Patterns of bryophyte and lichen diversity in interior and coastal cedar-hemlock forests of British Columbia.

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Rich cyanolichen community in an inland rainforest, Upper Adams river valley, British Columbia

Abstract

This project examined the patterns of bryophyte and lichen diversity in cedar-hemlock forests of interior and coastal British Columbia. Our study provides a better understanding of the distribution ecology of bryophytes and lichens, and of the relationship between sensitive species and their habitat and offers insight that can be used to minimize the impact of forestry operations on biological diversity.

We investigated the patterns of lichen and bryophyte diversity at three scales of ecosystem organization: 1) at a within-stand scale examining microdistributional ecology of species on various substrates; 2) at a meso-scale focussing on differences in species distribution and abundance in forests of different ages; and 3) at broader geographical scales assessing landscape and regional differences in species composition and developing predictive tools for the distribution of cyanolichens. Our work mainly took place in the ICHmw, ICHwk, and ICHvk subzones of the Kamloops Forest Region and in the CWHvm subzone of the Vancouver Forest Region. Our studies on the distribution of cyanolichens on conifers also included information from various regions of the Northern Hemisphere.

We found that many factors affect the patterns of bryophyte and lichen diversity in ICH and CWH forests. At a small scale the type and number of microhabitats are an important predictor of the number and type of species present. For example, conifer trees influenced by nearby *Populus* trees often have circumneutral bark pH and are strongly correlated with cyanolichen diversity. Other important habitats for bryophytes and lichens include include large rotten logs, and large leaning trees and snags . At the stand level, the number of species of bryophytes and lichens is consistently higher in old-growth forests compared to young forests in both the Interior Cedar-Hemlock Zone and in the Coastal western Hemlock Zone. However, this relationship between species diversity and stand age is complex and will vary for certain groups of species across ecological gradients. For example old cedar-hemlock stands in the inland rainforests located on toe slope positions contain unique assemblages of epiphytic lichens, many of which are rare or infrequent, that are not found on adjacent old-growth forests located on mid-slope positions in the same biogeoclimatic variant. These findings clearly show that ecosystem representation at a finer scale than the biogeoclimatic variant is essential for the designation of old-growth management areas to minimize the loss of biological diversity in managed landscapes. Our data also clearly shows that no single stand management practice will satisfy the requirements of all sensitive lichens and bryophytes.

Our detailed comparisons of macrolichen, Calicioid lichen, and bryophyte diversity in old and young unmanaged forests is unparalleled elsewhere in British Columbia and complements work comparing old-growth and young managed forests in other forests of the world. Some of our work is not only contributing to knowledge on the distribution ecology of cyanolichens in British Columbia but is also providing new insights into patterns observed at the scale of the Northern Hemisphere. We have presented our results in many operational forestry meetings, public meetings, provincial and international scientific conferences, peer reviewed Journal and Proceeding papers. Some of our findings have already assisted the land use planning in the Kamloops Forest Region.

Introduction

Bryophytes and lichens although relatively small in size form a significant component in many forest ecosystems. In addition to their large biomass and valuable role in ecosystem function (i.e. biogeochemical cycles) bryophytes and lichens represent a large portion of forest biodiversity. Several species of bryophytes and lichens (particularly epixylics; species growing on wood) are dependent upon old-growth forests for their survival. The conversion of a large proportion of the landbase to second-growth forests may eventually result in the loss of these species. A better understanding of the patterns of bryophyte and lichen diversity, and of the relationship between sensitive species and their habitat, will provide a rare opportunity to minimize the impact of forestry operations on biodiversity.

The importance of bryophytes and lichens in British Columbia is considerable. With over 850 species of mosses and hepatics, the province's bryoflora is one of the richest in North America and contains the largest percentage of endemic species and genera on the continent. The Coastal Western Hemlock Zone (CWH) is characterized by extraordinary bryophyte richness (Schofield 1988) and contains the majority of Western North American endemic species and genera. Many of the species that grow in this zone are unknown elsewhere in Canada.

British Columbia is also home to an estimated 1600 lichens and many new species await discovery. They are amongst the most poorly documented macroscopic flora of British Columbia (Goward 1994). Many lichens are sensitive to environmental changes and have been used successfully as bioindicators of air quality. Lichens like bryophytes lack root systems and species often have developed a close relationship with substrate type. Antique cedar-hemlock stands in both the coastal and inland rainforests contain unique assemblages of epiphytic lichens. A detailed analysis and comparison of the patterns of species diversity and of species-habitat relationships in coastal and interior cedar-hemlock forests will provide information which will be useful in the development of strategies for the conservation of bryophytes and lichens in managed forest landscapes of British Columbia.

Few studies have examined bryophyte community structure and its relation to substrata in forests of British Columbia. In a study of patterns of bryophyte diversity in old-growth temperate forests of British Columbia I found that despite considerable variation, the species-substratum association was significant at the community level (Arsenault 1995). Species could be divided into two main groups related to woody vs. non woody substrates. Species growing on wood could be arranged along a successional gradient reflecting the various decay stages of wood. This chronosequence has also been described in temperate deciduous forests of North America and Europe (Jovet and Jovet 1944; Shuster 1949; Muhle and Leblanc 1975) and in the boreal forests of Sweden (Soderstrom 1988). This influence of forest structure on the bryophyte community may have serious management implications. Few studies have examined changes in bryophyte community structure following forest harvesting. Soderstrom (1988) demonstrated that the occurrence of epixylic (wood) hepatics decreased in managed forest stands, and that differences in species occurrence with old-growth stands could be related to humidity and the availability of logs in different stages of decay. Managed stands are more frequently exposed to drought and have uneven supply of logs in different stages of decay. Similarly a study in Montana showed that hepatics on logs in old-growth stands were more diverse than in second-growth forests (Lessica et al. 1991).

In forest ecosystems, lichens growing on wood or adapted to unique old-growth conditions are the most susceptible to changes resulting from forest harvesting. Cyanolichens and crustose caliciales appear particularly sensitive to forestry practices. In a survey of deciduous woodlands in the British Isles, Rose (1976) found a positive correlation between lichen diversity and forest age. He introduced the idea that lichens could be used as historical indicators. Old-growth dependent lichens are mostly epiphytic and since Roses' work several other investigators have discovered old-growth dependent lichens throughout the world (Selva 1994; Lessica et al. 1991; Tibell 1992; Goward,1994). Goward (1994) proposed two hypotheses to explain why older forests have higher epiphytic lichen species diversity. The first hypothesis suggests that environmental conditions in the past were more favourable to lichen colonization than they are at present, while the second hypothesis proposes that lichen diversity is simply higher in older forests as a result of a longer period of environmental continuity. In British Columbia evidence suggests that differences in epiphytic lichen communities not only exist between second-growth and old-growth forests but can also be found between old-growth and antique forests (“old old-growth”). This distinction is important because at present landscape planning does not distinguish between different categories of old-growth. The possibility that old-growth or antique dependent lichens disappear due to forest harvesting before their species are even described exists. It is our responsibility to make a stronger effort in the documentation of lichens and their ecology to find positive solutions that will ensure their survival and maintain successful forestry operations in British Columbia.

General Objectives

1. Compare the patterns of bryophyte and lichen diversity of coastal and interior cedar-hemlock forests of different age.

2. Develop species concepts for undescribed lichens (mostly crustose lichens like the Calciales) inhabiting coastal and interior cedar-hemlock forests.

3. Compare bryophyte and lichen species-habitat relationships in interior and coastal cedar-hemlock forests of different ages.

4. Compare the floristic composition and affinities between the coastal and interior rainforest bryophyte and lichen floras.

Our studies on lichen and bryophyte diversity were organized into the following ten main themes:

Theme 1. Pattern of lichen diversity in young and old forests

The primary objectives of this project were: 1) to capture trends in macrolichen and calicioid diversity and distribution in old and young ICH and CWH forests of southern British Columbia, with emphasis on oldgrowth-dependency; and 2) to correlate these trends to stand age and other potentially controlling environmental factors, and 3) to provide tentative recommendations for the maintenance of lichen diversity in managed forests.

Theme 2. The *Populus* dripzone effect

The objectives of this project were three-fold: 1) to document cyanolichen microdistribution over conifer branches in young conifer forests in inland British Columbia; 2) to establish whether a correlation exists between cyanolichen colonization of conifers and proximity to Populus; and 3) assuming such a correlation does exist, to propose a hypothesis by which to account for it.

Theme 3. Predictive tool for cyanolichen diversity

In this project, we attempted to contribute to a basic understanding of cyanolichen distributional ecology in intermontane British Columbia. Our specific objectives are: 1) to summarize the most important environmental factors promoting cyanolichen diversity in inland forests; and 2) to propose a simple method by which cyanolichen diversity can be reliably predicted at an operational scale, based on readily available information.

Theme 4. Regional and global distribution of cyanolichen diversity on conifers

The objectives of this project were threefold: first to conduct a detailed survey of the occurrence of epiphytic cyanolichens in the forests of British Columbia; second to contrast the resulting patterns, especially with respect to conifers, with corresponding patterns in other regions of the world at similar latitudes; and third, to organize these observations into a summarizing hypothesis regarding circumpolar epiphytic cyanolichen distribution.

Theme 5. Evaluating floristic habitat sampling versus plot sampling for determining bryophyte species diversity

This project contrasted patterns of bryophyte diversity, using Floristic Habitat Sampling (FHS) and traditional plot sampling (PS) techniques in the same study area. More specifically this projects addresses the questions, 1) Are there differences in bryophyte diversity using FHS or PS within only the forest mesohabitats? 2) What are the differences bryophyte diversity using FHS or PS for all mesohabitat types found within temperate rainforest stands? 3) Are the patterns of diversity similar for both sampling techniques? and 4) What are the relationships between sampling intensity, area, and diversity for different mesohabitats using FHS?

Theme 6. Bryophyte communities of ICH and CWH forests

This study compares the community composition of the ICH and CWH biogeoclimatic zones. The objectives of this study are to determine 1) which environmental factors are associated with bryophyte vegetation patterns in cedar-hemlock forest, 2) the definable relationships between stands, species and environmental variables if all ICH and CWH stands are considered, 3) the floristic, taxonomic or morphologic affinities associated with bryophyte vegetation patterns in the CWH and ICH, 4) what are the indicator species for the ICH and CWH, and do these biogeoclimatic zones have the same indicator species for young and old-growth forests.

Theme 7. Assessing patterns of bryophyte diversity in cedar-hemlock forests of southern British Columbia

This project compared patterns of bryophyte diversity in young and old forests of the ICH and CWH. More specifically our objectives were to 1) determine if bryophyte diversity changes following stand replacing disturbances in the ICH and CWH, 2) assess whether a stand classification built on species composition will adequately partition species richness, 3) analyse the pattern of bryophyte diversity and its relationship with environmental variables at a regional scale, 4) assess whether a discriminate model of regional diversity can predict species richness given a set of environmental variables for the ICH or CWH.

Theme 8. Quantifying the influence of the number and type of mesohabitat on bryophyte diversity

The purpose of this study is to investigate the patterns of bryophyte diversity in cedar-hemlock forest mesohabitats. Specifically, the objectives of this study are to determine 1) how bryophyte diversity is distributed across the different mesohabitat types within similar large scale disturbances, and biogeoclimatic zones 2) what the environmental variables effect patterning of species richness in mesohabitats, 3) within individual mesohabitat types, what the factors are that influence bryophyte diversity, 4) How species are associated with one another in a given mesohabitat, 5) What are the mesohabitat requirements of old-growth indicator species within the interior cedar-hemlock (ICH) or coastal western hemlock (CWH).

