

Growth rate responses of *Lobaria pulmonaria* to canopy structure in even-aged and old-growth cedar–hemlock forests of central-interior British Columbia, Canada

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Abstract

The ability of cyanolichens to sustain growth in even-aged forests that develop after clear-cut harvesting is a major conservation biology concern in British Columbia's inland rainforest. This and other conservation issues have led to proposals advocating partial-cut rather than clear-cut harvesting to better maintain the structures that support biodiversity in old-growth forest stands. However, evaluating the potential impacts of alternative harvesting practices cannot occur without first understanding lichen growth responses to the existing range of natural variability in canopy structure. Using transplant experiments with thalli of *Lobaria pulmonaria* (a tripartite foliose cyanolichen), we evaluate growth responses to canopy structure in both naturally occurring 120 year old small-patch even-aged stands and in adjacent old-growth uneven-aged forest stands. Canopy microclimate was also measured in old-growth reference trees, allowing calculation of energy conversion efficiency for old-growth *L. pulmonaria* thalli. Growth rates of *L. pulmonaria* transplants showed a strong correlation with canopy light transmission (CLT). Mean annual lichen dry matter gain over the 2-year measurement period ranged from less than 5% on branches in closed canopy even-aged stands ($<1 \text{ mol m}^{-2} \text{ day}^{-1} \text{ CLT}$) to near 20% on branches under canopy gaps in old-growth stands ($>18 \text{ mol m}^{-2} \text{ day}^{-1} \text{ CLT}$). Intercepted irradiance of hydrated *L. pulmonaria* thalli (I_{wet}) under old-growth stand conditions was 24.7 and 45.5 MJ m^{-2} annually in years 2 and 3 of the study, resulting in an energy conversion efficiency of 1.33 and 0.61%, respectively. Open sky (gap fraction) above lichen transplants in old-growth stands was much greater than that found in even-aged stands, allowing for longer duration sunfleck events in the lower canopy of the old-growth forest stands. These findings suggest that the creation of small openings by partial-cut harvesting in the inland rainforest may result in conditions favourable to continued growth of the dominant canopy cyanolichen, *L. pulmonaria*. They also support existing concerns about future cyanolichen growth in even-aged forests regenerating after clear-cut harvesting.

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1. Introduction

Epiphytic cyanolichens have been identified as old-growth associates in the wet-temperate inland rainforest located on the windward slopes of British Columbia's interior mountain ranges (Arsenault and Goward, 2000; Goward and Spribille, 2005). Of these cyanolichens, *L. pulmonaria*, a tripartite species containing both green-algal and cyanobacterial photobionts, is perhaps the most widespread. Its presence is often associated with a complex of other canopy cyanolichens, both bipartite (containing only cyanobacterial photobionts) and tripartite; including *Collema auriforme*, *Lobaria hallii*, *L.*

retigera, *L. scrobiculata*, *Nephroma helveticum*, *N. isidiosum*, *N. parile*, *Pseudocyphellaria anomala*, and *Sticta fuliginosa* (Campbell and Fredeen, 2004; Radies and Coxson, 2004). This species assemblage is sometimes known as the Lobarion group, but will be referred to hereafter as cyanolichens.

As a group, canopy cyanolichens face major conservation biology threats. Landscapes that were historically dominated by old-growth stands (DeLong et al., 2003) are subject to widespread habitat loss, both from direct impacts of clear-cut forest harvesting, and from secondary impacts associated with forest fragmentation and edge effects (Goward, 1994; Goward and Arsenault, 2000). The recent study of Radies and Coxson (2004), which found few cyanolichens growing in even-aged stands, 120 years after establishment, raises additional concerns about lichen persistence in landscapes where most plantations will be harvested in under 100 years time. One possible way in

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which these impacts may be mitigated is through the adoption of partial-cut techniques. Partial cutting is one of several approaches that try to ensure that some old-growth characteristics are retained, or develop through time, within managed forest stands (Franklin, 1989; Peck and McCune, 1997; Stevenson and Coxson, 2003).

Although the rationale for proposing the adoption of alternative harvesting approaches is sound, we have little information on the response of canopy cyanolichens to changes in canopy structure, let alone to the natural range of variability that is found within these forests (DeLong et al., 2003). Campbell and Fredeen (2004) found that *L. pulmonaria* was an important old-growth associate in British Columbia's interior wet-temperate rainforests. Other studies have found that *L. pulmonaria* can adapt to changes in canopy light environments (Gauslaa and Solhaug, 2001; Mackenzie et al., 2004). However, this work is largely based on collections from seasonally variable deciduous forest canopies, and may not apply to *Lobaria* populations growing in coniferous forest canopies. In Pacific Northwest old-growth coniferous stands *Lobaria* thalli reached their greatest abundance in the lower canopy, where light transmission shifts from predominantly direct to mainly indirect light exposure (McCune et al., 1997; Parker, 1997), a pattern of vertical lichen distribution also observed by Benson and Coxson (2002) in old-growth inland rainforest stands. This raises the question as to whether or not canopy cyanolichens have a point of optimal light exposure in old-growth canopies, beyond which lichen thalli decline. On the other hand, diminishing abundance of lichen thalli in mid- to upper canopy environments may reflect other environmental gradients, such as wind scouring of thalli, as was proposed for *Alectoria sarmentosa* by Coxson and Coyle (2003).

The response of the canopy cyanolichen *L. pulmonaria* to gradients of light availability has now been addressed in a series of transplant experiments in temperate rainforests of the upper Fraser River watershed. Thalli were transplanted from an old-growth stand environment into a range of canopy light exposures, both in naturally occurring 120-year old even-aged (EA) stands and in >450 year old old-growth (OG) stands. All thalli were transplanted into mesic lower canopy environments, minimizing the effects of physical fragmentation and desiccation from wind scouring. Lichen growth rates were subsequently evaluated during a three-year period, leading to some of the first direct observations of lichen growth rate responses to the range of natural variation in canopy openings and light availability in British Columbia's inland rainforests. Lichen thallus microclimate was concurrently monitored in a set of OG cedar trees, allowing the derivation of energy conversion efficiency (e) values for *Lobaria* thalli growing within OG forest stands of the inland rainforest.

2. Materials and methods

2.1. Study sites

Study areas were located approximately 120 km east of Prince George, British Columbia (BC), Canada, in the upper Fraser

River watershed, within the very wet cool Interior Cedar–Hemlock (ICHvk) biogeoclimatic zone (Ketcheson et al., 1991). This area is part of the 'Inland Rainforest', as described by Arsenault and 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) (Reynolds, 1997).

