Lobaria pulmonaria abundance as an indicator of macrolichen diversity in Interior Cedar–Hemlock forests of east-central British Columbia

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Abstract: Orographic precipitation over interior mountains has resulted in the formation of the inland temperate rainforest, where certain stands are potentially antique and support a rich flora of epiphytic macrolichens. We documented macrolichen diversity across three age-classes in forests of the Interior Cedar–Hemlock biogeoclimatic zone (i.e., ICHwk3 subzone) east of Prince George, British Columbia. Our objectives were to report changes in lichen communities with stand age, identify potential indicators of antiquity, and investigate the functional role of dominant species in the ecosystem. We identified 41 taxa, including 4 alectorioid lichens, 21 foliose chlorolichens, and 16 old-growth-associated chlorolichens and cyanolichens. Older forests supported more species than young or mature forests. The abundance of *Lobaria pulmonaria* (L.) Hoffm. was strongly correlated with this increase in diversity and may therefore be an appropriate indicator of stand age in the ICH. The increase in *L. pulmonaria* and other N_2-fixing cyanolichens with stand age may have significant implications for forest nitrogen budgets in the interior of British Columbia, where atmospheric nitrogen deposition is relatively low and biological N_2 fixation accounts for nearly all of the nitrogen lost to forest harvesting. We hope that this greater understanding of lichen ecology across age-classes will promote sustainable stewardship of the remaining old-growth forests of inland British Columbia.

Key words: macrolichen diversity, Interior Cedar–Hemlock zone, *Lobaria pulmonaria*, indicator species, cyanolichens, stand age.

Résumé : La précipitation orographique sur les montagnes de l’intérieur a conduit à la forêt ombrophile continentale, où certains peuplements sont potentiellement anciens et supportent une riche flore de macrolichens épiphytes. Les auteurs ont étudié la diversité des macrolichens, selon trois classes d’âge, dans ces forêts continentales à cèdre et pruche (c.-à-d., zone biogéoclimatique ICHwk3), à l’est de Prince George, en Colombie-Brittanique. Les objectifs étaient de faire état des changements survenant dans les communautés de lichens selon l’âge du peuplement, d’identifier des indicateurs potentiels d’ancienneté et d’étudier le rôle fonctionnel des espèces dominantes dans l’écosystème. On a ainsi identifié 41 taxons, incluant 4 lichens alectoriaux, 21 chlorolichens foliacés et 16 chlorolichens et cyanolichens associés aux vieilles forêts. Les forêts plus vieilles supportent plus d’espèces que les forêts jeunes ou matures. L’abondance du *Lobaria pulmonaria* (L.) Hoffm. montre une forte corrélation avec l’augmentation de la diversité et pourrait conséquemment constituer un bon indicateur de l’âge des peuplements d’ICH. L’augmentation du *L. pulmonaria* et autres cyanolichens fixateurs de l’azote, selon l’âge du peuplement, pourrait avoir des implications significatives quant au budget de l’azote en Colombie-Brittanique continentale, où la déposition atmosphérique de l’azote est relativement faible et où la fixation biologique de l’azote constitue presque la moitié de tout l’azote perdu par la récolte forestière. Les auteurs souhaitent que cette compréhension accrue du rôle écologique des lichens, selon les classes d’âge, permettra de promouvoir une gestion durable des forêts anciennes restantes, en Colombie-Brittanique continentale.

Mots clés : diversité des macrolichens, forêt continentale à cèdre et pruche, *Lobaria pulmonaria*, espèces indicatrices, cyanolichens, âge des peuplements.

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Introduction

The Interior Cedar–Hemlock (ICH) forests of British Columbia are characterized by relatively infrequent disturbances and unparalleled biological diversity. Wet ICH subzones are comparatively undisturbed by stand-replacing events with fire frequencies ≥1000 years (Sanborn et al. 2001). This has resulted in a preponderance of old ICH forests that are typically >350 years old and that have the potential of being much older than the oldest tree, a condition defined as “antique” by Goward (1994). As a possible consequence of this infrequent disturbance regime, the ICH biogeoclimatic zone (Ketcheson et al. 1991) has the greatest tree-level diversity among British Columbia forest zones

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(Meidinger and Pojar 1991) and supports more species of epiphytic (tree-dwelling) lichens than any other inland ecosystem of North America (Goward and Arsenault 2000*a*).

Two general groups of epiphytic macrolichens are found in ICH forests: generalists and old-growth-associated species (Types A and B, respectively, sensu Goward 1993). Generalists include both alectorioid species and foliose chlorolichens that occur throughout the ICH irrespective of stand age and condition and appear to tolerate the fluctuating environmental conditions characteristic of younger developing forests (Goward 1994). By contrast, old-growth-associated species are a group of primarily cyanolichens that are generally found in coastal environments, where prolific rainfall affords the exposure to liquid water necessary for net positive gas exchange (Lange et al. 1986, 1993). For the present study, these lichens are collectively referred to as "oceanic" because of the maritime nature of much of their range. Some of these species are now known to occur in the humid, windward slopes of the interior mountain ranges (Goward and Arsenault 2000*b*). Inland, they tend to proliferate only with relative environmental stability (Goward 1994), conditions that are increasingly satisfied with increased forest age. Goward (1993) postulates the existence of two oceanic species assemblages. The first group comprises species that have relatively broad ecological tolerances (including most notably *Lobaria pulmonaria* (L.) Hoffm.) and are thus fairly widespread. The second group includes species such as *Nephroma occultum* Wetmore and *Sticta oroborealis* Goward & Tønsberg (Tønsberg and Goward 2001) that are rare in the ICH and are generally limited to humid locales in the oldest stands. The fact that these assemblages primarily consist of N_2-fixing cyanolichens has significant implications for nitrogen (N) budgets in these ecosystems, particularly in those where N is limiting (Rhoades 1995).

In the face of increased or sustained harvesting of our oldest and potentially antique ICH forests, the need to understand the effect of stand age on the diversity of rare species and ecological function of dominant macrolichens has never been greater. Similarly, suitable biological indicators of stands antiquity and biodiversity in the ICH are needed for sound forest management and conservation planning.

In British Columbia and elsewhere, certain lichen species have been used as indicators of biodiversity, old-growth forests, forest health, and certain moisture and light regimes (Negi and Gadgil 2002). Unfortunately, the relative paucity of managers who can identify lichens coupled with the rarity and epiphytic nature of many species greatly decreases the operational practicality of using groups of lichens as indicators of stand condition. This impediment led Harrison and Delong (2000) to suggest the use of the easily identified and easily seen gold dust lichen (*Chrysothrix candelaris* (L.) J.R. Laundon) as an indicator of lichen biodiversity. This paper is presented in response to the need for empirical data supporting this hypothesis and a general requirement for information on lichens in the ICH. Our specific objectives are (1) to examine patterns in the composition of epiphytic macrolichen communities across stand age in the ICH; (2) to identify potential positive correlations between stand diversity and stand structure or composition as prospective ground-based indicators of epiphytic diversity; and (3) to quantify the biomass of dominant epiphyte taxa and relate this to the overall N budget for forest ecosystems.

Methods and materials

Study area description

The study sites were located in the Robson Valley within the wet-cool variant of the Interior Cedar–Hemlock biogeoclimatic zone (ICHwk3), approximately 170 km southeast of Prince George in east-central British Columbia. Young (age-classes 4–6: 61–120 years), mature (age-class 8: 141–250 years), and old (age-class 9: 251+ years) stands in mesic to subhydric sites were explored between Clyde Creek (53°18′N, 120°10′W) at the southeastern boundary to Crescent Spur (53°35′N, 120°41′W), at the northwestern boundary of the ICHwk3 subzone. A combination of past forest harvesting, dead trees attributed to hemlock looper (*Lambdina fiscellaria* Hulst.), and site inaccessibility made it impossible to extend the study area any farther to the northwest of the subzone. We attempted to confine our study to toe slopes because of observations of increased cyanolichen species richness in sites of water collection (Goward and Arsenault 2000*b*). However, the additive effects of agriculture, forest harvesting, and residential development significantly reduced the availability of contiguous forests at toe slope locations within the ICHwk3. We therefore focused on sites with prolific growth of devil's club (*Oplopanax horridus* Miq.) as an indicator of seepage, localized nutrient enrichment, and high site productivity (Klinka et al. 1989). Goward and Arsenault (2000*c*) suggested that nutrient enrichment in microhabitats surrounding *Populus* species is in part responsible for increased lichen species richness. Sites containing either cottonwood (*Populus balsamifera* subsp. *trichocarpa* (Torr. & A. Gray) Bradshaw) or aspen (*Populus tremuloides* Michx.) could not be consistently located at each site, and so were avoided entirely. Three sites were selected in each of young, mature, and old forest types.