Theme 9. The influence of microhabitats on bryophyte diversity
This study addressed the following questions regarding the relationship between microhabitats and bryophyte diversity.
1) Do microhabitats have variable species richness, species communities and indicator value?
2) Are their temporal differences (different age classes) in the patterning of bryophyte diversity on microhabitats within either the ICH or CWH? 3) Are there differences in the patterning of bryophyte diversity on microhabitats between biogeoclimatic zones?

Methods

The following is a general summary of the methods used during our study. A more detailed description is available in the publications listed in the next section.

Study area

The majority of our studies in inland British Columbia took place in the lower elevation forests of Wells Gray Provincial Park along a north south gradient between the Murtle Plateau and Azure Lake, and in the Upper Seymour river and Upper Adams river valleys. We sampled in a range of sites in the ICHmw3, ICHwk1, and ICHvk1 biogeoclimatic Variants. Our work in coastal British Columbia mainly took place in the lower elevation forests of the Capilano river and Seymour river valleys near Vancouver. The bryophyte project also included portions of the following watersheds on Vancouver Island: Clayoquot river , Sidney river, Toffino river, and Walbran river. The majority of the stands studied belonged to the CWHvm1 biogeoclimatic variant.

Forest stand description

In each of the selected stands, we established a circular plot 20 m in diameter. A soil profile was described within each plot, and all vascular plants were assessed for percent cover. Standing trees greater than 1 cm dbh and snags (standing dead trees) greater than 10 cm dbh were also recorded using the methods given in Arsenault & Bradfield (1995). For trees between 1 cm and 10 cm dbh, two cross-sections were collected for representative trees of each tree species; these were stored for later dendrochronological analysis. Trees greater than 10 cm dbh were cored at 30 cm height.

Fallen trees greater than 10 cm dbh were measured at 1.3 m above the root collar, and were evaluated for decay class, cause of death and, in the case of uprooted trees, orientation. Fallen trees rooted outside the plot were measured at their largest diameter within the plot and evaluated for decay class. Coarse woody debris was assessed along two 50 m transects, with measurements taken on size and structural class (Arsenault & Bradfield 1995).

Notes on several additional site characteristics were also taken: aspect, slope, elevation, biogeoclimatic variant (Lloyd et al. 1990), mesoslope position, and hygrotope. Percent covers were also recorded for various forest layers, including the moss, herb, shrub, sapling, understory tree, and canopy tree layers.

Lichen sampling approach

Macrolichen frequency and/or abundance was recorded using a five-point frequency/abundance scale (See below). A detailed explanation of the rationale behind our decision to adopt this scale is given in Goward & Arsenault (1997).

Unit	Description
1	2 or fewer colonies per trunk (and associated branches) for epiphytic species, or per 16m2 for terricolous species
2	3-5 colonies per tree or per 16m2
3	6 colonies as above, or up to 20% cover (under optimum conditions)
4	from 21% to 50% cover (under optimum conditions)
5	51% cover or greater (under optimum conditions)

Macrolichens were recorded on a variety of substrates during our studies. For example during our study comparing lichen diversity in young and old forests of Wells Gray Park we studied the distribution of macrolichens for 21 substrate units distributed among living trees, snags, shrubs, and the forest floor. The specific substrates investigated were: 1) branches and trunks of *Thuja*; 2) branches and trunks of *Populus trichocarpa*; 3) branches and trunks of *Betula*, *Pinus*, and *Pseudotsuga* -- all early successional trees with acid bark; 4) branches and trunks of *Abies* and *Picea* -- both early to late successional species with acid bark; 5) trunk bases of conifers excluding *Tsuga*, 6) live saplings excluding *Tsuga*; and 7) conifers occurring within the drip zone of old *Populus trichocarpa*. In addition, *Tsuga* -- the most common tree species in our plots -- was subdivided into five substrate units: 8) root collar; 9) trunks; 10) young, living branches; 11) old, dead branches; 12) saplings; and 13) shrubs. Other substrates included: 14) dead decorticated saplings, 15) snags (defined as dead decorticated trees greater than 1 m tall and 15 cm dbh); 16) ground; 17) mossy rock; 18) logs without bark; 19) logs with bark; 20) stumps; and 21) tip-up mounds.

In order to assess the extent to which our plots captured total lichen diversity within the stands, we also conducted more general "walk-abouts" outside the plots. Here we recorded any species not previously recorded in the adjacent plot. The walk-abouts varied somewhat in extent, depending on the area of the available stand, but in general measured approximately 40 m wide by 150 m long. (The rectilinear shape reflects our effort to examine only the "toe" topographic position, which tends to form a narrow band at the base of hillslopes). They were restricted to stands similar to the adjacent plot in age and, to a large extent, hygrotopic position. Some variation in soil moisture regime was tolerated, though forests located over mesic or xeric soils were excluded. Each plot required about eight hours to perform, i.e., 4 hours for the basic survey, and another 4 hours for the walk-about.

Calicioid lichens

Initially we adopted circular plots 20m in diameter as our basic sampling unit. This approach was well suited for our study of macrolichens (for further details, see Arsenault & Goward, in prep.), but proved unsatisfactory for calicioid species, which tend to require highly specific microniches (Rikkinen 1995), and hence are more stochastic in distribution. We therefore abandoned circumscribed plots in favour of more informal "walkabouts", in which the size of the sampling area is dictated both by the availability of suitable habitat and by a maximum sampling effort of four hours. As calicioid species are often difficult to identify in the field, no attempt was made to quantify their abundance; they were recorded as simply present or absent and the substrate over which they occurred were noted.

Bryophyte sampling approach

A stand is defined as a standing growth of trees with similar physiognomy. In this study, stands are defined by the dominant tree species, its age, structure, elevation, slope position, and aspect. They consist of a mosaic of dominant and restricted mesohabitats on the landscape. In each stand, one mesohabitat represents the dominant mesohabitat (the forest), and encloses numerous restricted mesohabitats (e.g., cliffs, streams).

This study expands on the sampling methodology used by Belland & Brassard (1988) and Belland & Vitt (1995). It incorporates forest stands and their mesohabitats to present a complete biodiversity analysis. For discussion this method is termed, *floristic habitat sampling* (FHS). FHS is similar to a floristic survey since it provides a method that records all species within a study area. The stand is the plot and mesohabitats are the sampling units. This method differs from plots in several respects 1) Plots are bounded by a relatively small sampling area; FHS is bounded by the actual stand, 3) plots are used for vegetation classification or population and community dynamics; FHS is ideal for biodiversity studies. FHS provides an extensive list of species and habitat characteristics, from which many ecological and environmental questions can be answered.

FHS is completed after all the potential mesohabitats and microhabitats have been identified. This is accomplished by systematically walking a grid of transects through the study area. The sampling units are the mesohabitats/microhabitats, and sampling is completed in the following two steps:

1) List all the species for each microhabitat (See table 1) that occurs within the dominant forest mesohabitat. An example of this would be recording all the bryophyte species that occur on rocks (one microhabitat), and on the forest floor. New microhabitats (e.g., logs) are surveyed until all the microhabitats within the dominant mesohabitat are thoroughly sampled. Adequately sampled means that, microhabitats (e.g., rocks) are examined until no new species are recorded
2) Sample all restricted mesohabitats and list all the species and microhabitats for each type of restricted mesohabitat (i.e., stream, cliff, seep, waterfall).

PS can be completed after a centre point and 20 m sampling unit boundaries are located within the stand. All the species and their percent cover within a 20 m diameter circular plot are recorded.

Table 1. Description of microhabitats and mesohabitats used for recording the distribution and abundance of bryophytes.

Microhabitat	DMH	RMH			
	Forest	Cliff	Stream	Water	Seep
Coniferous tree species	x	x	x	x	x
Deciduous tree species	x	x	x	x	x
Size of tree (10-25 cm dbh, 30-60 cm dbh, > 70 cm DBH)	x	x	x	x	x
Position on tree (trunk or base - 50 cm above tapered bowl)	x	x	x	x	x
Snag (dead coniferous or deciduous trees)	x	x	x	x	x
Twig (CWD < 10 cm diam.)	x	x	x	x	x
Log size (10-30 cm, 30-60 cm dbh, > 70 cm DBH)	x	x	x	x	x
Log decay class (D1,D3 or D5 – CWD codes)	x	x	x	x	x
Organic soils (LFH)	x	x	x	x	x

Mineral soil (sand, silt, loam, clay)	x	x	x	x	x
Moist depression (small isolated pools of water/mud)	x	x	x	x	
Intermittent stream (narrow and ephemeral)	x	x			x
Rock (sample type, pH)	x	x	x	x	x
Tree stump	x	x	x	x	x
Upturned tree roots ("tip-up")	x	x	x	x	x
Adjacent bank (sand, silt, clay, loam, gravel, cobble, rock)	x	x	x	x	x
Submerged habitat (rocks or logs)			x	x	x
Shallow bars (sand, silt, clay, loam, gravel or cobble; dry/wet)			x		
Waterfall (< 1 m, 1-2 m, 2-5 m, 5-10 m, >10 m)			x	x	
Depth (< 10 cm, 10-30 cm, > 30 cm)			x		
Rapid (flow rate (m/second))			x	x	
Crevice (horizontal/vertical; < 5 cm, .5-1 m, > 1m; wet/dry; seepage, soil cover, sand, silt, clay, loam)		x	x	x	
Ledges (size, wet/dry, seepage, soil covered)		x	x	x	
Caves (size, wet/dry, seepage)		x	x	x	
Vertical rock face (size, wet/dry, seepage)		x	x	x	
Talus		x	x	x	
Rock surface (rough/smooth)		x	x	x	

Sample size and plot locations

Floristic habitat sampling (FHS) and plot sampling (PS) were used to assess patterns of diversity in cedar-hemlock rainforests over two field seasons. In 1996, 104 stands were sampled in the interior cedar-hemlock (ICH) biogeoclimatic zone. Stands were chosen from the Wells Gray, upper Adams River, and Seymour watersheds. Within these watersheds, sampling was evenly distributed between stands that were burned approximately 80 years ago, and old growth stands of 250+ years in age. In 1997, 185 stands were sampled in the coastal western hemlock biogeoclimatic zone (CWHvm1). Stands were chosen from the Capilano and Seymour watersheds along the mainland coast and in the Sidney, Clayoquot, Tofino, and Walbran watersheds along the western coast of Vancouver Island. Extensive logging activities in the Capilano and Seymour watersheds allowed balanced sampling among stands that were burned approximately 80 years ago, stands that were logged 80 years ago, and old growth stands (>250 years). Sampling on Vancouver Island was limited to older stands due to the relatively recent logging activity and lack of fire history.

Sampling within a stand was influenced by time, space, and by natural stand or habitat boundaries. Fourteen hours (maximum) was spent at each stand, within each stand, the circular plot was used as the starting point for collecting species data from microhabitats using FHS. Only the restricted mesohabitats within a one km radius of the plot were sampled. Sampling continued in the stand until all mesohabitats and microhabitats had been thoroughly sampled. Recording in this manner facilitated a comparison of the data from PS and FHS. In restricted mesohabitats, sampling was conducted in successively larger areas to quantify the relation of plot size to species richness. Sample areas started at one square metre, and increased in size for seven areas (i.e., 1 m^2, 2 m^2, 4 m^2, 16 m^2, 64 m^2, 144 m^2, >400 m^2).

