

Macrolichen colonization on 120–140 year old *Tsuga heterophylla* in wet temperate rainforests of central-interior British Columbia: a comparison of lichen response to even-aged versus old-growth stand structures

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Abstract: Canopy lichen abundance was assessed by size class on regenerating hemlocks, comparing trees of similar size and age (c. 120–140 yrs) growing in the understorey of old-growth cedar-hemlock stands with those growing in adjacent even-aged hemlock stands (natural origin patches c. 1–3 ha in size). Five chlorolichen taxa were associated with old-growth understorey trees: *Cavernularia hultenii*, *Hypogymnia vitata*, *Parmelia hygrophila*, *Platismatia norvegica*, and *Usnea* spp. *Lobaria pulmonaria* was the most abundant cyanolichen on regenerating hemlock in the old-growth forest stands, particularly in lower canopy (under 12 m) exposures. However, other cyanolichen taxa such as *Nephroma helveticum*, *Sticta fuliginosa*, and *Pseudocyphellaria anomala*, reached their greatest abundance at mid-canopy (12–24 m) positions. Smaller cyanolichen thalli (<9 cm²) were abundant on regenerating hemlocks across all canopy positions in the old-growth forest, raising the question as to whether or not cyanolichen thalli in mid- to upper-canopy environments represented long-established individuals facing severe growth constraints, or were simply thalli that had experienced higher rates of fragmentation, and thus did not achieve larger sizes. In comparison, cyanolichens of all taxa were essentially absent from the small-patch even-aged forest stands. Given that dispersal of propagules was not likely a major limiting factor, these 120–140 year old even-age stands may not yet have attained sufficient old-growth characteristics (especially canopy microclimate and canopy through-flow enrichment) to support cyanolichen growth. These findings have major conservation biology implications for wet interior cedar-hemlock forests in British Columbia, where forest harvesting is creating a mosaic of even-aged stands, whose projected age at the time of next harvest (rotation age) will be 120 years or less.

Key words: canopy microclimate, cyanolichens, forest management, Fraser River valley, inland rainforest, interior cedar-hemlock forest, lichen biodiversity, *Lobaria*.

Introduction

Rapid loss of old-growth forests has led to recent concerns over the possible extirpation of organisms dependent on these environments (Lesica *et al.* 1991; Goward 1994). Such concerns have challenged the research community to obtain a deeper understanding of the mechanisms underlying old-growth dependency and the degree to which

these processes can be emulated in managed forests. Key to this effort are studies designed to determine how forest organisms will adapt to silvicultural treatments of different kinds (Stevenson & Jull 1996; Franklin *et al.* 1997).

One group of organisms that has received considerable attention in recent years, especially in the US Pacific Northwest, is epiphytic (tree-dwelling) lichens. Epiphytic lichen communities vary considerably with forest age, some species associated mainly with old stands (Sillett 1995; Pike *et al.* 1977; McCune *et al.* 2000), while others occur mainly in younger forest types (Hyvärinen *et al.* 1992; Neitlich 1993;

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Arsenault & Goward 1997; Holien 1998). Most studies have used lichen 'functional groups', such as alectorioid lichens, chlorolichens, cyanolichens, and bryophytes, as the primary unit of assessment (Clement & Shaw 1999; Lyons *et al.* 2000; Campbell & Coxson 2001). These groups typically show strong preference by age class and height position within coniferous forests in Western North America (McCune 1993).

A conceptual framework for many of these studies was provided by the 'similar gradient hypothesis', developed by McCune and co-workers, which asserts that epiphytic lichen functional groups are ordered in parallel along three temporal and spatial gradients, namely, time, height, and moisture (McCune 1993). The similar gradient hypothesis predicts that as a stand matures, a spatial sequence of dominance will develop among the four functional groups. In a young, regenerating stand, only chlorolichens and alectorioid lichens are present; but as the stand matures, these groups migrate upwards, to be replaced by cyanolichens and, in time, bryophytes.

Lyons *et al.* (2000) made a further important distinction between lichen distribution patterns in old-growth stands where trees had originated from previous stand destroying events (within the last several hundred years), and old-growth stands where trees had largely originated in understorey old-growth environments, the latter old-growth type referred to by Goward (1994) as 'antique.' The process of epiphytic succession would, of course, be expected to differ significantly between these two forest types.

In this paper, we ask to what extent the broad patterns predicted by the similar gradient hypothesis are reflected in the distributions of individual species from within a lichen functional group. More specifically, we take up the challenge of Lyons *et al.* (2000) to undertake "direct comparisons of epiphyte abundance in trees of known ages in young versus old stands", comparing epiphytic macrolichen distribution patterns on trees of similar age growing in even-aged, single-generational stands versus multi-generational, old-growth stands. These

studies were conducted in wet-temperate interior cedar-hemlock (ICH) rainforests of north-central British Columbia. Lichen sampling was based on destructive removal of branches, using single-rope climbing techniques to obtain access within the canopy.

Methods

The study area was located approximately 120 kilometres east of Prince George, British Columbia (BC), Canada, in the upper Fraser River watershed, within the wet-cool Interior Cedar-Hemlock (ICHvk) Biogeoclimatic zone (Ketcheson *et al.* 1991). This area has been characterized as belonging to the 'Inland Rainforest' formation of Arsenault & Goward (2000). Mean annual precipitation in the ICHvk totals 839.8 mm, most of this falling as snow (465.5 mm water equivalent in winter), which plays an important role in maintaining high soil moisture levels during the summer period (Ketcheson *et al.* 1991).