Three western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees were selected at each of the nine sites (Table 1), with the exception of site 9-3, where only two trees were climbed because of an early snowfall. Hemlock was chosen instead of western redcedar (*Thuja plicata* Donn ex D. Don) because of greater observed epiphyte diversity in hemlock over cedar (Goward and Arsenault 2000*a*). Structural safety and a high level of epiphytic species richness were the sole criteria for candidate tree selection. Lichen species richness was assessed from the forest floor through ground-level observations at each candidate site. The trees with the most species within the visible lower canopy were chosen and subsequently rigged, climbed, and sampled vertically at various heights.

Mensuration and site measurements

A circular study plot was established surrounding each study tree and divided into a 0.05-ha inner circle (12.3 m radius) and a 0.1-ha outer circle (17.8 m radius). The stand composition of the inner circle was sampled by recording species and diameter at breast height (DBH) for each tree with a DBH between 10 and 25 cm. For every tree within the inner and outer plot exceeding 25 cm in DBH, we recorded (1) species; (2) health (alive or dead); (3) DBH;

Table 1. Location and basic site descriptions of nine field sites for epiphytic lichen biodiversity comparisons within the ICHwk3.

Site	Map sheet and polygon	Age-class	Approximate location	Forest cover
5-1	93H39-617 (E2s/L)	5	Clyde Creek	CS (HB)
5-2	93H38-420	6[a]	Lamco Road (West Twin Creek)	SH (FB)
5-3	93H47-391	4[a]	Confluence of Milk River and Goat River	SHB (At)
8-1	93H48-412	8	West Twin Creek	H (CS)
8-2	93H68-97	8	Morekill River	HC (SB)
8-3	93H48-541	8	Between West Twin Creek and Clyde Creek	HC (S)
9-1	93H47-69 (E2s)	9	Lower Goat River	CH (S)
9-2	93H68-163	9	Morekill River	CSH (B)
9-3	93H48-167	9	West Twin Creek	HC

Note: Forest cover abbreviations are as follows: C, western redcedar (*Thuja plicata*); S, hybrid spruce (*Picea engelmannii* × *Picea glauca*); H, western hemlock (*Tsuga heterophylla*); B, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.); F, interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco); At, trembling aspen (*Populus tremuloides*).

[a] Because of the relative scarcity of age-class 5 stands containing *Thuja plicata* or *Tsuga heterophylla* in the ICH, age-classes 4 and 6 stands were used to complete the young samples. These are henceforth collectively referred to as “young” stands.

Table 2. Abundance scales for gold dust lichen (*Chrysothrix candelaris*).

Abundance scale	Corresponding lichen biomass
1	One or two discrete colonies per tree trunk
2	Three to six discrete colonies per tree trunk
3	Greater than six discrete colonies per tree bole to 20% trunk cover
4	20%–50% trunk cover
5	>50% trunk cover

Note: A discrete colony was defined as a patch of lichen that was discontinuous with other patches of lichen.

Table 3. Overlap classes defining the spatial relationship between the study tree (in which lichen biodiversity was assessed) and the surrounding trees.

Class	Definition
1	No overlap, open, all branches completely clear of other trees
2	Tips of branches touching other trees on 1–180° of the study tree circumference
3	Tips of branches touching other trees on 181–270° of the study tree circumference
4	Main branch axes overlapped by branches on 1–180° of the study tree circumference
5	Main branch axes overlapped by branches on 181–270° of the study tree circumference
6	Tree totally overlapping with adjacent trees on 360° of the study tree circumference

(4) height of lowest branch; (5) visual appearance: crown condition, bark retention, and wood condition (5-point scales according to Meidinger 1998); (6) wildlife use; (7) height of gold dust lichen using the scale described in Table 2; and (8) abundance of *L. pulmonaria* (assessed as the number of “clumps” per plot, after Benson and Coxson 2003). Abundances of *L. pulmonaria* and gold dust lichen were estimated using ground-level observations, because of their potential use as indicators of epiphytic lichen biodiversity. Based on Meidinger (1998), coarse woody debris quality and quantity were recorded along transects beginning at plot centre and extending for 15 m in two randomly selected directions.

Canopy measurements

The distance to and DBH of the tree nearest the study tree in each of eight directions (east, southeast, south, southwest, west, northwest, north, and northeast) were recorded. The degree of overlap of the study tree with the surrounding trees was recorded using a 6-point scale (Table 3). Finally, the study tree and 2–3 surrounding trees were cored using an increment borer to obtain tree ages. Any spruce (*Picea engelmannii* Parry ex Engelm. × *Picea glauca* (Moench) Voss) in the vicinity (even if they did not fall within the plot) were cored in an attempt to obtain an accurate age, as most western hemlock and western redcedar in the stands had some degree of heart rot.

All branches that could safely be accessed using the single rope technique (Perry 1978) were assessed for lichen composition and abundance. The clump method (Campbell et al. 1999) was used to estimate biomass for three dominant taxa: *Alectoria* (which was predominantly *Alectoria sarmentosa* (Ach.) Ach., but also included rarer occurrences of *Ramalina thrausta* (Ach.) Nyl. and *Usnea* Dill. ex Adans. spp.), *Bryoria* (including *Bryoria* Brodo & D. Hawksw. spp. and *Nodobryoria* Common & Brodo spp.), and *Platismatia glauca* (L.) Culb. & C. Culb. Biomass of *L. pulmonaria* was estimated using a modification of the clump method (Benson 2001). Briefly, the amount of lichen present was compared to a "clump" of lichen with a known biomass (*Alectoria* and *Bryoria* clump = 2.5 g; *Platismatia glauca* clump = 1.5 g; and *L. pulmonaria* clump = 5 g) and recorded as a multiple of that clump.

The canopy was divided into three distinct height zones based on vertical changes in lichen species composition. The upper canopy was characterized by abundant *Bryoria* (particularly nonsorediate species), the middle canopy by copious *A. sarmentosa* and *Platismatia glauca*, and the lower canopy by the presence of cyanolichens (primarily *L. pulmonaria*).

Stand-level biomass and N

Representative samples of the dominant epiphytic macrolichens were sampled along vertical transects for each of the study trees in all young and old sites. Macrolichen biomass per area was estimated by multiplying biomass of the dominant macrolichens (described previously) by the density of western hemlock in the stands. Biomass samples were oven dried at 55 °C for 3 d before they were weighed, ground to a fine powder in a mortar and pestle, and total N was determined by a flash combustion of duplicate 5-mg subsamples (NA 1500 NC Elemental Analyzer, Fison Instruments, Milan, Italy). Finally, estimates of stand-level N were calculated by multiplying stand-level macrolichen biomass by macrolichen N content.

Species identification

Three sample branches were removed from each of the three height zones per tree. Effort was made to collect the branch with the greatest lichen species richness from each height stratum. Each branch was carefully cut into 20- to 40-cm segments, labelled for branch reconstruction, and bagged in paper for long-term storage. The number of discrete thalli (i.e., disconnected from other thalli of the same species) >3 mm in length was counted for each species encountered on all parts of the branch. Lichens such as *Fuscopannaria* P.M. Jörg. spp., which are not expected to grow >3 mm (Brodo et al. 2001), were counted when observed, regardless of size.

Statistical analysis

Lichen species were categorized as chlorolichens or cyanolichens for preliminary analysis using Systat 10 (SPSS Inc. 2000). An analysis of variance (ANOVA)with a Bonferroni adjustment was used to compare differences in species richness (number of species per tree) and species abundance across age-classes. Species diversity patterns were assessed using the Shannon–Wiener function (H′), because it is particularly sensitive to rare species (see Krebs 1999). A one-way ANOVA with a Tukey's post hoc test was used to compare the maximum height to which cyanolichens were found across age-classes.