Species abundance was recorded for each microhabitat within the dominant forest mesohabitat. Abundance was measured on a scale of one to three following Vitt et al. (1995): 1) one to few occurrences, < 20% cover; 2) several occurrences to frequent in one or some areas of the micro/mesohabitat, 30-50% cover; 3) frequent throughout the micro/mesohabitat, > 70% cover.

Bark pH and chemistry
In our study of the dripzone effect of Populus on cyanolichen distribution we collected branches of conifers for chemical analysis. The branches resulting were air-dried, ground, and placed overnight in deionized water. pH readings were taken using a Fisher pH meter calibrated using buffers at pH 4.0 and pH 7.0. In addition the samples were air-dried, ground, and later subjected to the barium chloride method for exchangeable cations (Hendershot & Duquette 1989). The exchanged cations in the resulting solutions were quantified by ICAP (Inductively Coupled Argon Plasma) spectrometry.

Data analysis
We described our data structure using a variety of tools including graphical analysis, ordinations, and classifications. We interpreted our data structure by examining univariate and multivariate relationships between species composition, community attributes, and environmental variables using correlations with univariables and multivariables, Anovas, Canonical Correspondance Analysis, and regression. A general description of our data analysis is provided below. More details are available in the research publications listed in the next section.

Species Diversity
Several indices of species diversity were calculated for macrolichens. These included mean species richness and total species richness, as well as the Shannon- Wiener diversity, and the Simpson Index of Dominance calculated with PC-ORD. Differences between young and old forests were tested statistically using t-tests and the number of species exclusive to one age class or the other was also computed. Finally, the contribution of the 21 substrate categories to overall macrolichen species richness as well as to species richness in specific macrolichen groups was examined. For calicioid we could only use species richness as a diversity index because the species were recorded by presence/absence only.

Bryophyte diversity was analyzed at several scales following the structure and terminology proposed by Whittaker (1972). Point diversity was calculated for British Columbia's temperate rainforest (epsilon diversity), biogeoclimatic zones, variants, watersheds and mesohabitats (gamma diversity), and stands (alpha diversity). Indices based on species richness and proportional frequencies were calculated for biogeoclimatic zones, variants, and watersheds for stands stratified by disturbance (logging, fire, old growth). These indices were chosen because of their use of species richness (S), number of individuals (N), mean species richness (α), and their suitability to well-sampled communities (Magurran 1988). Indices were calculated using Krebs/WIN (Krebs 1997). Species richness in stands (alpha diversity) was compared using ANOVAS.

Analysis of communities
Patterns of lichen species composition were investigated using multivariate analysis. Several techniques were used, e.g. Detrended Correspondance Analysis (DCA) and Principal Components Analysis (PCA), to explore the organization of lichen communities in young and old forests. The interpretation of the ordinations involved correlating sample scores and species abundance for macrolichens and presence/absence for calicioid lichens. In addition, age classes were plotted on the ordination. Differences in community structure between young and old forests were tested using a Kruskall-Wallis test on the sample scores of the first three DCA axes.

Patterns of bryophyte community composition was explored using multivariate techniques. TWINSPAN was used to group all 417 cedar-hemlock stands according to species interactions.

Ordination techniques such as Canonical Correspondence Analysis (CCA) was used to ordinate all 287 stands using 29 environmental variables to constrain the ordination (ter Braak, 1998). The ordination generated axis scores for each stand, with the axes correlated to the most important environmental variables in the analysis. Positional variables (latitude, longitude, watershed and biogeoclimatic zone) and allogenic variables (mean annual temperature, degree days, 6 month mean temperature and rainfall) were used as covariables in the CCA analysis. TWINSPAN Stand group classifications from TWINSPAN were superimposed onto the CCA stand and species ordination. This analysis identified the species that are associated with specific stand groups and significantly correlated environmental variables.

The relative importance of an indicator species within its community was estimated using the method of Dufrêne and Legendre (1997). PC-ORD software (McCune & Mefford 1997) was used to analyze indicator values for species within each of the TWINSPAN groups. The "indicator value" combines, by multiplication, the abundance of a species in each TWINSPAN group relative to its abundance in all groups, with that species's frequency of occurrence in the sample units of the designated group. The "indicator value" describes a species' reliability for indicating a TWINSPAN group, and is expressed as a percentage of perfect indication. Monte Carlo analyses was used to asses statistical significance based on the proportion of 1,000 randomized trials that equalled or exceeded the maximum indicator value for a species.

Host Characteristics

In our analysis of the role of *Populus* on the pattern of epiphytic lichen distribution and abundance on conifers we adopted individual trees as the basic unit of comparison. For each tree species, we calculated the mean and standard deviations for the following ecological attributes: diameter at breast height (dbh), height, age, and percent of live branches within two metres of the ground, and distance to the closest *Populus*. Using Spearman rank correlation, we then analysed the relation of each of these attributes to total number of lichen species, and to total number of cyanolichens.

Bark pH

The mean and standard deviations of bark pH of *Picea* were calculated for 13 branch samples associated with *Parmeliopsis ambigua*, and 13 branch samples associated with *Lobaria pulmonaria*. Differences were assessed using a T-test. Within-tree differences were assessed on the basis of subsamples from different portions of two trees supporting both lichen species. T-tests were used to assess differences in cation concentration. Comparisons of bark pH for 40 *Picea* branch samples growing inside and 40 corresponding branch samples growing outside the dripzone of *Populus* were also assessed in the same manner. The combined effects of slope position and overstory condition were assessed using a two-way Anova.

Spatial Distribution of Epiphytic Lichens

The spatial distribution of lichen species was described in two ways. First, the frequency occurrence of each lichen species was calculated as a function of distance from the nearest *Populus*. The following five distance classes were used: 1 = 0-5 m, 2 = 6-10 m, 3 = 11-15 m; 4 = 15-20 m; and 5 = 20-25 m. Second, for 35 *Picea* trees having asymmetrical loadings of *Lobaria pulmonaria*, we calculated the discrepancy (in degrees) between the compass bearing of the *Lobaria* "node" against the compass bearing of the nearest *Populus* tree.

Analysis of regional and global distribution of epiphytic cyanolichens.

We have analysed the distributional patterns of cyanolichens in the intermontanes regions of British Columbia based largely on field studies conducted by Trevor Goward over a period of twenty years, and summarized, in part, in Goward (1994, 1995, 1996, 1999), Goward and Ahti (1992, 1997), Goward and Arsenault (1997), Goward et al. (1994), as well as in several unpublished studies undertaken in the Kamloops, Nelson, Prince George, Prince Rupert and Vancouver Forest Regions (Goward, unpublished reports). In addition, more than 40,000 herbarium specimens housed at the Canadian Museum of Nature (CANL) in Ottawa, the University of British Columbia (UBC) in Vancouver, and the University of Victoria (VC) in Victoria have been examined and mapped (Goward, in prep.). More recently, the authors have assembled quantitative data on 40 stands supporting epiphytic cyanolichens (Goward and Arsenault, in prep.); for a summary of our field methods, see Goward and Arsenault (1997).

We have further compared the distribution of epiphytic cyanolichen species on broadleaf and conifers based exclusively on herbarium material on deposit at the University of British Columbia (UBC). More specifically, we recorded substrate and distributional data for 933 specimens belonging to the *Peltigerineae* and *Lichinaceae* (sensu Tehler 1996). Our decision to limit this study to herbarium material proceeds from two assumptions concerning the representativeness of the lichen holdings at UBC. Our first assumption is that these collections accurately portray the relative frequency occurrence of cyanolichens on different trees species. Our second assumption is that they provide an accurate cross-section of cyanolichen distribution at a regional scale. Here it is pertinent to observe that lichen holdings at UBC now include a rich material of specimens collected in connection with studies specifically designed to record cyanolichen diversity and phorophyte selection (Goward, various reports and publications). Indeed, more than half of the available material has derived from such studies. For an up-to-date summary of lichen collecting localities in British Columbia, see Map 1 in Goward (1999).

We have also assembled data on the occurrence of cyanolichens on conifer branches in other parts of the world at temperate and boreal latitudes. Some of this information was gleaned from the literature, but most has been kindly supplied by colleagues specializing in epiphytic lichen ecology.

Taxonomy

Taxonomically difficult lichen specimens were collected in connection with this project. These were air dried, sorted, curated, packaged, labelled, and examined in the laboratory using a dissecting microscope, a compound microscope, and chemical reagents where appropriate. Several specimens of Caliciales were subsequently forwarded to Dr. Leif Tibell for confirmation. Voucher specimens have been deposited in the herbaria of the Kamloops Forest Region and the University of British Columbia Department of Botany (UBC). Our taxonomy and nomenclature follow Esslinger and Egan (1995) in most regards for macrolichens and Goward (1999) for calicioid lichens. Some of the collections made during this study contributed to Goward (1999).

Phytogeographic categorization follows that of Belland (Belland 1999) for mosses and Godfrey (1977) and Schofield (1988) for hepatics. Taxonomic categorization of the lineages of *Bryidae* and *Sphagnidae* follow Vitt (1984) with suborders raised to order rank; within the lineages Jungermanniales, *Metzgeriales* and *Marchantiales* follow Stotler and Crandel-Stotler (1977). Species nomenclature follows Anderson *et al.* (1990) for bryophytes and Stotler & Crandall-Stotler (1977) for Hepatics. Collections were made at each stand for common and rare species. Voucher specimens were prepared and deposited at the University of Alberta Cryptogamic Herbarium, Kamloops Forest Region Herbarium and University of British Columbia Herbarium.

Results and Discussion

Stand level comparisons

Distribution of lichens and bryophyte in young and old forests.
All of our studies have consistently recorded higher overall diversity of lichen and bryophyte species in old forests compared to young forests in the ICHmw3, ICHwk1, ICHvk1, and CWHvm1. Bryophyte diversity was approximately twice as high in old forests and increased with annual precipitation across the biogeoclimatic variants examined (Figure 1.). In the CWH, the oldest and most continuous stands (Sidney Fjord, Clayoquot and Walbran Watersheds on the west coast of Vancouver Island) had the highest bryophyte diversity. These old-growth cedar-hemlock forests have a rich flora of oceanic and suboceanic western North American endemics. 15% of the bryoflora of British Columbia is confined to western North America (Schofield 1988).

