

Riparian alder ecosystems as epiphytic lichen refugia in sub-boreal spruce forests of British Columbia

Matthew Doering and Darwyn Coxson

Abstract: Alder-dominated riparian forests represent only a small proportion of the landscape in central-interior British Columbia. However, they possess a suite of attributes that may allow them to function as refugia for canopy macrolichens. These include their deciduous habitat, their location in moist nutrient receiving sites, and their distribution as narrow corridors that cross broad regional landscapes. We have examined their potential role as lichen refugia by assessing canopy macrolichen communities in 75 riparian alder forests across a 200 km longitudinal gradient in central-interior British Columbia. Study sites were stratified equally between three climate subzones of the Sub-Boreal Spruce biogeoclimatic zone. Forty-nine macrolichen taxa were observed, including the old-growth indicator cyanolichen species *Lobaria scrobiculata* (Scop.) DC., *L. retigera* (Bory) Trevisan, *Nephroma isidiosum* (Nyl.) Gyelnik, and *Sticta limbata* (Sm.) Ach. Canonical correspondence analysis identified mean annual temperature, mean annual precipitation, age of adjacent conifer forest, and abundance of large stems (dbh >10 cm) as significant explanatory variables. Regional precipitation gradients explained the exclusion of many lichen species from both the most westerly and most easterly riparian forests, with drier summer conditions and heavy winter snowpack, respectively, being major limiting factors. Lichens preferentially occupied large leaning stems, which may provide greater precipitation interception and continuity of substrate, when compared with smaller upright alder stems. We conclude that alder-dominated riparian forests represent a major refugium for old-growth dependent lichens in British Columbia's sub-boreal spruce landscapes and as such may provide valuable dispersal corridors between remnant old-growth coniferous forest patches.

Key words: *Alnus*, riparian gallery, canopy macrolichens, sub-boreal spruce, old growth, lichen indicator species.

Résumé : Les forêts riveraines dominées par les aulnes ne représentent qu'une faible proportion du paysage dans la région du centre-intérieur de la Colombie Canadienne. Cependant, elles possèdent un ensemble d'attributs qui pourraient leur permettre d'agir comme refuge pour les macrolichens de la canopée. Ceux-ci incluent leur habitat décadu, leur localisation sur des sites recevant des embruns nutritifs, et leur distribution le long d'étroits corridors traversant un ensemble de paysages régionaux. Les auteurs ont examiné leur potentiel comme refuge pour les lichens, en évaluant les communautés de macrolichens de la canopée dans 75 forêts riveraines le long d'un gradient longitudinal de 200 km, dans le centre-intérieur de la Colombie Canadienne. Les sites d'études furent également stratifiés entre trois sous-zones de la zone biogéoclimatique de la pessière sub-boréale. Les auteurs ont observé 49 taxons de macrolichens, incluant les *Lobaria scrobiculata* (Scop.) DC., *L. retigera* (Bory) Trevisan, *Nephroma isidiosum* (Nyl.) Gyelnik et *Sticta limbata* (Sm.) Ach., des espèces de cyanolichens indicatrices des forêts surannées. L'analyse des correspondances canoniques identifie comme variables explicatives significatives, la température annuelle moyenne, la précipitation annuelle moyenne, l'âge des forêts conifériennes adjacentes, et l'abondance de tiges à fort diamètre (dhp >10 cm). Les gradients de précipitation régionale expliquent l'exclusion de plusieurs espèces de lichens le long des forêts riveraines à la fois les plus à l'ouest et les plus à l'est, subissant respectivement des conditions estivales plus sèches et d'enneigement hivernal plus importantes qui agissent comme facteurs limites. Les lichens occupent de préférence les longues branches traînantes qui peuvent permettre une interception plus importante des précipitations et une continuité de substrat, lorsqu'on les compare aux plus petites tiges dressées des aulnes. Les auteurs concluent que les forêts riveraines dominées par des aulnes constituent un refuge de premier ordre pour les lichens dépendant de forêts surannées dans les paysages de la pessière sub-boréale de la Colombie Canadienne, en fournissant des corridors utiles entre les aires de forêts conifériennes surannées.

Mots-clés : *Alnus*, galerie riveraine, macrolichens de la canopée, pessière sub-boréale, espèces de lichens indicatrices d'âge avancé.

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M. Doering and D. Coxson.¹ Ecosystem Science and Management Program, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada.

¹Corresponding author (e-mail: darwyn@unbc.ca).

Introduction

Riparian forests 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 montane

forests, riparian forests and adjacent wetlands may provide refugia from disturbance events such as forest fires, which can skip over or have reduced severity in wet microsites (Dwire and Kauffman 2003). In central-interior British Columbia, first- and second-order streams typically support narrow riparian corridors of green-alder (*Alnus crispa* subsp. *crispa* (Ait.) Pursh) and mountain-alder (*Alnus incana* subsp. *tenuifolia* (Nuttall) Breitung). Although individual alder stems in these patches may not be very long-lived, senescing alder stems can 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 long periods of time (Bramble and Byrnes 1972; Nierig et al. 1986).

This raises the question as to whether alder riparian forests in central-interior British Columbia may function as refugia for old-growth associated canopy lichens. We know from previous studies that old-growth coniferous forest stands in these landscapes can support rich canopy lichen communities (Campbell and Fredeen 2004; Radies and Coxson 2004). Little information is known about the development of canopy lichen communities within riparian forests in these landscapes, although 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 forests 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 circa 52°N to 57°N latitude, and from 122°W to 128°W longitude (Meidinger and Pojar 1991). Although this landscape was 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 alders within SBS riparian forests in central-interior British Columbia. We were particularly interested in the response of lichen communities to regional climate gradients, from wet and cool sites in the east, to warmer and drier sites in the west. We have also investigated the role of changes in substrate availability and canopy structure on lichen community composition in riparian alder forests. We would hypothesize that riparian zone alders in the SBS may serve as refugia for old-growth associated canopy macrolichens. If this is the case, these forests would provide valuable connectivity between remnant old-growth coniferous forests in the surrounding landscapes. They may also provide an important source population for recolonization of lichens into adjacent second-growth plantation forest stands.

Methods

Site selection

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 climate subzones of the SBS climate zone (Fig. 1). From east to west, wettest to driest, respectively, these climate subzones are the very wet and cool climate subzone variant (SBSvk), the Willow variant of the wet and cool climate subzone (SBSwk1), and the Mossvale variant of the moist and cool climate subzone (SBSmk1). We subsequently refer to these climate subzones in the text as the very wet, wet, and moist climate subzones, respectively. Climate subzone boundaries used followed the boundaries published by B.C. Ministry of Forests and Range (Victoria, B.C.).

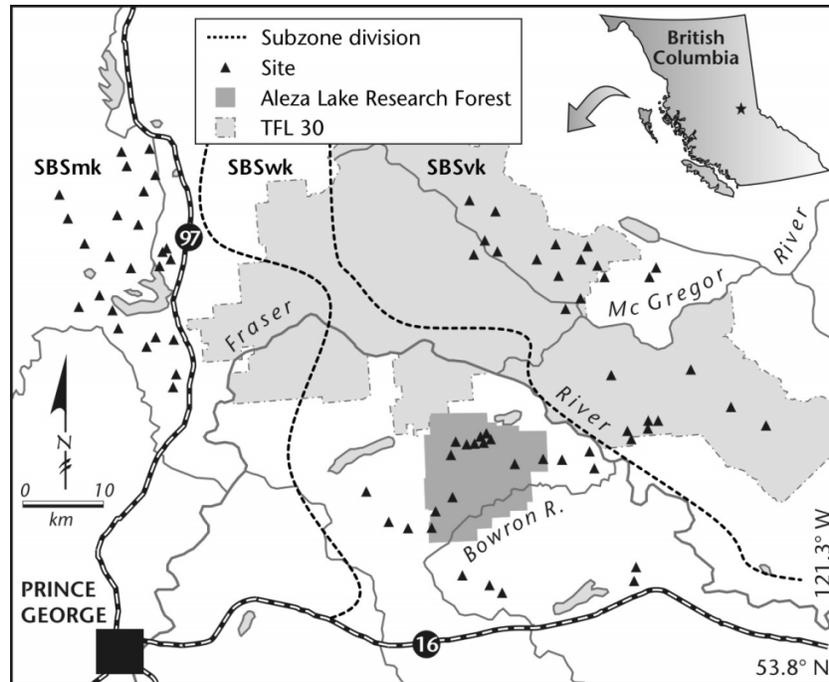
All the sampled riparian forests were in wet depressions along streams with relatively similar understory vascular vegetation. *Alnus incana* (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung was the predominant species of alder. *Alnus crispa* (Ait.) Pursh subsp. *crispa* was present in four of the sites in the very wet climate subzone and in one site in the moist climate subzone. Willows (*Salix* spp.), red osier dogwood (*Cornus sericea* L.), and devil's club (*Oplomanax horridus* (Sm.) Miq.) were occasionally present in some sites. The main herbs observed included lady fern (*Athyrium filix-femina* Roth), spiny wood fern (*Dryopteris expansa* (C. Presl) Fraser-Jenk. and Jermy), oak fern (*Gymnocarpium dryopteris* (L.) Newman), skunk cabbage (*Lysichiton americanus* Hulten and 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. *Alnus incana* subsp. *tenuifolia* ranged in height from 2 to 5 m. The height of the trees in the adjacent, mature forest was upwards of 15 m.