We used paired study sites of Benson and Coxson (2002) located on Viking Ridge (53°51'38"N, 121°33'50"W) and in the Lunate watershed (53°49'53"N, 121°28'44"W). These sites were between 900 and 1000 m a.s.l. on north to northwesterly facing slopes with an inclination of between 7° and 23°. One stand at each site was composed of 120 year old even-aged western hemlock (*Tsuga heterophylla*) trees (Benson and Coxson, 2002), believed to have originated after hemlock looper (*Lambdina fuscicollis*) outbreaks in the late 1800s (these EA stands designated as VIKY and LUNY, respectively). Average canopy height within the EA stands was 20.2 m, with a mean stand density of 1930 trees ≥ 1 cm dbh ha⁻¹; average canopy height within the OG stands was 32.4 m, with a mean stand density of 766 trees ≥ 1 cm dbh ha⁻¹ (Benson and Coxson, 2002).

These small-patch EA stands (most trees were less than a tree length from adjacent OG stands) were surrounded by extensive areas of old-growth forest, the latter dominated by western hemlock and western red cedar (*Thuja plicata*), with minor stand components of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (adjacent OG stands were designated as VIKO and LUNO, respectively). Tree-ring chronologies can be established for up to 450 year in the outer shells of OG cedar and hemlock at the VIKO and LUNO sites (Benson and Coxson, 2002). However, most trees examined by Benson and Coxson had heart rot and could not be dated to their time of establishment. The infrequent occurrence of charcoal layers indicates that fire return intervals may be much longer than the age of the oldest trees present (Sanborn et al., 2006).

A continuous moss layer, composed mainly of *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, and *Pleurozium schreberi*, dominated the forest floor surface in the EA stands. Shrub layers were largely absent, with *Cornus canadensis*, *Chimaphila umbellata*, and *Pyrola secunda* forming a sparse herb layer. Ground cover in the OG stands was dominated by oak ferns (*Gymnocarpium dryopteris*), a common indicator of hygic 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 *C. canadensis*, while the moss layer was composed largely of *H. splendens*, *R. triquetrus*, and *P. schreberi*.

2.2. Lichen growth rates

Growth rates of the dominant canopy cyanolichen *L. pulmonaria* were measured from June 2002 to June 2004. Sample lichens were collected from lower canopy small diameter branches at the edge of gaps in the LUNO site in early June 2001. Thalli readily detached from these small diameter, often decorticated, branches. Lichen thalli were chosen so as to obtain a relatively uniform size range, choosing naturally



Fig. 1. Thallus of *Lobaria pulmonaria* held within a field growth enclosure “cage”.

occurring pieces ca. 10 cm × 12 cm in size (mean air-dry weight on initial placement of 2.15 g). These typically consisted of multiple lobes, joined at a common point of attachment (see thallus illustrated in Fig. 1). Thalli were held in the dark under cool dry conditions (ca. 15 °C and 60% R.H.) after collection, except for a short period when they were spread out on lab benches for sorting. Within 2 weeks of initial collection, 20 replicate thalli were placed in mesh enclosures and suspended from branches in each of the four stands. The collection and subsequent placement of transplant thalli in early to mid-June, typically a cool, wet period in the study area, should minimize initial transplant “shock”, though transition to warm dry conditions can occur rapidly in July and August.

Lichen enclosures consisted of a 15 cm × 20 cm plastic tray (1 cm × 1 cm grid) surrounded by translucent mesh (Fig. 1). Light transmission under this mesh varied by less than 5% from light transmission outside the mesh. Placement of these lichen “cages” within the stand followed a sampling design used by Coxson and Stevenson (2005) for lichen litterfall traps, with a single lichen cage placed in the nearest co-dominant canopy tree (hemlock or cedar) at 10 locations chosen at random along two 100 m transects, the transect placed along the contour interval in each stand (giving a total of 20 cages placed within each stand). Cages were hung on the first major lower branch of each sample tree ca. 1 m from the bole, usually between 5 and 10 m from the forest floor (though sometimes as high as 12 m from the forest floor where available branches so dictated) at whatever orientation the available branch presented. Sample trees that fell within the dripzone of isolated deciduous trees present within the canopy (mainly *Populus balsamifera*) were excluded from consideration.

Changes in the mass of enclosed lichen thalli were determined at annual intervals, starting in June 2002 and continuing through June 2004. Mass determinations were conducted in a temperature and humidity controlled weighing room (25–27 °C and 40% relative humidity), where thalli were held for 48 h before being weighed to the nearest 0.001 g. Lichen growth rates from June 2002 to June 2003 (year 2), and June 2003 to June 2004 (year 3), were subsequently used to

assess response to transplant environments. We regarded the initial year’s placement of lichen cages in the canopy (year 1, June 2001 to June 2002) as an equilibration period after transplanting, and do not use mass determinations from this period in our present analysis of lichen responses to canopy light environment.

2.3. Canopy light environments

The canopy light environment of lichen enclosures was measured using hemispherical (fisheye) photographs, taken at the point of placement of each lichen cage within the lower canopy. An 8 mm Sigma lens mounted on a Nikon F90X was used to obtain canopy images in late May and early June 2004. Images were photographed under clear-sky conditions. Digitized images were subsequently analyzed using Gap Light Analyzer 2.0 (<http://www.rem.sfu.ca/forestry/index.htm>); an imaging software program that extracts canopy structure and gap light transmission indices from fisheye photographs (Frazer et al., 1999) using calculated daily values of solar angle and solar maximum (incident radiation above canopy) at that latitude to determine annual light availability (canopy light transmission) from each fisheye photograph. Parameters subsequently calculated for all cage locations were canopy light transmission (CLT) ($\text{mol m}^{-2} \text{day}^{-1}$) and % canopy openness. Although photographs were taken in the early summer period, given the dominant coniferous forest cover at these sites, we would not expect significant changes in seasonal canopy closure. Additional calculations were made for one EA cage location (Enclosure VIKY-38) and one OG cage location (Enclosure VIKO-08) having CLT values in the midrange of those in EA and OG stands, respectively. These calculations were the potential number and duration of discrete sunfleck events, and gap fraction (ratio of sky pixels to total pixels per sky-region segment), partitioned by zenith angle (degrees from vertical) (Frazer et al., 1999).

2.4. Canopy microclimate

Canopy microclimate was assessed in the LUNO OG stand from the time of initial cage placement (June 2001) to the end of the 2-year measurement period (June 2004). These assessments were conducted on six replicate *L. pulmonaria* thalli growing on separate branches in each of three replicate cedar trees (mean branch height of 11 m, maximum branch height 16 m). *Lobaria* thalli were chosen using the same criteria as those used for selecting growth rate thalli. Lichens in western-red cedar were chosen to provide data on canopy microclimate in the dominant tree within these OG stands. Canopy access for placement of microclimate probes was gained using single-rope climbing techniques. Campbell Scientific data loggers recorded average sensor output for the preceding interval (since last record) at 10 min intervals during periods when thalli were hydrated, and 3 h intervals when thalli were desiccated.