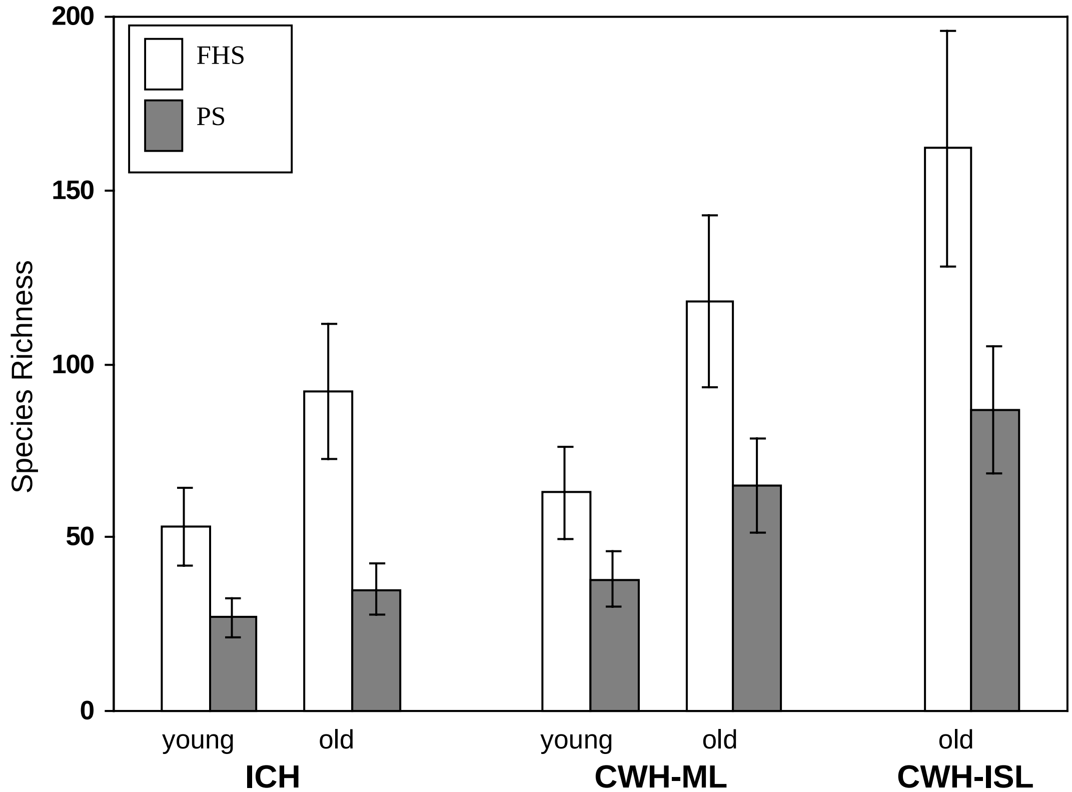

Figure 1. Alpha diversity of stands assessed using floristic habitat sampling (FHS including all mesohabitats) and plot sampling (PS) sampling. Cedar hemlock forests are divided into inland (ICH), coastal mainland (CWH-ML), coastal oceanic (CWH-ISL), and by age classes (class 4, young = 80 years and class 9, old >250 years). Error bars represent two standard errors on either side of the mean.

In the ICHmw3 of Wells Gray Provincial Park old forests were found to support a higher number of species, though mean species richness was not significantly different between the two age classes. Twenty-five species, however, were confined to old stands, as compared with eight species restricted to young stands. Epiphytic community structure was strongly correlated with precipitation in the old stands, but not in the young stands (Figure 2). Here the old-growth stands at the wetter end of our study area, near the outlet of Clearwater lake, function as range extenders (See Goward 1995) for several hygrophytic species (Figure 3) including *Graphis scripta*, *Hypogymnia oceanica*, *H. rugosa*, *H. vittata*, *Parmelia pseudosulcata*, *Platismatia norvegica*, *Sphaerophorus globosus*, and *S. tuckermanii*.

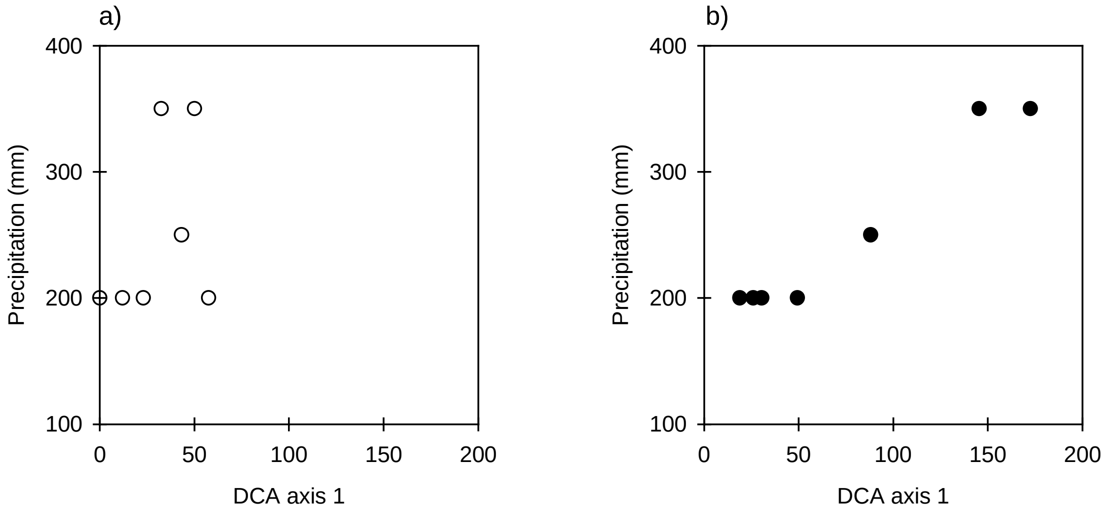

Figure 2. Epiphtic macrolichen species composition summarized by the first axis of a DCA ordination as function of annual precipitation for paired a) young forests and b) old forests stands.

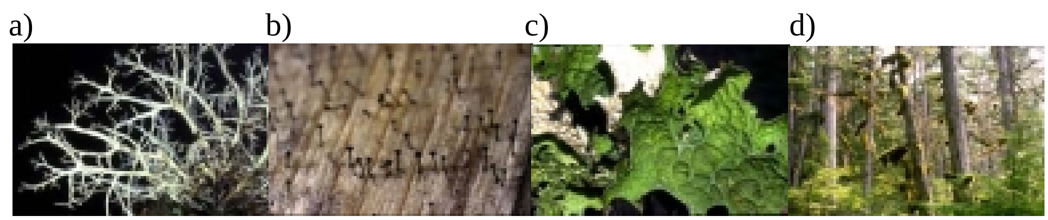

Figure 3. Examples of organisms examined during this project. a)*Sphaeophorus tuckermanii*, an hygrophytic macrolichen, b) *Chaenothecopsis nana*, an epixylic calicioid lichen. c) *Lobaria pulmonaria*, an epiphytic cyanolichen, d) *Antritichia curtipendula*, an hygrophytic moss species shown here on branches of western hemlock trees in Wells Gray Provincial park. Photographsfor a, b, and c by Anna Roberts, and d by André Arsenault; reproduction not permitted.

Conversely, calicioid lichen diversity was strongly correlated with stand age (Figure 4). This relationship became stronger when the veteran trees and snags present in young forests were removed from the analysis. More specifically, species richness has been shown to increase for at least 200 years after stand initiation, and possible much longer. These observations echo the findings of European workers, e.g., Tibell (1992), Hyvärinen et al. (1992), and Holien (1996), who have pointed to similar age-related increases in calicioid richness. They do not, however, lend overwhelming support to the hypothesis of Selva (1994), that floristic richness among calicioid species can by itself be used as an indicator of relative forest continuity. Rather, the data suggest that levels of calicioid species richness are increasingly difficult to predict with increasing stand age. While it is true that a high level of species richness correlates well with advanced stand age, relatively low levels of species richness can also occur both in young stands and in very old stands.

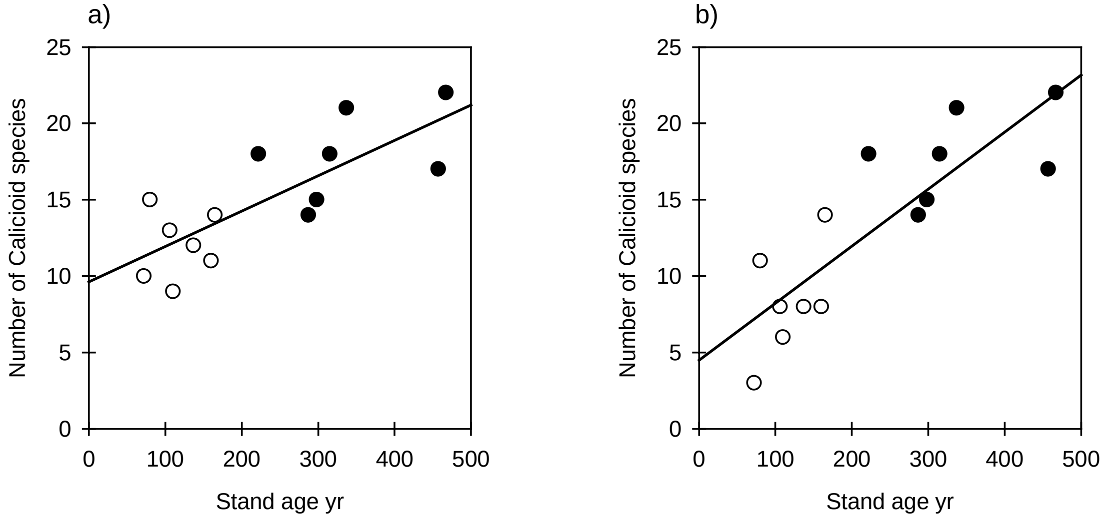

Figure 4. a) Calicioid species richness as a function of stand age, b)Calicioid species richness as a function of stand age excluding veteran trees and snags in young forests.

Several crustose calicioids, are oldgrowth-dependent: of the 37 species documented by us, ten were found to be restricted to oldgrowth. Six of these species were recorded exclusively in stands older than about 200 years (i.e., *Chaenotheca cinerea*, *Chaenotheca xyloxena*, *Chaenothecopsis epithallina*, *C.* sp. 4, *C.* sp. 9, and *Sclerophora amabilis*), while another four species were restricted to stands older than about 300 years (i.e., *Chaenothecopsis pusilla*, *C. tsugae*, *C.* sp. 6, and *Microcalicium alhlneri*).

Within-stand level comparisons

Microhabitats

Substrates occupied by calicioid species tend to be "selected" at a much higher scale of resolution. Holien (1996), for example, has shown that bark and lignum sheltered from direct exposure to rain are especially important. Four key microhabitats can be recognized: 1) leaning trees and snags; 2) "decay grottos" at the bases of trees; 3) branch-induced "rainshadows" around the trunks of large trees; and 4) large tip-up mounds. All of these microhabitats can be described as "legacies" of tree senescense. Not surprisingly, they are more characteristic of old stands than of young stands; and even within oldgrowth forests they appear to become increasingly well represented with increasing stand age (Goward & Arsenault, pers. obs.).

Bryophytes can be grouped into communities of epiphylous, epixylous, saxicolous and terricolous species. In both the ICH or CWH forests epiphytic communities can be further defined using tree type (i.e., deciduous or coniferous), size and vertical position on the tree. Species richness is highest on large trees (> 30 cm diam.), and stand age is an important integrated factor. These findings are supported in other epiphytic studies (Pike et al. 1975; Slack 1976; Sillett 1995). Epixylic communities in the ICH or CWH can be further defined using log size and decay class. The large logs (> 70 cm diam.) of decay class three offered the highest diversity of bryophytes with a large proportion of hepatic. These patterns are supported by research in other types of forests in Europe and the United States (Söderström; Rambo & Muir 1998). Forest floor bryophyte community composition is related to habitat heterogeneity.

The Populus dripzone effect

Several studies from Europe and North America have shown that cyanolichens are often adversely affected by forestry. This has potentially important management implications for British Columbia because cyanolichens not only contribute to biological diversity but also have the potential to influence ecosystem productivity because of their ability to fix atmospheric nitrogen. Thus we have focussed particular attention on the distribution of these organisms. during this project. In a study in a young forest on the Murtle Plateau of Wells Gray Provincial Park we found that cyanolichen diversity was relatively high and contained several species considered to be old-growth dependent elsewhere.