We used the study sites of Benson & Coxson (2002), two of which were located in the Viking Ridge watershed (53°51'38"N, 121°33'50"W) (now part of the newly created Sugarbowl-Grizzly Den Provincial Park and Protected Area) and one in the Hungary Creek watershed (53°49'53"N, 121°28'44"W). These sites were at elevations of between 900 and 1000 m a.s.l. on north to north-westerly facing slopes with an inclination of between 7° and 23°. Each site comprised a small 1–3 ha even-aged stand paired with the surrounding multi-aged old-growth stand.

The small patch (2–3 ha) 120–140 year old even-aged stands were composed exclusively of *Tsuga heterophylla*, which likely regenerated after hemlock looper (*Lambdina fuscicollis*) outbreaks in the late 1800s. Average canopy height within the even-aged stands was 20.2 m, with a mean stand density of 1930 trees ha⁻¹ (Benson & Coxson 2002). A continuous moss layer dominated the forest floor surface in the even-aged stands, composed mainly of *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, and *Pleurozium schreberi*. Shrub layers were largely absent, with *Cornus canadensis*, *Chimaphila umbellata*, and *Pyrola secunda* forming a sparse herb layer. These even-aged patches were surrounded by old-growth forest stands. Consequently, most trees within the even-aged stands were within one or two tree lengths (40–80 m) of the surrounding old-growth forest.

Old-growth sites were dominated by *Thuja plicata* and *Tsuga heterophylla* (Benson & Coxson 2002), with *Picea engelmannii* × *glauca*, *Abies lasiocarpa*, and *Pseudotsuga menziesii* as occasional stand components. Tree-ring chronologies extended for up to 450 yr in the outer shells of old-growth cedar and hemlock. However, most trees had heart rot and could not be dated to their time of establishment. The absence of charcoal layers indicates that these stands may be much older

than the oldest trees present (Sanborn *et al.* 2001). The average canopy height within the old-growth stands was 32.4 m. The mean height of regenerating hemlocks within the old-growth stand was 19.4 m. Mean old-growth stand density was 766 trees ha⁻¹ (Benson & Coxson 2002). Ground cover was dominated by oak ferns (*Gymnocarpium dryopteris*), a common indicator of hygric old-growth forest stands (Ketcheson *et al.* 1991). The shrub layer, although sparse, was dominated by *Oplopanax horridus*. Other members of the herb layer included *Rubus pedatus*, and *Cornus canadensis*, while the moss layer was composed largely of *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, and *Pleurozium schreberi*.

Sample trees were selected based on a pool of candidates sampled by Benson & Coxson (2002) for two main reasons: (1) the sites had known epiphytic biomass and functional group characteristics, which we could compare; and (2) the trees selected for sampling in this study had known structural attributes.

We randomly selected 2 sample trees from among a pool of 5 candidate trees at each of the 3 paired watershed sites. This resulted in a total of 12 sample trees: 6 from the even-aged stands and 6 from old-growth stands. In each sample tree, 15 branches, 5 each from the 'upper', 'mid', and 'lower' height levels (lower canopy from 0–11.9 m above ground, mid-canopy from 12–23.9 m, and upper canopy from 24–36 m) were selected randomly for sampling with a probability proportionate to the value of a predictive variable (Cochran 1977; Campbell & Coxson 2001). In this case, the predictive variable was the estimated abundance of the canopy epiphytic lichen *Alectoria sarmentosa*. As a highly visible macrolichen associated with the more-mesic mid- to lower-canopy exposures (Campbell & Coxson 2001), *A. sarmentosa* provided a surrogate for the initial identification of microsites having high humidity, and therefore more likely to support 'oceanic' species. In cases where there were less than five branches in the canopy region, all remaining branches were selected. The sample branches were then removed for subsequent lichen identification using within-tree climbing techniques (Campbell *et al.* 1999). Some sample branches were damaged during handling. A total of 128 branches were available for study, 67 from the even-aged forest stands and 61 from the old-growth forest stands (selected approximately equally from the three height categories).

All foliose macrolichens larger than 3 mm in diameter were identified using a binocular microscope and chemical spot tests. Taxonomically difficult species were verified by Trevor Goward (UBC Curator of Lichens). *Bryoria*, *Melanelia*, and *Usnea* fragments were often too small to be identified to species, and so were identified only to the genus level. Nomenclature follows Esslinger (1997), with the exception that '*Parmelia hygrophila*' could include a few specimens of *P. pseudosulcata*.

The relative abundance of each species on a branch was evaluated using a 5 point scale [0: 0% (absent); 1: 0.1–0.9% (rare); 2: 1–4.9% (sparse); 3: 5–19.9% (moderately abundant); 4: 20–49.9% (abundant); 5:

50–100% (copious)]. These categories represent the estimated percentage cover of the species in question in relation to the total lichen cover on each branch.

An additional (direct) estimate of lichen cover was made for cyanolichens on each branch. Each cyanolichen thallus noted was classed into one of 4 size categories and tallied by branch. These size categories were: 1: 0.9–2.25 cm² (very small); 2: 2.25–9 cm² (small); 3: 9–49 cm² (medium); 4: >49 cm² (large).

Tests of significance between sample groups were assessed with a Bonferroni t-test, using SYSTAT 8.0 (SPSS, Chicago, ILL). Categorical abundance data were converted to percentages prior to significance testing, by assigning the numerical value appropriate to the midpoint of each cover range.

Nonmetric multidimensional scaling (NMS) was used to examine trends in our data set. NMS is an ordination method that is well suited to data that are nonnormal or have discontinuous or otherwise arbitrary data sets (McCune & Mefford 1999). NMS is a distance-based ordination technique where a solution is based on minimizing stress, this is defined as a measure of the poorness of fit between the ordination and measured ecological distances. NMS was run using the ordination routines of PC-ORD Version 4.0 (MJM Software Design, Gleneden Beach, OR).