Instrumentation placed in each tree consisted of six fine-wire thermocouples held against the upper surface of *Lobaria* thalli, six impedance clips measuring thallus water content (after

Coxson, 1991), and three Li-Cor photosynthetically active radiation (PAR) sensors, these mounted on a horizontal plane adjacent to one thallus in each tree using branch-mounted swivels. Average CLT obtained from fish-eye photographs for individual branch locations at the LUNO microclimate station was $5.75 \text{ mol m}^{-2} \text{ day}^{-1}$.

Impedance clips for measurement of thallus hydration status were placed on new thalli each year to counter any degradation resulting from exposure to excitation voltages and potential movement of clips during storm events. The accuracy of impedance measurements across lichen thalli dropped as thallus temperatures fell below ca. $-2 \text{ }^\circ\text{C}$, with reduced voltage returns from frozen thalli becoming difficult to distinguish from reduced voltage returns in desiccated thalli. For the purposes of the present study, the hydration status of each thallus was therefore assumed to continue unchanged as temperatures fell below the $-2 \text{ }^\circ\text{C}$ threshold, until thawing allowed resumption of impedance measurements. These gaps in our measurement of thallus hydration typically occurred over diel cycles, during seasons when temperatures dropped below freezing each night (especially in spring and fall) or during extended periods of low temperature (often under snow cover) in mid-winter. Our assumption that relatively small changes in hydration status occurred when thalli were frozen was found to be accurate over most freeze-thaw episodes, with values on thawing usually within 10% of those recorded when impedance measurements ceased. When greater changes in thallus moisture content were observed over diel freeze-thaw events, these were typically increased hydration, caused by snow-melt events.

Instrumentation placed on *Lobaria* thalli monitored in canopy microclimate measurements precluded using the same thalli for lichen growth rate measurements. Energy conversion efficiency calculations for old-growth thalli therefore used growth rates from enclosed thalli with similar CLT values in the LUNO and VIKO stands. Thalli instrumented for canopy microclimate measurements were typically located on branches 1–2 m higher in the canopy than those used for transplant cage placements, this an artifact of branch availability on selected trees. This difference, however, is small against the overall height of the canopy (up to 55 m) and height range (from ground to $>30 \text{ m}$) over which *Lobaria* thalli grow (see Benson and Coxson, 2002). The selection of cages for calculations of energy conversion efficiency based on their CLT values (see below) further minimizes differences between canopy environments experienced in growth rate and microclimate thallus sets.

2.5. Data analysis

The relationship between mean annual dry matter gain [g (g DW)^{-1}] of enclosed lichens over the two year assessment period and canopy light transmission (or % canopy openness) was evaluated by linear regression using SYSTAT 8.0 (SPSS Inc., Chicago, IL). Indicator (dummy) variables were introduced as categorical variables to linear regressions (Neter et al., 1983) to determine whether study block type (OG or EA) significantly affected relationships between dry matter gain and

canopy light transmission/openness. Significance in statistical tests was assumed at a probability value of $p < 0.05$ in t -tests on individual coefficients. We excluded data from cages where growth rate measurements were obtained in only a single year, for instance in cases where thallus fragmentation resulted in unknown mass loss (as fragments often fell through the lower cage mesh) or where cages were damaged by tree-fall events or animals.

We calculated intercepted irradiance at the surface of hydrated lichen thalli (I_{wet}), defined as those whose thallus moisture content was above 20% water content by weight, this calculated as $((\text{wet weight} - \text{dry weight})/\text{dry weight}) \times 100$. I_{wet} values were calculated over two periods: (i) annually, during all episodes when hydrated thalli were above $0 \text{ }^\circ\text{C}$, and (ii) during the May to September period only, again when hydrated thalli were above $0 \text{ }^\circ\text{C}$. Calculations of energy conversion efficiency (e) were made for both of these I_{wet} periods using a subset of lichen growth rate measurements corresponding to cages that had similar CLT values (mean CLT at climate station $\pm 1 \text{ mol m}^{-2} \text{ day}^{-1}$) after Palmqvist and Sundberg (2000). Conversion of lichen growth rates to area based denominators used a mean lichen mass of $187.3 \text{ g dry weight m}^{-2}$ (S.E. of 9.4), taken from 20 replicate 1 cm^2 thallus segments (these taken from collections obtained for the LUNO transplant set). Terminology and conversion factors for energy content of photons and energy content of lichen dry matter follow Palmqvist and Sundberg (2000). These provide only an approximation of available radiant energy, as spectral distribution of measured PAR will vary from one period to another, depending on the proportion of direct and indirect light availability.

3. Results

Thallus temperature measurements showed extreme seasonality, with absolute recorded maximum and minimum temperatures during the 3-year measurement period ranging from -32 to $+30 \text{ }^\circ\text{C}$ (Fig. 2a and b). During the winter period thalli often remained hydrated, but frozen under snow on branches within the canopy. The longest of these episodes (between thaw periods) was 3 weeks, in January/February 2004. Snowmelt events within the canopy were common in the late winter–early spring period. Under these conditions hydrated thalli were exposed to daily freeze/thaw events (Fig. 3). Snowmelt events represented one of the few sets of conditions under which hydrated thalli faced prolonged periods of relatively high insolation exposure.

The duration of thallus wetting events during rainfall was greatest in the months of July and August. The mean duration of thallus hydration events was 37.7 h over the 3-year study period (8 wetting events per month on average) (Fig. 2c). Hydrated thalli, however, experienced a much narrower range of operating temperatures (Fig. 2b) compared to overall thallus temperature measurements (Fig. 2a), with maximum recorded temperatures of hydrated thalli reaching only $16.6 \text{ }^\circ\text{C}$.

Two types of wetting events were common in the data set. Major precipitation events, characterized by extended periods