Our data indicate, that *Picea* branches growing within five metres of *Populus* on average support twice as many cyanolichen species (mean = 3.9) as similar branches growing at greater distance (mean = 1.8) (Figure 5). In our study of 80 branch samples devoid of lichens, we determined that conifer branches growing within the dripzone of *Populus* have a mean pH of 5.8, where as similar conifer branches growing at distance from *Populus* exhibited a pH of 4.9. An Anova examining both the effects of overstory condition and slope position confirmed the statistical significance (P <0.001) associated with the dripzone of *Populus*, but revealed no statistical significance with slope position.

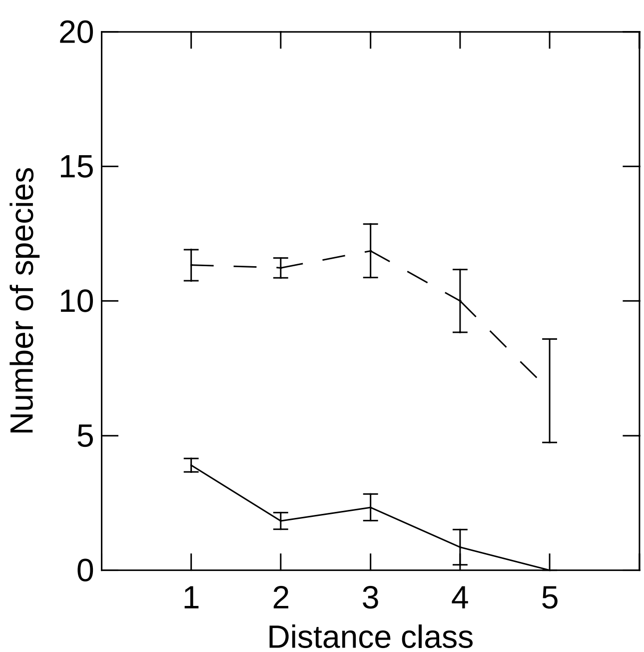

Figure 5. The average number of lichens (dotted line) and cyanolichens (solid line) living on spruce branches at different distances away from the nearest *Populus* tree. Distance classes are; 1 = 0-5 metres, 2 = 5-10 metres 3 = 10-15 metres, 4 = 15-20 metres, 5 = 20-25 metres.

From these observations it can be concluded that: 1) the presence of cyanolichens is positively correlated with an elevated pH; 2) an elevated pH is positively correlated with the dripzones of *Populus*; and 3) cyanolichens alone cannot be totally responsible for the elevated pH of their host branches. Collectively, these conclusions suggest the hypothesis that the pH of *Picea* branches is being elevated by some form of extraneous nutrient enrichment (Figure 6).

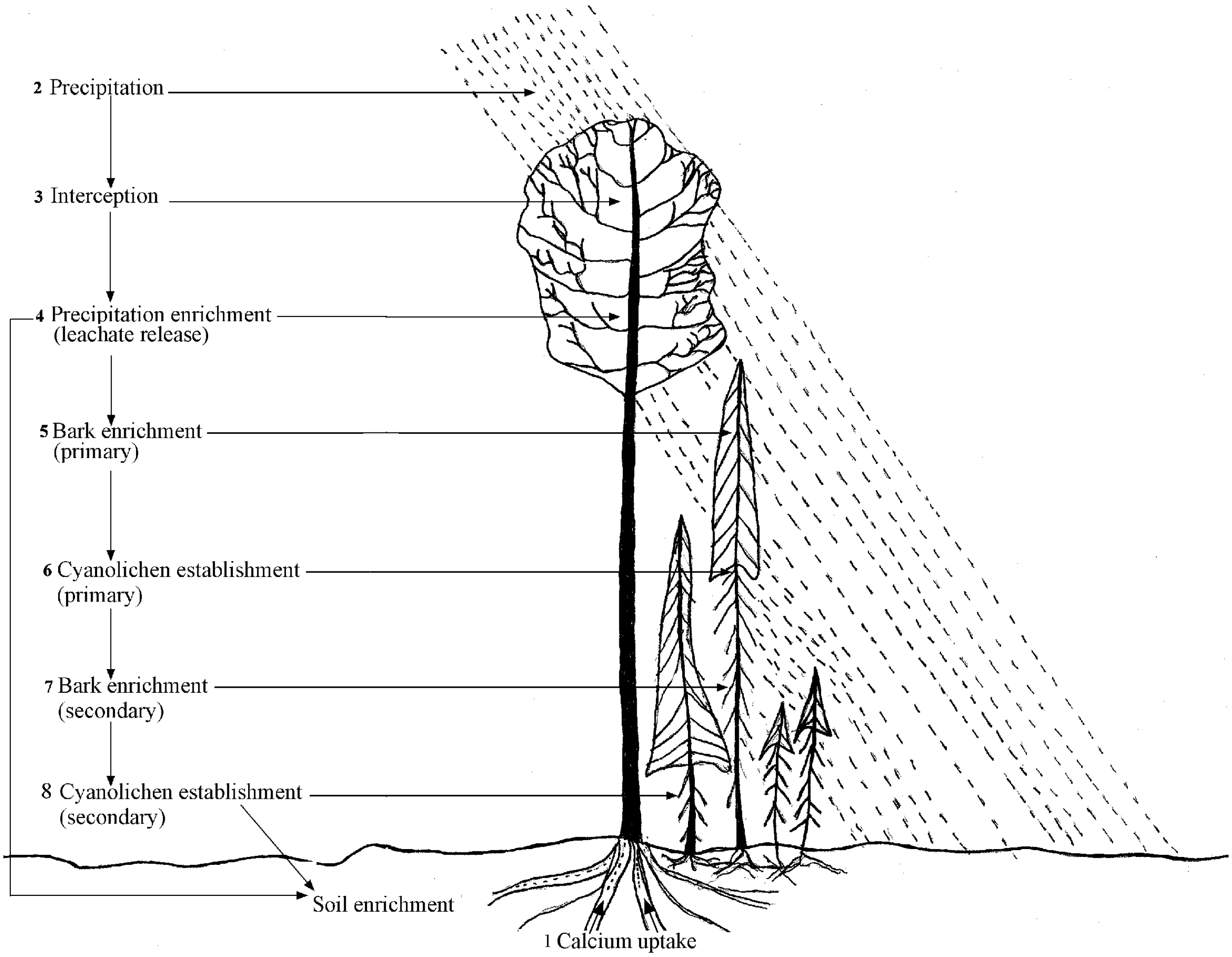

Figure 6. The dripzone hypothesis.

Broad scale distribution of bryophyte and lichens

Bryophytes

Our ordination (Figure 7) of cedar hemlock stands using bryophyte communities at the regional scale clearly distinguishes the Interior cedar Hemlock Zone from the Coastal Western Hemlock Zone. Our comparisons of the ICH and CWH quantitatively support previous observations (Schofield 1988). Several disjunct (Western Europe or Asia) species are common in the CWH, but only locally abundant in the ICH (for example *Herbertus aduncus, Porella cordaeana, Antitrichia curtipendula, Claopodium bolanderi,* and others). However, our contrasts of the CWH and ICH indicate that there are many differences between the bryoflora of the CWH and ICH even though species richness (gamma diversity) is very similar (i.e., ICH 300 spp, CWH 317 spp.). Some species are found exclusively in either the CWH (114 species - 36%) or ICH (98 species - 33%). Species with Circumboreal distributions are more common in the ICH. Conversely, species with temperate distributions are more common in the CWH. There are more western North America endemics in the CWH than the ICH, some of which are exclusive to the

CWH. Environmental conditions and habitat limitations limit development of the bryoflora. Some microhabitats will be more common to either the ICH or CWH. Climate greatly influences the microhabitats that are available in either biogeoclimatic zone. For example, the communities that are unique to big leaf maple (*Acer macrophyllum*) are unlikely to develop in the ICH since the species is restricted to the coast. However, some habitats are not related to climate but also limit community development within a biogeoclimatic zone. Specific species of bryophytes are often associated on either acidic or basic rock, which provides microhabitat for unique communities (Belland & Schofield 1984). Rock microhabitats are chiefly acidic in the CWH and predominantly basic in the ICH (Montgomery 1997). Although rock microhabitats are present in forest, they were not a primary environmental variable explaining the community composition of bryophytes in the cedar hemlock landscape.

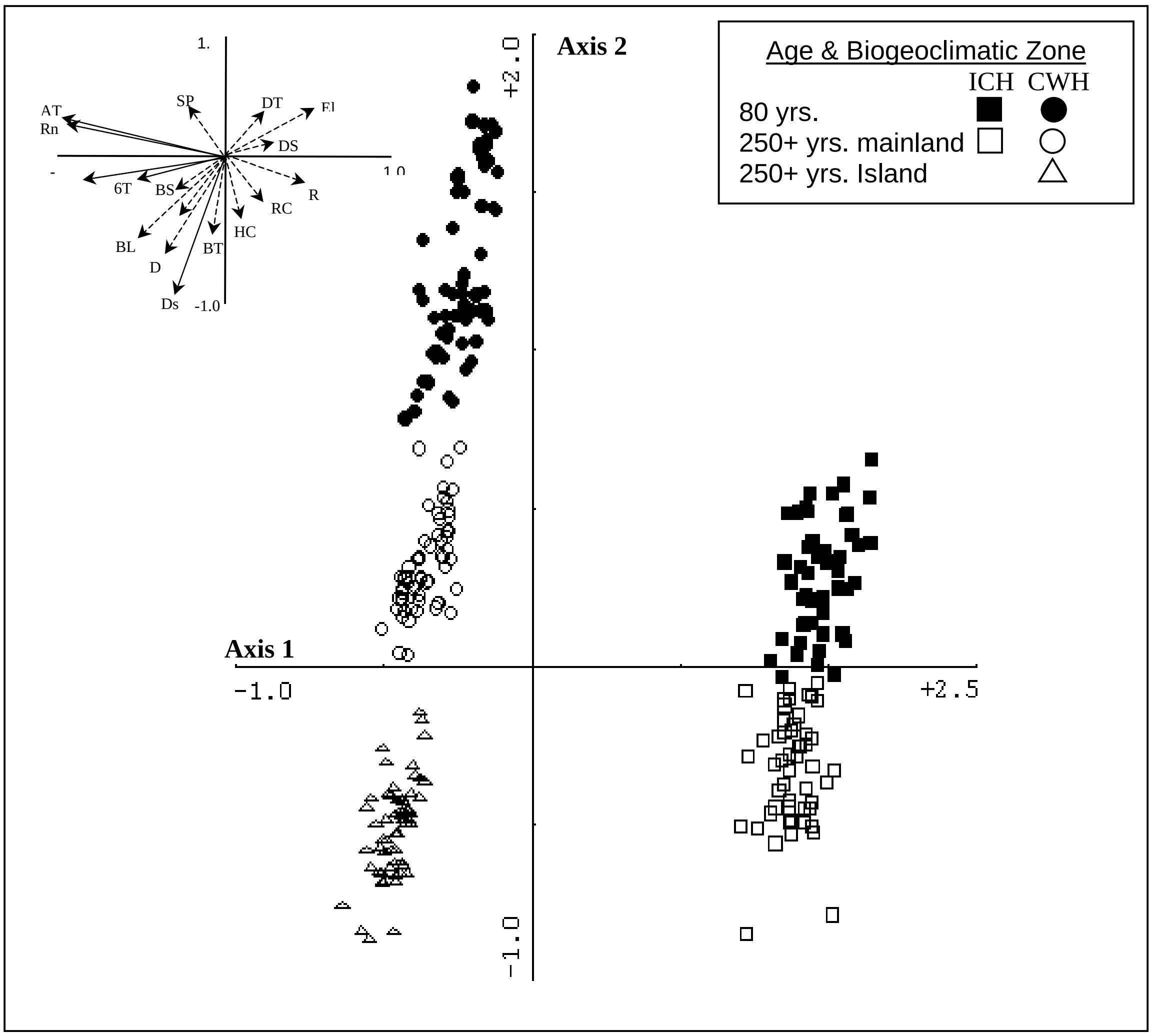

Figure 7. CCA ordination of 287 stands, 417 species, 24 environmental variables. The abbreviations for each variable are listed in Table 1 of Newmaster 2000.

