Canadian Journal of Forest Research

Forest edge-induced damage of cephalo- and cyanolichens in northern temperate rainforests of British Columbia

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2018-0187.R2
Manuscript Type:	Article
Date Submitted by the Author:	13-Nov-2018
Complete List of Authors:	Gauslaa, Yngvar; Norges miljø- og biovitenskapelige universitet, Faculty of Environmental Sciences and Natural Resource Management Bartemucci, Paula; Gentian Botanical Research, Solhaug, Knut Asbjørn; Norges miljø- og biovitenskapelige universitet Fakultet for veterinærmedisin og biovitenskap, Faculty of Environmental Sciences and Natural Resource Management
Keyword:	Canopy retention, Edge effect, Epiphytic lichen, Logging disturbance, Temperate rainforest
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

SCHOLARONE™
Manuscripts

**Forest edge-induced damage of cephalo- and cyanolichens in northern
temperate rainforests of British Columbia**

Yngvar Gauslaa^{1*}, Paula Bartemucci², and Knut Asbjørn Solhaug¹

¹ Faculty of Environmental Sciences and Natural Resource Management, Norwegian
University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway.

² 4861 Nielsen Road, Smithers, BC V0J 2N2 British Columbia, Canada

* Corresponding author: yngvar.gauslaa@nmbu.no (Y. Gauslaa)
<https://orcid.org/0000-0003-2630-9682>

Abstract: Retention of trees after logging is a method of preserving epiphytic lichens; however, epiphytes' responses to logging disturbance are insufficiently known. We aimed to characterize four viability measures - effective PSII yield (Φ_{PSII} ; a proxy for photosynthesis), maximal photosystem II efficiency (F_V/F_M ; a proxy for photoinhibition), chlorophyll *a* content, chlorophyll *a/b*-ratio, - and the functional parameter specific thallus mass (STM; a proxy for water storage) in sympatric populations of two old-growth lichens (*Lobaria retigera*, *L. oregana*) and the less old-growth dependent *L. pulmonaria* along recently-logged forest edge gradients of retained forest patches. All species experienced substantially reduced chlorophyll contents near edges, whereas Φ_{PSII} was lower in the two old-growth lichens than in *L. pulmonaria*. STM, and thus lichen water storage, did not respond to logging, probably because chlorophyll degradation reduced the carbon-gain required for necessary acclimation. Reported edge effects on lichen viability were so strong that the epiphytic lichens in most of the retained forest patches were affected. Measured viability variables improved linearly with distances up to ≈ 120 m from the edge. To avoid logging-induced adverse impacts on the threatened epiphytic lichens of these old-growth rainforests, there is a need to retain forest patches wider than 240 m.

Keywords: Canopy retention; Edge effect; Epiphytic lichens; Logging disturbance; Temperate rainforest;

34 Introduction

35 Forest canopy lichens often show reduced survival along edges after logging (Dettki and
36 Esseen, 2003) because they rapidly become damaged when exposed to sudden increases in
37 light levels (Gauslaa and Solhaug, 1996). Lichens surviving the logging, and this sudden
38 high-light exposure, afterwards exhibit greatly reduced growth rates in the low-light
39 environments of early successional regeneration stages (Gauslaa et al., 2006; 2007). The
40 decline of canopy lichens after logging may also reflect inefficient dispersal and low
41 establishment success by the increasingly fragmented lichen population (Ardelean et al.,
42 2015; Ellis and Coppins, 2007; Nordén et al., 2014; Ronnås et al., 2017), which can lead to
43 extirpation (Ellis, 2017; Jönsson et al., 2017; Snäll et al., 2005). Logging may even affect
44 canopy lichens in forest stands beyond the forest edges (Esseen and Renhorn, 1998; Rheault
45 et al., 2003).

46 The Kispiox Valley in north-western British Columbia is part of the northern temperate
47 rainforest of the Pacific coast of North America. This rainforest exists because of a
48 combination of high humidity, cool temperatures and frequent but relatively low levels of
49 summer rain (DellaSala et al., 2011). The region is transitional between wet rainforests of the
50 coast and the drier, colder interior continental forests. It is rich in rare old-growth canopy
51 lichens, and has a unique epiphytic lichen flora in the sense that the nitrogen-fixing cephalo-
52 and cyanolichens account for nearly half of the total epiphytic macrolichen diversity, an
53 incidence hardly equalled in other parts of North America (Goward and Pojar, 1998).