Within each of the three climate subzones, 25-point latitude and longitude coordinates, confined to sites within 1 km of road access points, were generated randomly. The nearest first- or second-order stream with an adjacent riparian alder zone was subsequently sampled using a 100 m transect line, as outlined below. Taken together these three sets of 25 sites (75 sites total) constitute our longitudinal gradient across the SBS zone in this region (Fig. 1).

At each site, a 100 m long lichen sampling transect was established parallel to the stream course, halfway between the stream bank and the edge of the alder strip. This was typically located at a distance of between 3 and 5 m from the stream edge. Sampling of alder stems and associated lichen communities was conducted at 10 m intervals along these transect lines. Sampling for lichens on alder stems at each 10 m point along the transect lines was based on a search for one of each of the following types of stems: (1) the nearest live alder stem with a diameter at breast height (dbh) of less than 10 cm; (2) the nearest dead alder stem with a dbh of less than 10 cm; (3) the nearest live alder stem with a dbh of between 10 and 15 cm; (4) the nearest dead alder stem with a dbh of between 10 and 15 cm; (5) the nearest live alder stem with a dbh of greater than 15 cm; (6) the nearest dead alder stem with a dbh of greater than 15 cm. Alder stems in each of these six categories were not always present in each of the sites sampled. The range of stems sampled along each transect line in our study was from 10 to 47 stems. All transects were placed a minimum of 50 m from the nearest road.

The sampled region on each stem began 0.5 m above the ground and extended for 2 m along the stem. Within this re-

Fig. 1. Map of the study region in British Columbia showing the locations of the 25 study sites in each climate subzone (total of 75 sites).



gion all macrolichens were identified to species level 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, ≤ 3 thalli present; 2, $>3 \leq 6$ 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 or absence binary data were 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% 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 m point along the lichen sampling transect, canopy cover was measured with a spherical densiometer, and averaged for each transect line. In each site, the five largest living alder stems were cored to determine their ages. The three largest conifers adjacent to each alder transect were cored to estimate stand age. The average width of each sampled stream was also recorded.

Elevation-corrected Climate B.C. data (version 3.2, Uni-

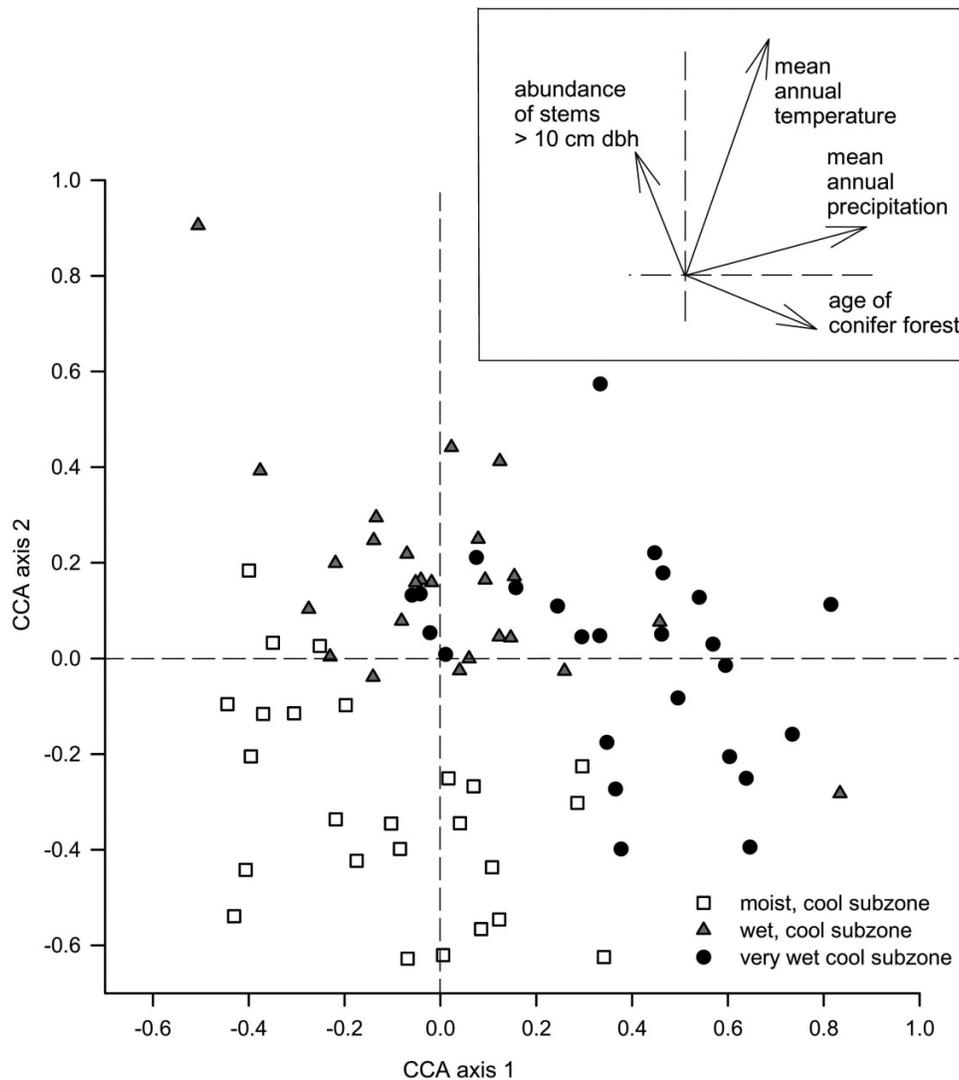
versity of British Columbia, Vancouver), using modeled mean data from 1971 to 2000 (Wang et al. 2006), were obtained for each of the sampled sites.

Data analyses

The average abundance of each of the 49 macrolichen taxa in each of the 75 sites was calculated. These values were subsequently examined using canonical correspondence analysis (CCA) in CANOCO version 4.5 (ter Braak and Smilauer 2002). Biplot scaling, with downweighting of rare species, was used for ease of interpretation (CCA runs without downweighting were examined, but were not used in the present analysis). We used 499 permutations with random starts to assess the significance of canonical axes. The plots of the first two axes provided by CANOCO provided the least-cluttered view of points in ordination space and are presented herein. The ordination axes in CCA were constrained to be linear combinations of the four significant 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 their 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 climate 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, following

Fig. 2. Canonical correspondence analysis of the relationship between alder sites in each of the three climate subzones of the Sub-Boreal Spruce biogeoclimatic zone and the four significant ($p < 0.05$) environmental variables, of the set of seven used, based on abundance data of macrolichen species in each site. 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. The first two eigenvalues were 0.08 and 0.052.