Cyanolichens

A key to cyanolichen diversity

In the intermontane forests of British Columbia, 31 epiphytic (tree-dwelling) cyanolichens are known to colonize conifers, including nine species that can be considered rare or infrequent in the province as a whole. In this study we developed a simple key for predicting stand-level epiphytic cyanolichen diversity on conifers (Figure 8). The key is based on several readily mappable environmental factors, and is useful at an operational scale. Maximum cyanolichen diversity is shown to occur in lowland oldgrowth rainforests established over nutrient-rich soils, and subject a rainfall pH above about 5.0. In practice, such stands are generally restricted to the base of hillslopes in the wettest subzones of the Interior Cedar-Hemlock Zone. Here they not only support one of British Columbia's richest assemblages of rare cyanolichens, they also themselves represent one of the province's rarest and most endangered forest ecosystems. Preliminary field testing of the key is promising and suggest that it could be a powerful tool to assist landscape planning.

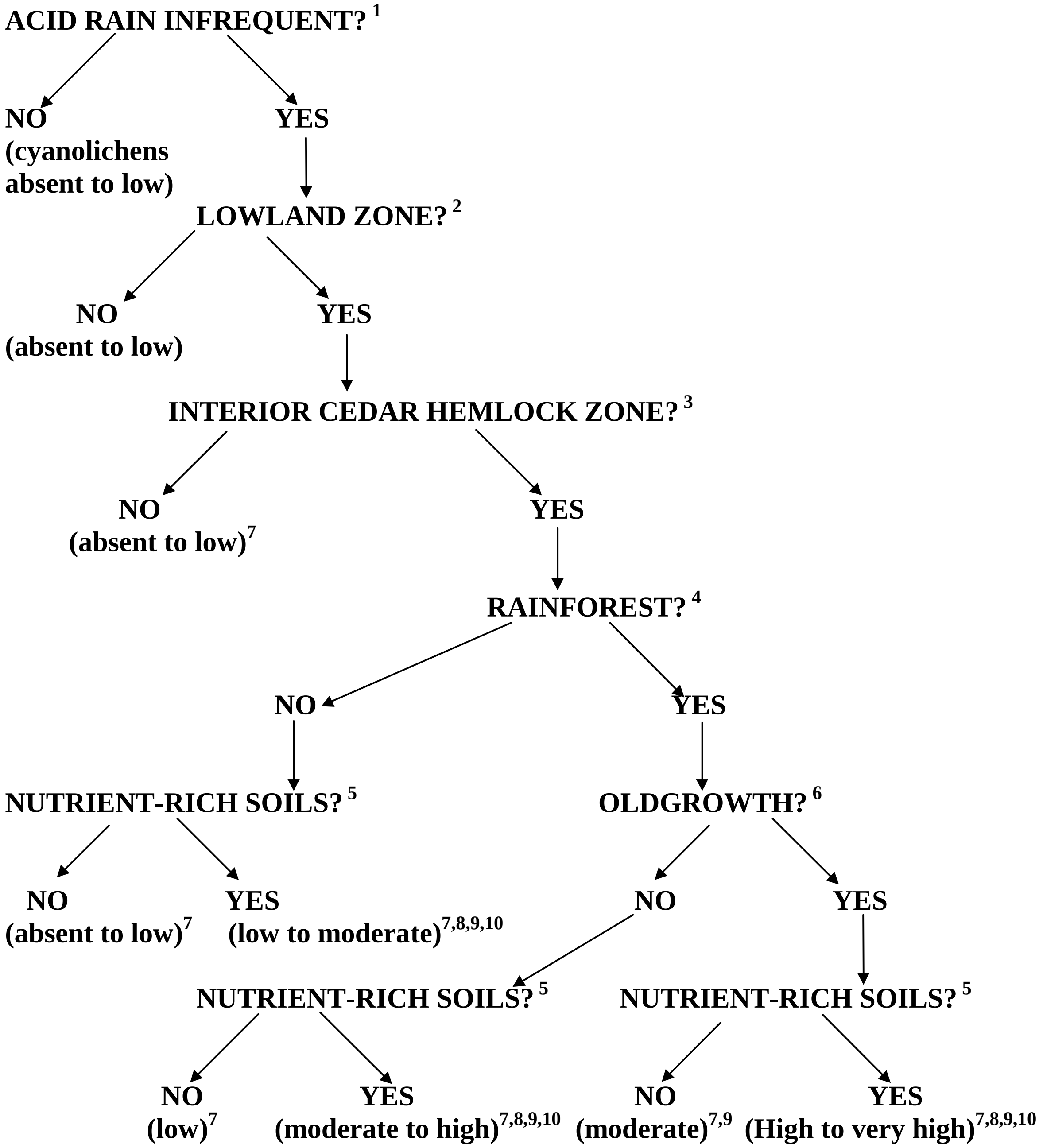

Figure 8. Provisional key to epiphytic cyanolichen diversity on conifer branches in intermontane British Columbia. [1]I.e., rainfall pH averages more than 5.0. [2]I.e., the Bunchgrass Zone, the Ponderosa Pine Zone, the Interior Douglas-fir Zone, the Interior Cedar - Hemlock Zone, the Sub-boreal Spruce Zone, the Boreal Black and White Spruce Zone,

and the Spruce - Willow - Birch Zone (further details are provided in Meidinger and Pojar 1991). [3]I.e., western red-cedar (*Thuja plicata*) and/or western hemlock (*Tsuga heterophylla*) present in mature stands on mesic sites. [4]I.e., oak fern (*Gymnocarpium dryopteris*) and/or devil's club (*Oplopanax horridus*) often present in mature stands on mesic sites. [5]I.e., aspen or cottonwood (*Populus* spp.) present, especially in the "toe-position" at the base of hillslopes. [6]Snags and trees in all age classes present; *Populus* sparse or absent. [7]Occurrence within the sprayzones of waterfalls can enhance cyanolichen diversity, assuming nutrient-rich aerosols. [8]Occurrence within the "dripzone" of *Populus* can enhance cyanolichen diversity, assuming nutrient-rich soils. [9]Hygric sites often support higher cyanolichen diversity than mesic or xeric sites. [10]Open stands support higher cyanolichen diversity than closed stands.

Regional and global distribution of cyanolichens on conifers

Based on a survey of 933 herbarium specimens collected from British Columbia, the substrate ecology and "lifezone" we broadly summarized distribution of 48 species of epiphytic cyanolichens. Conifers belonging to the Pinaceae provide habitat for at least 43 cyanolichen species, 12 of which occur exclusively on conifers. Hardwoods support a similar number of cyanolichens, but provide exclusive habitat for only four species. Cyanolichen diversity on conifer branches is shown to increase along a gradient of increasing summer precipitation (figure 9).

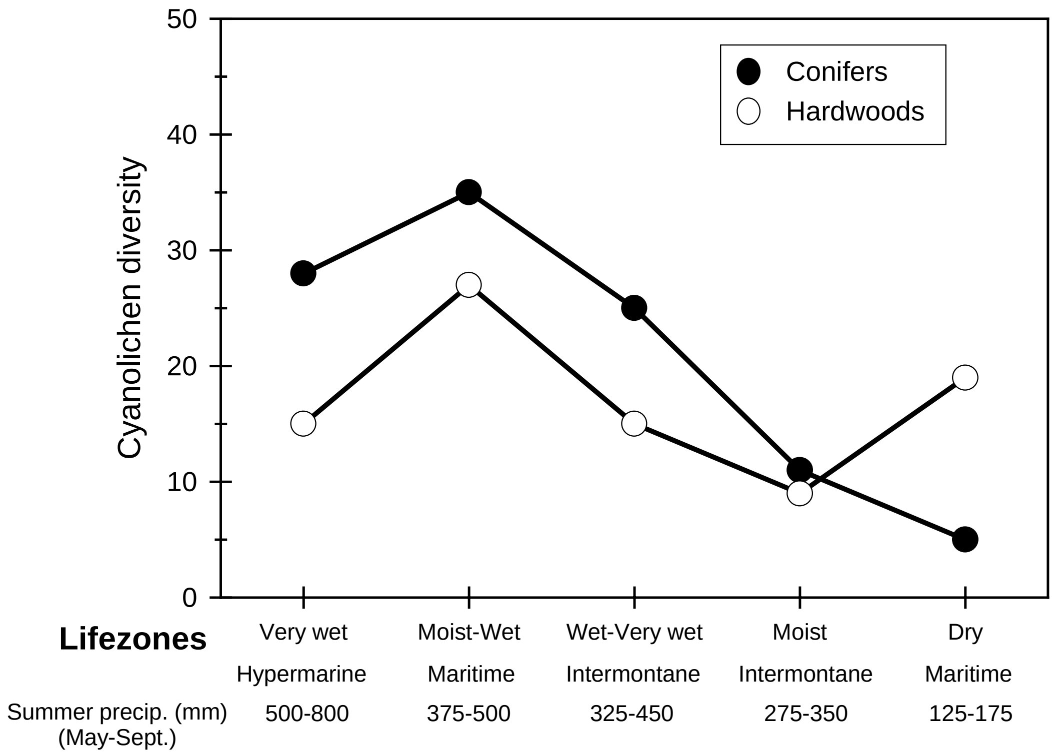

Figure 9. Epiphytic cyanolichen diversity: conifers versus hardwoods across five lifezones in British Columbia.

Figure 10 summarizes the reported and "potential" (i.e., pre-industrial) distribution of cyanolichens on members of the Pinaceae at temperate and boreal latitudes. For convenience, the occurrence of cyanolichens on conifer branches will henceforth be referred to as the "CC phenomenon". The patterns displayed in Figure 10 permit five observations regarding this phenomenon: 1) it can be captured within the distribution areas of four conifer genera, i.e., *Abies*, *Picea*, *Pseudotsuga*, and *Tsuga*; 2) it is restricted to regions in which summer mean temperatures (May through September) are lower than about 15°C; 3) it is limited to humid areas, in which measurable precipitation (including fog-induced "occult precipitation") occurs on at least sixty days each summer; 4) it is not excluded by high continentality per se (sensu Tuhkanen 1984); and 5) it extends northward only as far as the middle subzone of the boreal bioclimatic zone (sensu Tuhkanen 1984). Thus circumscribed, the distribution area of the CC phenomenon roughly corresponds to the combined ranges of several hygrophytic lichen species, including *Cladonia umbricola*, *Parmotrema arnoldii*, *Peltigera britannica*, *P. horizontalis*, *Usnea longissima*. Potential "hot spots" thus include northwestern North America (especially north of northern California), northeastern North America (north of New Hamshire), western Europe (excluding Mediterranean regions), and eastern Asia (northeast China and southeast Russia).