54 In the past four decades, logging in Kispiox Valley has greatly reduced the extent of old
55 forests and the unique suite of old-growth lichens (Goward and Pojar, 1998) associated with
56 them. Recent forest management direction aims at retaining groups of trees around rare lichen
57 occurrences because successful retention of groups of old trees in clearcuts may allow canopy

lichens to persist through the forest harvest cycle, and lifeboat them to the regenerating forests (Rosenvald and Lõhmus, 2008). There is, however, little known about how well these species will survive in retained forest patches. Due to on-going logging pressure on these epiphyte-rich forests, there is an immediate need for a rapid assessment of how far the detrimental effects of logging on canopy lichens extend into the forest retention patches.

For the present study, we sampled canopy lichens six months after logging in two old-growth forest patches that were retained after clearcut logging. We aimed to characterize how naturally established epiphytic lichens respond physiologically to edge formation, and to complement earlier forest edge studies in which lichens had been transplanted along edge gradients at some time after the edge was formed (Coxson and Stevenson, 2007; Stevenson and Coxson, 2008). Specifically, we examined viability parameters, including effective PSII yield (Φ_{PSII} ; a proxy for photosynthesis), maximal photosystem II efficiency (F_v/F_m ; a proxy for photoinhibition), chlorophyll *a* content, and the chlorophyll *a/b*-ratio in three lichens sampled from the recently-logged forest edges into the interior of retained forest patches. We compared two old-growth canopy lichens *Lobaria retigera* (Bory) Trevisan (cyanolichen) and *Lobaria oregana* (Tuck.) Müll. Arg. (cephalolichen) with the widespread and less old-growth dependent cephalolichen *Lobaria pulmonaria* (L.) Hoffm. Only these species were sufficiently abundant to be regularly sampled in the studied forest patches. The objective was to quantify the length and severity of the edge effect and to recommend minimum sizes of retained forest patches to avoid adverse effects on these lichens.

In particular, we want to test the following hypotheses: (1) the widespread *Lobaria pulmonaria* experiences less high-light damage and has higher viability closer to the recently logged edges than *L. retigera* and *L. oregana*, which unlike *L. pulmonaria* are associated with old growth forests (Goward and Pojar, 1998). (2) Between the two old forest species, the cyanolichen *L. retigera* is more susceptible to recently-logged edge effects than the

cephalolichen *L. oregana*. The second hypothesis was proposed because *L. retigera*, unlike *L. oregana*, is listed as a threatened species under Canada's species at risk (<https://www.canada.ca/en/environment-climate-change/services/committee-status-endangered-wildlife/status-reports-preparation.htm>) and because longer-term growth reductions in lichen transplants along hard edge transects were shown to be strong in *L. retigera* (Stevenson and Coxson, 2008). *Lobaria oregana* with its coarse marginal lobules acting as diaspores could simply be an old-growth forest associate because it disperses more poorly (Sillett et al., 2000) than *L. retigera* with smaller diaspores (soredia). Finally, we wanted to quantify the important functional trait, specific thallus mass (STM), an easily measured proxy of thallus thickness shaping the water-holding capacity of lichens and thus the duration of physiologically active periods in poikilohydric organisms (Gauslaa, 2014). Because STM can acclimate and compensate for increasing evaporative demands (Merinero et al., 2015), our last hypothesis (3) assumes that STM after logging increases as an acclimation to stronger evaporative demands near the forest edge. By quantifying early damage and acclimation along edge gradients, we establish basic knowledge of important physiological events taking place in lichens shortly after logging, facilitating formulation of action plans for rare canopy lichens.

Materials and methods

Study sites

We studied lichen viability in response to recent logging in Kispiox Valley of north-western British Columbia, Canada (55° 32' N, 128° 02' W; 530-620 m) hosting old-growth northern temperate forests. The two selected cut-blocks of old-growth forest (forest patches) lie within the Hazelton variant of the moist cold subzone of the Interior Cedar-Hemlock biogeoclimatic

zone (ICHmc2; Banner et al., 1993). However, this area is transitional to the ICHmc1, which occurs at slightly higher elevations than the ICHmc2, and has a very humid local climate. Summers are wet, cool and cloudy because moist cold weather systems pass through the Coast Mountains up large river valleys like the Skeena, shedding warmth and moisture into the Kispiox area, just east of the Coast Mountains (Banner et al., 1993). Forests patches are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Amabilis fir (*Abies amabilis* (Douglas ex Loudon) Douglas ex Forbes).

Annual precipitation is relatively low (625-800 mm; Environment Canada, 2018; Wang et al., 2012), but as much as 45% of the days in the three warmest months receive rain (151 mm in total; weather data from the closest long-term weather station, 20 km south of study area, Hazelton, BC; Environment Canada 2018). Fire return intervals are 150 to 350 years depending on topographical position and microclimate (Parminter, 1991).

