*, *Tuckermannopsis orbata*, and *Vulpicida pinastri*, are commonly found in open pine and spruce forests of British Columbia (Goward et al. 1994). *Kaernefeltia merrillii*, a rare species that we observed

only in the SBSmk, also tends to colonize sites in drier locations (Goward et al. 1994). *Collema furfuraceum*, rare in the alder swales sampled, was found only in the warmest of the SBSmk alder swales reflecting the general preference of many cyanolichens for warmer wet sites (Goward et al. 1994). Therefore, it would be hypothesized that *C. furfuraceum* would be able to colonize alder swales of the SBSwk which were generally warmer and wetter.

Four of the indicator species of the SBSwk, Lobaria hallii, L. pulmonaria, Platismatia norvegica, and Sticta fuliginosa, were listed among oceanic macrolichens of cedar-hemlock forests in B.C.'s interior by Goward and Spribille (2005) and Radies (2008). They hypothesized that summer drought was the predominant limiting factor for the growth of these species in inland regions, supporting the stronger association with the wetter SBSwk. Although the SBSvk is wetter, other factors, including the heavier winter snowpack, may limit the occurrence of these oceanic species in the SBSvk. Of the species unique to the SBSwk, Collema subflaccidum, Leptogium burnetiae, and Peltigera collina are rare species, though may be representative of bipartite cyanolichens in that they are typically observed in sheltered humid forests (Goward et al. 1994). Along with Lobaria retigera, an old-growth associated species (Goward et al. 1994; Goward and Spribille 2005), we tended to observe these four cyanolichens in warmer than average sites that had higher than average abundances of large alder stems. These aspects of their distribution coincide with characteristics of the alder swales in the SBSwk. Hypogymnia bitteri, another rare species in our data set and in the study region as a whole (Goward et al. 1994), was found only in the SBSwk alder swales, generally in sites with a rich epiphyte flora and a high density of alders greater than 10 cm dbh.

The age of surrounding coniferous forests was identified by CANOCO as an additional major variable predicting the abundance of canopy lichens in alder swales.

Certainly, we would expect that alder swales immediately adjacent to old-growth coniferous forests would show higher lichen diversity. Alder swales were typically quite narrow, only 15-20 m across at their widest point, well within the dispersal range of lichen soredia from adjacent old forests (Armstrong 1990, 1994). However, the vector of age of conifer forests in surrounding landscapes was strongly correlated with the vector of mean annual precipitation along our east to west longitudinal transects, with fire return intervals ranging from ca. 100 years in SBSmk regions, to over 900 years in SBSvk sites (DeLong 1998), making it difficult to separate the potential influence of these two factors. The strongest correlations between these two variables were present among the sites of the SBSmk, the subzone where subzone variation in precipitation levels would be expected to most greatly impact both the frequency of stand-destroying fires and the suitability of the habitat for cyanolichens.

One factor that we have not examined is the short-term impacts of the removal of adjacent coniferous forests on lichens of riparian forests. As alder swales were generally located in topographic depressions with abundant standing water and/or surface seepage areas, we would expect that they would be somewhat buffered from changes in fetch characteristics of surrounding upland forests. Further, these conditions of greater light availability (compared to surrounding closed canopy coniferous forests) and enhanced humidity in alder swales should favor retention of old forest lichens, as they do in canopygaps over seepage areas in adjacent cedar-hemlock forests (Coxson and Stevenson 2007) or in spruce swamp-forests in Finland (Kuusinen 1996b). Radies (2008) also noted that stands with a more open canopy structure generally indicated sites better suited to the establishment of many old-growth associated macrolichens.

Looking at east-west climate gradients in the SBS biogeoclimatic zone, we would expect that arboreal lichens with green algal bionts would be more tolerant of drought (Hajek