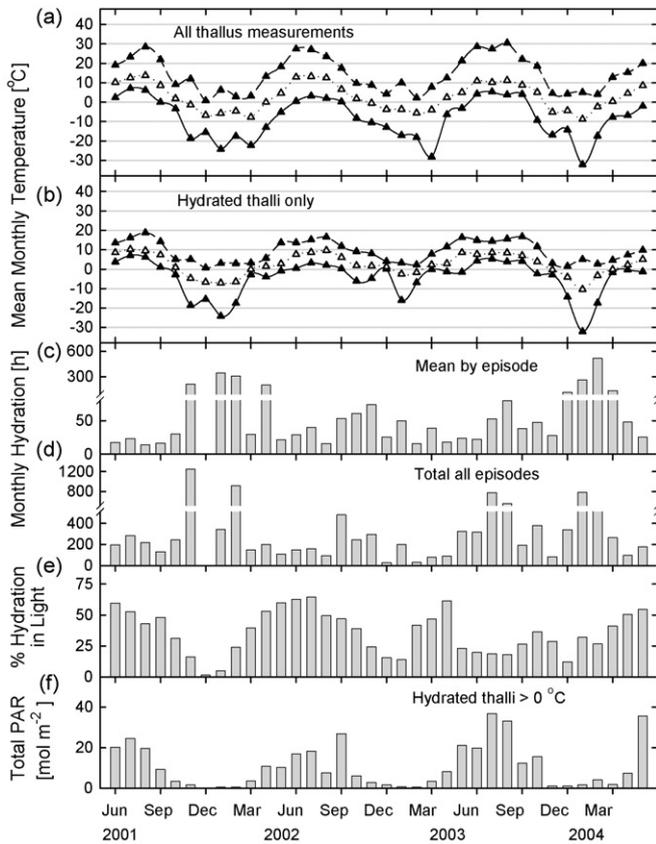


Fig. 2. Monthly summary of canopy microclimate parameters recorded at the surface of *Lobaria pulmonaria* thalli from June 2001 to May 2004. From top: (a) maximum (upper solid line, closed triangles), mean (middle dotted line, open triangles), and minimum (lower solid line, closed triangles) thallus temperatures; (b) maximum (upper solid line, closed triangles), mean (middle dotted line, open triangles), and minimum (lower solid line, closed triangles) temperatures of hydrated thalli; (c) mean duration of hydration episodes; (d) total duration of hydration episodes; (e) percentage of time that hydrated thalli were in light; and (f) total photosynthetically active radiation (PAR) exposure during periods of thallus hydration.

of low cloud and fog (especially during spring and fall storms), resulted in fairly low (almost isothermal) thallus temperatures, usually under 10°C , with incident light exposure rarely exceeding $100\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PAR (Fig. 2). In contrast, hydration episodes that accompanied convective shower events (thunderstorms) during the summer months often began in late afternoon or evening, with thalli rapidly drying the following morning as insolation exposure increased (Figs. 4 and 5). Notwithstanding this trend of overnight hydration episodes, percent hydration exposure during daylight hours in the summer period was greater than 60% (Fig. 2).

PAR exposure by hydrated thalli was greatest during the month of July, in both 2001 and 2003 (at 24.5 and $36.8\ \text{mol m}^{-2}$, respectively), and in September, during 2002 ($26.9\ \text{mol m}^{-2}$) (Fig. 2). Monthly PAR exposure by hydrated thalli was low during the mid-winter period, with December values ranging from 0.175 in 2001 to $1.26\ \text{mol m}^{-2}$ in 2003.

Mean annual dry matter gain of lichen thalli was higher during year 2, than in year 3 (Table 1). Growth rate calculations for a subset of lichen cages with CLT values similar to those recorded

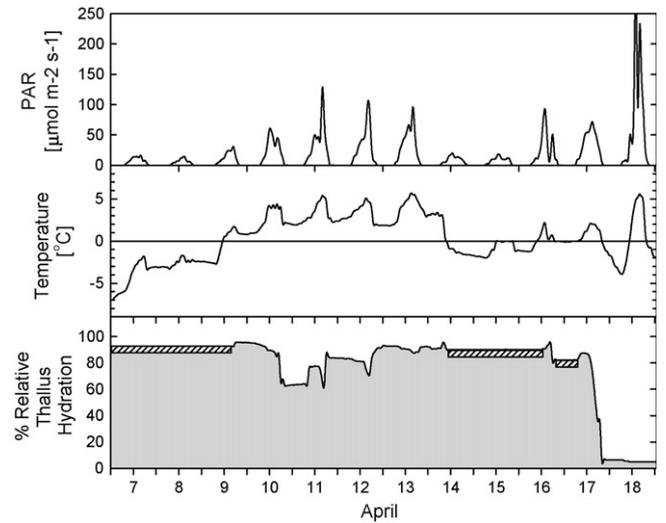


Fig. 3. Canopy microclimate at surface of *Lobaria pulmonaria* thalli, April 7–18, 2001. From top: mean photosynthetically active radiation (PAR) ($n = 9$), mean thallus temperature ($n = 18$), and mean percent relative thallus hydration (expressing the maximum thallus water content held by each thalli as 100%) ($n = 18$). Diagonal bars on hydration plots indicates periods when thalli were frozen in snowmelt run-off.

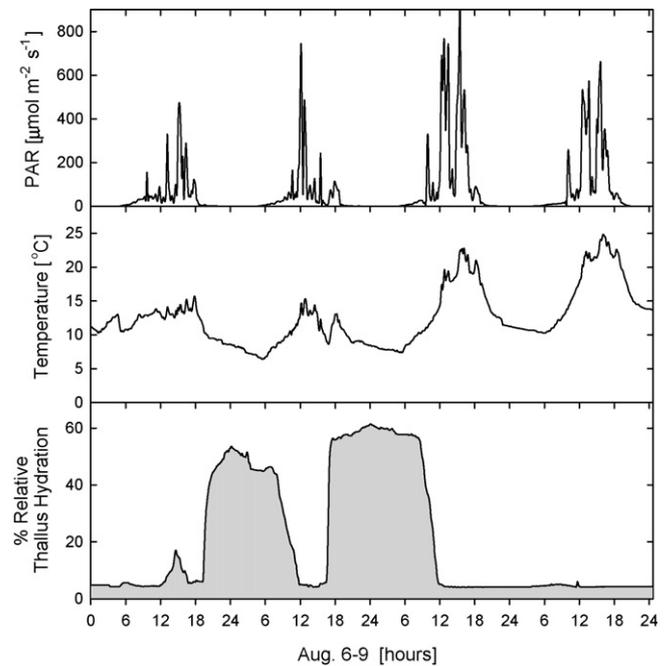


Fig. 4. Canopy microclimate at surface of *Lobaria pulmonaria* thalli, August 6–9, 2001. From top: mean photosynthetically active radiation (PAR), mean thallus temperature, and mean percent relative thallus hydration.

at the canopy microclimate station also showed lower growth rates in year 3 (Table 2), even though I_{wet} values were actually higher during year 3. These contrasting trends resulted in lower energy conversion efficiencies in year 3 (0.77 in 2003–2004).

Regression plots of canopy light transmission versus lichen growth response showed a strong correlation between mean annual dry matter gain (2-year average) and CLT (Fig. 6). In both EA and OG stands, dry matter gain increased linearly with light transmission (Fig. 6), but the rate of increase was significantly

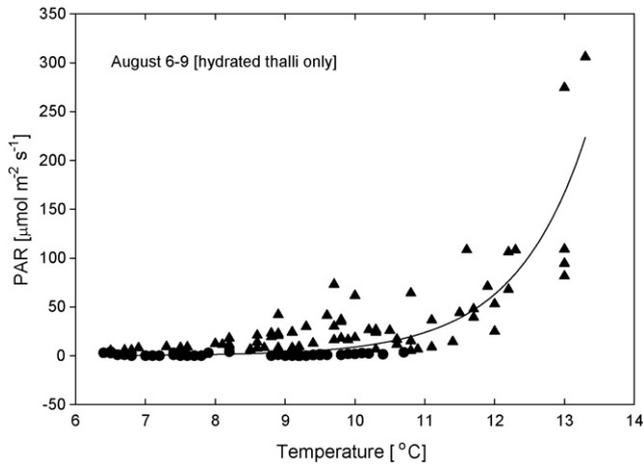


Fig. 5. Scattergram of mean photosynthetically active radiation (PAR) at the surface of *Lobaria pulmonaria* thalli against mean thallus temperature at time of measurement for hydration episodes on August 6–9, 2001.