We established three line transects through one forest patch (3.7 ha). Only two transects could be made in the second forest patch (4.5 ha) due to its somewhat irregular shape. Forest retention patches were located in two nearby cut-blocks (one km apart), and were the only available cut-blocks of reasonable size for this year. All five parallel transect lines were oriented east-west originating from the recently logged edge of the forest patch (eastern edge) and ran west into the interior of the patch. Distances between parallel transects ranged from 80 to 140 m; the lengths of the five transects ranged 63-150 m.

Sampling distances along transects varied depending on where the target species could be found in close proximity. The farthest possible distance from any logged edge in studies transects varied from 63 to 150 m, depending on the dimensions of the retention patches. The spatial position of each sampling location was mapped using Avenza PDF Maps on a Samsung Galaxy tablet (≤ 10 m accuracy). The distance to the edge for each sampling

131 location was computed from the geo-referenced data.

132 *Lichen material*

133 At each transect position, one specimen of each of the three target species (*Lobaria retigera*,
134 *L. oregana*, *L. pulmonaria*) was collected as close to each other as possible. In some cases,
135 only two species could be found at a given position. From the five transects in total, this
136 resulted in 23 transect locations, all of which had *Lobaria pulmonaria* and *L. retigera*, but
137 only 16 of them had *L. oregana*. After drying the thalli at room temperature, they were stored
138 in a freezer (-18 °C) until lab measurements could be made. The collection of thalli was done
139 on August 31, 2017, and all measurements (see below) were completed within 10 d.

140 We measured air-dry mass after 24 h drying at 20°C in the lab for each thallus. Five
141 additional thalli were oven-dried 24 h at 70°C to measure oven dry mass (DM). We used the
142 oven-dried/air-dried mass ratio from these additional thalli to calculate dry mass (DM) for all
143 experimental thalli. All thalli were photographed in the hydrated state to compute the
144 hydrated thallus area (A) by ImageJ 1.48 (Rasband, 2014). Specific thallus mass (mg cm^{-2})
145 was computed as $\text{STM} = \text{DM}/\text{A}$.

146 *Chlorophyll fluorescence*

147 After removing the thalli from the freezer, they were preconditioned. We sprayed them with
148 de-ionized water and placed them in a controlled temperature room at 15°C under dim light
149 ($\approx 5 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) for 24 h to optimize detection of the more lasting photoinhibitory
150 damage (Solhaug, 2018).

151 After the preconditioning, we quantified maximal photosystem II efficiency, F_V/F_M , after 15
152 min of dark-adaption, using an Imaging-PAM MAXI-version (Heinz Walz GmbH, Effeltrich,
153 Germany). Then, all thalli were acclimated to $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ from a LED panel
154 (Model SL-3500, Photon System Instruments, Brno, Czech Republic) with red light for 30

min before we recorded the effective PSII yield (Φ_{PSII} , a proxy of photosynthesis) with the Imaging-PAM using measuring light, actinic light and saturating light pulses from red LEDs. The saturating light pulses for measurement of the maximal fluorescence from dark-adapted (F_M) and light-adapted thalli (F_M') were $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$. For measurements of Φ_{PSII} , we used actinic light of $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Each fluorescence parameter was assessed as the average for each entire thallus, including visually damaged as well as normal patches.

Chlorophyll measurements

After measurement of chlorophyll fluorescence, each specimen was ground to a fine powder in an Eppendorf tube with a ball mill (Retsch MM 301, Retsch GmbH, Haan, Germany). To extract chlorophylls, we added 10 to 12 mg DM from each specimen to an Eppendorf tube with 1.5 ml of DMSO saturated with MgCO_3 , following Palmqvist and Sundberg (2002). The tubes were incubated at 60°C in an ultrasonic water bath (Ultrasonic cleaner, USC 200TH) for 40 min, and vortexed every 10 min. Afterwards, extracts were centrifuged at 18000 rpm for 5 min and the absorbance of the supernatant was measured (Shimadzu UV2001 PC spectrophotometer) at 665 and 649 nm. The baseline absorbance at 750 nm was subtracted from the absorbance at 649 and 665 nm before contents of chlorophyll *a* and *b* (only present in cephalolichens) were calculated according to Wellburn (1994) and converted to area-based values (mmol m^{-2}).