et al. 2001) and better able to sustain physiological activity in dry conditions, due to their ability to rehydrate under conditions of high atmospheric humidity (Lange et al. 2004). In contrast, the requirement of cyanolichens for liquid water to sustain rehydration may impose narrower habitat requirements for many species (Antoine 2004). Additionally, carbon assimilation and nitrogen fixation in many foliose cyanolichens are particularly limiting at low temperatures (Sundberg et al. 1996). Taken together, these contrasting trends in temperature and precipitation may play a critical role in structuring lichen communities of alder swales. Green-algal lichen species such as Parmelia sulcata Taylor, Hypogymnia physodes (L.) Nyl., and Platismatia glauca (L.) Culb. and C. Culb. were widely distributed across all of our alder swales, while fewer foliose cyanolichens were found in the SBSmk alder swales. Some lichens may also have been absent from the SBSvk sites due to temperature limitations. Lobaria retigera, for instance, tended to be more strongly influenced by temperature than precipitation. The large stems that Collema subflaccidum and Leptogium burnetiae tended to colonize more frequently may have moderated temperature extremes (Hengst and Dawson 1993) in the warmer SBSmk and SBSwk sites.

Regional gradients in temperature and precipitation availability are, of course, modified by site specific substrate factors. The most notable of these in our alder swales were the influence of stem diameter and stem lean. In all three subzones, leaning large diameter stems (which tend to be moss covered) were a major predictor of lichen abundance and diversity. These stems tend to intercept more precipitation, thereby providing wetter microsites for lichen colonization. They typically have greater moss growth on their upper stem surfaces, providing a substrate with much greater water holding capacity. This was seen in our CANOCO vectors, which showed percent moss cover and stem diameter as two of the most important variables predicting lichen species distribution on alder stems.

These characteristics may be of particular importance to cyanolichens such as *Lobaria retigera* and *Collema subflaccdium* and chlorolichens such as *Ramalina farinacea* and *Hypogymnia austeroides*, which preferentially colonized alder stems with dbh larger than 8 cm. In the SBSmk and SBSwk, the majority of the cyanolichens tended to plot along the percent moss cover vector, however in the SBSvk, only species of *Nephroma* species plotted along this vector with other cyanolichens tending to be found only on large alder stems. The identification of *N. parile*, the most abundant species of *Nephroma* in the alder swales, as an indicator species of the SBSvk further supports the association of *Nephroma* species with wetter sites. The only other taxa that failed to plot along the stem diameter vector were *Cladonia* spp and *Vulpicida pinastri*. *Cladonia* is a terrestrial lichen genus and *V. pinastri*, while being epiphytic, tends to establish in habitats with more terrestrial characteristics such as the lower portions of trees and shrubs (Goward et al. 1994).

Although increases in precipitation can be a positive indicator for lichen abundance, seasonal distribution of precipitation must also be considered. Submersion beneath winter snowpack has previously been shown to have a deleterious influence in a range of different ecosystems. Prolonged burial by snowpack can lead to much higher respiratory carbon loss (Kappen and Breuer 1991), which over time can greatly increase lichen mortality rates (Benedict 1990). For this reason, slow-growing species may be more tolerant of subnivean environments than fast growing species. Marsh and Timoney (2005) further note that prolonged periods of saturation under snowpack can increase mortality rates of lichens even after the saturation stress is removed. One group of sensitive lichens in our riparian swales may be green-algal biont lichens such as *Hypogymnia physodes, Tuckermannopsis chlorophylla, Parmelia sulcata, Platismatia norwegica,* and Platismatia glauca. These lichens were widespread in the alder swales of the SBSmk and SBSwk, however they were

restricted to large diameter stems in the SBSvk swales. These large diameter stems are far less likely to bend under the weight of winter snow pack, and thus may be a more viable substrate for canopy lichens in SBSvk alder swales. When we consider all climatic variables, the SBSwk, with its intermediate level of precipitation, lower snowpack (than the SBSvk), and the warmest climate, would appear to provide the best climate for the development of arboreal lichen communities in the alder swales. The SBSwk supported both the greatest species richness and the most rare and old-growth associated species.

Historically, the wetter Sub-Boreal Spruce landscapes (i.e. the SBSwk and SBSvk) in central-interior British Columbia were dominated by old-growth forests. Natural range of variability estimates for percent of forested area older than 140 years is 43-61% for the SBSwk and 84-89% for the SBSvk (DeLong 2007). These landscapes, however, have seen a dramatic transformation over the last 50 years. Logging and fire have reduced the proportion of old-growth coniferous forest cover in the SBSwk to less than 30%, and to less than 70% in the SBSvk (unpublished data, Prince George Timber Supply Area - Landscapes Objectives Working Group, B.C. Ministry of Agriculture and Lands, March 2005). By regulation these can be further reduced to 26% for the SBSwk and 50% for the SBSvk. In addition, lodgepole pine-dominated forests, which are common in the SBSwk, have been impacted by mountain pine beetle and may no longer be suitable for many arboreal lichens. Thus, wet alder patches may be important refugia for old growth-dependent canopy lichens and an important source of propagules for recolonization of surrounding second-growth forests, thereby validating the current policy of not converting alder swales to forest.