Results

Thirty-one lichen species and 3 genera (*Bryoria* spp., *Usnea* spp., and *Melanelia* spp.) were identified (Table 1). Of these 34 taxa, 33 were found in old-growth stands, and 24 in even-aged stands. Twenty-two taxa were classified as foliose chlorolichens, three belonged to the alectoroid functional group, and nine were cyanolichens. Moss cover on branches was very sparse, being most frequent in the lower canopy of the old-growth stands, where *Orthotrichum* was the most common genus.

Most foliose chlorolichen species were equally abundant between the two stand types. Exceptions ($P < 0.05$) were *Cavernularia hultenii*, *Hypogymnia vittata*, and *Parmelia hygrophila*, which were significantly more abundant in the old-growth stands, and *Hypogymnia metaphysodes*, which was significantly more abundant in the even-aged stands. Dominant foliose chlorolichens species include, in order of decreasing abundance: *Platismatia glauca*, *Parmelia sulcata*, *P. hygrophila*, *Hypogymnia occidentalis*, *H. physodes*, *Tuckermannopsis chlorophylla*, *Hypogymnia tubulosa* and *H. metaphysodes*.

TABLE 1. Frequency of occurrence and percent relative cover [mean and standard error (SE) of the mean] of foliose chlorolichens, cyanolichens, and alectorioid lichens on branches from old-growth and even-aged 'second-growth' stands.

Lichen Species by Group	Old-growth stand branches			Even-aged 'second-growth' stand branches		
	% Frequency (n=61)	% Relative lichen cover		% Frequency (n=67)	% Relative lichen cover	
		Mean	SE		Mean	SE
Foliose Chlorolichens						
<i>Cavernularia hultenii</i> *	52	0.46	0.093	24	0.131	0.028
<i>Hypogymnia austerodes</i>	5	0.02	0.013	7	0.041	0.018
<i>H. bitteri</i>	10	0.082	0.047	4	0.066	0.05
<i>H. enteromorpha</i> **	2	0.007	0.007	0	0	0
<i>H. metaphysodes</i> *	52	0.388	0.086	52	1.303	0.254
<i>H. occidentalis</i>	85	3.425	0.645	80	4.549	0.578
<i>H. physodes</i>	85	3.963	0.828	55	3.525	0.862
<i>H. rugosa</i>	16	0.122	0.049	16	0.369	0.214
<i>H. tubulosa</i>	75	1.194	0.228	52	1.066	0.170
<i>H. vittata</i> *	33	0.149	0.028	6	0.033	0.016
<i>Kaernefeltia merrillii</i>	0	0	0	1	0.008	0.008
<i>Melanelia</i> spp.	3	0.015	0.01	1	0.008	0.008
<i>Parmelia hygrophila</i> *	100	5.172	0.534	66	1.164	0.168
<i>P. sulcata</i>	100	2.821	0.370	69	1.893	0.178
<i>Parmeliopsis ambigua</i>	11	0.052	0.019	12	0.107	0.052
<i>P. hyperopta</i>	39	0.216	0.051	34	0.230	0.056
<i>Platismatia glauca</i>	100	32.31	3.061	91	29.26	3.704
<i>P. norvegica</i>	18	0.881	0.329	10	0.377	0.219
<i>Tuckermannopsis chlorophylla</i>	80	1.037	0.218	54	1.32	0.578
<i>T. ciliaris</i>	2	0.007	0.007	0	0	0
<i>T. orbata</i>	24	0.187	0.065	19	0.107	0.026
<i>T. platyphylla</i>	2	0.045	0.045	1	0.008	0.008
Cyanolichens						
<i>Collema auriforme</i>	3	0.015	0.01	0	0	0
<i>Lobaria hallii</i>	2	0.007	0.007	0	0	0
<i>L. pulmonaria</i> *	54	9.366	2.230	0	0	0
<i>L. scrobiculata</i> *	13	0.06	0.02	0	0	0
<i>Nephroma helveticum</i> *	36	1.0	0.328	1	0.008	0.008
<i>N. isidiosum</i>	8	0.075	0.047	0	0	0
<i>N. parile</i>	5	0.022	0.013	0	0	0
<i>Pseudocyphellaria anomala</i> *	15	0.112	0.049	0	0	0
<i>Sticta fuliginosa</i> *	23	0.216	0.078	0	0	0
Alectorioid Lichens						
<i>Alectoria sarmentosa</i>	100	24.07	2.839	89	29.81	2.98
<i>Bryoria</i> spp.*	87	6.366	1.475	80	21.57	3.664
<i>Usnea</i> spp.*	75	1.41	0.284	28	0.197	0.055

**t*-test probabilities (old-growth versus 'second-growth') <0.05.

**Insufficient data for test.

Kaernefeltia merrillii was found once in the even-aged stand, while *Hypogymnia enteromorpha* occurred once in the old-growth stand.

Cyanolichens were found only on sample branches from the old-growth stand regeneration trees. The one exception was a small thallus of *Nephroma helveticum* found in the

upper canopy of a regenerating tree in the even-aged stand. The association with old-growth stands was statistically significant for *Lobaria pulmonaria*, *L. scrobiculata*, *Nephroma helveticum*, *Pseudocyphellaria anomala* and *Sticta fuliginosa*. The remaining species were too infrequent for statistical analysis. *Lobaria pulmonaria* and *N. helveticum* dominated on most branches, the other species being present in lesser quantities.