Statistical analyses

Because cyanolichens (*L. retigera*) are deficient in chlorophyll *b*, only chlorophyll *a* was subjected to statistical analyses. In the first analysis, measured parameters averaged across all edges and distances were analysed with a one-way ANOVA during which differences between species were tested by All Pairwise Multiple Comparison Procedures (Holm-Sidak method).

Regression analyses were run for Φ_{PSII} , F_V/F_M , STM, chlorophyll *a*, chlorophyll *a/b*-ratio with distance from the edge used as a continuous predictor, and species (*Lobaria pulmonaria*, *L. oregana*, *L. retigera*) and forest patch (random variable) as categorical predictors. The species x distance interaction was also included in the model. For the parameters with no significant effects of species or species x distance interaction, the overall regression line for all species combined with 95% confidence intervals was given in plots. For the parameters with a significant effect of species or species x distance interaction, the species-specific regression lines were shown. All statistical analyses were done in Minitab v18 (Minitab Inc., State College, PA, USA). All parameters satisfied the Equal Variance Test, and all except F_V/F_M passed the normality test. F_V/F_M was therefore transformed prior to analysis.

Results

By visual inspection, most cephalolichen thalli (*L. oregana* and *L. pulmonaria*) at and near the edge were fully or partially bleached with extensive white portions, but the level of visual bleaching decreased rapidly with distance from the forest edge. The cyanolichen (*L. retigera*) showed less bleaching, but its color had changed from the normal dark brown or grey to dirty pink near the logged edge. These visual color changes concurred with distinctly lowered chlorophyll *a* contents for forest edge thalli compared to those from the interior parts of the stands, consistent with substantial chlorophyll degradation near the edge. There was a strong, linear increase in chlorophyll *a* content with increasing distance from the edge (Fig. 1A; Table 2). The chlorophyll *a* content did not vary among species (Table 1), and there was no significant interaction between distance and species (Table 2). This implies that the chlorophyll *a* content in all species responded in similar ways to the distance from the exposed edge. Likewise, the chlorophyll *a/b* ratio did not differ between the two cephalolichens having green algae as their main photobiont (Table 1), and the ratio significantly increased with increasing distance from the forest edge (Fig. 1C; Table 2).

Like the chlorophyll *a* content, Φ_{PSII} increased with distance from the edge (Fig. 1B; Table 2), although not as strongly as the chlorophyll. Φ_{PSII} strongly differed among the species (Table 1-2); the mean Φ_{PSII} across transects and distances was highest in the widespread *L. pulmonaria* and significantly lower in the old-growth associates *L. oregana* and *L. retigera* (Table 1). Also the frequently used viability parameter, F_v/F_m responded to the forest edge gradient (Fig. 1D; Table 2), but the slopes of these species-wise regressions did not differ (insignificant interaction between distance and species; Table 2). The linear increase in measured viability parameters up to a distance of 120 m from the logged edge (Fig. 1) suggests an edge effect of approximately 120 m.

Forest patch did not influence the viability parameters Φ_{PSII} , F_v/F_m and the chlorophyll *a/b*-ratio, and just weakly affected the chlorophyll *a* content ($P = 0.038$; Table 2), contrasting the strong effect of distance. The mixed linear regression models thus imply that species responses to the distance from edge were fairly similar in the two forest patches.

The functional hydration trait specific thallus mass (STM) did not significantly change along the gradient (Table 2). However, STM differed among the species (Table 1-2). Despite the fact that *L. oregana* had the largest thalli, 1.8 times larger than in *L. retigera*, it had the lowest STM (Table 1). Unlike all recorded viability parameters, STM was significantly affected by forest patch (Table 2). Lichens in first patch had lower STM than in the second. However, this contrast was due to the lower frequency of the thin *L. oregana* in transects of the second forest patch, and thus has minimal ecological significance.

Discussion

The chlorophyll *a* content of the examined lichens strongly increased along the forest edge gradient. The large bleached portions of many thalli at and near the logged edge suggest that many photobiont cells had been killed after logging. Because the number of photobiont cells

228 in healthy *Lobaria* is fairly constant over time, and because new photobiont cells are only
229 formed in young, apical tissues, not in older tissues even if some are killed (Schofield et al.,
230 2003), the reported chlorophyll degradation likely implies a serious, lasting loss of photobiont
231 cells. Photobiont cells in *Lobaria* growing in deciduous forests are able to adjust to the slow
232 and gradual, but substantial seasonal changes in light during fall and spring (MacKenzie et
233 al., 2004). This seasonal reconfiguration of photosynthetic systems (MacKenzie et al. 2004)
234 likely makes them more tolerant to the sudden increases in light after logging compared to
235 *Lobaria* growing in northern conifer forests that naturally experience less extreme light in
236 late winter-early spring.