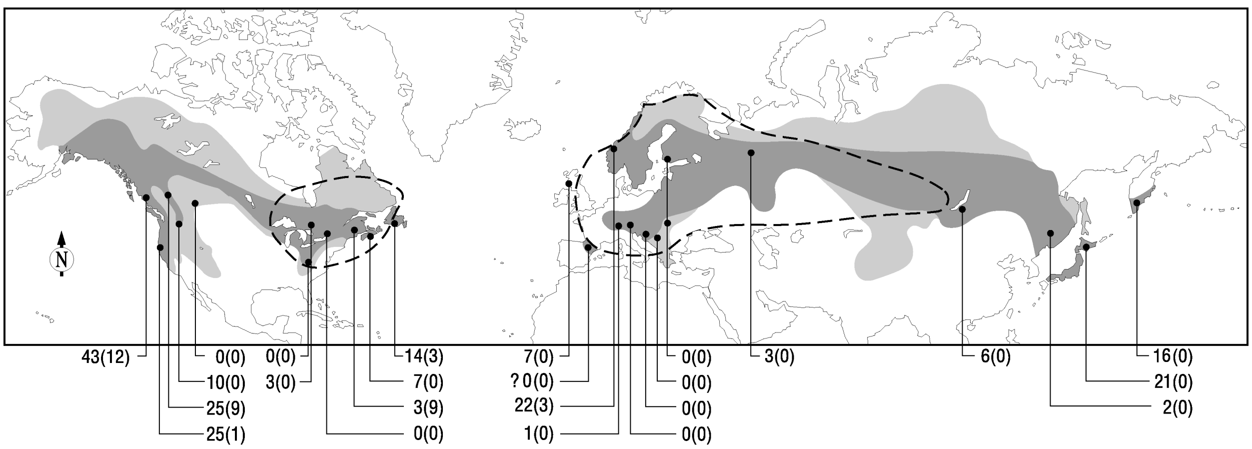

Figure 10. Reported and "potential" occurrence of cyanolichens on conifer branches at middle latitudes in the northern hemisphere. Greyed area: distribution area of Pinaceae, excluding *Larix* and *Pinus* (from Florin 1963; Jalas & Suominen 1973; Brockman 1979; Hultén & Fries 1986). Blackened area: potential distribution area of cyanolichens on conifer branches (see text). Dotted lines: distribution area of "acid rain effect" on lichens (from Wolseley 1995). Paired numbers indicate cyanolichen occurrence on conifers in selected regions (and cyanolichen species restricted to conifers). Regional sources: T. Ahti (Finland), I.M. Brodo (central Canada), S.R. Clayden (eastern Canada), B. Coppins (Britain), J. Etayo (Spain), B. Goffinet (Alberta), H. Holien (Norway), G. Insarov (Russia), H. Kashiwadani (Japan), S. Kondratyuk (Ukraine), B. McCune (Montana), W. Maass (eastern Canada), S. Ozimec (Croatia), J. Prügger (Slovenia), C. Scheidegger (Switzerland), S. Sillett (Pacific United States), T. Tønsberg (general), R. Türk (Austria), G. Urbanavichyus (Russia), M. Zhurbenko (Russia).

It can also be observed that the CC phenomenon declines sharply with increasing distance from the continental coastlines (Figure 10). The inland "rainforests" of south-central British Columbia constitute a notable exception to this rule, with 25 epiphytic cyanolichens having been recorded. Admittedly conditions are thermally rather oceanic in this region (Goward 1994), though winter temperatures as low as -40°C have been recorded. Farther south, in slightly drier, but otherwise corresponding portions of Idaho and Montana, the CC phenomenon is restricted to only ten species. The Pyrenees of northern Spain, with 11 species, constitute another "inland" node of cyanolichen diversity on conifers (Figure 10).

Wolseley (1995) has provided a global map summarizing those regions in which lichens have been adversely affected by acid precipitation. When this map is compared against our Figure 10, a clear correspondence between acid rain and low epiphytic cyanolichen diversity on conifers emerges. This correspondence is especially apparent in most regions of western Europe, where the CC phenomenon is almost entirely absent, even in areas supporting extensive conifer forests.

Interestingly, the CC phenomenon is well developed in west-central Norway, one of the least polluted parts of Europe (Gauslaa & Holien 1998). We suggest that these observations are unlikely to be coincidental. Instead, they can probably be viewed as artifacts of environmental deterioration associated with the relatively recent spread of acid precipitation over large areas (Richardson 1991).

The Inland rainforests phenomenon

The coastal rainforests of western North America have long provided an international flashpoint for environmental concern. By contrast, their inland counterparts -- the rainforests of intermontane British Columbia -- are still poorly known even to researchers. Located at between 51°N and 54°N along the windward slopes of the Columbia and Rocky Mountains (Figure 1), the inland rainforest phenomenon is unique to British Columbia. It is restricted to a region of anomalously humid climate, in which a plentiful snow-melt during late spring is followed by ample rainfall during the height of the growing season. More specifically, inland rainforests are confined to the wettest subzones of the Interior Cedar-Hemlock Zone (i.e, the ICHwk and ICHvk); in no other region of the world has a similar integration of humidity and continentality been documented.

Oceanic species

By their high ambient humidity, inland rainforests favour colonization by numerous oceanic species, i.e., species more often associated with maritime environments. For example, hanging moss (*Antitrichia curtipendula*) forms thick hanging mats on the boughs of western red-cedar and western hemlock trees. A number of oceanic vascular species also occur here, including deer fern (*Blechnum spicant*) and red huckleberry (*Vaccinium parviflorum*). Perhaps most fully represented, however, are various oceanic epiphytic lichen genera, including *Chaenotheca*, *Chaenothecopsis*, *Collema*, *Fuscopannaria*, *Lichinodium*, *Lobaria*, *Nephroma*, *Parmeliella*, *Polychidium*, *Pseudocyphellaria*, *Sphaerophorus*, and *Sticta*. Many species belonging to these genera are oldgrowth-dependent in this portion of their range, and are rare or infrequent in British Columbia as a whole. Perhaps our most significant finding to date is that rare species are not uniformly distributed in oldgrowth forests, but tend to associate with forests characterized by us as antique. Similarly, antique inland rainforests are themselves not distributed randomly across the landscape; rather they are situated in gullies, toe positions and other moist to hygric sites that tend repeatedly to escape wildfire. This observation would seem to have important implications for the establishment of future oldgrowth management areas.

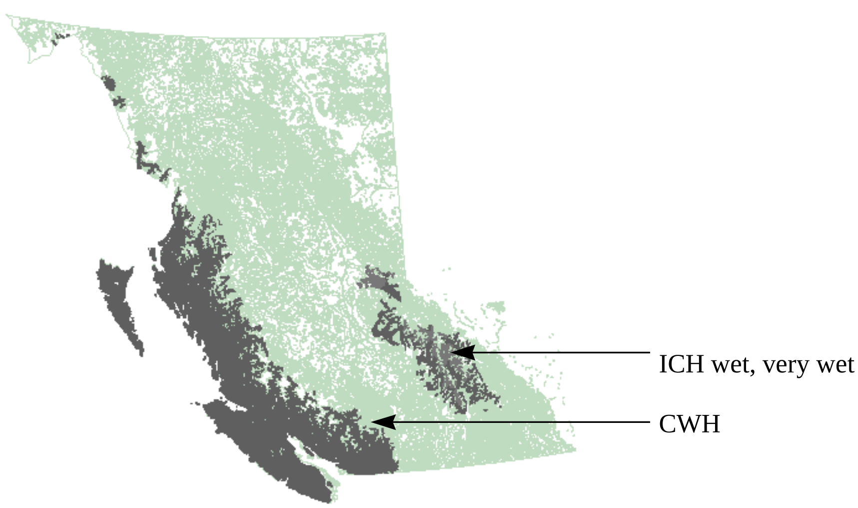

Figure 11. The occurrence of coastal rainforests and inland rainforests (ICH wet and very wet subzones) in British Columbia.

Extension

We had the opportunity to provide extension related to this project to wide variety of audiences including the general public, students and teachers from an elementary school and from several Universities , operational foresters and forest planners from forest companies and from the Ministry of Forests, environmental groups, ecosystem specialists from the Ministry of Environment, policy makers, and research scientists.

Newmaster, S. 2000. ***Patterns of bryophyte diversity in interior and coastal cedar-hemlock forests of southern British Columbia.*** Ph.D. Thesis University of Alberta.

Goward, T. and A. 2000. ***Cyanolichen distribution in young un-managed forests: a dripzone effect?*** The Bryologist 103(1):28-37

Goward, T. and A. Arsenault (Submitted for publication). **Notes on the *Populus* "dripzone effect" in well ventilated stands in east-central British Columbia.**

Arsenault, A. and T. Goward.(Submitted for publication). ***Patterns of macrolichen diversity in old and young unmanaged forests along a moisture gradient in humid inland British Columbia.***

Goward, T. and A. Arsenault.(Submitted for publication). ***Patterns of calicioid diversity in old and young unmanaged forests along a moisture gradient in humid inland British Columbia.***

Arsenault, A. (in press). ***Coarse woody debris management in British Columbia: a cultural shift for professional foresters.*** Proceedings of the ecology and management of deadwood in western forests conference, Reno, 1999.

Goward, T. and A. Arsenault. (in press). ***Cyanolichens and conifers in British Columbia: implications for global conservation.*** Proceedings of the International conference on lichen conservation biology held in Switzerland in August 1999.

Arsenault, A. and T. Goward (in press). ***The dripzone effect: new insights into the distribution of rare lichens.*** Proceedings of the B.C. species at risk conference held in Kamloops at UCC in February 1999.

Goward, T. and A. Arsenault (in press). ***Inland old-growth rainforests: Safe havens for rare lichens?*** Proceedings of the B.C. species at risk conference held in at UCC in February 1999.

Arsenault, A. and T. Goward (in press). ***Ecological characteristics of inland rainforests.*** Proceedings of the B.C. species at risk conference held in at UCC in February 1999

Arsenault, A. and T. Goward, 1998. ***Patterns of lichen diversity and distribution in old and young forests of the Interior Cedar-Hemlock Zone of British Columbia.*** *in:* Jull *et al*. (eds.): Proceedings of the ecosystem dynamics and silvicultural systems

in interior wet-belt ESSF and ICH forests workshop, June 1997, UNBC.

Arsenault, A. 1999. ***Coarse woody debris management in British Columbia: a cultural shift for professional foresters.*** Presented in Reno at the ecology and management of deadwood in western forests conference in November 1999.

Arsenault, A. and T. Goward 1999. ***Epihytic lichens an emerging biodiversity issue.*** Presented at the Managing forests for lichens: The mountain caribou issue conference in Revelstoke in September 1999.

Goward, T. and A. Arsenault 1999. ***Cyanolichens and conifers in British Columbia: implications for global conservation.*** Presented at the International conference on lichen conservation biology held in Switzerland in August 1999.

Arsenault, A. and T. Goward 1999***. The dripzone effect: new insights into the distribution of rare lichens.*** Presented at the B.C. species at risk conference held in at UCC in February 1999.

Goward, T. and A. Arsenault 1999***. Inland old-growth rainforests: Safe havens for rare lichens?*** Presented at the B.C. species at risk conference held in at UCC in February 1999.