Table 1
Annual dry matter gain [g (g DW)⁻¹]^a for *L. pulmonaria* thalli in old-growth and even-aged stands

	2002–2003	2003–2004
Old-growth		
Mean (S.E.)	0.1123 (0.010)	0.0788 (0.009)
Even-aged		
Mean (S.E.)	0.0986 (0.005)	0.0634 (0.006)

^a Pooled values, all stands. *n* = 38 per stand type.

lower in EA stands (0.0435 g (g DW)⁻¹/mol m⁻² day⁻¹) than in OG stands (0.0810 g (g DW)⁻¹/mol m⁻² day⁻¹) (*n* = 53, *t* = 3.5, *p* < 0.001). If this comparison was constrained to growth rates obtained from lichen cages within the range of CLT overlap between OG and EA stands (from 2.26 to 7.45 mol m⁻² day⁻¹) then no significant differences were seen between growth rate responses to CLT (*n* = 37, *t* = 1.518, *p* = 0.138). Treatment of the pooled data set with a second-order polynomial regression (*r*² = 0.63) provided a response slope intermediate to that of the individual linear regressions obtained for even-aged and old-growth data (Fig. 6). Comparisons of CLT growth rate responses between Viking and Lunate sites were not significant (*n* = 53, *t* = 1.3, *p* = 0.196).

A strong linear relationship was seen between calculated CLT (mol m⁻² day⁻¹) and % canopy openness (*r*² = 0.84) for

Table 2
Annual dry matter gain (calculated as g (g DW)⁻¹ and g m⁻²)^a, intercepted irradiance when wet (*I*_{wet})^b, and energy conversion efficiency (*e*) for *Lobaria pulmonaria* thalli

Year	Annual dry matter gain (g (g DW) ⁻¹ [g m ⁻²])		<i>I</i> _{wet} (MJ m ⁻²)		<i>e</i> (%)	
	Mean	S.E.	Annual	May–September	Annual	May–September
2002–2003	0.101 [18.8]	0.007	24.7	19.7	1.33	1.67
2003–2004	0.065 [12.1]	0.012	34.5	27.4	0.61	0.77

Annual dry matter gain was placed against *I*_{wet} of hydrated thalli (to determine *e*) over 2 time periods: from June 1 to May 31 of each year (annual); and from May 1 to September 30 of each year.

^a Includes only lichen “cages” with CLT values between 4.55 and 6.95 mol m⁻² day⁻¹ (*n* = 13).

^b Limited to time periods when hydrated thalli were above 0 °C.

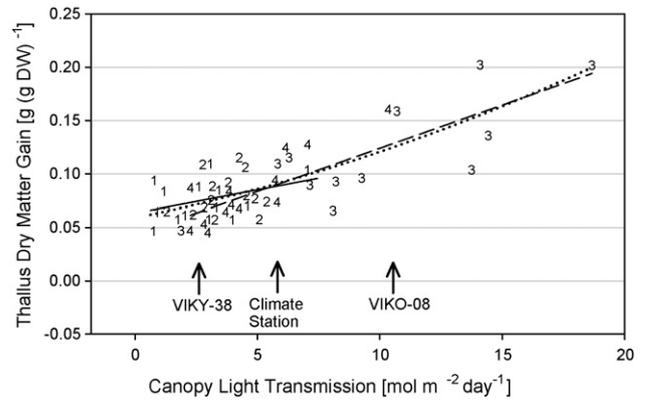


Fig. 6. Mean annual dry matter gain [g (g DW)⁻¹] over 2-year measurement period (from June 2002 to June 2004) in Lunate even-aged, Viking even-aged, Lunate old-growth, and Viking old-growth stands (using 1, 2, 3, and 4 as respective plot symbols for these stands) as a function of canopy light transmission. Linear regressions for old-growth and even-aged stand lichen growth measurements are indicated by dashed and solid lines, respectively (*r*² of 0.69 and 0.128, respectively), while a second-order polynomial regression (*r*² of 0.63) is indicated by the dotted line. The light availability at lichen cages VIKY-38 and VIKO-08 (used as representative cages for gap fraction plots) and at the canopy microclimate station are shown by the arrows.

individual branch plots (Fig. 7). The greater light transmission at most branch locations in the OG stands reflected the presence of larger canopy gaps. Comparison of frequency distribution plots for the duration of sunfleck events between representative EA and OG branch samples (from VIKY-38 and VIKO-08, respectively) illustrates these differences (Fig. 8). Though lichens in both locations potentially experience many small sunfleck events, longer duration sunfleck events (over 20 min in length) occurred almost exclusively in the OG stand. The greater proportion of gaps recorded at low zenith angles (near overhead in the canopy) (Fig. 9) at the VIKO-08 branch plot led to much greater calculated daily insolation exposure during the summer period (Fig. 10). Proportionally, sunfleck exposure in the EA stand was distributed more evenly throughout the year (Fig. 10).

4. Discussion

Cyanolichen growth environments are shaped by interactions between three main climatic influences: the availability of moisture to hydrate lichen thalli, be it from snowmelt, rainfall, fog interception, or dewfall; the availability of light at the surface of hydrated lichen; and the temperatures under which

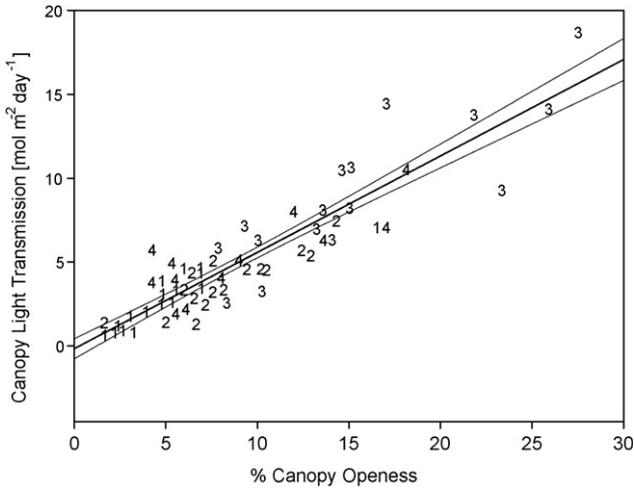


Fig. 7. Canopy light transmission ($\text{mol m}^{-2} \text{day}^{-1}$) vs. % canopy openness for branch plot lichen growth cages. Linear regression and 95% confidence intervals ($r^2 = 0.84$) are shown by solid lines on plot.