237 Maximal photosystem II efficiency (F_V/F_M) records photoinhibition that can be dynamic or
238 chronic. Our protocol using 24 h of preconditioning at low light, not in darkness, is required
239 to capture chronic photoinhibition and not the easily reversible one (Solhaug, 2018). Even
240 when measured this way, F_V/F_M is mainly an informative viability measure when the
241 photosystem II actually becomes damaged. After the damage has killed photobiont cells ,
242 they no longer contribute to lower F_V/F_M -values (Gauslaa and Solhaug, 2000). If a few living
243 photobiont cells are left in good shape, as for thalli at and near the edges, F_V/F_M -values can
244 reach normal values despite significant photobiont damage. Therefore, in the time scale of 6
245 months post-logging, F_V/F_M is likely a less useful measure of logging-induced damage.

246 The Φ_{PSII} results were consistent with our first hypothesis which predicted better performance
247 and less damage in the widespread species *Lobaria pulmonaria*. The two old-growth forest
248 lichens (*L. retigera* and *L. oregana*) had overall lower Φ_{PSII} than *L. pulmonaria*. The second
249 hypothesis that inferred more damage in the cyanolichen *L. retigera* than to *L. oregana* was
250 not supported. The substantially lower F_V/F_M in *L. retigera* is not a sign of damage, but is
251 caused by the unique construction of the photosynthetic apparatus in cyanobacterial
252 photobionts (Campbell et al., 1998). Despite the fact that hydrated cyanolichens are more

susceptible to high-light exposure than green-algal lichens with or without cephalodia (Demmig-Adams et al., 1990), the cyanolichens, even from moist and shaded old-growth forests, are remarkably more tolerant than cephalolichens to high light when dry (Gauslaa et al., 2012). Thus, following logging, cyanolichens dry fast under high light and are not damaged until wetted and exposed to a combination of moisture and high light.

Our last hypothesis was that the specific thallus mass (STM) would be higher near the forest edge as the lichens acclimate to drier and brighter conditions after logging. However, this was not supported by the data we collected, STM did not significantly change with distance from the edge (Table 2). The lack of acclimation was likely due to the substantial reduction in chlorophyll contents reducing the carbon gain needed to grow in thickness and thus acclimate. Thus, the reported STM likely reflects the pre-logging conditions in a closed canopy. In fact, the STM of *L. pulmonaria* matches the STM of thalli from intact closed canopies in the wet Robson Valley, northern British Columbia (Gauslaa and Coxson, 2011). The widespread *L. pulmonaria* has higher STM than *L. oregana*. Because of the tight link between STM and water holding capacity (WHC) (Esseen et al., 2015; Gauslaa, 2014), *L. pulmonaria* stores more water, allowing longer hydration periods (Gauslaa et al., 2017; Longinotti et al., 2017) than *L. oregana*. The STM of *L. retigera* does not differ from the STM of the two cephalolichens. Being a cyanolichen, *L. retigera* not only needs liquid water to achieve photosynthetic activation (Lange et al., 1986), but it also needs more water to fill its internal water holding capacity than *L. pulmonaria* (Gauslaa and Coxson, 2011). Using the species-wise conversion factors between STM and WHC which were developed for lichens from the wet Robson Valley further east in northern B.C. (Gauslaa and Coxson, 2011), the WHC for *L. pulmonaria* from Kispiox could be estimated at 15.6 mg H₂O cm⁻² versus 18.0 mg H₂O cm⁻² for *L. retigera*. Assuming a similar WHC/STM-ratio for both cephalolichens, the WHC of *L. oregana* should then be just 12.8 mg H₂O cm⁻². Thus a rainfall of just 0.13

mm should be enough to fill the internal water storage of the thinnest lichen *L. oregana*, whereas *L. retigera* would need 0.18 mm rain. This implies rarer, but longer photosynthetically active hydration periods experienced by *L. retigera* than by the other two species. Nevertheless, the relatively low WHC of these three lichens should allow them to efficiently utilize the frequent, but low intensity rainfall occurring during the three warmest months. However, climate change models for the Kispiox predict drier summers (Wang et al., 2012), which may seriously impact cyanolichens like *L. retigera*.