An indirect ordination analysis was used to describe species patterns as a function of measured environmental variables. An NMS (nonmetric multidimensional scaling, NMS PC-ORD, version 4, McCune and Mefford 1999) was chosen as an ordination technique, because of the reputed robustness when analyzing non-normal and discontinuous data (McCune and Grace 2002). Species were grouped by tree to elucidate species patterns across varying stand ages. Rare species were retained in our analysis because we wanted to describe the diversity of species as a function of the environmental variables (as per McCune and Mefford 1999). There were 41 species (Table 4) and 26 plots in the primary matrix and 16 environmental variables and 26 plots in the secondary matrix. The environmental variables were age-class, canopy overlap, average distance to nearest tree, minimum distance to nearest tree, maximum distance to nearest tree, minimum tree DBH, maximum tree DBH, average plot DBH, height of lowest limb in study tree, average height of gold dust lichen in plot, average biomass of *L. pulmonaria* in plot, amount of coarse woody debris in plot, percent cedar composition in plot, percent hemlock composition in plot, and tree density in plot. Species data were log transformed to reduce skewness in the data. We used the "slow and thorough" autopilot mode with a Sorenson distance measure and a random starting configuration. The ordination was produced following 43 iterations and had a stability criterion of 0.00001. The resulting ordination graph was rotated by the secondary matrix variable "age" to improve interpretability. Simple correlations were used to test the relationship between macrolichen diversity and environmental factors.

A Kruskal–Wallis nonparametric ANOVA with a multiple mean comparison post hoc test with adjustments for unequal sample size and tied ranks was used to compare differences across age-classes in *A. sarmentosa*, *Bryoria* spp., *Platismatia glauca*, and *L. pulmonaria* biomass and across all species and age-class combinations for macrolichen N content (Zar 1984).

Results

There were 41 lichen taxa observed across the 26 trees in our study (Table 4), 37 of which were identified to the species level. Because of time constraints, *Bryoria*, *Parmelia*, and *Usnea* were identified only to genus level, and *Pannaria* Delise. and *Fuscopannaria* were identified only to family level (Pannariaceae). The species assemblage included 4 alectorioid lichens, 21 foliose chlorolichens found generally across the stand (i.e., generalists or Type A, sensu Goward 1993), 6 old-growth-associated chlorolichens, and 10 old-growth-associated cyanolichens (oceanic or Type B, sensu Goward 1994).

We observed a greater total number of lichen species (chlorolichens and cyanolichens) in older forests, an observation consistent with the literature (Benson and Coxson 2003; Pike et al. 1977; Sillett and Neitlich 1996). Out of 41 possible taxa, 35 were found in old stands, 33 in mature stands, and 25 in young stands (Table 4). Young stands supported a significantly lower number of epiphytic macrolichen species (15.4 ± 0.6 species per tree; $n = 9$) than did mature and old stands, with 20.7 ± 0.6 ($n = 9$) and 24.0 ± 1.2 ($n = 8$) species per tree, respectively ($F_{[2,23]} = 26.33$, $p < 0.0001$; Fig 1A). These observations translated into a trend of increasing diversity (H′) for epiphytic lichen species with increasing forest age (Fig. 1B). By contrast, there was an inconsistent and small decline in evenness (E) from the young stands to the mature and old stands (Fig. 1C).

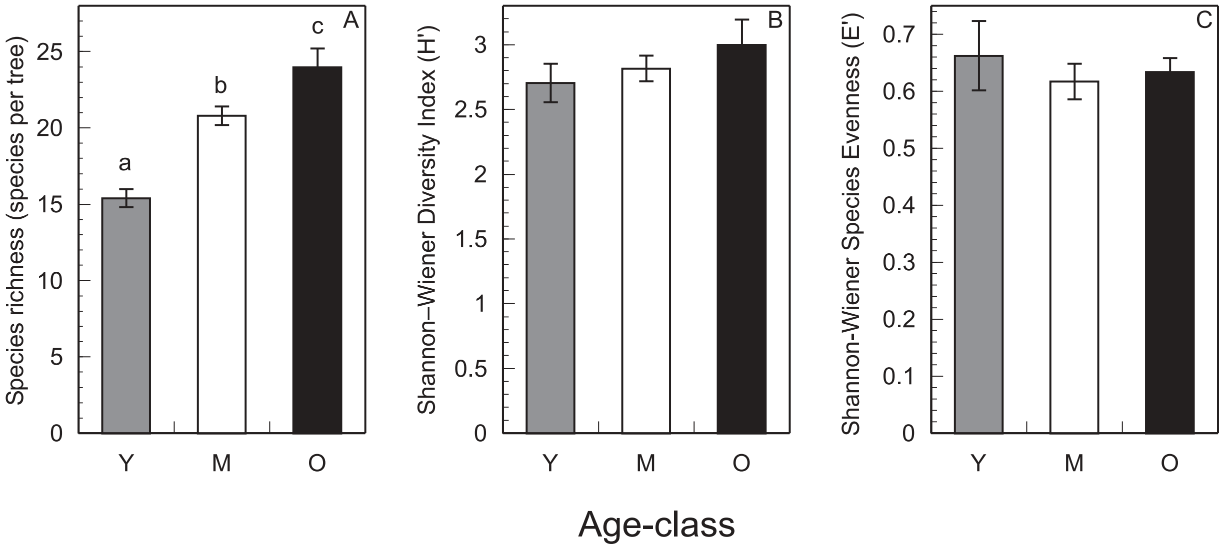
Many of the generalist chlorolichens (i.e., *A. sarmentosa*, *Bryoria* spp., *Platismatia glauca*, *Parmelia* Ach. spp.,

Table 4. Green and cyanophytic macrolichens observed on three branches in young (age-class 5), mature (age-class 8), and old (age-class 9) trees in the Interior Cedar–Hemlock biogeoclimatic zone.

		Presence		
	Species code	Young	Mature	Old
Generalist species				
Alectorioid chlorolichens (4 spp.)				
Alectoria sarmentosa	ALESAR	T	T	T
Bryoria spp.	BRYSPP	T	T	T
Usnea spp.	USNSPP	A	A	A
Ramalina thrausta	RAMTHR	VS	—	VS
Foliose chlorolichens (21 spp.)				
Evernia mesomorpha	EVEMES	VS	—	—
Hypogymnia austerodes	HYPAUS	S	A	T
Hypogymnia bitteri	HYPBIT	S	S	A
Hypogymnia imshaugia	HYPIMS	—	VS	—
Hypogymnia metaphysodes	HYPMET	A	A	T
Hypogymnia occidentalis	HYPOCC	T	T	T
Hypogymnia oroborealis	HYPORO	VS	S	S
Hypogymnia physodes	HYPPHY	T	T	T
Hypogymnia tubulosa	HYPTUB	T	A	T
Imshaugii aleurites	IMSALE	VS	VS	VS
Kaernefeltia merrillii	KAEMER	VS	—	—
Melanelia subaurifera	MELSUB	VS	—	—
Parmeliopsis ambigua	PARAMB	T	T	T
Parmeliopsis hyperopta	PARHYP	T	T	T
Parmelia spp.	PARSPP	T	T	T
Platismatia glauca	PLAGLA	T	T	T
Tuckermanopsis americana	TUCAME	S	S	S
Tuckermanopsis chlorophylla	TUCCHL	T	T	T
Tuckermanopsis orbata	TUCORB	A	A	A
Tuckermanopsis platyphylla	TUCPLA	S	VS	S
Vulpicida canadensis	VULCAN	—	VS	—
Old-growth-associated species (oceanic)				
Foliose chlorolichens (6 spp.)				
Cavernularia hultenii	CAVHUL	—	VS	VS
Hypogymnia oceanica	HYPOCE	—	VS	—
Hypogymnia rugosa	HYPRUG	S	A	A
Hypogymnia vittata	HYPVIT	A	A	A
Platismatia herrei	PLAHER	—	—	VS
Platismatia norvegica	PLANOR	—	VS	VS
Foliose cyanolichens (10 spp.)				
Lobaria pulmonaria	LOBPUL	—	A	A
Lobaria hallii	LOBHAL	—	—	S
Lobaria scrobiculata	LOBSCR	—	VS	VS
Nephroma helveticum	NEPHEL	—	S	A
Nephroma isidiosum	NEPISI	—	—	A
Nephroma occultum	NEPOCC	—	—	VS
Nephroma parile	NEPPAR	—	S	A
Pannaria spp.	PANSPP	—	VS	VS
Pseudocyphellaria anomala	PSEANO	—	VS	S
Sticta fuliginosa	STIFUL	—	VS	S

Note: *Bryoria*, *Parmelia*, *Usnea*, and *Pannaria* were identified to genus because of time considerations. Abundance is recorded as follows: (—), absent; VS, very sparse (one or two thalli per branch); S, sparse (found on up to one-third of sample branches); A, abundant (found on over one-third of sample branches); T, total (found on every sample branch).