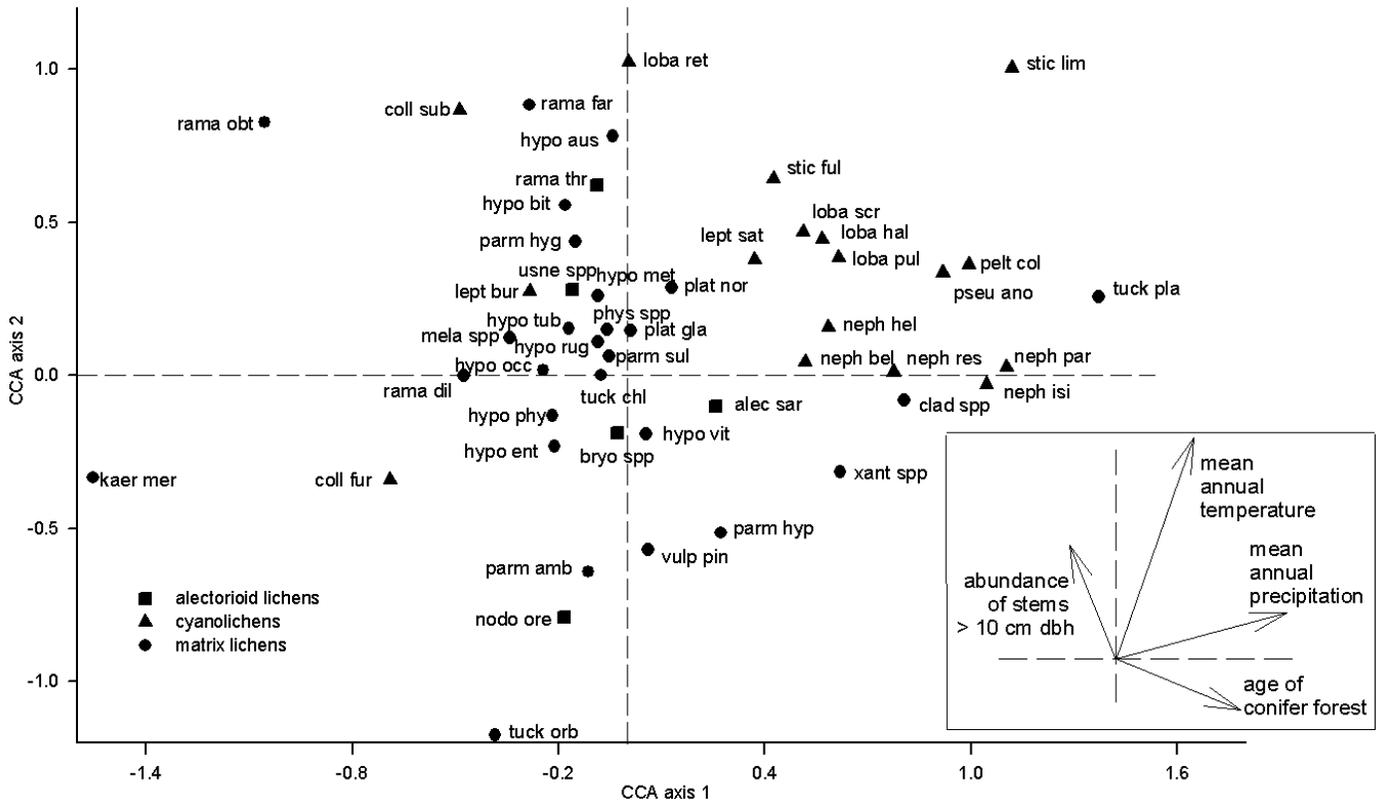


Okland et al. (2003). Our preliminary analysis of CCA runs conducted without downweighting (data not presented) did not suggest markedly different outcomes. Variables were included in the plot if they were significant at $p \leq 0.05$, as determined through forward selection with Bonferroni adjustments. This ensured that only those variables that 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, 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. These variables are similar to those identified in previous studies as major environmental influences (e.g., McCune et al. 2002; Öckinger et al. 2005). Stream width,

slope, and mean annual precipitation described soil moisture conditions. Canopy cover and stem density described the humidity environment. The time since disturbance was approximated using the age of the adjacent conifer forest. The abundance of large alder stems described the range of substrate characteristics present in the sites. The climate of the site was assessed using modeled estimates of mean annual precipitation and mean annual temperature. The presentation of CCA results in Figs. 2 and 3 are based on analysis of the same data set (site level data), with Fig. 2 presenting sites, and Fig. 3 presenting species space.

The ability of the species within each climate subzone to act as indicators of that climate 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 climate subzone was calculated as the product of 100, mean abundance of the species in the

Fig. 3. Canonical correspondence analysis of the relationship between the abundance of lichen taxa and site characteristics in the 75 alder sites. The species abbreviations and functional groups are as in Table 2. The inset shows the four significant ($p < 0.05$) environmental variables, of the set of seven used, 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. The first two eigenvalues were 0.08 and 0.052.



climate subzone, and the relative frequency of occurrence of the species in the climate 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 climate 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 climate subzones. Inter-set correlations and statistics for the environmental variables used in CCA analysis are provided in Appendices 1 and 2; these, respectively, presenting site level analyses (across all climate subzones), and stem level analyses (within each of the moist, wet, and very wet climate subzones). The Appendices also include canonical coefficients and t values for variables identified as significant through forward selection.

Results

The average temperature in sampled alder forests was lowest in the moist climate subzone, at the western end of our longitudinal transect (Table 1). A marked east to west precipitation gradient was predicted, with the eastern-most sites having both greatest annual precipitation and greatest winter snowfall accumulation. In the moist subzone, the age range of alders sampled was between 3 and 71 years, while in

the wet subzone the alders ranged from 3 to 65 years, and in the very wet subzone the alders ranged from 3 to 54 years old. The average age of the oldest alders in each site was fairly consistent across the three subzones, 33 years in the wet climate subzone, 32 years in the moist climate subzone, and 29 years in the very wet climate subzone. No significant differences were found between the ages of alders sampled in different subzones or between the canopy cover of the sites among the subzones. The age range of adjacent conifer forests in the moist subzone was 39–171 years, in the wet subzone it was 41–157 years, and in the very wet subzone it was 42–158 years. Average alder canopy cover ranged from 87% in the moist climate subzone, to 82% in the wet climate subzone, and 85% in the very wet climate subzone. These differences were not statistically significant. Overall, canopy cover estimates ranged from 37% to 96%.

Mean annual temperature (ANOVA $F = 6.98$; $df = 2$; $p = 0.0017$) and mean annual precipitation (ANOVA $F = 7.52$; $df = 2$; $p = 0.0011$) were not uniform across the subzones. Mean annual temperature was highest in the wet subzone and lowest in the moist subzone. Mean annual precipitation increased among the sites from the moist to the wet to the very wet subzone, with the greatest increases occurring from the wet to the very wet subzones.

Alder forests in the moist climate subzone were associated with lower mean annual precipitation and lower mean annual temperatures than were alder forests in the other two climate subzones (Fig. 2). Alder forests in the wet climate

Table 1. Range of climate data for sampled alder sites (mean in parentheses), by climate subzone of Sub-Boreal Spruce (SBS), based on modeled mean annual data from 1971 to 2000 obtained from Climate B.C. version 3.2.

SBS climate subzone	Temperature (°C)			Mean annual precipitation (mm)	Mean annual snowfall (mm)
	Mean annual	Mean January	Mean July		
Moist (mk)	2.1–2.9 (2.7)	–12.3 to –9.6 (–10.7)	13.2–14.8 (14.1)	657–889 (734)	272–365 (287)
Wet (week)	2.9–3.4 (3.3)	–12.3 to –8.8 (–10.9)	14.2–15.3 (12.4)	717–886 (791)	270–353 (292)
Very wet (vk)	2.5–3.5 (3.3)	–11.3 to –8.9 (–9.7)	14.1–15.3 (14.9)	845–1135 (918)	327–462 (340)

subzone were associated with a greater abundance of large stems, compared with sites in the very wet climate subzone (Fig. 2).