Earlier forest edge studies have reported light and/or drying effects to extend from 15 to 70 m into the adjacent forest: 15 to 20 m (Nelson and Halpern, 2005), 45 m (Baldwin and Bradfield, 2005), 30 to 60m (Chen et al., 1999) and 65 to 70 m (Burton, 2002), although the edge influence depends on macroclimate, aspect (north vs. south, hill slope position) and by amount of windthrow. Our data show that the viability of canopy lichens in Kispiox Valley is affected at further distances from the edge than those reported in the cited studies, but matches better the required 100 m no-timber-harvest-buffer for the rare *Erioderma pedicellatum* (Cameron and Toms 2016). A number of wind-thrown trees were seen near the edges. More trees will likely fall during autumn-winter storms, and retained patches will become even smaller in the next coming years which will likely amplify edge effects on the epiphytic community. In a longer time frame, we thus cannot exclude further adverse effects resulting from factors such as climate change, and altered hydrology and humidity regimes. Furthermore, edge effects would presumably be longer on south-facing edges than on our east-facing edges.

In conclusion, reported edge effects on lichen viability were so strong that the epiphytic lichens in the entire retained forest patches in the Kispiox area appeared affected by the logging. Measured short-term viability variables were impaired at greater distances from the edge than were reported for long-term growth rates in lichens transplanted along hard edge

gradients (Coxson and Stevenson, 2007; Stevenson and Coxson, 2008). The stronger edge effect than in most other lichen studies is likely because the rainforest epiphytes in Kispiox inhabit forests that are at the drier end of their tolerance limits. Along natural and stable forest edges of coniferous forests, edge influence on lichens may extend more than three times the tree height (Esseen, 2006). With a 30m tree height in our stands this would mean an edge effect of ≥ 90 m, which is slightly shorter than the edge effect reported here (120 m). In the Kispiox rainforest, there is thus a need to retain forest patches substantially larger than 240 m in width (> 5.7 ha) in future logging operations in order to avoid negative impacts on the unique and threatened epiphytic lichens of these old growth forests.

Acknowledgements Thanks to Darwyn S. Coxson for suggesting a study in the Kispiox Valley and for introducing the authors. We are grateful to David Richardson for comments to an earlier draft of this manuscript, and to Philip Burton and two anonymous reviewers for help during the revision. Thanks to Noreen O'Hara and Steve St. John from BC Timber Sales for supporting this research with maps and logging information.

References

- Ardelean, I.V., Keller, C. and Scheidegger, C., 2015. Effects of management on lichen species richness, ecological traits and community structure in the Rodnei Mountains National Park (Romania). *Plos One*, 10(12).
- Baldwin, L.K. and Bradfield, G.E., 2005. Bryophyte community differences between edge and interior environments in temperate rain-forest fragments of coastal British Columbia. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 35(3): 580-592.

- 325 Banner, A. et al., 1993. A field guide to site identification and interpretation for the Prince Rupert
326 Forest Region. Land Management Handbook No. 26. British Columbia Ministry of Forests,
327 Victoria.
- 328 Burton, P.J., 2002. Effects of clearcut edges on trees in the Sub-boreal Spruce Zone of Northwest-
329 central British Columbia. *Silva Fennica*, 36: 329-352.
- 330 Cameron, R. P. and Toms, B.. 2016. Population decline of endangered lichen *Erioderma pedicellatum*
331 in Nova Scotia, Canada. *Botany*, 94: 565-571.
- 332 Campbell, D., Hurry, V., Clarke, A.K., Gustafsson, P. and Öquist, G., 1998. Chlorophyll fluorescence
333 analysis of cyanobacterial photosynthesis and acclimation. *Microbiology and Molecular*
334 *Biology Reviews*, 62(3): 667-683.
- 335 Chen, J.Q. et al., 1999. Microclimate in forest ecosystem and landscape ecology - Variations in local
336 climate can be used to monitor and compare the effects of different management regimes.
337 *Bioscience*, 49(4): 288-297.
- 338 Coxson, D.S. and Stevenson, S.K., 2007. Influence of high-contrast and low-contrast forest edges on
339 growth rates of *Lobaria pulmonaria* in the inland rainforest, British Columbia. *Forest Ecology*
340 *and Management*, 253(1-3): 103-111.
- 341 DellaSala, D.A. et al., 2011. Temperate and boreal rainforests of inland northwestern North America.
342 In: D.A. DellaSala (Editor), *Temperate and boreal rainforests of the World*. Island Press,
343 Washington, pp. 82-110.
- 344 Demmig-Adams, B., Adams III, W.W., Green, T.G.A., Czygan, F.C. and Lange, O.L., 1990. Differences in
345 the susceptibility to light stress in two lichens forming a phycosymbiodeme, one partner
346 possessing and one lacking the xanthophyll cycle. *Oecologia*, 84: 451-456.
- 347 Dettki, H. and Esseen, P.A., 2003. Modelling long-term effects of forest management on epiphytic
348 lichens in northern Sweden. *Forest Ecology and Management*, 175: 223-238.
- 349 Ellis, C.J., 2017. When is translocation required for the population recovery of old-growth epiphytes
350 in a reforested landscape? *Restoration Ecology*, 25(6): 922-932.