Arsenault, A. and T. Goward 1999. ***Ecological characteristics of inland rainforests.*** Presented at the B.C. species at risk conference held at UCC in February 1999

Arsenault, A. 1998. ***Ecology of lichens and bryophytes in the ICH: Why should foresters care?*** Winter Sisco. Presented at the winter meeting of the Southern Interior Silviculture Committee in Penticton

Arsenault, A. and T. Goward, 1997***. Patterns of lichen diversity and distribution in old and young forests of the Interior Cedar-Hemlock Zone of British Columbia.*** Presented at the Ecosystem dynamics and silvicultural systems in interior wet-belt ESSF and ICH forests workshop in June 1997, UNBC.

Summer 1998. ***Inland rainforest ecology.*** Lead a field trip in the Upper Seymour river watershed for a group working on the Okanagan/Shuswap Land and Resources Management Plan.

Summer 1998, 2000. ***Coarse woody debris management workshops***. Organized 2 field workshops for the Kamloops, and Clearwater Forest Districts in 1998 and 2 in Penticton and Merritt Forest Districts in 2000 aimed at improving coarse woody debris management in the Kamloops Forest Region.

Arsenault A. 2000. ***A comparison of the ecology of coastal and inland rainforests of southern British Columbia.***Presented at the ICH stewardship conference in Sept. 2000 at the University of Northern British Columbia.

Arsenault, A. 1999. ***From the virtual to the operational: applying ecological data into forest management.*** Seminar presented at UBC in a conservation biology course in November 1999.

Arsenault, A. 1999. ***Deadwood management in British Colombia: a cultural shift for professional foresters.*** Presented at the winter meeting of the Southern Interior Guest lecture presented to the Silviculture Committee in Penticton in March 1999.

Arsenault, A. 1999. ***Old-growth dependent species: Myth or reality?*** Keynote address at the first annual conference on B.C. ancient forests held at UBC in February 1999.

Vitt, D.H. 1999. ***What are the attributes and patterns of Rare Bryophytes.*** Presented at International Botanical Congress in St. Louis, MO.

Vitt, D.H. ***Attributes of rarity of bryophytes.*** Presented at the European Conservation Congress in Trondheim, Norway, in August, 1998.

Vitt, D.H.1999. ***Patterns of rarity in mosses.*** Presented at the Department of Biological Sciences, University of Alaska at Anchorage.

Arsenault A. 1998. ***Temperate rainforest ecology.*** Invited by the Bamfield Marine Station to provide 2 lectures and 1 field workshop, and 1 lab exercise for the temperate rain forest ecology undergraduate course.

Goward, T. 1998. ***Lichens and inland rainforests.*** Presented to the Kamloops Naturalist Club.

Manuscripts in preparation

Arsenault, A. and T. Goward. (in preparation). ***Distribution of epiphytic cyanolichen in forests of British Columbia: implications for landscape unit planning.***

Arsenault, A., and T. Goward (in preparation). ***Patterns of lichen diversity in young and old forests of the Coastal temperate rainforests of southern British Columbia.***

Newmaster, S. G., R. Belland, D.H. Vitt, and André Arsenault. (in preparation). ***The ones we left behind: Comparing plot sampling and floristic habitat sampling for estimating bryophyte diversity.***

Newmaster, S. G., R. Belland, D.H. Vitt, and André Arsenault. (in preparation). ***Bryophyte community composition in Oceanic and continental cedar-hemlock Biogeoclimatic Zones of British Columbia, Canada.***

Newmaster, S. G., R. Belland, D.H. Vitt, and André Arsenault. (in preparation***). Patterns of bryophyte diversity in cedar-hemlock forests***.

Newmaster, S. G., R. Belland, D.H. Vitt, and André Arsenault. (in preparation***). Mesohabitat quality and quantity: Basic ingredients for bryophyte diversity.***

Newmaster, S. G., R. Belland, D.H. Vitt, and André Arsenault. (in preparation). ***Forest Microhabitat: the lowest level in patterning bryophyte diversity.***

Media Liaisons: This project has been featured on CBC radio, in local newspapers and a Ministry of Forests article for National Forest Week, and in a documentary.

Summary and conclusions

Lichens and bryophytes in young and old forests

- Our studies in the ICHmw3, ICHwk1/ ICHvk1, and CWHvm1 have shown without exception that old forests overall always contained a higher number of species of lichens and bryophytes. However this trend differed amongst groups of species. For example, in the ICHmw3 although more species were recorded overall in old forests there was no significant correlation between species richness and stand age. Also in the ICHmw3 the majority of old-growth dependent macrolichens were essentially associated with the wetter end of the precipitation gradient. Conversely calicioid lichen richness was very strongly correlated with stand age and old-growth dependent species in this group were not related to the precipitation gradient.

Within stand distribution of bryophytes and lichens

- Our studies has shown that elucidating factors underlying the distribution of lichens and bryophytes within stands is key to understand the broader patterns of species distribution. These factors are not only coarse level attributes, e.g. large trees, logs, and snags, that are often listed in the forest management literature but also involve small-scale structural diversity as well as complex interactions between tree species.

- We have shown that *Populus* trees appear critical for the maintenance of cyanolichens on conifers in young un-managed forests. Cyanolichens present on conifers were associated with higher bark pH and higher concentrations of Calcium. We have proposed the dripzone hypothesis; *Populus* trees provide extraneous enrichment to the bark of nearby conifers thereby modifying the chemistry of conifer bark enough to allow colonization and development of cyanolichen species. This study has provided new insight into the distribution ecology of cyanolichen species in young forests and has contributed to our development of a predictive tool for cyanolichen diversity.

- The type and number of microhabitats also influence strongly the distribution ecology of lichens and bryophytes. Large trees (>30cm) were associated with the greatest numbers of epiphytic bryophytes while large logs (>70cm) in intermediate stages of decomposition were associated with very high diversity of hepatics. Over 90% of the terricolous lichen species surveyed were situated on elevated woody substrates showing the importance of coarse woody debris. Calicioid diversity was associated with four key microhabitats including leaning trees and snags, decay grottos at the base of trees, branch induced rain shawdows on large trees, and large tip-up mounds.

- Western redcedar is a keystone species for the maintenance of epiphytic and epixylic bryophyte and lichen diversity in young and old forests.

Broad patterns of lichen and bryophyte distribution

- Our ordination of cedar hemlock stands using bryophyte communities at the regional scale clearly distinguishes the Interior cedar Hemlock Zone from the Coastal Western Hemlock Zone. Our comparisons of the ICH and CWH quantitatively support previous observations (Schofield 1988). Several disjunct (Western Europe or Asia) species are common in the CWH, but only locally abundant in the ICH (for example *Herbertus aduncus, Porella cordaeana, Antitrichia curtipendula, Claopodium bolanderi*, and others).

- Our studies on cyanolichen distribution in the intermontane forests of British Columbia suggests that we can predict levels cyanolichen diversity using readily available information. We developed a predictive tool to that effect and preliminary results evaluating this tool in the field are encouraging and could be useful for landscape planning.

- We have shown that cyanolichen diversity on conifers increases with increasing precipitation across five major lifezones in British Columbia. We have also provided new insight into the global distribution of cyanolichens on conifers addressing the intriguing question of why are cyanolichens almost exclusively found on broadleaf trees in Europe while in British Columbia conifers actually harbour relatively high numbers of cyanolichen species. We have suggested that regions in which the “Cyanolichen on conifer phenomenon” is well developed might be characterized as environmentally "pristine", at least in the sense that epiphytic cyanolichens still occupy their original, pre-industrial ecological amplitude. In comparison, epiphytic cyanolichen assemblages in regions affected by acid precipitation are more likely to be "relictual", that is, they are restricted to a considerably reduced assemblage of phorophytes. This observation clearly shows the global significance of British Columbia’s old-growth conifer inland and coastal rainforests in the conservation biology of cyanolichens.

Management Implications

- 20 yr. plantations examined in the ICHvk1 and in the CWHvm1 had the lowest diversity of lichens and bryophytes and often lacked rare species. Because we are evolving rapidly from an unmanaged forest dominated landscape to a mostly managed forest landscape further work is needed to assess what factors are limiting colonization and development of these organisms in plantations.

- Our comparison of the pattern of macrolichen and calicioid lichen diversity illustrates that different groups of organisms require different types of old-growth forests or old-growth forest attributes even within the same biogeoclimatic variant. Our results would suggest that not one type of old-growth management area or a single set of old-growth legacies in managed forests will satisfy the requirements of all species.

- Our studies indicate that it would be wise to complement coarse level indicators of our impact on biodiversity (e.g. seral stage distribution) with the monitoring of key species or community attributes of bryophytes and lichens. We propose that cyanolichens, calicioid lichens and hepatics represent excellent bioindicators of our impact on forest biodiversity.

- We propose that many oldgrowth-dependent calicioid species are tied to structural attributes not usually deemed requisite to the maintenance of biological diversity. Indeed, our study suggests that traditional concepts of habitat requirement may need to be broadened. In particular, we urge forest managers to accord greater significance to the maintenance of leaning trees and snags. While granting the desirability, in some situations, of removing snags to ensure worker safety, we recommend that leaning snags be promoted both through the designation of retention patches as "no work zones", and through "stubbing", i.e., leaving only the bottom 5 metres of trees or snags.

- Finally we have also shown that it is important to take a global perspective when we are assessing our impact on biological diversity. Our study on patterns of cyanolichen distribution illustrates the global importance of our old-growth inland rainforests and that of their coastal counterparts for the maintenance of biological diversity and for the study of cynolichen ecology.

Benefits resulting from this project

- This project has gathered important baseline data on lichens and bryophytes in forests of the Coastal Western Hemlock Zone and Interior Cedar Hemlock Zone. In particular we have advanced the state of our knowledge particularly with cyanolichens and calicioid lichens, organisms often used as biological indicators in other forests of the world. Our data on the distribution of rare species in inland rainforests of British Columbia has already assisted the Kamloops and Okanagan/Shuswap Land Use and Resource Management Plans. Our description of the requirements for old-growth dependent species provides insight into key habitat characteristics to maintain in managed stands and landscapes to minimize our impact on biological diversity.

- Our approach to develop predictive relationships between environmental characteristics and the distribution of non-vascular plants has tremendous potential for landscape planning.

- We evaluated two sampling techniques for assessing bryophyte diversity in forests.

- We have communicated available results to a wide range of audiences (see previous section) at various stages of our research to optimize the potential benefits from this project.

- We have provided extension on the role of coarse woody debris for non-vascular plants to many audiences involved with forestry policy, planning, and operations in British Columbia.

- Education and training was provided to Steve Newmaster who successfully defended his Ph.D. Thesis earlier this year. In addition two of the recent biology graduates who have worked on this project have continued to work successfully on other projects in the field of ecological research in British Columbia.

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PART 2: Statement of Expenditures

2. Breakdown of project costs for the period from April 1 2000 to December 1 2000 (Project extension period.)

Name of Accounting Officer: Lynn Diduck Phone No.250-828-4984

Categories	**Budget for this period**	**Actual Expended this period**	**Expended to date (total)**
a) Salaries & Stipends: (not including benefits)		$11,686.00	
b) Employee Benefits:			
c) Equipment:			
d) Travel			
e) Materials/Supplies			
f) Others:			
g) Indirect Costs:			
h) Administration Costs:			
TOTAL:	$13,375	$11,686.00	

Total Expended to Date: ______________________________________

Total Funds Received to Date: ______________________________________

Funds Requested for Next Period: ______________________________________

Please note: A complete listing of all expenditures being claimed, including a listing of invoices and cheque numbers, must be attached to this report.
In addition: Attach a narrative explaining any significant deviations (+/- 10%) between ACTUAL and BUDGETED expenditures.