Cyanolichen thalli, at least of the smallest size class, were found at all canopy heights on hemlock branches in the old-growth stand (Fig. 1). *Lobaria pulmonaria* showed greatest affinity for lower-canopy positions, while the remaining cyanolichens were found in greatest abundance in mid-canopy position branches of regenerating trees. Apart from *L. pulmonaria*, which dominated the cyanolichen group in overall abundance, most cyanolichen specimens had surface areas of 9 cm² or less (small or very small). Exceptions were 8 thalli of *Nephroma helveticum* and 1 thallus of *Lobaria scrobiculata* found in the medium surface area category. Thalli of *Nephroma parile*, *Lobaria hallii* and *Collema auriforme* (data not plotted) were infrequently encountered (small thalli on 2 branches each), found on middle and lower canopy branches. Alectorioid lichens, including *Alectoria sarmentosa*, *Bryoria* spp., and *Usnea* spp., were equally abundant in both stands. *Usnea* spp. were more frequent and abundant in the old-growth stand, while *Bryoria* spp. were significantly more abundant in the even-aged stand (Table 1).

NMS ordination showed a spatial separation of even-aged versus old-growth hemlock branches along Axis 1 (Fig. 2). Canopy position (upper to lower) separated more clearly along Axis 2 of the NMS branch ordination. No clear separation of branches based on size class was seen in the NMS plot.

Two broad patterns of lichen distribution patterns were recognized; species with ‘generalist’ distribution patterns, and species with ‘old-growth-associated’ distribution patterns. Species that had a ‘generalist’ type distribution pattern showed no clear preference for old-growth or even-aged ori-

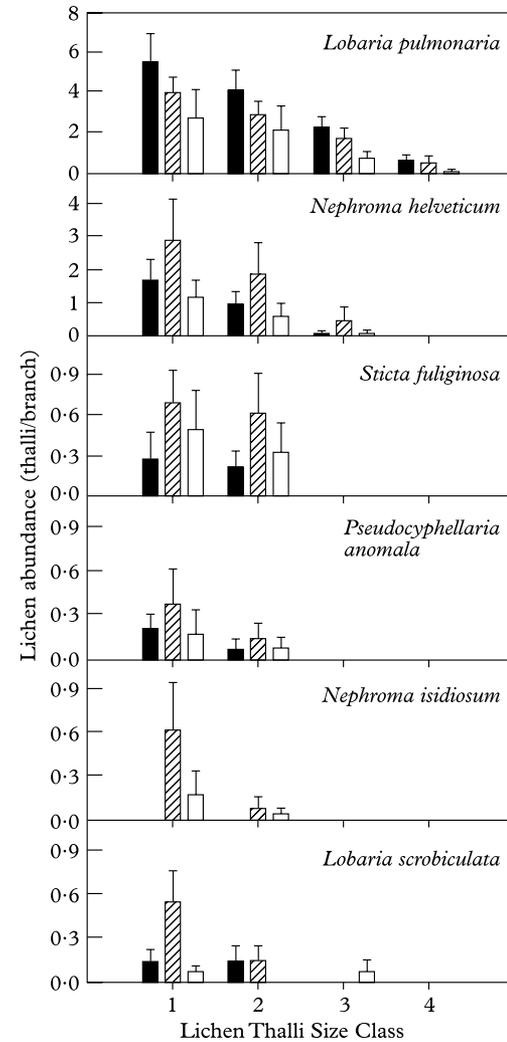


FIG. 1. Mean cyanolichen abundance (+1 SE) by lichen thallus size class (1=0.9–2.25 cm²; 2=2.25–9 cm²; 3=9–49 cm²; 4=over 49 cm²) on branches of regenerating hemlock (n=61) growing in the understory of old-growth cedar-hemlock forest stands. ■, lower canopy branches (n=15); ▨, middle canopy branches (n=12); □, upper canopy branches (n=11).

gin branches. This group was composed entirely of chlorolichens. Species from mid- to upper-canopy positions included *Tuckermannopsis orbata*, *Hypogymnia physodes* (Fig. 3), *H. tubulosa*, *H. metaphysodes*, *Bryoria* spp. (Fig. 4), and *Parmelia sulcata*. Lichen generalists that were found predominantly in mid-canopy positions