Chapter Five. Physiology of six common cyanolichens in alder swales of central-interior British Columbia.

Introduction

Lichens are important to the cycling of nutrients in forests (Knops et al. 1996). By intercepting precipitation they change the chemistry of that precipitation reaching the ground (Knops et al. 1996). In arctic regions, cyanolichens contribute a significant amount of fixed nitrogen to the environment (Alexander & Schnell 1973). In forested regions, cyanolichens are generally more abundant in old-growth forests than in young forests (Goward 1994; Sillett and McCune 1998) and may fix as much as 5 kg N/ha/year in some coastal forests (Franklin et al. 1981). Hardwoods often support rich cyanolichen communities (Goward and Arsenault 2000a), in some cases richer than those found in old-growth forests (Peterson and McCune 2003) and may therefore be important in the cycling of nitrogen in many landscapes. In central British Columbia, hardwoods, such as alders and willows, are commonly found along first order streams. Riparian alders are able to support rich lichen communities that include rare and old-growth associated cyanolichens (see Chapter 4). Therefore these sites have a potential role in the cycling of nitrogen in these landscapes. The objectives were 1) to examine the physiological responses (rates of acetylene reduction, photosynthesis, and respiration) of common cyanolichens, collected from the same community, to a temperature gradient, and 2) to determine their relative contributions to the nitrogen budget of the sub-boreal spruce biogeoclimatic zone.

Methods

Biomass estimates of six cyanolichen species were made on the sampled stems within each of the 75 sites in the biogeoclimatic subzone. These six species were *Lobaria pulmonaria*, *Lobaria hallii*, *Lobaria scrobiculata*, *Sticta fuliginosa*, *Nephroma parile*, and *Pseudocyphellaria anomala*. These six species were the most abundant cyanolichens in the sites sampled and so were selected for physiological analyses. A circular reference thallus size of 4.5 cm diameter was used to approximate biomass in the field for a two meter interval along the stems starting 50 cm above ground level. The number of reference-sized clumps of each species on each sampled tree was estimated visually. For analysis, thalli that were approximately 4.5 cm in diameter were collected as thalli of this size were optimal for fitting into the incubation dishes. The dry weights of these same thalli were used in all further calculations. The average dry mass of a clump of *S. fuliginosa* was 0.48 g, of *L. hallii* 0.49 g, of *L. scrobiculata* 0.54 g, of *L. pulmonaria* 0.34 g, of *P. anomala* 0.43 g, and of *N. parile* 0.84 g.

The density of each of the six categories of stem vigor and diameter were estimated through the nearest individual method (Cottam et al. 1953) with distances from the transect to the nearest stems being taken every 10 m along the transect line. The dry weights of thalli that were collected for physiological analysis were used to determine the average mass of the reference clump for each of the six species (n=50 for each species). The average biomass of each cyanolichen species was found for each category of stem diameters and was multiplied by the density stems in that category. Biomass of each species in each site was expressed on a per hectare basis. This estimate was then doubled to account for unsampled portions of the stems, based on the observation that unsampled portions of the alder stems had comparable biomasses of the six cyanolichens studied. Small stems, under four meters in height,

generally did not support these six cyanolichens. To relate the amount of acetylene reduced to amount of nitrogen fixed per unit time by each species we used the theoretical ratio of 3 C_2H_4 : 1 N₂ (Hardy et al. 1973). Annual estimates of the amount of nitrogen fixed assumed a 150 day growing season with fixation occurring for half of that period at a mean temperature of 14 °C. This likely represents an overestimate of the annual amount of nitrogen fixed.