Nine species of lichen-forming fungi were found in only one climate subzone, with an additional nine species not observed in one of the three climate subzones. One species, *Tuckermannopsis platyphylla* (Tuck.) Hale, was found only in the very wet climate subzone. Five species, *Collema subflaccidum* Degel., *Hypogymnia bitteri* Lyngé Ahti, *Leptogium burnetiae* C.W. Dodge, *Lobaria retigera* (Bory) Trevisan, and *Peltigera collina* (Ach.) Schrader, were found only in the wet climate subzone. 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 moist climate subzone. The species that were not observed in the moist climate subzone were *Nephroma helveticum* Ach., *Pseudocyphellaria anomala* Brodo and Ahti, *Hypogymnia austeroides* (L.) Nyl., and *Sticta limbata* (Sm.) Ach. *Ramalina obtusata* (Arnold) Bitter and *Xanthoria* spp. were not observed in the sites of the wet climate subzone. *Tuckermannopsis orbata* (Nyl.) M.J. Lai and *Hypogymnia metaphysodes* (Asahina) Rass. were not observed in the very wet climate subzone sites (Table 2). Indicator species analysis suggested the presence of three indicator species for the moist climate subzone, nine for the wet climate subzone, and one for the very wet climate subzone (Table 3).

The ordination based on the average abundances of each of the macrolichen taxa in the sites indicated that the significant ($p < 0.05$) 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 (Figs. 3 and 4). These four vectors explained 84% of the variation in the weighted averages of species with respect to the environmental data. The eigenvalues for the first four axes were 0.08, 0.052, 0.035, and 0.02, and the cumulative percentage of species data explained by each additional axis were 38%, 62%, 77%, and 85%, respectively. These low eigenvalues indicate that higher unconstrained axes contribute to the total variation, and that the set of variables used are inadequate to account for the entire set of differences in species composition between sites. However, the first ($p = 0.002$) and all the canonical axes ($p = 0.002$) were significant, as determined with Monte Carlo tests, using 499 permutations, indicating that the environmental variables used, while not explaining the full amount of variation, are influential in determining these species distributions. The species environment correlations with each axis were 0.765, 0.684, 0.743, and 0.557, respectively. 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. The high correlations with the environmental data are due to the highly significant canonical axes. The analogue to r^2 calculated by dividing the explained variance by the total variance was 0.239.

All the observed cyanolichens, with the exception of four species, were associated with increased mean annual precipitation as a major environment trend (Fig. 3). These four exceptions were *Collema subflaccidum*, *Leptogium burnetiae*, *Lobaria retigera* (Bory) Trevisan, and *Collema furfuraceum*.

In each of the three climate subzones, stem diameter, percent moss cover, and angle of lean were the most important variables for determining species abundances on individual stems (Fig. 4). The cyanolichens responded most strongly to stem diameter and percent moss cover in all three climate subzones (Fig. 4). The first three eigenvalues from the ordination of sampled stems in the moist climate subzone were 0.049, 0.023, and 0.022. The cumulative percentages of species data explained by each additional axis were 27%, 53%, and 67%, respectively (Fig. 4A). The species environment correlations with each axis were 0.724, 0.611, and 0.582, respectively, and the analogue to r^2 was 0.358 (Fig. 4A). In the ordination based on the sampled stems of the wet subzone, the first three eigenvalues were 0.077, 0.024, and 0.023, respectively, and the cumulative percentages of species data explained by each additional axis were 36%, 62%, and 74%, respectively. (Fig. 4B). The species environment correlations with each axis were 0.761, 0.623, and 0.588, respectively, and the analogue to r^2 was 0.415 (Fig. 4B). In the ordination based on the sampled stems of the very wet subzone, the first three eigenvalues were 0.081, 0.046, and 0.037, and the cumulative percentages of species data explained by each additional axis were 40%, 66%, and 75%, respectively (Fig. 4C). The species environment correlations with each axis were 0.785, 0.692, and 0.641, respectively, and the analogue to r^2 was 0.273 (Fig. 4C). Inter-set correlations and statistics for the environmental variables used in CCA analysis are provided in Appendices A and B. These, respectively, present site-level analyses (across all climate subzones), and stem-level analyses (within each of the moist, wet, and very-wet climate subzones). The Appendices also include canonical coefficients and t values for variables identified as significant through forward selection.

Discussion

An often overlooked component of conservation biology planning in boreal and sub-boreal forests is the role that riparian forests may play in conserving lichen biodiversity. Alder-dominated riparian forests constitute only a small proportion of regional landscapes, less than 1% of our

Table 2. Species list with abbreviation (Abbr.), functional groups (Func.), and percent frequency occurrence in the plots of each climate subzone of the Sub-Boreal Spruce (SBS) biogeoclimatic zone.

Species	Percent frequency occurrence by SBS climate subzone				
	Abbr.	Func.	Moist (mk)	Wet (week)	Very wet (vk)
<i>Alectoria sarmentosa</i> (Ach.) Ach.	alec sar	A	96	100	100
<i>Bryoria</i> spp. Brodo and D. Hawksw.	bryo spp	A	100	96	96
<i>Cladonia</i> spp. P. Browne	clad spp	M	4	32	16
<i>Collema furfuraceum</i> (Arnold) Du Rietz	coll fur	C	4	0	0
<i>Collema subflaccidum</i> Degel.	coll sub	C	0	4	0
<i>Hypogymnia austeroidea</i> (Nyl.) Räsänen	hypo aus	M	0	12	4
<i>Hypogymnia bitteri</i> (Lynge) Ahti	hypo bit	M	0	4	0
<i>Hypogymnia enteromorpha</i> (Ach.) Nyl.	hypo ent	M	56	52	28
<i>Hypogymnia metaphysodes</i> (Asahina) Rass.	hypo met	M	8	20	4
<i>Hypogymnia occidentalis</i> L. Pike	hypo occ	M	56	48	12
<i>Hypogymnia physodes</i> (L.) Nyl.	hypo phy	M	92	96	64
<i>Hypogymnia rugosa</i> (G. Merr.) L. Pike	hyo rug	M	20	20	8
<i>Hypogymnia tubulosa</i> (Schaerer) Hav.	hypo tub	M	80	72	40
<i>Hypogymnia vittata</i> (Ach.) Parrique	hypo vit	M	40	32	20
<i>Kaerenfeltia merrillii</i> (Du Rietz) Thell and Goward	kaer mer	M	4	0	0
<i>Leptogium burnetiae</i> C. W. Dodge	lepr bur	C	0	4	0
<i>Leptogium saturninum</i> (Dickson) Nyl.	lept sat	C	8	36	12
<i>Lobaria halii</i> (Tuck.) Zahlbr.	loba hal	C	0	52	28
<i>Lobaria pulmonaria</i> (L.) Hoffm.	loba pul	C	24	72	52
<i>Lobaria retigera</i> (Bory) Trevisan	loba ret	C	0	8	0
<i>Lobaria scrobiculata</i> (Scop.) DC.	loba scr	C	12	56	48
<i>Melanelia</i> spp. Essl.	mela spp	M	92	96	64
<i>Nephroma bellum</i> (Sprengel) Tuck.	neph bel	C	16	44	16
<i>Nephroma helveticum</i> Ach.	neph hel	C	0	40	16
<i>Nephroma isidiosum</i> (Nyl.) Gyelnik	neph isi	C	12	44	16
<i>Nephroma parile</i> (Ach.) Ach.	neph par	C	20	76	80
<i>Nephroma resupinatum</i> (L.) Ach.	neph res	C	16	56	36
<i>Nodobryoria oregana</i> (Tuck.) Common and Brodo	nodo ore	A	12	0	0
<i>Parmelia hygrophila</i> Goward and Ahti	parm hyg	M	44	68	40
<i>Parmelia sulcata</i> Taylor	parm sul	M	100	100	88
<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.	parm amb	M	100	68	64
<i>Parmeliopsis hypteropta</i> (Ach.) Arnold	parm hyp	M	72	36	56
<i>Peltigera collina</i> (Ach.) Schrader	pelt col	C	0	12	0
<i>Physcia</i> spp. (Schreber) Michaux	phys spp	M	48	56	32
<i>Platismatia glauca</i> (L.) Culb. and C. Culb.	plat gla	M	80	84	48
<i>Platismatia norwegica</i> (Lynge) Culb. and C. Culb.	plat nor	M	8	48	20
<i>Pseudocyphellaria anomala</i> Brodo and Ahti	pseu ano	C	0	52	36
<i>Ramalina dilacerata</i> (Hoffm.) Hoffm.	rama dil	M	84	80	28
<i>Ramalina farinaceae</i> (L.) Ach.	rama far	M	4	8	4
<i>Ramalina obtusata</i> (Arnold) Bitter	rama obt	M	4	0	4
<i>Ramalina thrausta</i> (Ach.) Nyl.	rama thr	A	4	8	12
<i>Sticta fuliginosa</i> (Hoffm.) Ach.	stic ful	C	0	32	12
<i>Sticta limbata</i> (Sm.) Ach.	stic lim	C	0	4	4
<i>Tuckermannopsis chlorophylla</i> (Willd.) Hale	tuck chl	M	84	88	72
<i>Tuckermannopsis orbata</i> (Nyl.) M.J. Lai	tuck orb	M	24	4	0
<i>Tuckermannopsis platyphyla</i> (Tuck.) Hale Syn	tuck pla	M	0	0	8
<i>Usnea</i> spp. Dill. ex Adans.	usne spp	A	92	96	84
<i>Vulpicida pinastri</i> (Scop.) Mattsson and M.J. Lai	vulp pin	M	92	60	76
<i>Xanthoria</i> spp. (Fr.) Th. Fr.	xant spp	M	12	0	4