these conditions are realized. Although rates of net photosynthesis and nitrogen fixation in cyanolichens are generally optimal at temperatures of 20–25 °C or higher (Kershaw, 1977; Kershaw and MacFarlane, 1982; Pannewitz et al., 2000; Sundberg et al., 1997), in many cases hydrated lichen thalli operate under suboptimal temperature and light conditions, reflecting the conditions that often accompany precipitation

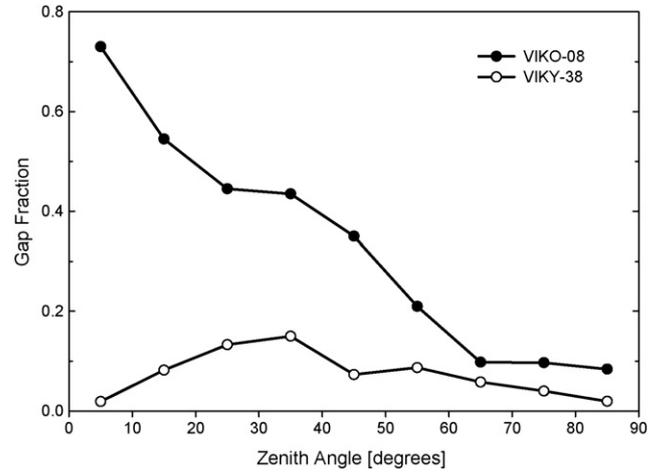


Fig. 9. Gap fraction plotted within 10° zenith angle class intervals for lichen cage measurements from old-growth (VIKO-08) and even-aged (VIKY-38) stand locations.

events, especially in boreal and montane environments (Coxson and Coyle, 2003; Palmqvist and Sundberg, 2000). These limitations on lichen growth rates were evident in *L. pulmonaria* thalli from our inland rainforest study sites. In August, the warmest month at our sites, though maximum thallus temperatures reached 27.5 °C, the mean temperature of hydrated thalli during daylight hours was only 10.1 °C. Wetting

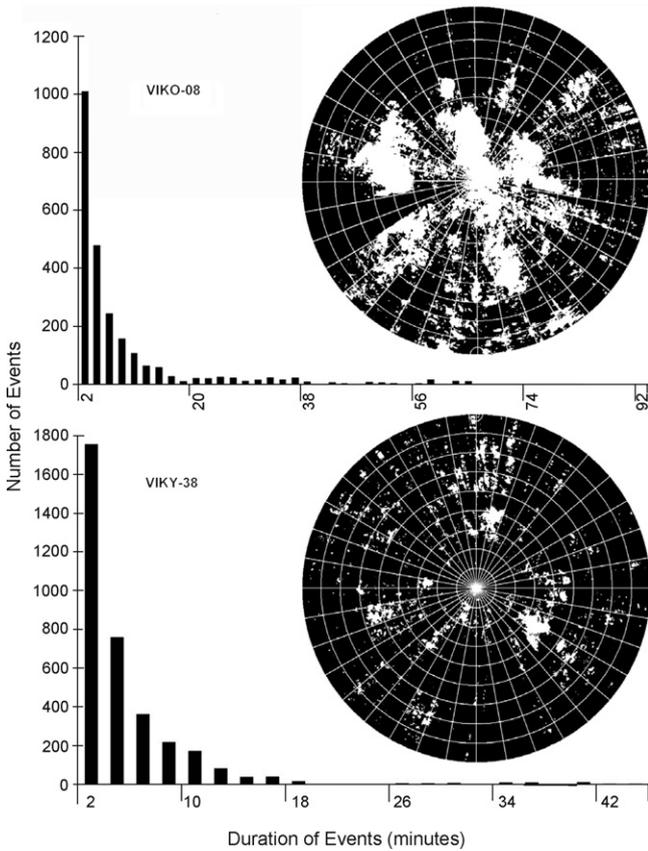


Fig. 8. Frequency distribution of sunfleck events by duration for lichen cage measurements from old-growth (VIKO-08) and even-aged (VIKY-38) stand locations.

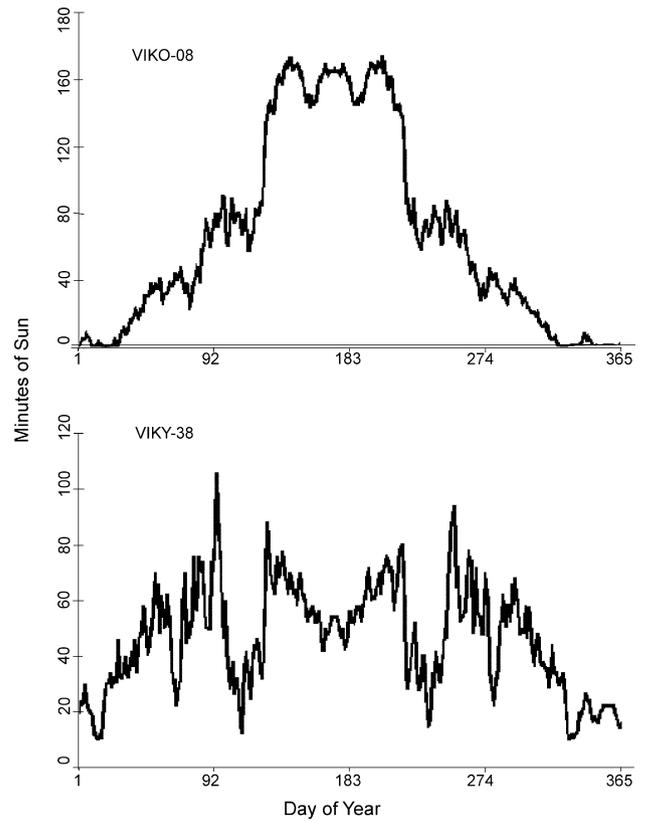


Fig. 10. Minutes of direct insolation exposure (sunflecks) by day of year in branch plots from old-growth (VIKO-08) and even-aged (VIKY-38) stand locations.

events that occurred during warmer fair weather conditions, often as late evening thunderstorms, were typically followed by rapid drying of thalli the next day, limiting PAR utilization by limiting the duration of physiological activity, i.e. when thalli were hydrated.

PAR exposure of hydrated thalli (above 0 °C) was low from October through early-March of each year, with reduced solar angles and height of the surrounding canopy interacting to shade lichen thalli for most of each day. Further, thalli were commonly frozen under snow pack on canopy branches for extended periods, presumably a major constraint on physiological activity. Although we have not separately measured winter period growth rates, our microclimate data would suggest that little growth can be sustained during the mid-winter period, in contrast to observations made in coastal wet-temperate rainforests, where winter rainfall provides a major period of physiological activity and growth (Muir et al., 1997).