Fig. 1. Mean epiphytic macrolichen (A) species richness (species per tree) and Shannon–Wiener (B) diversity and (C) evenness for hemlock trees in three age-classes, young (Y), mature (M), and old (O), of the Interior Cedar–Hemlock inland rainforest (ICHwk3) in east-central British Columbia. Mean values are shown ±SE, and only those values with different letters differ significantly for an α of 0.05.



Parmeliopsis ambigua (Wulfen) Nyl., *Parmeliopsis hyperopta* (Ach.) Arnold, *Hypogymnia physodes* (L.) Nyl., *Hypogymnia occidentalis* L. Pike, *Hypogymnia tubulosa* (Shaerer) Hav., and *Hypogymnia metaphysodes* (Asah.) Rass.) were ubiquitous throughout canopies of all ages and were observed over nearly every branch in the study (Table 4). Minor increases in the number of thalli of most other generalist chlorolichens were observed with increasing stand age (Figs. 2A and 2B). There were two notable exceptions: *Platismatia glauca*, which had significantly more individual thalli in older stands (Kruskal–Wallis test statistic (2) = 9.517, p = 0.009), and *Tuckermannopsis chlorophylla* (Willd.) Hale, which showed irregular relationships with stand age compared with other species. Also note that *Evernia mesomorpha* Nyl. and *Kaernefeltia merrilli* (Du Rietz) Thell & Goward (Thell and Goward 1996) were found only in young stands, and *Hypogymnia imshaugii* Krog and *Vulpicida canadensis* (Räsänen) J.-E. Mattsson & M.J. Lai were found only in mature stands. However, these species are omitted from Fig. 2 because of the single observation of each in the study.

Old-growth-associated chlorolichens included *Cavernularia hultenii* Degel., *Hypogymnia vittata* (Ach.) Parrique, *Hypogymnia rugosa* (G. Merr.) L. Pike, *Hypogymnia oceanica* Goward, and *Platismatia norvegica* (Lynge) Culb. & C. Culb. (as per Goward 1994). *Cavernularia hultenii*, *H. oceanica*, and *Platismatia norvegica* were all absent from young stands. *Hypogymnia vittata* and *H. rugosa*, by contrast, were found in young stands, but they were observed in the older stands with exponentially increasing abundance (Figs. 2C and 2D).

Cyanolichens were even more strongly associated with old-growth forests than were chlorolichens. There were no old-growth-associated cyanolichen species found on sample branches in young stands, and increases in the number of thalli per branch from mature to old stands were significant ($F_{[2,18]}$ = 5.926, p = 0.01; Figs. 2E and 2F). For example, we observed average branch loadings for *Nephroma helveticum* Ach. and *L. pulmonaria* (the two most common cyanolichens) of 2.1 ± 1.2 and 22.4 ± 7.8 discrete thalli, respectively, in mature stands. This compared with 33.6 ± 22.8 and 83.2 ± 34.6 thalli counted for *N. helveticum* and *L. pulmonaria*, respectively, on comparable branches in old stands (Fig. 2E). Furthermore, three of the 10 cyanolichen species occurred only in old stands (Table 4), and only one cyanolichen species (*L. pulmonaria*) was found in young stands.

The maximum height to which old-growth-associated chlorolichens and cyanolichens were found increased significantly with stand age. In young stands, oceanic species were rarely found on coarse woody debris and never in the study trees, suggesting the height of oceanic species colonization in these stands is <50 cm. By contrast, the maximum height to which oceanic species were found in mature and old stands was significantly higher at 15.6 m and 26.5 m, respectively ($F_{[2, 23]}$ = 104.787, p < 0.0001).

Forty-one lichen taxa were analyzed using an NMS ordination (Fig. 3). The final ordination, achieved after 40 runs with real data had a final instability of 0.0001 and a final stress of 12.37628. Two axes captured most of the variance in the lichen communities, with axes 1 and 2 accounting for 74.4% and 16.5% of the variance, respectively. Higher dimensions improved the model very little and thus were excluded from the analysis. Axis 1 was strongly correlated both with the average age of the stand (r^2 = 0.822) and with the abundance of *L. pulmonaria* in the plot (r^2 = 0.816). Axis 2 was related to the parameters of stand density (r^2 = 0.589) and stand DBH (r^2 = –0.531).

Lobaria pulmonaria was also well correlated with macrolichen richness at the site scale (r^2 = 0.687, Fig. 4A). By

Fig. 2. The average number of (A, B) generalist chlorolichen; (C, D) old-growth-associated chlorolichen; and (E, F) old-growth-associated cyanolichen thalli per branch across three age-classes. Note different abundance scales on the *y*-axis. *Lobaria hallii* (Tuck.) Zahlbr. was found on one branch in an old stand but was omitted from (F) because of its extreme rarity. In addition, alectorioid species are also excluded because biomass, not number of thalli, was quantified.