Note: The functional groups are alectorioid (A), cyanolichen (C), and matrix (foliose macrolichens with a green algal biont) lichens (M). $n = 25$ in each climate subzone.

122 000 ha study area (M. Doering and D. Coxson, unpublished data). However, their significance for canopy lichen communities may extend far beyond their actual area, given that they occur as corridors that cross regional landscapes,

providing potentially important connectivity between different habitat patches. Further, the disturbance processes that have drastically reduced the amount of old-growth coniferous forests in British Columbia's sub-boreal spruce landscapes

Table 3. Indicator species, and their indicator values (*), of epiphytic lichens in each climate subzone of the Sub-Boreal Spruce (SBS).

Species	SBSmk	SBSwk	SBSvk	<i>p</i>
<i>Parmeliopsis ambigua</i>	62*	11	15	0.0001
<i>Tuckermannopsis orbata</i>	23*	0	0	0.0022
<i>Vulpicida pinastri</i>	41*	13	26	0.0421
<i>Leptogium saturninum</i>	0	32*	1	0.0047
<i>Lobaria hallii</i>	0	40*	7	0.0004
<i>Lobaria pulmonaria</i>	2	41*	19	0.0044
<i>Nephroma resupinatum</i>	2	28*	14	0.0408
<i>Parmelia hygrophila</i>	8	38*	11	0.0145
<i>Platismatia glauca</i>	21	45	10	0.0058
<i>Platismatia norvegica</i>	1	35	4	0.0011
<i>Sticta fuliginosa</i>	0	28	2	0.0061
<i>Tuckermannopsis chlorophylla</i>	30	41	12	0.0199
<i>Nephroma parile</i>	1	33	43	0.0029

Note: *p* values are from Monte Carlo tests. SBSmk, the Mossvale variant of the moist and cool climate subzone; SBSwk, the Willow variant of the wet and cool climate subzone; SBSvk, the very wet and cool climate subzone variant.

may operate with reduced frequency in alder forests, both because of their topographic position in wet depressions that may be skipped by fires (Dwire and Kauffman 2003), 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 with herbicide or mechanical treatments as a deliberate policy to increase the proportion of the landscape with coniferous forest cover (C. DeLong, personal communication 2008), fortunately, this practice has been decreasing because of changes in policy and the high cost of conducting these conversions.

Against this backdrop, our finding that many of the lichens growing within our riparian forests are species that have previously been described as old-growth associated lichen species 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* (Lyngé) Culb. are common in alder forests in all of the three sampled climate subzones. The comparison is even more dramatic when we consider old-growth cyanolichens listed by Campbell and Fredeen (2004), 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 wet and very wet alder forests. This would suggest that alder forests represent important refugia for old-growth dependent lichens in sub-boreal spruce landscapes. McCune et al. (2002) similarly found that deciduous forests growing adjacent to montane streams in western Oregon were important refugia for canopy cyanolichens, although their study indicated that rare species were more often found along large streams, rather than along smaller upland streams.

Clearly one of the factors that promotes lichen diversity in alder forests must be their persistence over time, which

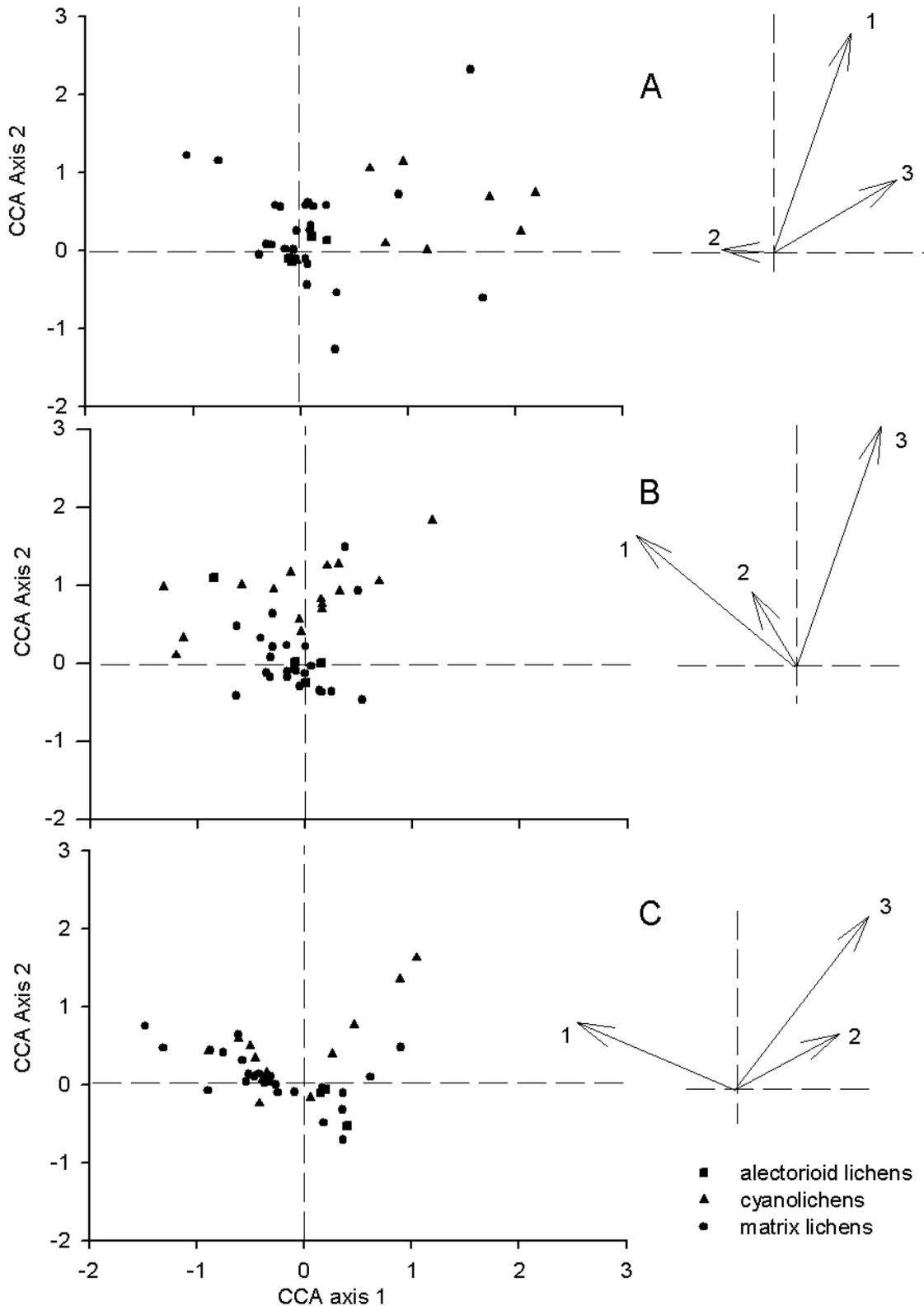
allows for the gradual accumulation of old-growth forest species. The widespread presence of *Ramalina dilacerata* (Hoffm.) Hoffm. in our alder forests is instructive in this regard. Its presence has previously been associated with fire-free refugia that have long site continuity (Karström 1992). Although 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 forests 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 Snäll et al. (2005) and Kuusinen (1994) showed the importance of deciduous stand elements for retention of epiphytic lichens in Scandinavian boreal forests. However, Snäll et al.'s (2005) 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 forests, which may function as refugia through multiple disturbance events.