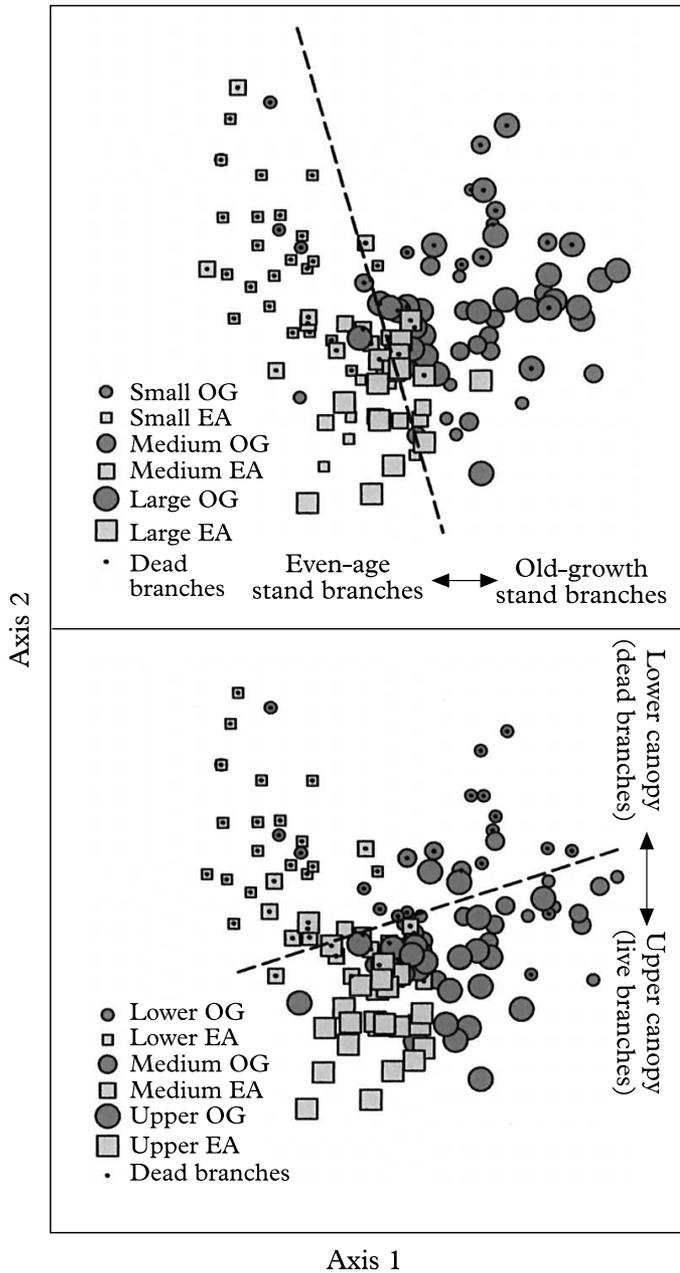


FIG. 2. NMS ordination, with branch size class [small (<2 cm diameter), medium (2–3 cm diameter), large (>3 cm diameter)] and stand type (old-growth [OG] versus even-aged [EA]) indicated for each plot (sample branches).

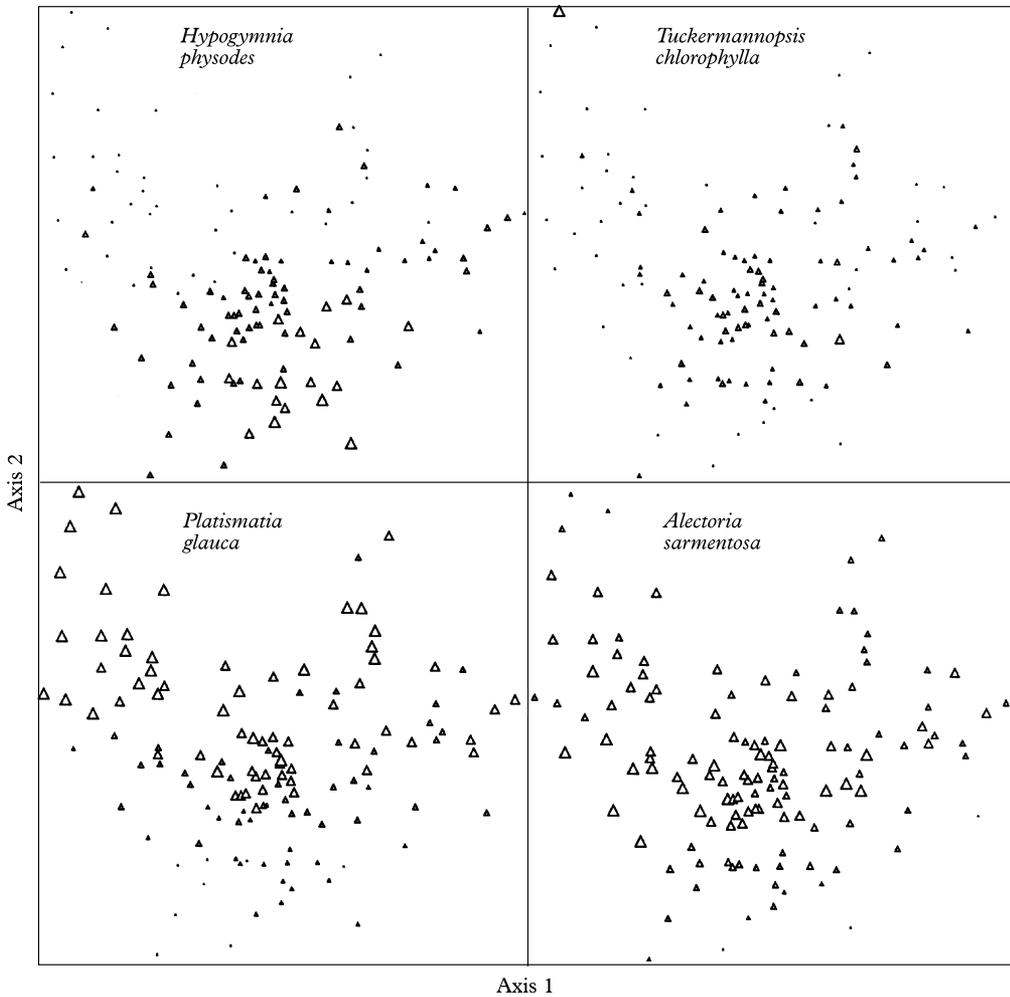


FIG. 3. Nonmetric multidimensional scaling (NMS) ordination plots for *Hypogymnia physodes*, *Tuckermannopsis chlorophylla*, *Platismatia glauca*, and *Alectoria sarmentosa*. Each point represents an individual stand-level plot (branch) measurement for the species in question; their respective placement along axes 1 and 2 provided by the NMS ordination scores. Symbol size is proportional to percent relative cover for each species.

included *Parmeliopsis ambigua*, *P. hyperopta*, *Hypogymnia occidentalis*, and *Tuckermannopsis chlorophylla* (Fig. 3). Lichen generalists from mid- to lower-canopy positions included *Alectoria sarmentosa* (Fig. 3) and *Platismatia glauca* (Fig. 3), where they occurred both on live and dead branches.