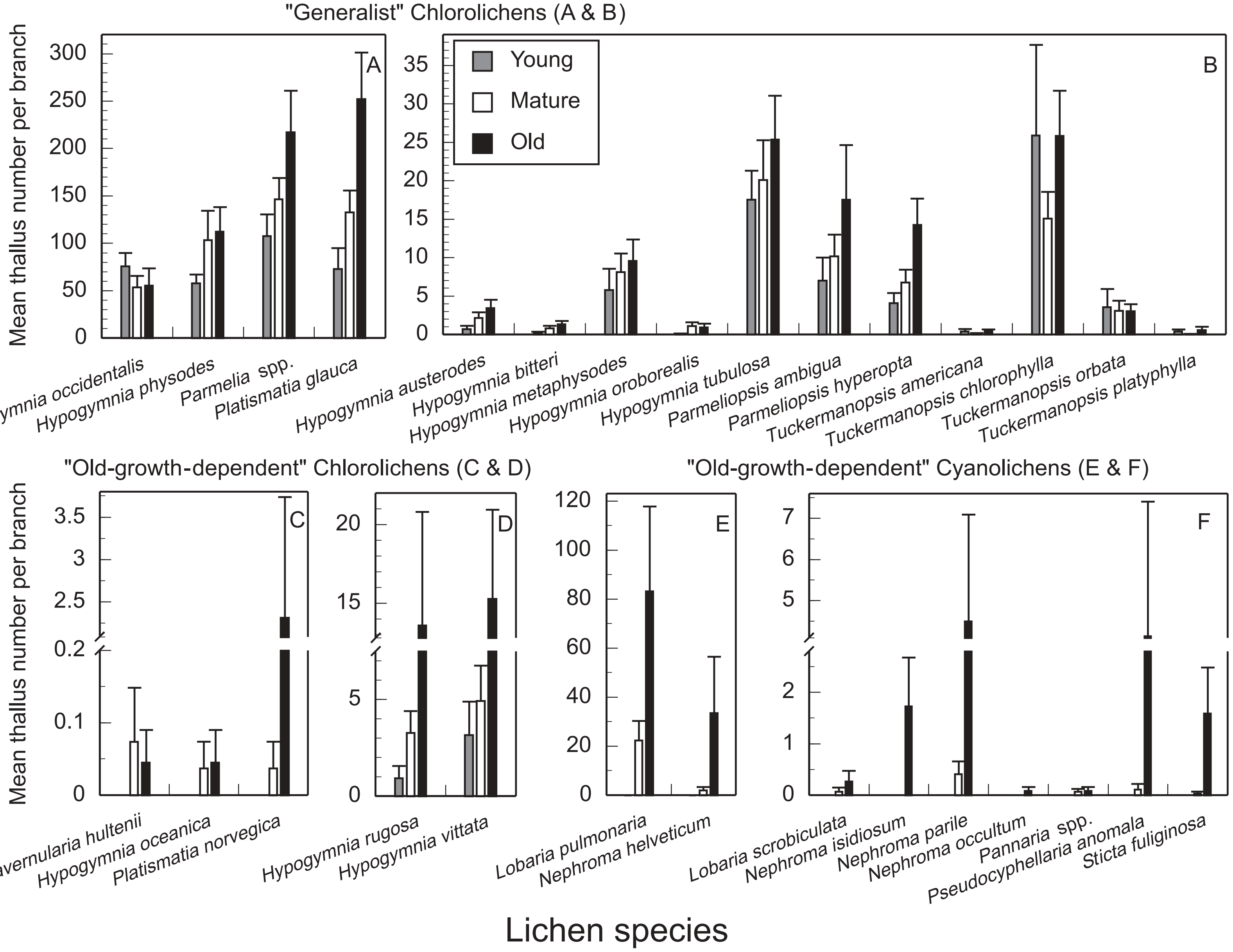


Fig. 3. NMS ordination results showing the gradients in species composition along two dimensions. Axis 1 is strongly correlated with the parameters of stand age ($r^2 = 0.619$) and *Lobaria pulmonaria* abundance ($r^2 = 0.578$) and accounts for 77.3% of the variance in the model. Axis 2 captured much of the remaining variance (12.4%) and was related to the parameters of tree density ($r^2 = 0.359$) and tree diameter ($r^2 = 0.243$). Overlays group species into generalists (alectorioid and foliose chlorolichens) and old-growth-associated cyanolichens and chlorolichens.

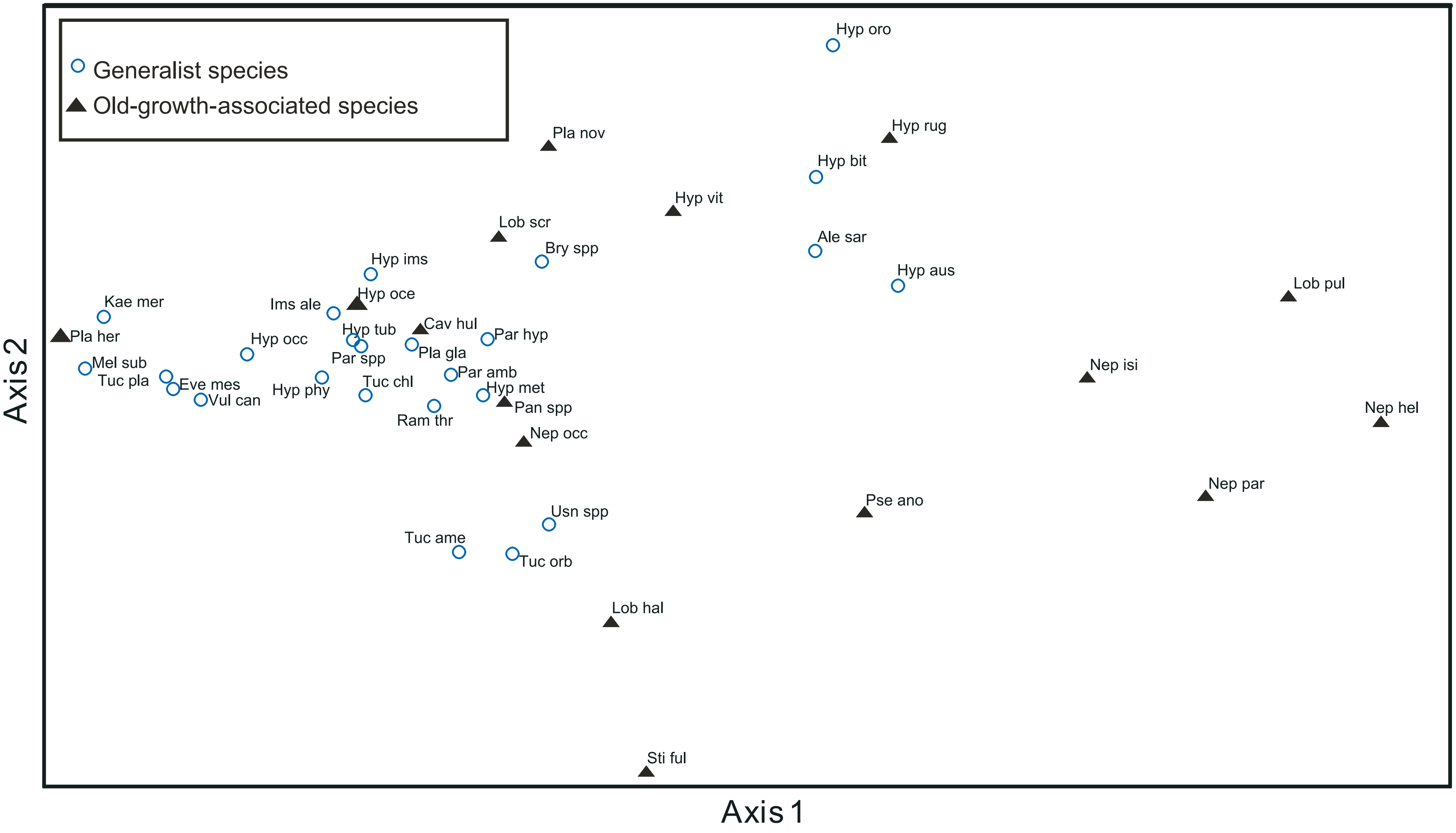


Fig. 4. The relationship between the average number of macrolichen species observed in the study tree and abundance of (A) *Lobaria pulmonaria* and (B) *Chrysothrix candelaris* (gold dust lichen) in the 0.1-ha sample plot surrounding the study tree. *Lobaria pulmonaria* abundance was recorded as biomass, while gold dust lichen was recorded on the abundance scale described in Table 2.

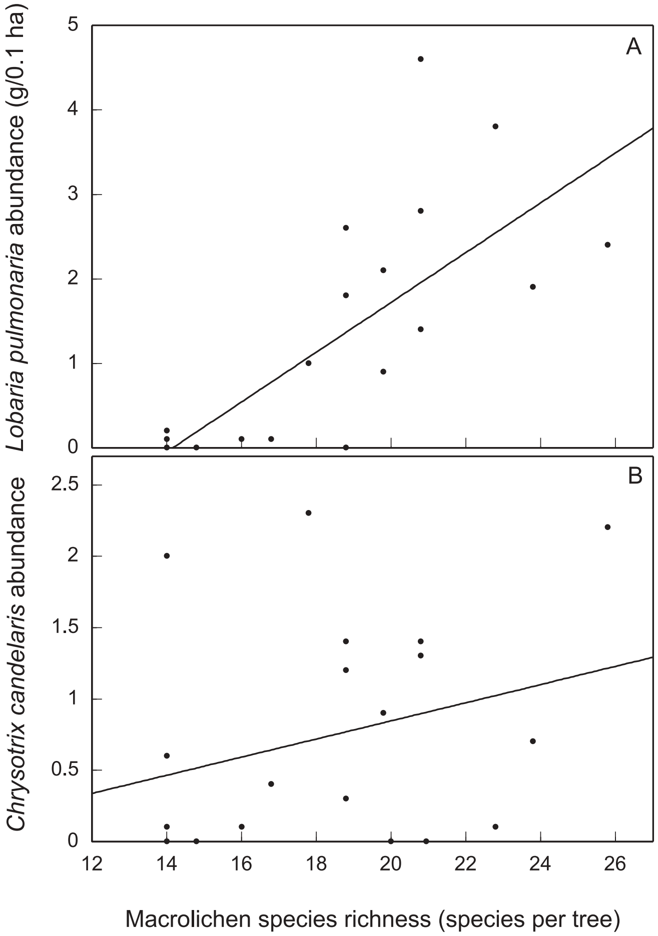
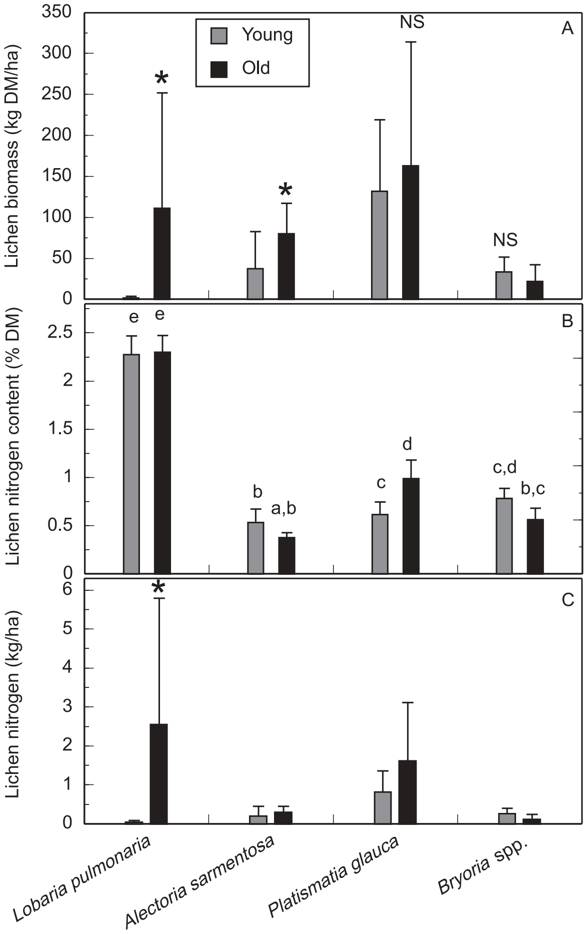