When considering the accumulation of old-forest associated lichens in alder forests, we must look at both the suitability of available habitat and dispersal limitations from source populations (Öckinger 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 US Pacific Northwest. Similar limitations may exist in our riparian forests, where old-growth associated cyanolichens such as *Lobaria retigera* and *Sticta limbata* were often absent from seemingly suitable habitat. If we use old-growth indicator criteria of Goward et al. (1994) and Goward and Spribille (2005), 6 of the 14 old-growth associated lichen species in our data set were present in five or fewer sites. Okland et al. (2003) suggest that difference in species composition (vascular plants and bryophytes) between otherwise similar swamp forest patches must reflect the balance between “windows of opportunity” for colonization of new propagules, and persistence of established populations. These two factors would similarly apply to colonization by lichens in geographically dispersed alder patches.

A common limitation on the establishment and survival of canopy epiphytes is nutrient availability and the pH of stem-flow precipitation (Hauck et al. 2002). The position of alder forests in groundwater receiving topographic position may enhance nutrient availability for canopy epiphytes, especially when compared with 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 the inland mountain ranges of British Columbia. However, the profusion of cyanolichens on both deciduous (Goward and Arsenault 2000a) and coniferous substrates in wet SBS climate subzones (Goward and Arsenault 2000b; Goward and Spribille 2005) suggests that substrate pH may not be a limiting factor in this region.

Another important set of environmental variables that influence lichen communities in alder forests is that of 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

Fig. 4. Canonical correspondence analysis of the relationships between each of the lichen taxa and the stem characteristics in each of the three climate subzones (25 sites in each subzone) of the Sub-Boreal Spruce (SBS) biogeoclimatic zone: (A) moist climate subzone (SBSmk), the first two eigenvalues were 0.049 and 0.023; (B) wet climate subzone (SBS week), the first two eigenvalues were 0.077 and 0.024; (C) very wet climate subzone (SBS vk), the first two eigenvalues were 0.081 and 0.046. The three significant environmental variables, of the set of five included, are shown to the right of each plot. Vector 1, stem diameter; 2, angle of lean; 3, percent moss cover.



and McCune 2004; Giordani 2006; Gauslaa et al. 2007). Climate B.C. model results predicted greatest precipitation at the easternmost end of our longitudinal transect, in the very wet climate subzone, declining in the more western transect locations (moist climate subzone) alder forests. One caution that we would add to the interpretation of significant environmental variables identified by our CCA analysis (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) is that although these variables had high r^2 values, their eigenvalues were relatively low. This may indicate the existence of high correlations along relatively short gradients, which would be consistent with the spatial distribution pattern of our riparian alder forests, in narrow corridors along small streams.

Our indicator species of the moist climate subzone, *Parmeliopsis ambigua*, *Tuckermannopsis orbata*, and *Vulpicida pinastri*, were commonly found in open pine and spruce forests, characteristic of many of our adjacent stands (Goward et al. 1994). *Kaerenfeltia merrillii*, a rare species only found in the moist climate subzone, also tended to colonize those sites in drier locations (Goward et al. 1994).

Four of the indicator species of the wet climate subzone, *Lobaria hallii*, *L. pulmonaria*, *Platismatia norvegica*, and *Sticta fuliginosa*, were listed among oceanic macrolichens in cedar-hemlock forests of central-interior British Columbia by Goward and Spribille (2005). 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 wet subzones. Although the very wet subzone sites may have even greater moisture availability, there may be other reasons (i.e., heavy snowpack) that limit the occurrence of these species in the very wet subzone sites. Of the species unique to the wet climate subzone, *Collema subflaccidum*, *Leptogium burnetiae*, and *Peltigera collina* are rare species that 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 forests in the wet climate subzone. *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 wet climate subzone alder forests, 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 forests. Certainly, we would expect that alder forests immediately adjacent to old-growth coniferous forests would show higher lichen diversity. Alder forests 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. However, the age of forests in surrounding landscapes is strongly correlated with the precipitation gradients found along our east to west longitudinal transects, with fire return intervals ranging from circa 100 years in western SBS regions, to over 900 years in eastern SBS sites (DeLong 1998), making it

difficult to separate the potential influence of these two factors.

One factor that we have not examined is the short-term impacts of the removal of adjacent coniferous forests on riparian forest lichens. As alder forests 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, although Hylander et al. (2005) found significant changes in lichen and bryophyte communities within 20 m buffer strips left along streams that ran through clearcuts in northern Sweden. The conditions of high light and humidity that we would expect to find in our riparian alder forests should favor the development of rich canopy lichen communities, as previously noted, for instance, in canopy gaps over seepage areas in cedar-hemlock forests (Coxson and Stevenson 2007), or in spruce swamp forests in Finland (Kuusinen 1996).

Looking at east-west climate gradients in the SBS climate 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, because of their ability to rehydrate under conditions of high atmospheric humidity (Lange et al. 2001). 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. 1997). Taken together, these contrasting trends in temperature and precipitation may play a critical role in structuring lichen communities of alder forests. 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 forests, while fewer foliose cyanolichens were found in the driest (most westerly) alder forests.

Regional gradients in temperature and precipitation availability are, of course, modified by site-specific substrate factors. The most notable of these in our alder forests was the influence of stem diameter and stem lean. In all climate 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 subflaccidum* and chlorolichens such as *Ramalina farinacea* and *Hypogymnia austerooides*, which preferentially colonized alder stems with dbh larger than 8 cm. In the moist and wet climate subzones, the majority of the cyanolichens tended to plot along the percent moss cover vector, however in the very wet climate subzone, 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 forests, as an indicator species of the very wet climate subzone 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 forests may be green algal biont lichens such as *Hypogymnia physodes*, *Tuckermannopsis chlorophylla*, *Parmelia sulcata*, *Platismatia norvegica*, and *Platismatia glauca*. These lichens were widespread in the moist and wet climate subzones riparian alders, however, they were restricted to large diameter stems in the very wet climate subzone riparian alder forests. These large diameter stems are far less likely to bend under the weight of winter snowpack, and thus may be a more viable substrate for canopy lichens in very wet climate subzone alder forests. When we consider all climatic variables, the wet climate subzone, with its intermediate levels of precipitation, lower snowpack (than the very wet climate subzone), and the warmest climate, would appear to provide the best climate for the development of arboreal lichen communities in the alder forests. The wet climate subzone supported both the greatest species richness and the most rare and old-growth associated species.

Although our study did not examine lichen communities on other riparian forest species in central-interior British Columbia, cottonwoods (*Populus balsamifera* subsp. *trichocarpa*), common on the floodplains of larger rivers in the British Columbia central interior, have been hypothesized to play an important role in promoting the growth and establishment of SBS lichen communities (Goward and Arsenault 2000c).

In conclusion, the significance of wet alder forests for rare and old-growth associated lichen species must also be placed in a regional context. Historically, SBS landscapes in central-interior British Columbia were dominated by old-growth forests. Natural range of variability estimates for the percentage of forested area older than 140 years are 43%–61% for the wet climate subzone and 84%–89% for the very wet climate subzone (DeLong 2007). These landscapes, however, have seen a dramatic transformation over the last 50 years. Logging, fire, and insect outbreaks have reduced the proportion of old-growth forests in the wet climate subzone (excluding pine stands) to less than 14%, and in the moist climate subzone to less than 6% (unpublished data,

Prince George Timber Supply Area - Landscapes Objectives Working Group, B.C. Ministry of Agriculture and Lands, March 2005). The situation for old-growth pine forests is even more dramatic, with most mature pine stands having been killed by the recent mountain-pine beetle outbreak (Aukema et al. 2006). Thus, alder forests, which dominate in riparian zones along small streams in the SBS, may represent an important refugium for old-growth dependent canopy lichen species and source of propagules for future colonization of surrounding forests. We would recommend that greater consideration be given to the conservation of alder-dominated riparian forests along small streams and watercourses in montane and interior plateau landscapes of British Columbia.