Old-growth-associated species included both chlorolichens and cyanolichens, both of which were generally most abundant in mid-canopy positions. Five taxa fell within the old-growth associated chlorolichen group.

This included *Cavernularia hultenii* (Fig. 4), *Hypogymnia vittata* (Fig. 4), *Parmelia hygrophila*, *Platismatia norvegica*, and *Usnea* spp. (Fig. 4). Members of this group showed clear affinities with the old-growth stands, but were nevertheless found also, though at lesser frequency, in the even-aged stands.

Nine species fell exclusively within the old-growth branch group, all of them cyanolichens (Fig. 5), including *Collema auriforme*, *Lobaria hallii*, *L. pulmonaria*, *L. scrobiculata*,

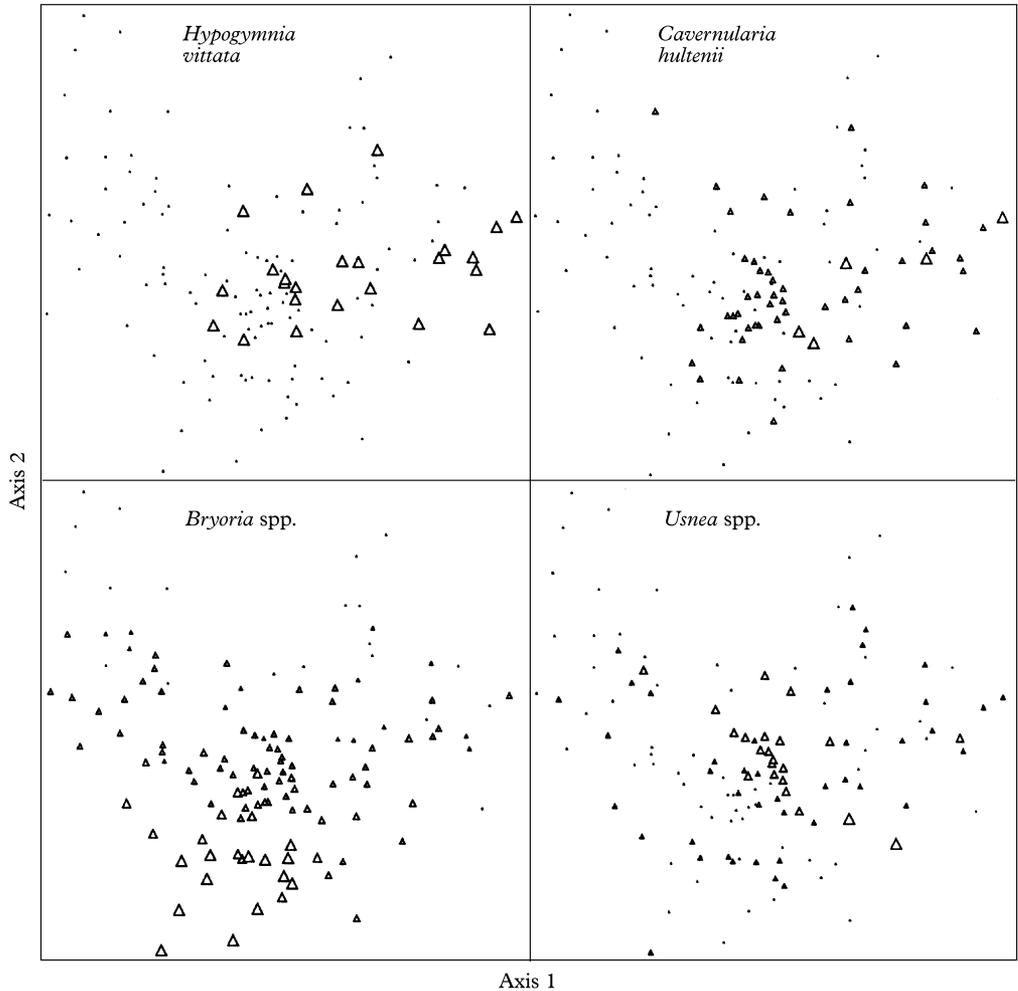


FIG. 4. Nonmetric multidimensional scaling (NMS) ordination plots for *Hypogymnia vittata*, *Cavermularia hultenii*, *Bryoria* spp., and *Usnea* spp. Plot details as in Fig. 3.

Nephroma helveticum, *N. isidiosum*, *N. parile*, *Pseudocyphellaria anomala*, and *Sticta fuliginosa*.

Discussion

A fundamental assumption of canopy biology studies is that vertical gradients in temperature, moisture, and light availability, interact with patterns of substratum availability and tree structure to shape the operating environment of canopy epiphytes (McCune 1993; McCune *et al.* 1997). This

includes both direct impacts on growth environments, such as epiphytes in mesic lower-canopy environments that may experience longer periods of hydration after precipitation events (Campbell & Coxson 2001), and indirect effects, such as wind-scouring of epiphytes from upper canopy exposures (Goward 1998). Additionally, canopy environments change, as stands age (Neitlich 1993), and disturbance events shape canopy structure (Benson & Coxson 2002). Thus, the distribution of canopy epiphytes at a given point in time can reflect