Fig. 5. Estimates of (A) areal dry biomass, (B) nitrogen content, and (C) areal total nitrogen for the dominant macrolichens in hemlock trees from young and old forest stands. Mean values are shown ±SE. Means with different letters differ significantly across all species and age-classes, while those with asterisks differ significantly from the other age-class within a particular species for an α of 0.05. DM, dry mass.



contrast, there was very little relationship between abundance of gold dust lichen and macrolichen biodiversity (r^2 = 0.004, Fig. 4B).

There were significant differences in biomass of all four dominant taxa across the three forest ages (Kruskal–Wallis (2) = 132.634, $p < 0.0001$). The average branch loading of *L. pulmonaria* in young stands was negligible (0.034 ± 0.020 g) and significantly less than biomass loadings on branches in mature and old stands, which averaged 2.8 ± 0.7 g and 7.2 ± 1.2 g, respectively. The differences in *L. pulmonaria* biomass were even more pronounced when whole tree loadings were compared, with old stands having over 100 times more *L. pulmonaria* biomass than young stands (Fig. 5A). Differences in the biomass of the three dominant chlorolichens across age-classes were also significant. *Alectoria sarmentosa* (Kruskal–Wallis (2) = 209.208, $p < 0.0001$) and *Platismatia glauca* (Kruskal–Wallis (2) = 73.165, $p < 0.0001$) were both consistently more abundant in mature and old stands than in young stands. *Bryoria* biomass, by contrast, was greatest in mature stands (Kruskal–Wallis (2) 28.463, $p < 0.0001$). These abundances, when extrapolated to a per-hectare level, resulted in 80, 20, and 163 kg/ha in old stands compared with 38, 34, and 132 kg/ha in young stands for *Alectoria*, *Bryoria*, and *Platismatia glauca*, respectively (Fig. 5A).

To determine the potential significance of high biomass lichen loadings (particularly *L. pulmonaria*) to the N budgets of ICH forests, percent N was determined for the four most abundant epiphytes: *L. pulmonaria*, *A. sarmentosa*, *Bryoria* spp., and *Platismatia glauca*. N contents were significantly higher in *L. pulmonaria* (the lone cyanolichen) than in the three chlorolichen taxa (Fig. 5B). When these N contents were scaled up to a per-hectare level we found that *L. pulmonaria* was the most important source of N in old stands (Fig. 5C). Total N (from the dominant lichens) was in fact over 3-fold higher in old stands (4.6 kg N/ha) than in young stands (1.3 kg N/ha). These estimates are likely extremely conservative, because they were based on lichen biomass estimates and tree density for hemlock only (which made up 55.6%, 61.5%, and 48.1% of the stand in young, mature, and old stands, respectively).

Discussion

The ICH biogeoclimatic zone is one of the most biologically rich forested zones of British Columbia (Ketcheson et al. 1991). Within this wealth of life is a relatively little known and poorly understood community of epiphytic lichens. Several studies (Goward and Arsenault 2000*b*; Goward 1994, 1995, 1996; Radies 2002) have documented species diversity across a range of ICH forest types. The present study complements existing knowledge by providing information regarding the patterns of macrolichen diversity across age-classes, reporting on physical and biological characteristics that may be used as indicators of this diversity, and offering insight into the function of dominant epiphytes in the ICHwk3.

Patterns in macrolichen species composition across age-classes

Forty-one macrolichen taxa were observed over 26 western hemlock trees in the ICHwk3. Note that this level of species diversity was observed only in the oldest stands (Fig. 4). Our data show that old ICH forests have the greatest diversity of epiphytic macrolichens (Fig. 1A), with 35 of the 41 total taxa identified overall found in old stands (Table 4). By contrast, mature stands contained 33 taxa, and young stands contained only 25 different taxa. This same trend was mirrored at the tree level, with old, mature, and young trees containing 24, 21, and 15 species per tree, respectively.

With perhaps two exceptions, lichen species found in young forests were generalists and accounted for less than two-thirds of the total number of species. The remaining macrolichens were the more rare species, which, while prolific in old forests, were generally absent from young stands and sparse in mature stands (Table 4, Fig. 4).

The absence of these old-growth-associated species in younger forests may be attributed to microclimate unsuitability or slow rates of dispersal. Sillett and Antoine (2004) suggest the former: the higher levels of atmospheric moisture allow for the prolific cyanolichen accumulation in maritime forests. Ecophysiological studies on tolerance to desiccation concur, showing that cyanolichens require high levels of atmospheric moisture (Goward 1994; Sillett and Neitlich 1996) as well as liquid water for photosynthetic activity and growth (Büdel and Lange 1991; Lange et al. 1986, 1993).

Other studies, on the other hand, have demonstrated cyanolichen survival following transplantation to young forest environments (Sillett and McCune 1998) and thus support an alternate hypothesis of dispersal being a limiting factor (Sillett and Goslin 1999; Peck and McCune 1997; Sillett et al. 2000; Dettki et al. 2000). Goward (1994) suggested that the dearth of cyanolichens in younger forests was attributable to a slow rate of colonization into new locales and that old growth and the associated absence of stand-level disturbances may be required before a forest would begin to host an abundance of macrolichens. These authors intimate that if microclimate plays a role in limiting lichen colonization, it must be functioning in concert with dispersal limitations. This may be particularly true of lichens in ICH forests because they are in a relatively thin elevational band of rainforest, isolated from the coastal cedar–hemlock forests that may be the original source of these oceanic species.

Our results, which show an extreme impoverishment of oceanic species in younger stands (Fig. 4), give credence to both hypotheses. The hypothesis that we are putting forth in the present study combines the two: dispersal limits lichen colonization in young ICH forests, but the disparity in diversity between mature and old stands is more a result of microclimatic differences. Three observations substantiate this hypothesis. First, there was a relatively low abundance of oceanic species within mature stands (Fig. 4), and only two oceanic species were observed with more than very sparse abundance (Table 4). One of the two oceanic species was *L. pulmonaria*, which is a cephalodiate species in which the N_2-fixing cyanobacteria may be protected from desiccation. This species would not likely be subjected to the same ecological limitations as noncephalodiate cyanolichens. Its presence in young and mature stands is generally limited to coarse woody debris and very low branches, respectively, where forest-floor water may create a moisture-enriched microclimate that is not generally indicative of young or mature canopy conditions.

Second, although some oceanic species were found in mature stands, we observed an upper vertical limit of oceanic species colonization. It appears that the height to which cyanolichens are commonly found in the stand increases significantly with stand age (Fig. 6). Therefore, it is conceivable that this height physically represents the upper limit of permissive atmospheric moisture conditions. The zone in which oceanic species are found in mature stands is only a fraction of what it is in old stands perhaps, which may explain the dramatic increase in the abundance of cyanolichen lichen thalli found from old to mature forests.

Third, a comparison of lichen species richness between the two wettest subzones in the ICH reveals that although species richness is comparable across the wet ICH subzones, there is a significantly higher abundance of rare cyanolichens in the ICHvk (very wet cool; Radies 2002) than in the ICHwk (wet cool). The ICHvk, being of a similar latitude, tree species composition, and geography, differs from the ICHwk only in its greater annual precipitation (Reynolds 1997[2]). Thus the observed difference between the epiphytic communities is likely attributable to higher levels of atmospheric moisture characteristic of the ICHvk.