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References

- Antoine, M.E. 2004. An ecophysiological approach to quantifying nitrogen fixation by *Lobaria oregana*. *Bryologist*, **107**(1): 82–107. doi:10.1639/0007-2745(2004)107[82:AEATQN]2.0.CO;2.
- Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A., and Taylor, S.W. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography*, **29**(3): 427–441. doi:10.1111/j.2006.0906-7590.04445.x.
- B.C. Ministry of Forests and Range (Victoria, B.C.). Biogeoclimatic ecosystem classification program. Available from www.for.gov.bc.ca/HRE/becweb [accessed 21 September 2009].
- Benedict, J.B. 1990. Lichen mortality due to late-lying snow: Results of a transplant study. *Arct. Alp. Res.* **22**(1): 81–89. doi:10.2307/1551722.
- Bramble, W.C., and Byrnes, W.R. 1972. A long-term ecological study of game food and cover on a sprayed utility right-of-way. *Purdue University Agricultural Experimental Station of Research Bulletin*, **885**: 1–20.
- Bramble, W.C., and Byrnes, W.R. 1983. Thirty years of research on development of plant cover on an electric transmission right-of-way. *Journal of Arboriculture*, **9**: 67–74.
- Bratton, S.P., Haperman, J.R., and Mast, A.R. 1994. The lower Susquehanna River Gorge and floodplain (USA) as a riparian refuge for vernal forest-floor herbs. *Conserv. Biol.* **8**(4): 1069–1077. doi:10.1046/j.1523-1739.1994.08041069.x.
- Campbell, J., and Fredeen, A.L. 2004. *Lobaria pulmonaria* abundance as an indicator of macrolichen diversity in Interior Cedar-Hemlock forests of east-central British Columbia. *Can. J. Bot.* **82**(7): 970–982. doi:10.1139/b04-074.
- Coxson, D.S., and Stevenson, S.K. 2007. Growth rate responses of *Lobaria pulmonaria* to canopy structure in even-aged and old-growth cedar-hemlock forests of central-interior British Columbia, Canada. *For. Ecol. Manage.* **242**(1): 5–16. doi:10.1016/j.foreco.2007.01.031.

- DeFerrari, C.M., and Naiman, R.J. 1994. A multiscale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *J. Veg. Sci.* **5**(2): 247–258. doi:10.2307/3236157.
- DeLong, S.C. 1998. Natural disturbance rate and patch size distributions of forests in Northern British Columbia. *Northwest Sci.* **72**: 35–48.
- DeLong, C. 2007. Implementation of natural disturbance-based management in northern British Columbia. *For. Chron.* **83**: 338–346.
- Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* **67**: 345–366.
- Dwire, K.A., and Kauffman, J.B. 2003. Fire and riparian ecosystems in landscapes of the western USA. *For. Ecol. Manage.* **178**(1-2): 61–74. doi:10.1016/S0378-1127(03)00053-7.
- Gauslaa, Y., Palmqvist, K., Solhaug, K.A., Holien, H., Hilmo, O., Nybakken, L., Myhre, L.C., and Ohlson, M. 2007. Growth of epiphytic old forest lichens across climatic and successional gradients. *Can. J. For. Res.* **37**(10): 1832–1845. doi:10.1139/X07-048.
- Giordani, P. 2006. Variables influencing the distribution of epiphytic lichens in heterogeneous areas: A case study for Liguria, NW Italy. *J. Veg. Sci.* **17**(2): 195–206. doi:10.1111/j.1654-1103.2006.tb02438.x.
- Goward, T. 1999. The lichens of British Columbia Part 2 – Fruticose species. Research Program Ministry of Forests, Victoria, B.C.
- Goward, T., and Arsenault, A. 1997. Notes on the assessment of lichen diversity in old-growth Engelmann Spruce – Subalpine Fir forests. *In* Sycamore Creek silvicultural systems project: Workshop Proceedings, 24–25 April 1996, Kamloops, B.C. pp. 67–78.
- Goward, T., and Arsenault, A. 2000a. Cyanolichens and conifers: implications for global conservation. *For. Snow Land. Res.* **75**: 303–318.
- Goward, T., and Arsenault, A. 2000b. Inland old-growth rain forests: Safe havens for rare lichens? *In* Proceedings of a conference on the Biology and management of species and habitats at risk, 15–19 February 1999, Kamloops, B.C. p. 759–766.
- Goward, T., and Arsenault, A. 2000c. Inland The Drip Zone Effect: New Insights Into the Distribution of Rare Lichens. *In* Proceedings of a conference on the Biology and management of species and habitats at risk, 15–19 February 1999, Kamloops, B.C. p. 767–768.
- Goward, T., and Spribille, T. 2005. Lichenological evidence for the recognition of inland rainforests in western North America. *J. Biogeogr.* **32**(7): 1209–1219. doi:10.1111/j.1365-2699.2005.01282.x.
- Goward, T., McCune, B., and Meidinger, D. 1994. The lichens of British Columbia Part I – Foliose and squamulose species. Research Program Ministry of Forests, Victoria, B.C.
- Hajek, J., Bartak, M., and Gloser, J. 2001. Effects of thallus temperature and hydration on photosynthetic parameters of *Cetraria islandica* from contrasting habitats. *Photosynthetica*, **39**(3): 427–435. doi:10.1023/A:1015194713480.
- Hauck, M., Hesse, V., and Runge, M. 2002. The significance of stemflow chemistry for epiphytic lichen diversity in a die-back affected spruce forest on Mt. Brocken, Northern Germany. *Lichenologist*, **34**(5): 415–427. doi:10.1006/lich.2002.0415.
- Hylland, K., Dynesius, M., Jonsson, B.G., and Nilsson, C. 2005. Substrate form determines the fate of bryophytes in riparian buffer strips. *Ecol. Appl.* **15**(2): 674–688. doi:10.1890/04-0570.
- Jovan, S., and McCune, B. 2004. Regional variation in epiphyte macrolichen communities in northern and central California forests. *Bryologist*, **107**(3): 328–339. doi:10.1639/0007-2745(2004)107[0328:RVIEMC]2.0.CO;2.
- Kappen, L., and Breuer, M. 1991. Ecological and physiological investigations in continental Antarctic cryptogams. II. Moisture relations and photosynthesis of lichens near Cassey Station, Wilkes Land. *Antarct. Sci.* **3**(03): 273–278. doi:10.1017/S0954102091000330.
- Karström, M. 1992. Steget före — en presentasjon. *Sven. Bot. Tidskr.* **86**: 103–114.
- Kuusinen, M. 1994. Epiphytic lichen diversity on *Salix caprea* in old-growth southern and middle boreal forests of Finland. *Ann. Bot. Fenn.* **31**: 77–92.
- Kuusinen, M. 1996. Importance of spruce swamp-forests for epiphytic diversity and flora on *Picea abies* in southern and middle boreal Finland. *Ecography*, **19**(1): 41–51. doi:10.1111/j.1600-0587.1996.tb00153.x.
- Lange, O.L., Green, T.G., and Heber, U. 2001. Hydration-dependent photosynthetic production of lichens: what do laboratory studies tell us about field performance? *J. Exp. Bot.* **52**(363): 2033–2042. doi:10.1093/jexbot/52.363.2033.
- Marsh, J.E., and Timoney, K.P. 2005. How long must northern saxicolous lichens be immersed to form a waterbody trimline? *Wetlands*, **25**(2): 495–499. doi:10.1672/24.
- McCune, B., and Mefford, J. 1999. PC-ORD: Multivariate Analysis of Ecological Data. Version 5.01. MjM Software, Gleneden Beach, Ore.
- McCune, B., Dey, J., Peck, J., Heiman, K., and Will-Wolf, S. 1997. Regional gradients in lichen communities of the Southeast United States. *Bryologist*, **100**: 145–158.
- McCune, B., Hutchinson, J., and Berryman, S. 2002. Concentration of rare epiphytic lichens along large streams in a mountainous watershed in Oregon, U.S.A. *Bryologist*, **105**(3): 439–450. doi:10.1639/0007-2745(2002)105[0439:CORELA]2.0.CO;2.
- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. Special Report Series 6. Research Branch, Ministry of Forests, Victoria, B.C.
- Meilleur, A., Veronneau, H., and Bouchard, A. 1994. Shrub communities as inhibitors of plant succession in Southern Quebec. *Environ. Manage.* **18**(6): 907–921. doi:10.1007/BF02393620.
- Mundfrom, D.J., Perrett, J.J., Schaffer, J., Piccone, A., and Roozeboom, M. 2006. Bonferroni adjustments in tests for regression coefficients. *Multiple Linear Regression Viewpoints*, **Vol. 32**. American Educational Research Association's Special Interest Group on Multiple Linear Regression: The General Linear Model. Northern Illinois University, DeKalb, Ill. pp. 1–6.
- Naiman, R.J., Decamps, H., and Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecol. Appl.* **3**(2): 209–212. doi:10.2307/1941822.
- Neitlich, P.N., and McCune, B. 1997. Hotspots of epiphytic lichen diversity in two young managed forests. *Conserv. Biol.* **11**(1): 172–182. doi:10.1046/j.1523-1739.1997.95492.x.
- Niering, W.A., Dreyer, G.D., Egler, F.E., and Anderson, J.P., Jr. 1986. Stability of a *Viburnum lentago* shrub community after 30 years. *Bull. Torrey Bot. Club*, **113**(1): 23–27. doi:10.2307/2996230.
- Öckinger, E., Niklasson, M., and Nilsson, S.G. 2005. Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capacity or habitat quality? *Biodivers. Conserv.* **14**(3): 759–773. doi:10.1007/s10531-004-4535-x.
- Okland, R.H., Rydgren, K., and Okland, T. 2003. Plant species composition of boreal spruce swamp forests: closed doors and windows of opportunity. *Ecology*, **84**(7): 1909–1919. doi:10.1890/0012-9658(2003)084[1909:PSCOBS]2.0.CO;2.
- Peterson, E.B., and McCune, B. 2003. The importance of hotspots for lichen diversity in forests of western Oregon. *Bryologist*, **106**(2): 246–256. doi:10.1639/0007-2745(2003)106[0246:TIOHFL]2.0.CO;2.