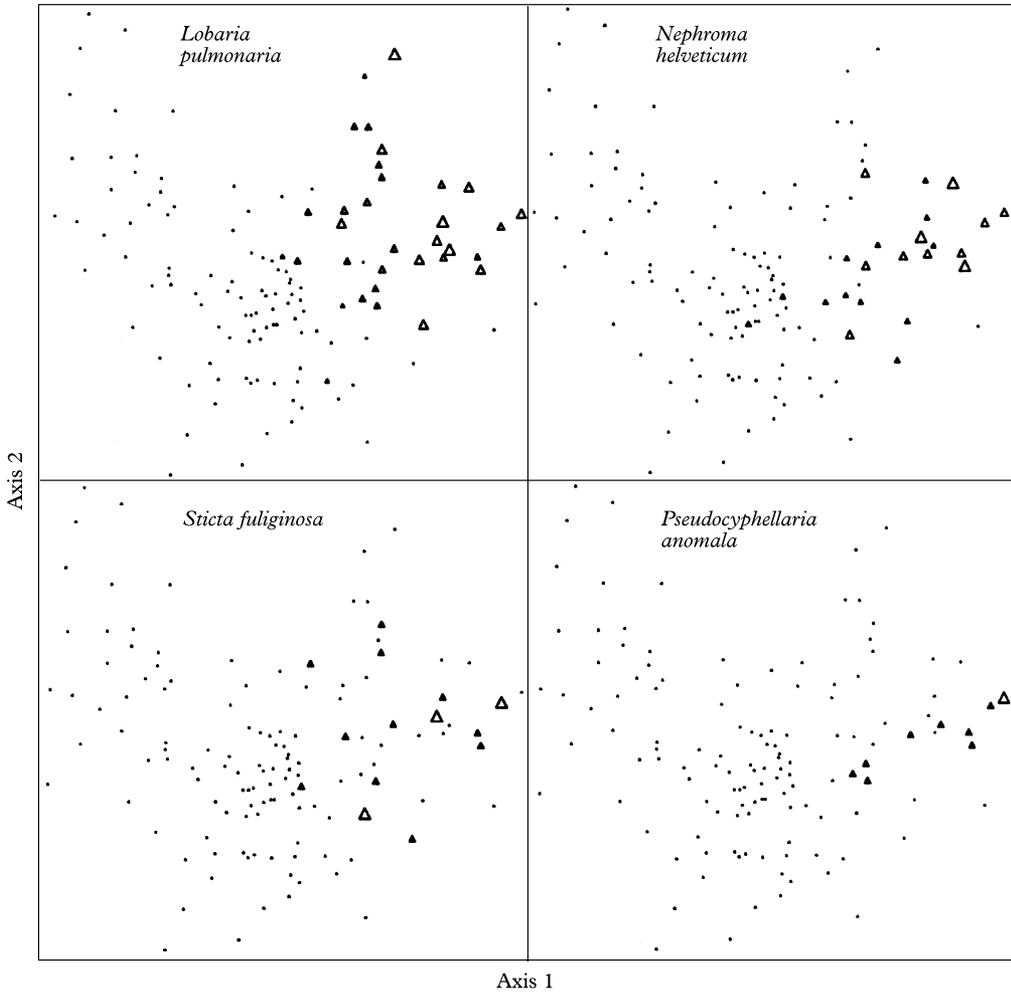


FIG. 5. Nonmetric multidimensional scaling (NMS) ordination plots for *Lobaria pulmonaria*, *Nephroma helveticum*, *Sticta fuliginosa*, and *Pseudocyphellaria anomala*. Plot details as in Fig. 3.

both current growth environments and past dispersal and/or establishment events.

Parker (1997) noted that in a coastal wet-temperate old-growth rainforest (Douglas-Fir/Western Hemlock), canopy cyanolichens attained much greater abundance in the lower canopy, near the point at which light transmittance shifted primarily from direct to diffuse transmission. Parker contrasted this with vertical gradients of light availability in younger even-aged forest stands, where the greater (and more evenly distributed) biomass of upper canopy foliage results in darker understory canopy

environments, which are presumed to have a negative effect on lichen establishment and survival.

A confounding variable in many studies on lichen establishment in even-aged forests is that of limitations on lichen dispersal, particularly where even-aged forest stands originated from clear-cut harvesting, and may now be some distance from the nearest lichen propagule sources. Benson & Coxson (2002) addressed this question in a study that examined lichen abundance in small patches (2–3 ha) of even-aged coniferous forest that had originated naturally (from

insect outbreaks in the late 1800s) and had been surrounded since stand inception by an old-growth forest matrix. In findings similar to those of Parker, they noted that canopy cyanolichens reached their greatest abundance in lower canopy environments in the old-growth stands, but were largely absent from the embedded even-aged younger forest patches. Benson & Coxson (2002) suggested that canopy stratification within these inland rainforest canopies could be viewed as a stand-level attribute, i.e. lichen loading on individual branches was better predicted by the position of branches within the overall canopy, than the position of branches on their host trees or size of host trees.

These conclusions were based on sampling that used visual (non-destructive) lichen assessments, taken within four major lichen functional groups. Alectorioid lichens were divided into *Alectoria* and *Bryoria* functional groups; foliose lichens were divided between cyanolichen and chlorolichen functional groups. McCune *et al.* (1997) noted that this approach (assessments within broadly defined lichen functional groups) can mask divergent behaviour of individual lichen species, particularly for the diverse chlorolichen functional group. The present study confirms this assessment. Detailed analysis of a subset of branches used by Benson & Coxson (2002) revealed two major groupings: generalist chlorolichen species on regenerating trees (of the same age) in both old-growth and even aged stands (including species such as *Hypogymnia physodes* in mid- to upper-canopy positions, *Tuckermannopsis chlorophylla* in mid-canopy positions, and *Platismatia glauca* in mid- to lower-canopy positions); and specialist species, such as *Hypogymnia vittata* and *Platismatia norvegica*, that showed clear affinities for regenerating hemlocks within the old-growth stands, but could be found, though at lesser frequencies, in the even-aged stands.