Overall, it seems likely that the maintenance of rare, oceanic macrolichens within the globally unique ICH bioregion may depend both on a low frequency of stand-level disturbance and long-term ecological continuity to facilitate dispersal and on zones of locally high atmospheric humidity to allow prolific accumulation. Stands that satisfy these criteria are considered likely to be antique and have an increased probability of supporting oceanic and potentially scarce lichens.

Indicators of lichen diversity

The primary impediment to sustainable management of these potentially antique stands (i.e., stands that are older

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[2] R.R. Reynolds. 1997. Climatic data summary for the biogeoclimatic zones of British Columbia. B.C. Ministry of Forests, Research Branch, Victoria, B.C. Unpublished report.

than the oldest trees) and the level of diversity observed in older ICH stands is that there is no "blanket" method for distinguishing between mature, old, and even antique forests. Tree ages themselves are difficult to determine with standard dendrochronological techniques (i.e., increment borer), since the dominant tree species in the ICH zone (western redcedar and western hemlock) are highly susceptible to heart rot (Peterson et al. 1998), and the techniques are in any case incapable of determining the age of antique stands. Sanborn et al. (2001) suggest that carbon dating of charcoal layers in the soil may be an effective method of aging certain stands. However, this method is expensive and geographically limited to toe slope locations where the probability of land movement affecting the charcoal layers is low.

An alternative to determining the age of the stand is to use the presence, absence, or abundance of an ecosystem trait or value (e.g., seral stage distributions), specific vegetation complexes, or indicator species to indicate forest age. International studies have shown that the diversity of epiphytic lichens is an ideal indicator for such purposes. It is a good measure for diversity in many other taxa (Negi and Gadgil 2002) and an ideal indicative feature for potential habitats of threatened species (Johansson and Gustafsson 2001). Indeed, within the ICH, certain cyanolichens have been found to be absent in all younger forests (Goward and Arsenault 2000*b*). The presence of high epiphytic cyanolichen biodiversity might therefore be used to identify antique stands. Unfortunately, using epiphytic lichens as an indicator of stand age uses circular logic in that high epiphyte biodiversity would be employed to locate stands of antiquity, which in turn would be used to identify areas of high biodiversity. Nonetheless, relatively few managers can identify lichens to the species level in the field, and so the indicator potential of these lichens is generally not practical. Thus a more easily measured indicator is required.

For candidate indicator measures, we turn to the results of our ordination. Correlations were significant between lichen biodiversity and (1) increasing stand age, (2) decreasing stand density, (3) increasing tree diameter, and (4) increasing *L. pulmonaria* abundance. There is little possibility of using stand age, as discussed previously, because of the ineffectiveness of standard dendrochronological techniques with ICH trees. Although both stand density and tree diameter are well correlated with biodiversity, the relationships are not strong enough to provide accurate proxy measures of diversity.

The remaining correlate, *L. pulmonaria*, was the most promising indicator of those evaluated. It was found in all age-classes, and the abundance increased with stand age and was strongly and positively correlated with macrolichen biodiversity (Fig. 3A). *Lobaria pulmonaria* is also large, is easily recognizable by its distinctive morphology, occurs low in the canopy, and is readily quantified because of its relatively uniformly sized foliose thalli (Benson 2001). Fortunately, the precedent for using epiphytic lichens in assessments of habitat suitability has already been made. Armleder et al. (1992) developed a handbook for estimating the abundance of epiphytic alectorioid (forage) lichens for use by forest managers in evaluating potential caribou habitat. These methods could easily be expanded to include *L. pulmonaria* in appraising stand antiquity or biodiversity.

Although *L. pulmonaria* abundance appears to be an ideal indicator for biodiversity, it needs to be used cautiously on three levels. First, only the relative abundance of this lichen is indicative of age. The relative ubiquity of *L. pulmonaria* negates the ability to predict stand conditions by the presence alone. By the same token, the absence of *L. pulmonaria* reveals very little, as many factors could account for the lack of thalli in specific ecosystems, and stands without *L. pulmonaria* could not be automatically classified as taxonomically poor. Second, *L. pulmonaria* abundance should only be employed as a preliminary indicator of stand age, a "flag" to highlight which stands should be prioritized for further research. Third, currently *L. pulmonaria* can only be used as an indicator in sites over similar spatial scales and with similar stand and geographic conditions as those in the present study. The variable habitat conditions under which *L. pulmonaria* can proliferate in other ecosystem types makes it unpredictable as a general forest management tool. For example, in the conifer forests of British Columbia, *L. pulmonaria* tends to be locally abundant over nutrient-rich soils and on particular species of trees (e.g., *Populus balsamifera* subsp. *trichocarpa* and *Betula papyrifera* Marsh.) regardless of stand age. Another example of *L. pulmonaria*'s heterogeneous ecology can be found in eastern mixed-wood forests, where *L. pulmonaria* is typically an epiphyte on maple (*Acer* spp.) and is only rarely found on conifers (MacKenzie et al. 2001).

Epiphytic lichen biomass and the overall N budget for forest ecosystems

Others have persuasively demonstrated that increases in biodiversity do not necessarily reflect the functional implications of that diversity and that presence of functional groups can be as or more important than overall species numbers (Hooper and Vitousek 1997) to roles such as N_2 fixation. Atmospheric N deposition is relatively low in the interior of British Columbia, and so biological N_2 fixation can account for nearly all of the N lost to forest harvesting (see Brockley et al. 1992). Still, annual inputs are likely low. For example, in adjacent higher elevation Engelmann spruce – subalpine fir forests, total N inputs are less than 1 $kg \cdot ha^{-1} \cdot year^{-1}$ (Hope 2001). N inputs from epiphytes are therefore potentially important, particularly in old ICH forests where the average total N pool contained in epiphytic lichens was >4 kg/ha. Although non-N_2-fixing species (*A. sarmentosa*, *Bryoria* spp., and *Platismatia glauca*) were found in substantial abundance, particularly with increasing age (Fig. 5A), it was the presence of N_2-fixing cyanolichens, particularly *L. pulmonaria*, that contributed most to this N pool and has the largest potential impact on N budgets (Fig. 5B). The absence of most N_2-fixing cyanolichens from young and even mature stands, and the over 100-fold increases in *L. pulmonaria* biomass from young to old stands, resulted in a great disparity in potential across stand ages. Compare an N pool of >4 kg/ha recorded for old stands with the slightly less than 1 kg/ha observed in young stands (Fig. 5C). While annual N inputs from these sources into the forest system are not indicated by pool sizes alone, it is significant that old-growth forests have considerably more lichen N than do the younger forests.

Conclusions

The western redcedar – western hemlock forests of the British Columbia interior (ICH) are remarkable both for their low frequency of stand-replacing disturbance events such as fire and their associated high levels of biodiversity. A substantial component of the macrobiotic biodiversity in these forests is contained in an impressive array of epiphytic macrolichens (41 species), particularly in the oldest stands, many of which are known to be older than the oldest trees contained in them, a state that has been termed antique. This paper contributes to the growing body of evidence suggesting that antique stands are distinctive from young and even mature stands, both in containing higher overall biodiversity (i.e., total number of species of macrolichen) as well as in significantly elevated functional diversity (i.e., total number and abundance of N_2-fixing cyanolichens). In fact, the only cyanolichen present in young, mature, and old ICH stands was *L. pulmonaria*. Our work suggests that abundance of *L. pulmonaria*, which increases from young to old stands, is a useful biotic indicator of macrolichen diversity in wet and cool ICH forests in east-central British Columbia. With further research, it may prove to be a similarly useful indicator of diversity in other forest types.

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References

Armleder, H.M., Stevenson, S.K., and Walker, S.D. 1992. Estimating the abundance of arboreal forage lichens. B.C. Ministry of Forests, Victoria, B.C. Land Management Handbook Field Guide. Insert 7.

Benson, S. 2001. Lichen colonization in natural gap disturbances and old-growth stands. M.Sc. thesis, University of Northern British Columbia, Prince George, B.C.

Benson, S., and Coxson, D.S. 2003. Lichen colonization and gap dynamics in wet temperate rainforests of northern interior British Columbia. Bryologist, **105**: 673–692.