- Radies, D.N., and Coxson, D.S. 2004. Macrolichen colonization on 120–140 year old *Tsuga heterophylla* in wet temperate rainforests of central-interior British Columbia: a comparison of lichen response to even-aged versus old-growth stand structures. *Lichenologist*, **36**(3–4): 235–247. doi:10.1017/S0024282904014227.
- Ruchty, A., Rosso, A., and McCune, B. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. *Bryologist*, **104**(2): 274–281. doi:10.1639/0007-2745(2001)104[0274:CIECAT]2.0.CO;2.
- Rykken, J.J., Moldenke, A.R., and Olson, D.H. 2007. Headwater riparian forest-floor invertebrate communities associated with alternative forest management practices. *Ecol. Appl.* **17**(4): 1168–1183. doi:10.1890/06-0901. PMID:17555226.
- Sillett, S.C., McCune, B., Peck, J.E., and Rambo, T.R. 2000. Four years of epiphyte colonization in Douglas-fir forest canopies. *Bryologist*, **103**(4): 661–669. doi:10.1639/0007-2745(2000)103[0661:FYOECI]2.0.CO;2.
- Snäll, T., Pennanen, J., Kivistö, L., and Hanski, I. 2005. Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos*, **109**(2): 209–222. doi:10.1111/j.0030-1299.2005.13616.x.
- Sonesson, M., Osborne, C., and Sandberg, G. 1994. Epiphytic lichens as indicators of snow depth. *Arct. Alp. Res.* **26**(2): 159–165. doi:10.2307/1551779.
- Sundberg, B., Palmqvist, K., Esseen, P.A., and Renhorn, K.E. 1997. Growth and vitality of epiphytic lichens. II. Modelling of carbon gain using field and laboratory data. *Oecologia (Berl.)*, **109**(1): 10–18. doi:10.1007/s004420050052.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**: 1176–1179.
- ter Braak, C.J.F., and Smilauer, P. 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, Ithaca, New York.
- Wang, T., Hamann, A., Spittlehouse, D., and Aitken, S.N. 2006. Development of scale-free climate data for western Canada for use in resource management. *Int. J. Climatol.* **26**(3): 383–397. doi:10.1002/joc.1247.

Appendices

Appendix A and Appendix B appear on the following page.

Appendix A. Inter-set correlations for the environmental variables stream width (SW), age of adjacent conifer (AGE), slope perpendicular to stream (SL), canopy cover (COV), stem density (DEN), abundance of stems >10 cm dbh (AB), mean annual temperature (TEMP), and mean annual precipitation (PREC) used in the site level CCA analyses, with canonical coefficient and *t* values provided for regression coefficients (on each canonical axis) for variables identified as significant through forward selection.

Environmental variables	Inter- set correlations								Canonical coefficients				<i>t</i> values			
	SW	AGE	SL	COV	DEN	AB	TEMP	PREC	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
SW	1.0000															
AGE	-0.0560	1.0000							0.4859	-0.0734	0.5895	0.6665	4.1952	-0.5397	3.7564	2.8048
SL	0.0112	0.0814	1.0000													
COV	-0.2742	0.0814	-0.0149	1.0000												
DEN	-0.1160	0.1091	0.0555	-0.1575	1.0000				-0.3295	0.4302	-0.486	0.7333	-2.7989	3.1131	-3.0464	3.0359
AB	0.0136	0.1107	0.0238	-0.0143	-0.0237	1.0000										
TEMP	0.1763	-0.1262	0.0829	-0.0993	-0.0150	0.2189	1.0000		0.2078	0.8533	0.6219	-0.3925	1.592	5.5699	3.5164	-1.4655
PREC	-0.0014	0.2065	0.0669	-0.2536	0.2890	0.1873	0.4009	1.0000	0.6571	-0.1736	-0.8985	0.0148	5.1185	-1.1523	-5.1652	0.0563

Appendix B. Inter-set correlations for the environmental variables stem diameter (SD), angle of stem lean (ANGLE), direction of stem lean (DIR), % bark cover (BARK), and percent moss cover (MOSS) used in the stem level CCA analyses of the moist, wet, and very wet subzones, with canonical coefficient and *t* values provided for regression coefficients (on each canonical axis) for variables identified as significant through forward selection.

Variables by subzone	Inter-set correlations					Canonical coefficients			<i>t</i> values		
	SD	ANGLE	DIR	BARK	MOSS	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Moist subzone											
SD	1.0000					0.7986	0.1673	-0.3713	12.4966	1.2803	-0.2418
ANGLE	-0.0943	1.0000				0.1515	-0.2963	-0.6262	2.6087	-2.4958	-4.6069
DIR	0.0284	0.0365	1.0000								
BARK	0.0465	0.0310	-0.0388	1.0000							
MOSS	0.3785	-0.0546	0.0060	0.0016	1.0000	-0.0804	0.4846	-0.2181	-1.2824	3.7809	-1.4861
Wet subzone											
SD	1.0000					0.3349	-0.9328	0.0878	-14.0334	-13.8192	0.042073
ANGLE	-0.0932	1.0000				0.3282	-0.3266	-0.4624	9.365914	2.212611	-0.16008
DIR	0.0166	-0.0302	1.0000								
BARK	0.0614	-0.0197	0.0768	1.0000							
Very wet subzone											
SD	1.0000					-0.4109	0.2778	-0.7539	-6.0188	2.6588	-5.7311
ANGLE	-0.1531	1.0000				0.2499	0.2075	0.0696	3.6821	1.9973	0.5323
DIR	-0.0199	-0.0234	1.0000								
BARK	0.0722	-0.0847	0.0037	1.0000							
MOSS	-0.0848	0.1623	0.0968	0.0053	1.0000	0.4101	0.8028	0.0166	6.0382	7.7223	0.1267
SD	1.0000					-0.4109	0.2778	-0.7539	-6.0188	2.6588	-5.7311