Greater exposure of hydrated thalli to high light environments was observed during snowmelt events in late March and April. However, it is unclear if *L. pulmonaria* thalli are able to utilize intercepted light during this period. Schofield et al. (2003) found that most light energy received by *L. pulmonaria* under winter (freezing) conditions was dissipated by the photosynthetic apparatus. This reduced excitation pressure on photosynthetic pathways, but resulted in greatly reducing the rate of photosynthetic carbon gain. Thus, although our growth measurements encompass an annual period, much of this growth may only be realized during late-spring and summer conditions.

Mean weight gain in *L. pulmonaria* thalli, at 18.8 and 12.1 g m⁻² in years 2 and 3, respectively, was well above that recorded for *L. pulmonaria* thalli by Palmqvist and Sundberg (2000) (only 1.3–3.8 g m⁻²); being closer in magnitude to their recorded values for terricolous *Peltigera*, which had values as high as 67.4 g m⁻² (for *P. canina* in their Ulterviken study site).

Table 3
Comparative studies on *Lobaria pulmonaria* growth rates

Citation	Study area	<i>n</i>	Growth (%)	Time period (months)	Energy conversion efficiency (<i>e</i>)
Antoine and McCune (2004)	Western Washington			12	
	47–52 m height class	36	13		
	29–37 m height class	36	10		
	17–24 m height class	36	4		
Denison (1988)	Western Oregon	10	8	12	
			17–36	36	
Gaio-Oliveira et al. (2004)	Portugal	30	68	10.5	1.7–1.9
	Sweden	30	1.9–9.5	15	0.1–0.4
Gauslaa et al. (2006)	Norway			3	
	Old forest	200	16.0		
	Young forest	200	8.3		
	Clear-cut	200	23.1		
McCune et al. (1996) ^a	Western Oregon	43	13	12	
		5	41	9	
		7	25	9	
Muir et al. (1997)	Western Oregon	58	28	12	
		57	47	24	
		39	69	36	
Palmqvist and Sundberg (2000)	Northern Sweden	49	–1.2	12	0.9
	Southern Sweden	49	–0.4	12	0.8
Renhorn et al. (1997)	Northern Sweden	256	4.4	16	
Shirazi et al. (1996)	Western Oregon	5	24.5	4	
Sillett et al. (2000)	Western Oregon				
	Old forest	200	14.8	12	
	Young forest	200	10.3	12	
	Clear-cut	200	15.2	12	
Sundberg et al. (1997) ^b	Northern Sweden				
	Forest edge	15	1.7	16	0.2 ^c
	Forest interior	16	2.9	16	1.0 ^c
This study	East-central British Columbia				
	Old growth	38	19	24	0.77–1.67
	Even age	38	16.1	24	

^a Excluding studies subsequently reported in other publications.

^b Based on a subset of samples of Renhorn et al. (1997).

^c Recalculated by Palmqvist and Sundberg (2000).

These values, however, must be placed in context of the greater I_{wet} values for *L. pulmonaria* thalli in our sites, up to 34.5 MJ m⁻² in 2003–2004, compared to values of 2.6–7.7 MJ m⁻² at sites of Palmqvist and Sundberg. When our growth rates were expressed as energy conversion efficiency (e) values (from 0.77 to 1.67% for the May–September period; Table 3), they were much closer to those seen by Palmqvist and Sundberg (from 0.8 to 1.0%) (see also studies of Sundberg et al., 1997 and Gaio-Oliveira et al., 2004), presumably reflecting underlying physiological constraints in *L. pulmonaria*.

A cautionary note to the interpretation of the current data set is that calculations of e derive from microclimate measurements taken on 3 trees (western-red cedar) within a single stand. Although the instrumented stand was representative of wet cedar–hemlock stands of the Upper Fraser River watershed in terms of tree species composition and structure, replication of microclimate instrumentation in additional stands may extend the range of observed e values. Growth rate comparisons can also be taken from data obtained from all four stands, however, comparisons with *Lobaria* growth rates obtained from thalli on branches in the shaded EA stands (where little or no *Lobaria* grows naturally, see Benson and Coxson, 2002) may not be appropriate (hence our use of a restricted CLT range above).

Several other studies have reported on *L. pulmonaria* growth rates (Table 3). Perhaps the most comparable studies are those from wet temperate coniferous rainforests in western North America, where mean values range from 4% over 12 months (Antoine and McCune, 2004) to 41% over 9 months (McCune et al., 1996). As noted above, a major difference between these coastal ecosystems and the interior rainforests is the prolonged periods of cover under snow and low temperatures within the canopy in our interior rainforests. This regional difference may account for the greater maximum growth rates reported in coastal ecosystems.

Large differences in light availability were found between lichen transplants in EA and OG stands. The greater light availability in our OG stands most likely results from single-tree gap dynamics, similar to those described by Daniels and Gray (2006) for coastal OG cedar–hemlock forests in BC. We expect that these would play a major role in creating the canopy openings that favor overhead light transmittance in our OG stands, as well as the multi-layered canopy structure that tends to reduce light transmission at high zenith angles. In contrast, canopy gaps in the EA stands were much smaller, and the gap fractions more widely distributed across all zenith angles. As a consequence, light transmission in our OG stands was three to four times higher than that calculated for our EA stands.

The response slope of *L. pulmonaria* growth rates to CLT was higher in the gap-dominated OG stands, where CLT values reached 20 mol m⁻² day⁻¹, than in EA stands, where CLT values only reached 7.45 mol m⁻² day⁻¹. This was true for both linear regressions (performed separately for OG and EA stands) and non-linear regressions (on the pooled data set). This may reflect covariate interactions of CLT with moisture availability and moisture retention in the more “gappy” OG stands (see also discussion below). Alternatively, support costs

for maintenance respiration of the fungal biont in low light environments may diminish the magnitude of growth rate responses, irrespective of stand type.

It should be noted that within the range of CLT values shared by OG and EA stands (from 2.26 to 7.45 mol m⁻² day⁻¹) lichen CLT growth rate response curves were not significantly different. The apparent equivalence of branches in the EA stands where canopy foliage was less dense with branches in OG stands where canopy foliage was more dense suggests that there are no other intrinsic factors associated with OG status that have a large influence on lichen growth rates.

Although our current data set focuses on light availability at the level of individual lichen thalli (calculated as CLT), the high correlation between CLT and % canopy openness provides a parallel measure against which manipulations of canopy structure could be assessed by silvicultural foresters. Variance observed between these two parameters (which were both calculated from the same canopy “fish-eye” images) reflects differences in the spatial location of canopy gaps from one branch to another. Some branches have gaps that are directly overhead, others are located at higher azimuth angles.