Thalli were collected on 17 October from riparian alders located at 54.10°N, 122.06°W and on 26 November 2008 from riparian alders located at 53.92°N, 121.75°W. Following collection, thalli were hydrated with deionized water and exposed to a 48 hour pretreatment period of 12 hours light at 15 °C and 200 μ mol/m²/s light intensity and 12 hours dark at 5 °C. Thalli were held at optimal water content during the incubations. Ten replicates of each species, from the first collection, were used for measurement of photosynthesis, respiration, and acetylene reduction assay (ARA) rates. Thalli of *S. fuliginosa, L. pulmonaria,* and *P. anomala,* collected from the second site in late November 2008 provided an additional 10 replicates of these species to verify the temperature response of ARA with an independent set of thalli.

For all physiology measurements, thalli of approximately 2 g dry weight were incubated at 200 µmol/m²/s at 7, 14, 21, and 28 °C in 100 mL glass chambers with the base covered with a flat glass plate sealed with vacuum grease. For ARA, 10 cm³ acetylene were injected prior to the three hour incubation. To measure respiration rates, the thalli were incubated between 2 and 10 minutes, with shorter durations at higher temperatures in the dark. For the ARA, the amount of ethylene converted from acetylene was quantified through gas chromatography using a Wennick SRI 8610A Gas Chromatograph (Wennick Scientific Corp, Ottawa, Canada) and associated software (Peak Simple 3.29, SRI Instruments, Torrance, USA). Rates of photosynthesis and respiration, as measured by changes in carbon

dioxide concentration, were measured using Li-Cor CO₂ Analyser Model LI-6251 (Li-Cor, Lincoln, USA). Following the incubations, all thalli were still saturated. Destructive sampling of the thalli was used to prevent any carry-over effects from the acetylene between incubations at each temperature.

Results & Discussion

In the SBSmk, only *L. pulmonaria* and *L. scrobiculata* were present (Table 5.1). All six species were present in both the SBSwk and SBSvks. *Nephroma parile* and *L. pulmonaria* made up the greatest mass in the SBSwk while in the SBSvk, *N. parile* was the dominant cyanolichen (Table 5.1). *Nephroma parile* fixed the greatest amount of nitrogen, among the species sampled, in the SBSwk and SBSvk. Average and maximum amounts of fixed nitrogen from these dominant cyanolichens are very low (Table 5.2), as compared to previous estimates of nitrogen fixation by cyanolichens, between 3 and 5 kg/ha/year, from old growth forests (Franklin et al. 1981). Denison (1973) estimated that 11.2 kg/ha/year of nitrogen may be fixed by *L. oregana* on Douglas fir trees. These estimates are much higher than we observed due to the greater biomass of the cyanolichens in those forests than in our study sites.

Though the lichen contribution to the nitrogen budget of alder swales is minimal, alders themselves contain cyanobacteria in root nodules and the nitrogen contributions from these root nodules represent a far more significant input of nitrogen to the ecosystem. Nitrogen fixation has been previously determined to be 43 kg N₂/ha/year in a 30 year old stand of *Alnus incana* (Johnsrud 1978) and as high as 320 kg N₂/ha/year in 20 year old stands of *Alnus rubra* (Newton et al. 1968).

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each subzone an	e indicated in par	entheses.				
		Lobaria	Lobaria		Pseudocyphellaria	Sticta
SBS subzone	Lobaria hallii	pulmonaria	scrobiculata	Nephroma parile	anomala	fuliginosa
	0 7 0	0.678 ± 1.107	0.098 ± 0.188	0 7 0		0 = 0
moist (mk)	(0)	(1.457)	(0.458)	(2.100)	(0) 0 ∓ 0	(0)
	2.582 ± 2.082	6.810 ± 4.473	2.320 ± 2.358	13.624 ± 10.069	0.996 ± 0.551	1.116 ± 0.617
wet (wk)	(2.882)	(5.525)	(2.750)	(12.600)	(0.838)	(0.891)
	2.312 ± 3.448	2.932 ± 3.978	2.446 ± 3.6	24.376 ± 18.27	2.066 ± 2.015	2.312 ± 2.256
very wet (vk)	(2.042)	(5.200)	(2.063)	(9.450)	(1.375)	(0.723)

of a color according Table 5.1. Average mass, ± SD, of dominant cyanolichen species in each subzone (g/ha) of the Sub-Boreal - - - - - -. 2 . Christe (CBC) his Table 5.2. Amount of nitrogen fixed annually (g N2/ha/yr), in each subzone of the Sub-Boreal Spruce (SBS) biogeoclimatic zone, by the dominant cyanolichens. Values from the site supporting the greatest biomass of each species in each subzone are indicated in parentheses.