A detailed analysis within lichen functional groups was similarly revealing for cyanolichens. Although most species were concentrated in the middle canopy, *Lobaria pulmonaria* (the most abundant species)

showed an increase in abundance toward the lower canopy. Moreover, all species, including *L. pulmonaria*, were distributed more or less evenly throughout the canopy of the 120–140 yr old hemlocks as small thallus fragments. This suggests that constraints on lichen growth after establishment and/or greater rates of fragmentation after establishment may play a disproportionate role in upper canopy environments. In studies on lichens from subalpine forest canopies, Coxson & Coyle (2003) found that observed lichen distribution patterns were not consistent with models of growth potential and suggested that biomass loss through fragmentation may play a more important role in determining levels of lichen abundance that can be sustained over vertical gradients within the canopy.

The diversity of cyanolichens in our old-growth stands would suggest that these sites meet Goward's definition of 'antique' forest stands (Goward 1994), sites that have had long ecological continuity, where regeneration of trees has been primarily through single-tree or small patch gap dynamics (Benson & Coxson 2002). The presence of *Collema auriforme* within our old-growth sites is noteworthy; this species is considered rare in British Columbia (Goward 1994).

An unexpected finding of our study was the extent to which cyanolichen abundance and diversity differed between the even-aged and old-growth forest stands for regenerating trees of the same age. Although cyanolichens were abundant on young trees in the old-growth forest matrix, they were essentially absent on trees of the same size, age class, and species, within the even-aged forest patches. We do not think that this reflects constraints on dispersal. Nearly all sample trees were within one to two tree lengths of the surrounding old-growth forest matrix. We suggest that for these study sites, constraints on establishment and/or growth of dispersing propagules are a major factor in excluding cyanolichens from even-aged forest stands. This conclusion differs from that of Sillett and McCune (1998), who used transplant studies to show that established cyanolichen thalli from old-growth stands

grew equally well upon relocation to second growth stands. Preliminary findings from cyanolichen transplant studies that we have initiated at the Benson & Coxson (2002) study sites (Coxson, unpublished data) suggest that growth rates are reduced in low light environments of the even-aged forest stands. An additional consideration may be that faster-growing hemlocks within the even-aged stands may have more unstable conditions on bark surfaces, reducing lichen establishment rates.

Another factor that must be considered when examining cyanolichen establishment is tree species composition. Goward & Arsenault (2000) hypothesize that enrichment of canopy throughflow from 'wolf-trees', for example large individual *Populus* trees, may enhance growth and establishment of cyanolichens on conifer branches. Hauck & Spribille (2002) further proposed that lichen establishment in coniferous forests is highly sensitive to Mg/Mn ratios, which are also influenced by the proximity of 'wolf-trees'. T. Goward (pers. comm.) has recently proposed that *Thuja* may similarly enrich adjacent canopy environments. Although cause and effect are difficult to separate, Collins *et al.* (2001), found that soils of cedar stands (in coastal forests) had much higher amounts of calcium and magnesium ions, increasing soil pH over that found in western hemlock leading stands. Lichens dispersing into our even-aged hemlock stands may therefore face unfavourable physicochemical environments, which, in combination with canopy microclimate gradients, preclude establishment of dispersing cyanolichen propagules.

If we base our predictions of cyanolichen response on the accumulation of biomass in the dominant canopy species, *Lobaria pulmonaria*, our findings are in close accord with the predictions of the similar gradient hypothesis, where total lichen abundance responds closely to the 'light transition zone' (McCune *et al.* 1997). An exception to this generalization can be seen in distribution patterns of smaller diameter cyanolichen thalli in the old-growth forest stands. Although one might expect small cyano-

lichen thalli to be sensitive to vertical placement within the canopy, due to lower water holding capacity and higher drying rates (Gauslaa & Solhaug 1998), small cyanolichen thalli were found across all canopy positions on regenerating hemlock trees.

This suggests two alternative scenarios. Small cyanolichen thalli from upper canopy positions may show the same relative growth rates as thalli from lower canopy positions, but suffer from greater biomass loss due to fragmentation. Alternatively, cyanolichens from mid- to upper-canopy exposures may stay small over long time periods (i.e. small upper canopy thalli may be as old as larger lower canopy thalli), in environments that limit the duration of their active growth periods. We are presently testing these hypotheses, using microclimate profiling approaches of Campbell & Coxson (2002) to examine lichen operating environments within the canopy of these inland rainforest communities.

The essential absence of cyanolichens from the 1–3 ha even-aged stands, 120–140 years after stand initiation, raises serious conservation biology concerns, given current forest management practices in the upper Fraser River watershed. Landscapes that were historically dominated by old-growth forests (DeLong *et al.* 2003) are increasingly being replaced by a mosaic of even-aged forest stands, where future harvesting (stand rotation age) is contemplated as occurring at intervals of 120 years or less. Our findings show that development of old-growth forest characteristics that support cyanolichen growth takes well in excess of 120–140 years, even under conditions of optimal lichen availability (conditions that would rarely be met under current clearfelling regimes). Alternative forest harvesting practices, such as partial cut harvesting (Stevenson & Coxson 2003), may provide a more viable means of insuring that old-growth stand characteristics, and associated canopy lichen communities, are retained over time outside of protected areas in these forested landscapes.

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