- 351 Ellis, C.J. and Coppins, B.J., 2007. Changing climate and historic-woodland structure interact to
352 control species diversity of the 'Lobarion' epiphyte community in Scotland. *Journal of*
353 *Vegetation Science*, 18(5): 725-734.
- 354 Environment_Canada, 2018. Canadian Climate Normals 1981-2010 Station Data. Environment
355 Canada, Climate Services, Vancouver, BC.
- 356 Esseen, P.-A., Olsson, T., Coxson, D. and Gauslaa, Y., 2015. Morphology influences water storage in
357 hair lichens from boreal forest canopies. *Fungal Ecology*, 18: 26-35.
- 358 Esseen, P.-A. and Renhorn, K.E., 1998. Edge effects on an epiphytic lichen in fragmented forests.
359 *Conservation Biology*, 12: 1307-1317.
- 360 Esseen, P.A., 2006. Edge influence on the old-growth forest indicator lichen *Alectoria sarmentosa* in
361 natural ecotones. *Journal of Vegetation Science*, 17(2): 185-194.
- 362 Gauslaa, Y., 2014. Rain, dew, and humid air as drivers of lichen morphology, function and spatial
363 distribution in epiphytic lichens. *Lichenologist*, 46: 1-16.
- 364 Gauslaa, Y. and Coxson, D., 2011. Interspecific and intraspecific variations in water storage in
365 epiphytic old forest foliose lichens. *Botany*, 89: 787-798.
- 366 Gauslaa, Y., Coxson, D.S. and Solhaug, K.A., 2012. The paradox of higher light tolerance during
367 desiccation in rare old forest cyanolichens than in more widespread co-occurring chloro- and
368 cephalolichens. *New Phytol.*, 195: 812-822.
- 369 Gauslaa, Y., Lie, M., Solhaug, K.A. and Ohlson, M., 2006. Growth and ecophysiological acclimation of
370 the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. *Oecologia*,
371 147: 406-416.
- 372 Gauslaa, Y. et al., 2007. Growth of epiphytic old forest lichens across climatic and successional
373 gradients. *Canadian Journal of Forest Research*, 37: 1832-1845.
- 374 Gauslaa, Y. and Solhaug, K.A., 1996. Differences in the susceptibility to light stress between epiphytic
375 lichens of ancient and young boreal forest stands. *Functional Ecology*, 10: 344-354.

- 376 Gauslaa, Y. and Solhaug, K.A., 2000. High-light-intensity damage to the foliose lichen *Lobaria*
377 *pulmonaria* within a natural forest: the applicability of chlorophyll fluorescence methods.
378 *Lichenologist*, 32: 271-289.
- 379 Gauslaa, Y., Solhaug, K.A. and Longinotti, S., 2017. Functional traits prolonging photosynthetically
380 active periods in epiphytic cephalolichens during desiccation. *Environmental and*
381 *Experimental Botany*, 141: 83-91.
- 382 Goward, T. and Pojar, J., 1998. Antique forests and epiphytic macrolichens in the Kispiox Valley.
383 *Forest Sciences, Prince Rupert Forest Region, Note 33*: 1-11.
- 384 Jönsson, M.T., Ruete, A., Kellner, O., Gunnarsson, U. and Snäll, T., 2017. Will forest conservation
385 areas protect functionally important diversity of fungi and lichens over time? *Biodiversity*
386 *and Conservation*, 26(11): 2547-2567.
- 387 Lange, O.L., Kilian, E. and Ziegler, H., 1986. Water vapor uptake and photosynthesis in lichens:
388 performance differences in species with green and blue-green algae as phycobionts.
389 *Oecologia*, 71: 104-110.
- 390 Longinotti, S., Solhaug, K.A. and Gauslaa, Y., 2017. Hydration traits in cephalolichen members of the
391 epiphytic old forest genus *Lobaria* (s. lat.). *Lichenologist*, 49(5): 493-506.
- 392 MacKenzie, T.B.D., Johnson, J. and Campbell, D.A., 2004. Environmental change provokes rapid
393 macromolecular reallocations within the photosynthetic system in a static population of
394 photobionts in the lichen *Lobaria pulmonaria*. *Lichenologist*, 36: 425-433.
- 395 Merinero, S., Martínez, I., Rubio-Salcedo, M. and Gauslaa, Y., 2015. Epiphytic lichen growth in
396 Mediterranean forests: Effects of proximity to the ground and reproductive stage. *Basic and*
397 *Applied Ecology*, 16: 220-230.
- 398 Nelson, C.R. and Halpern, C.B., 2005. Edge-related responses of understory plants to aggregated
399 retention harvest in the Pacific Northwest. *Ecological Applications*, 15(1): 196-209.
- 400 Nordén, B. et al., 2014. Effects of ecological continuity on species richness and composition in forests
401 and woodlands: A review. *Ecoscience*, 21(1): 34-45.