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	total	0.08 (2.72)	11.31 (22.24)	16.29 (27.16)
Sticta	fuliginosa	0.00 (0.00)	0.98 (1.56)	2.04 (3.27)
Pseudocyphellaria	anomala	0.00 (0.00)	0.51 (1.18)	1.05 (1.93)
	Nephroma parile	0.00 (1.53)	5.28 (9.15)	9.44 (13.93)
Lobaria	scrobiculata	0.06 (0.57)	1.46 (3.44)	1.54 (2.58)
Lobaria	pulmonaria	0.02 (0.63)	1.96 (2.37)	1.13 (2.23)
	Lobaria hallii	00.00 (00.00)	1.13 (4.54)	1.1 (3.21)
	SBS subzone	moist (mk)	wet (wk)	very wet (vk)

Photosynthesis rates followed the same trend for all six species with the rates increasing up to 21 °C and decreasing at higher temperatures (Figure 5.1). This pattern is typical of many lichens (Adams 1971; Lange et al. 1998). Respiration rates also followed the same trend for all six species with higher rates occurring at higher temperatures (Figure 5.2). This trend has been previously found for many lichens (Adams 1971; Lange et al. 1998).

ARA indicated that the six species responded in different ways to the various temperature conditions. *Sticta fuliginosa, Lobaria hallii,* and *Lobaria scrobiculata* had maximum rates of reduction at 7 °C. *Lobaria pulmonaria* had maximum rates at 21 °C. *Pseudocyphellaria anomala* had maximum rates of reduction at 28 °C. *Nephroma parile* had similar rates across all temperatures (Figure 5.3). The second set of ARA, based on thalli collected in late November 2008, indicated the same trends that were observed in the first set, though, in the second set of ARA analysis, the mean rates of fixation were lower in *S. fuliginosa* across the temperature gradient and were lower in *P. anomala* at the cool end of the temperature gradient and higher at the warm end of the gradient (Figure 5.4). Similar rates in *L. pulmonaria* were observed across the temperature gradient in the first and the second sets of ARA (Figure 5.4).



Figure 5.1. Effect of temperature on the photosynthetic rate of thalli of six cyanolichen species collected in mid October 2008. Error bars show standard error, n=10.



Figure 5.2. Effect of temperature on the respiration rate of thalli of six cyanolichen species collected in mid October 2008. Error bars show standard error, n=10.



Figure 5.3. Rate of acetylene reduction in six cyanolichen species across a temperature gradient based on thalli collected in mid October 2008. Error bars show standard error, n=10.



Figure 5.4. Rate of acetylene reduction in cyanolichen species across a temperature gradient, based on a second, independent collection made at the end of November 2008. Error bars show standard error, n=10.

The ecology and distribution of these cyanolichens is informative in explaining these various trends. *Nephroma parile* was present in the majority of the alder swales in the SBSwk and SBSvks (Chapter 4). We hypothesized that by frequently being present in these subzones and tending to colonize portions of stems within the winter snowpack, *N. parile* likely possesses unique adaptations to thrive in very wet, high elevation swales. The consistent rate of reduction in *N. parile*, across the temperatures analyzed, suggests that this species is well adapted to survive in habitats across the landscape so long as precipitation is not a limiting factor. Its distribution across the sampled landscape further supports this statement because it was one of the four cyanolichens to be found in all three subzones, was the second most frequently encountered cyanolichen in the sites of the SBSmk, after *Lobaria pulmonaria*, and was the most frequently encountered cyanolichen in the sites of the SBSwk and SBSvk (Chapter 4).