Growth response in *L. pulmonaria* did not show any decline at the highest light levels recorded in our study, nearly 20 mol m⁻² day⁻¹ in the VIKO OG stand. This finding is similar to that of Sillett et al. (2000) in western Oregon and Gauslaa et al. (2006) in Norway, both of whom found that *L. pulmonaria* sustained high rates of growth after being transplanted into a high light environment. This supports the hypothesis of Palmqvist and Sundberg (2000), that lichen dry matter gain during periods when photosynthetic capacity is fully reconstituted (i.e. when thalli are hydrated) is primarily controlled by light duration and photon flux density.

The response of *Lobaria* thalli to increasing light exposure may take two forms. Greater synthesis of fungal melanins is hypothesized to act as a “sun screen” for symbiotic green algae (Gauslaa and Solhaug, 2001). Although we did not quantify pigmentation changes in our transplanted thalli, our field notes indicate that thalli at the edge of canopy openings had a darker appearance when dry than those from more shaded habitats. Gauslaa and Solhaug note that increases in melanins would also increase absorbance of solar energy, potentially resulting in heat stress exposure. Although this may be a concern along forest edges after clear-cut harvesting, where prolonged insolation exposure is possible (Coxson and Stevenson, 2005), microclimate data from our canopy gaps under OG stand conditions do not show any evidence of high thallus temperatures.

A second form of adaptation to increasing light exposure may be that of macromolecular changes in photosynthetic systems. Mackenzie et al. (2004) found that *L. pulmonaria* growing in deciduous forest canopies showed rapid changes in light capture molecules of photobionts, especially during spring canopy leaf-out. However, the seasonal changes in temperature and light exposure under a deciduous forest canopy are likely to be much more rapid than those that were found in the present study, where overall seasonal changes in the mean temperature of hydrated thalli were generally less than 10 °C in magnitude.

Thalli of *L. pulmonaria* transplanted into EA stands showed continued, albeit low, rates of growth, this notwithstanding the virtual absence of *L. pulmonaria* thalli from these stands (Radies and Coxson, 2004). Sillett et al. (2000) found that transplanted thalli of *L. pulmonaria* performed well when placed in young Douglas-fir forests in western Oregon, and concluded that dispersal was the main factor limiting establishment in their younger stands. Given that our EA stands were close to the surrounding old-growth forest matrix, it is unlikely that availability of propagules was a primary limiting factor. However, constraints on the establishment of young thalli may still be quite important. The more uniformly dense foliage of even-aged stands may create drier lower canopy conditions due to interception and evaporation of rainfall in the upper canopy. This effect is likely compounded by thallus size, with small thalli experiencing a shorter duration of hydration after each wetting event, reflecting their greater relative surface area and reduced water holding capacity (Gauslaa and Solhaug, 1998).

The absence of *L. pulmonaria* thalli on hemlocks in the EA stands does not appear to be a function of substrate preferences. Radies and Coxson (2004) found abundant regenerating thalli on similarly sized hemlock within adjacent OG forests. Tree species diversity within forest canopies, however, can be an important consideration. Goward and Arsenault (2000) found greater lichen abundance on conifers under dripzones of large poplars (*Populus balsamifera*) compared to those with no dripzone influence, a factor which they attribute to enhanced Ca availability. Hauck and Spribille (2002) further suggest that changes in Mn/Ca and Mn/Mg ratios in poplar dripzones may influence recruitment of young thalli. Sites containing deciduous trees were excluded from our present study design, and were absent in any case from the even-aged stands.

Our study did not control for potential differences between lichen growth rates in cedar versus hemlocks. The EA stands were composed exclusively of hemlocks, whereas our OG stands had hemlock and cedar as codominant tree species (Benson and Coxson, 2002). Though hemlock-dominated OG stands can have lower lichen loadings than cedar-dominated stands, these differences are confounded by the relatively drier habitats of many of the hemlock-dominated stands in the inland rainforest (Ketcheson et al., 1991). In the present study sites, the relatively small size of the hemlock-dominated EA forest patches, where most trees were located less a tree length from adjacent OG stands, and the continuous nature of the forest cover should minimize what otherwise could be confounding effects of habitat type on moisture availability within the canopy. Lyons et al. (2000) suggest that for shade tolerant species such as hemlock, comparisons of epiphyte succession between trees in different stand types may be more dependant upon tree size and relative position than upon age.

It should be also noted that the gradients in light availability that we have documented within these cedar–hemlock forest stands will have strong interactions with gradients of moisture availability within the canopy, an important factor in interpreting lichen growth responses. Canopy gaps in cedar-leading OG stands will allow greater light and wind penetration

at lower canopy positions, normally factors associated with more xeric conditions. At the same time, however, reduced interception of precipitation in gaps will provide greater moisture availability, as may standing water at the forest floor surface in gaps. The present study does not directly evaluate or rank these possible covariate environmental parameters. Canopy light transmission (calculated from fisheye photographs) is rather presented as a readily measured environmental attribute that has a strong correlation with lichen growth rates. Even in the OG stands, where we did measure temperature, moisture, and light conditions experienced by a set of *Lobaria* thalli, we still rely upon lichen thalli to integrate the many source–sink relationships for temperature, moisture, and light availability. However, we would predict that silvicultural interventions that create small canopy gaps should also allow greater interception of direct precipitation by lichen thalli, mimicking natural gap-formation. It is more difficult to predict interactions with surface hydrology that may occur after harvesting small patch openings.

5. Conclusion

These findings suggest that thalli of *L. pulmonaria* may be surprisingly resilient to harvesting treatments that provide some opening of the canopy, while retaining propagule sources for future lichen establishment. We would recommend the determination of canopy light transmission under specific silvicultural treatments in BC's inland rainforests, following the example of Drever and Lertzman (2003) from coastal Douglas-fir forests in BC. As well, we need to know whether growth rates of *L. pulmonaria* decline at light levels higher than those observed in this study.

Our findings also raise the question of whether other old-growth-associated lichen species might also be more resilient than previously thought. Some lichen groups, such as the Caliciales, are highly dependant upon specific structural features that are present only in old-growth forest environments (Goward and Spribille, 2005). Sillett and McCune (1998) and Sillett et al. (2000) caution that while *L. pulmonaria* is capable of sustained high growth rates after transplantation into higher light environments, other foliose cyanolichens (*L. oregana* and *Pseudocyphellaria rainierensis* in their study sites) may have much greater mortality on high light exposure. Direct studies on other old-growth species in the inland rainforest, such as the bipartite lichen *L. retigera*, which has only a cyanobacterial photobiont, would be valuable to determine whether any other old-growth-associated species also tolerate high light levels. Increased understanding of the responses of old-growth associated lichens to canopy structure will improve our ability to predict which species can be maintained through alternative forestry practices, and which are dependent on unharvested conservation areas for their survival.

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