Brockley, R.P., Trowbridge, R.L., Ballard, T.M., and Macadam, A.M. 1992. Nutrient management in interior forest types. *In* Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests, Seattle, Wash., 12–14 February 1991. *Edited by* H.N. Chappell, G.F. Weetman, and R.E. Miller. University of Washington, College of Forest Resources, Seattle, Wash. pp. 43–64.

Brodo, I.M., Sharnoff, S.D., and Sharnoff, S. 2001. Lichens of North America. Yale University Press, New Haven, Conn.

Büdel, B., and Lange, O.L. 1991. Water status of green and blue green phycobionts in lichen thalli after hydration by water vapor uptake: Do they become turgid? Bot. Acta, **104**: 361–366.

Campbell, J., Stevenson, S.K., and Coxson, D.S. 1999. Estimating epiphyte abundance in high elevation forests of Northern British Columbia. Selbyana, **20**: 261–267.

Dettki, H., Klintberg, P., and Esseen, P.E. 2000. Are epiphytic lichens in young forests limited by local dispersal? Ecoscience, **7**: 317–325.

Goward, T. 1993. Epiphytic lichens: going down with the trees. *In* Community action for endangered species: a public symposium on B.C.'s threatened and endangered species and their habitat. *Edited by* S. Rautio. Federation of British Columbia Naturalists, Vancouver. pp. 153–158.

Goward, T. 1994. Notes on old-growth-dependent epiphytic macrolichens in inland British Columbia, Canada. Acta Bot. Fenn. **150**: 31–38.

Goward, T. 1995. Macrolichens of the old-growth forests of the Robson Valley. Part I: Goat River to Ptarmigan Creek. Robson Valley Forest District Special Report, McBride, B.C.

Goward, T. 1996. Lichens of British Columbia: rare species and priorities for inventory. B.C. Ministry of Forests, Research Branch, and B.C. Ministry of Environment, Lands and Parks, Habitat Protection Branch, Victoria, B.C. Working Paper 08.

Goward, T., and Arseneault, A. 2000*a*. Cyanolichens and conifers: implications for global conservation. For. Snow Landsc. Res. **75**: 303–318.

Goward, T., and Arseneault, A. 2000*b*. Inland old-growth rainforests: safe havens for rare lichens? *In* Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C, 15–19 February 1999. Vol. 2. *Edited by* L.M. Darling. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C., and University College of the Cariboo, Kamloops, B.C.

Goward, T., and Arsenault, A. 2000*c*. Cyanolichen distribution in young unmanaged forests: a dripzone effect? Bryologist, **103**: 28–37.

Harrison, M., and Delong, C. 2000. A comparison of ecological characteristics for age class 8 and 9 stands in the ICHwk3 and ESSFwk2: development of an index to assess old-growth features. Robson Valley Enhanced Forest Management Pilot Project.

Hooper, D.U., and Vitousek, P.M. 1997. The effects of plant composition and diversity on ecosystem processes. Science (Washington, D.C.), **277**: 1302–1306.

Hope, G. 2001. The soil ecosystem of an ESSF forest and its response to a range of harvesting disturbances. B.C. Ministry of Forests Research Program, Victoria, B.C. Extension Note 53.

Johansson, P., and Gustafsson, L. 2001. Red-listed and indicator lichens in woodland key habitats and production forests in Sweden. Can. J. For. Res. **31**: 1617–1628.

Ketcheson, M.V., Braumandl, T.F., Meidinger, D., Utzig, G., Demarchi, D.A., and Wikeem, B.M. 1991. Chapter 11. Interior Cedar–Hemlock zone. *In* Ecosystems of British Columbia. *Edited by* D. Meidinger and J. Pojar. B.C. Ministry of Forests, Victoria, B.C. Special Report Series 6. pp. 167–182.

Klinka, K., Krajina, V.J., Ceska, A., and Scagel, A.M. 1989. Indicator plants of coastal British Columbia. University of Washington Press, Seattle, Wash.

Krebs, C.J. 1999. Species diversity measures. *In* Ecological methodology. 2nd ed. *Edited by* C.J. Krebs. Addison Wesley Longman Inc., Menlo Park, Calif. pp. 410–452.

Lange, O.L., Büdel, B., Meyer, A., and Kilian, E. 1993. Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. Lichenologist, **25**: 175–189.

Lange, O.L., Kilian, E., and Ziegler, H. 1986. Water vapour uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. Oecologia, **71**: 104–110.

MacKenzie, T.D.B., MacDonald, T.M., Dubois, L.A., and Campbell, D.A. 2001. Seasonal changes in temperature and light drive acclimation of photosynthetic physiology and macromolecular content in *Lobaria pulmonaria*. Planta, **214**: 57–66.

Meidinger, D. 1998. Field manual for describing terrestrial ecosystems [online]. Tree attributes for wildlife (FS882-6) and coarse woody debris (FS882-7). B.C. Ministry of Environment, Lands and Parks and B.C. Ministry of Forests. Land Management Handbook 25. Available from http://www.for.gov.bc.ca/hfd/pubs/Docs/Lmh/Lmh25.htm [accessed 22 July 2004].

Meidinger, D., and Pojar, J. (*Editors*). 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Victoria, B.C. Special Report Series 6.

McCune, M., and Grace, J.B. 2002. Analysis of ecological communities [computer manual]. MjM Software Design, Gleneden Beach, Ore.

McCune, M., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.0 [computer program]. MjM Software, Gleneden Beach, Ore.

Negi, H.R., and Gadgil, M. 2002. Cross-taxon surrogacy of biodiversity in the Indian Garhwal Himalaya. Biol. Conserv. **105**: 143–155.

Peck, J.E., and McCune, B. 1997. Remnant trees and canopy lichen communities in Western Oregon: a retrospective approach. Ecol. Appl. **7**: 1181–1187.

Perry, D. 1978. A method of access into the crowns of emergent canopy trees. Biotropica, **10**: 155–157.

Peterson, E.B., Weetman, G.F., and Peterson, N.M. 1998. Silvics of western redcedar and western hemlock in British Columbia's ICH zone, and decision aids for their silviculture. Western Ecological Services Ltd., Victoria, B.C., and University of British Columbia, Vancouver, B.C.

Pike, L.H., Rydell, R.A., and Denison, W.C. 1977. A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. Can. J. For. Res. **7**: 680–699.

Radies, D.N. 2002. Macrolichen species distribution on 100-year-old western hemlock trees in even-aged and old-growth stands in the Interior Cedar–Hemlock zone, British Columbia. B.Sc. thesis. University of Northern British Columbia, Prince George, B.C.

Rhoades, F.R. 1995. Nonvascular epiphytes in forest canopies: worldwide distribution, abundance, and ecological roles. *In* Forest canopies. *Edited by* M.D. Lowman and N.M. Nadkarni. Academic Press, Toronto. pp. 353–408.

Sanborn, P., Geertsema, M., Jull, A.J.T., and Hawkes, B. 2001. Soil evidence for Holocene fires in an inland temperate rainforest: east-central British Columbia. *In* Canadian Quaternary Association Meetings, 2001: Program and Abstracts. Government of the Yukon, Heritage Branch, Whitehorse, Y.T. Occasional Papers in the Earth Sciences 1.

Sillett, S.C., and Antoine, M.E. 2004. Lichens and bryophytes. *In* Forest canopies. 2nd ed. *Edited by* B. Rinker and M. Lowman. Elsevier, San Diego, Calif.

Sillett, S.C., and Goslin, M.N. 1999. Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas-fir forest. Can. J. For. Res. **29**: 1204–1215.

Sillett, S.C., and McCune, B. 1998. Survival and growth of cyanolichen transplants in Douglas-fir forest canopies. Bryologist, **101**: 20–31.

Sillett, S.C., and Neitlich, P.N. 1996. Emerging themes in epiphyte research in westside forests with special reference to cyanolichens. Northwest Sci. **70**: 54–60.

SPSS Inc. 2000. Systat 10 [computer program]. SPSS Inc., Chicago, Ill.

Thell, A., and Goward, T. 1996. The new cetrarioid genus *Kaernefeltia* and related groups in the *Parmeliaceae* (Lichenized *Ascomycotina*). Bryologist, **99**: 125–136.

Tønsberg, T., and Goward, T. 2001. *Sticta oroborealis* sp. novum and other Pacific North American lichens forming dendriscocauloid cyanotypes. Bryologist, **104**: 12–23.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.