Little change was observed in rates of ARA between 7 and 15 °C, indicating a constant response to average temperatures, in *S. fuliginosa*, *L. hallii*, and *L. scrobiculata*. The average July temperature in all the swales was less than approximately 15 °C (Chapter 4). These three species were found to colonize large stems in the SBSwk that had high percent covers of moss (Chapter 4). These species were absent from the majority of the sites in the SBSvk due to higher snow levels and lower abundances of large stems and from the SBSmk due to inadequate levels of precipitation (Chapter 4). By minimizing the length of time covered by snow, maximum use can be made of spring and fall conditions, maximizing the growing season for these species since they also photosynthesize and respire at lower temperatures.
Low temperature optima, below 20 °C, for nitrogen fixation in cyanolichens have been previously documented (Kallio et al. 1972; Maikawa & Kershaw 1975) including for *S*. *fuliginosa* (Maikawa & Kershaw 1975) though procedural errors, including factors such as continuous hydration prior to the experiment, unstandardized pretreatment conditions, and drying of thalli during the experiment, may have caused some of those results (Kershaw 1985). To avoid the errors highlighted by Kershaw (1985), our pretreatment conditions allowed the thalli to dry out several times prior to the experiment, the same pretreatment was used for all the replicates of all the species, and all thalli were maintained at a constant level of hydration throughout the incubations. Therefore, our low temperature optima likely are not artifacts.

Our results, however, are not without precedents as low temperature optima for nitrogenase activity have been observed in experiments not susceptible to these criticisms (Rodgers 1978; Lennihan et al. 1994). These low optimal temperatures for fixation have been suggested to occur in cool climates (Rodgers 1978; Lennihan et al. 1994). Seasonal acclimation may also be an important factor leading to the different temperature optima of ARA in these species, as has previously been found in rates of nitrogen fixation in *Peltigera rufescens* (Hitch and Stewart 1973) and in free-living *Nostoc* (Lennihan et al. 1994). *Lobaria pulmonaria* experienced the lowest rates of acetylene reduction because it is a tripartite association with cyanobacteria present only within cephalodia.

Pseudocyphellaria anomala tended to be found in the wettest sites that would support cyanolichens and on large, leaning stems (Chapter 4). Leaning stems would be expected to intercept more light as a result of less shading of the stems by their own canopies. This greater exposure to light would result in more rapid drying of thalli, resulting in the presence of *P. anomala* in only the wettest of the sites capable of supporting cyanolichens. This rapid

drying would necessitate high rates of photosynthesis (Figure 5.1) and nitrogen fixation (Figure 5.3) while the thalli were still saturated. Although this species tends to colonize large stems, more of the stems supporting *P. anomala* would be covered by snow due to their greater lean. To compensate for this greater period of time submerged beneath the snowpack, this species exhibited the lowest rates of respiration among the six cyanolichens studied (Figure 5.2), thereby minimizing respiratory loss of carbon during the winter. Both ARA and photosynthesis measurements indicated that *P. anomala* positively responds to temperature, while minimizing respiration rates.

Lobaria pulmonaria exhibited the lowest rates of photosynthesis and ARA as well as very low rates of respiration, across the majority of the temperature gradient. All the thalli analyzed appeared healthy with no visible necrosis. *Lobaria pulmonaria* was quite common in all three subzones, though may not be tolerant of submersion beneath the winter snowpack as illustrated by its stronger association with large stems in the SBSvk than in either of the other subzones (Chapter 4) and is known to colonize forests of all ages (Campbell and Fredeen 2004). Optimal temperatures for nitrogen fixation have been previously identified to be between 20 and 30 °C for root nodules of many plants (Gibson 1971; Waughman 1977) and for free-living cyanobacteria (Fogg 1960; Pattnaik 1966). Many cyanolichens, including *L. pulmonaria*, have also been previously found to exhibit maximum rates of nitrogen fixation at temperatures above 20 °C (Hitch and Stewart 1973; Kallio 1973; Kelly and Becker 1975; Kallio et al. 1976).

Because optimal temperatures for the majority of cyanobacteria, in root nodules, freeliving, and lichenized, are above 20 °C, special adaptations are likely required to modify this state, as hypothesized for the other five cyanolichens studied. Therefore, *L. pulmonaria*

posesses none of the adaptations of the other five cyanolichens discussed because it is not adapted to any particular set of environmental conditions, beyond moist environments.

To more fully understand the seasonal changes in lichen physiology that may occur, these experiments should be repeated with summer collected thalli. This will provide further information into whether these species have different acclimation mechanisms and how those mechanisms are important to the survival of these species in the same habitat.

Chapter Six. Conclusion

Though wetland alder swale environments are limited in their aerial extent, they represent an ecologically important branching network spanning the many climatically different regions of the sub-boreal spruce biogeoclimatic zone. Their distribution and hypothesized longevity in a landscape otherwise more frequently disturbed by fire and harvesting, make them ideal for conserving lichen diversity. Alder swales function as important repositories of canopy lichen biodiversity, with 43 species and six additional genera of macrolichens present in alder swales, supporting rich arboreal lichen communities across the sampled landscape.

The composition of epiphytic communities changed across the landscape with rare species present in only one or two of the subzones. Diversity was greatest in the SBSwk, 20.8 species per site on average, reflecting the climatic gradient along which the sampled sites were established. Canopy macrolichen communities were less diverse in alder swales at both extremes of the climatic gradient, with an average alpha diversity of 15.1 species per site. Heavy winter snowpack may reduce lichen abundance in the cooler and wetter alder swales at the eastern end of our longitudinal transect. At the western end of the longitudinal transect, availability of summer precipitation is likely a limiting factor in sites. Alder swales that had intermediate climate supported the greatest diversity.

Canonical Correspondence Analysis identified mean annual temperature, precipitation, age of adjacent conifer forest, and abundance of large stems (dbh > 10 cm) as significant explanatory environmental variables. Regional precipitation gradients may explain the exclusion of many lichen species from both the most westerly and most easterly alder swales, with drier summer conditions and heavy winter snowpack respectively being major limiting factors in these sites. Lichens preferentially occupied large leaning stems

within individual alder swales, especially in the drier subzones. These stems provide greater precipitation interception, and with their well developed moss mats, provide long-lived substrates for many old-growth lichen species.

Physiological analyses, combined with the observed distributional pattern s, of six common cyanolichens, indicated four strategies for survival. *Sticta fuliginosa, Lobaria hallii*, and *Lobaria scrobiculata* appeared to be well adapted to spring and autumn conditions, thereby maximizing the length of their growing seasons. *Pseudocyphellaria anomala* was found to be adapted to warm, high light conditions. Both *Nephroma parile* and *Lobaria pulmonaria* were found to be tolerant of a wide range of environments, though *N*. *parile* was able to tolerate longer periods under the winter snowpack than was *L. pulmonaria*. These physiological adaptations correspond with their observed distributions in the 75 sampled alder swales. The cyanolichen contribution to the nitrogen budget is orders of magnitude less than that likely contributed by the root nodules of alders.

The abundance of old-growth associated macrolichens supported by alder swales is indicative of the ability of alder swales to function as refugia for canopy lichens and to function as a source of propagules for the colonization of second-growth forests. In addition, alder swales support important ecosystem processes such as nitrogen fixation and contribute to the cycling of nutrients in these areas. This supports the recognition of these previously neglected linear landscape attributes as old-growth arboreal lichen refugia in the land-use management policies of British Columbia. The epiphytic lichen diversity supported along non-fish bearing streams indicates that riparian buffers should be in place along all streams. In addition, avoiding activities, such as skidding across or along alder swales during the winter months, that disturb these riparian habitats should be avoided. Furthermore, as all of the alder swales that were sampled were adjacent to mature conifer forest, it would be

possible for the composition of the communities to change following the removal of this forest. The complete removal of the adjacent forests would result in the creation of windier, higher light conditions in the swales. This would result in drier microhabitats, even though the moisture that would be taken up by the forest would be redirected to the streams along which our alder swales occur.

Management should occur at both spatial and temporal scales, ensuring that enough potential habitat is present within the landscape to allow for natural variation to occur in the forests over time as the result of climate change, which predicts that this region will become warmer and wetter in the future. Therefore, the ability of the sampled alder swales of the SBSmk and SBSwk to function as refugia may be increased, so long as buffers are present along the alder swales. However, this is not to say that alder swales may be able to support the full complement of the diversity present in the SBS because alder swales do not represent the entire range of microhabitats present in the SBS and because the retention of many patches of all forest types will ensure that, even following climate change, that sufficient habitat is retained for all epiphytes, including rare and dispersal limited species which would be the first to vanish following the removal of adequate substrates. Further research is necessary in order to fully describe the extent of differences between the lichen communities of these riparian habitats and the adjacent conifer forests.

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