- 402 Palmqvist, K. and Sundberg, B., 2002. Characterising photosynthesis and respiration in freshly
403 isolated or cultured lichen photobionts. In: I. Kranner, R.P. Beckett and A.K. Varma (Editors),
404 Protocols in Lichenology. Culturing, Biochemistry, Ecophysiology and Use in Biomonitoring.
405 Springer-Verlag, Berlin, pp. 152-181.
- 406 Parminter, J., 1991. Fire history and effects on vegetation in three biogeoclimatic zones of British
407 Columbia. Proceedings of an international symposium, 20-24 Mar. 1990, Knoxville,
408 Tennessee., Fire and the environment: ecological and cultural perspectives. USDA For. Serv.
409 Gen. Tech. Rep. SE-69, Asheville, N.C., pp. 263-272.
- 410 Rasband, W.S., 2014. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA,
411 <http://imagej.nih.gov/ij/>
- 412 Rheault, H., Drapeau, P., Bergeron, Y. and Esseen, P.-A., 2003. Edge effects on epiphytic lichens in
413 managed black spruce forests of eastern North America. Canadian Journal of Forest
414 Research, 33(1): 23-32.
- 415 Ronnås, C. et al., 2017. Discovery of long-distance gamete dispersal in a lichen-forming ascomycete.
416 New Phytologist, 216(1): 216-226.
- 417 Rosenvald, R. and Löhmus, A., 2008. For what, when, and where is green-tree retention better than
418 clear-cutting? A review of the biodiversity aspects. Forest Ecology and Management, 255(1):
419 1-15.
- 420 Schofield, S.C., Campbell, D.A., Funk, C. and MacKenzie, T.D.B., 2003. Changes in macromolecular
421 allocation in nondividing algal symbionts allow for photosynthetic acclimation in the lichen
422 *Lobaria pulmonaria*. New Phytologist, 159(3): 709-718.
- 423 Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R. and Ruchty, A., 2000. Dispersal limitations of
424 epiphytic lichens result in species dependent on old-growth forests. Ecological Applications,
425 10: 789-799.
- 426 Snäll, T., Pennanen, J., Kivisto, L. and Hanski, I., 2005. Modelling epiphyte metapopulation dynamics
427 in a dynamic forest landscape. Oikos, 109(2): 209-222.

428 Solhaug, K.A., 2018. Low-light recovery effects on assessment of photoinhibition with chlorophyll
429 fluorescence in lichens. *Lichenologist*, 50: 139-145.

430 Stevenson, S.K. and Coxson, D.S., 2008. Growth responses of *Lobaria retigera* to forest edge and
431 canopy structure in the inland temperate rainforest, British Columbia. *Forest Ecology and*
432 *Management*, 256(4): 618-623.

433 Wang, T.L., Hamann, A., Spittlehouse, D.L. and Murdock, T.Q., 2012. ClimateWNA - High-resolution
434 spatial climate data for Western North America. *Journal of Applied Meteorology and*
435 *Climatology*, 51(1): 16-29.

436 Wellburn, A.R., 1994. The spectral determination of chlorophyll *a* and *b*, as well as total carotenoids,
437 using various solvents with spectrophotometers of different resolution. *Journal of Plant*
438 *Physiology*, 144(3): 307-313.

439
440

Figure Legends:

Fig. 1

Chlorophyll *a* content (A), effective PSII yield (B), chlorophyll *a/b*-ratio, (C) and maximal photosystem II efficiency (D) as a function of distance from the forest edge from a total of five separate transects/gradients through two forest patches. Filled circles: *Lobaria pulmonaria*; open circles: *L. oregana* and triangles: *L. retigera*. Solid, hatched or thick dotted lines show linear regression lines. Thin dotted lines (A, B) show 95% confidence intervals (only for parameters that did not differ between species). Shown regressions are as follows: Chlorophyll *a* content = $0.0545 + 0.000767 \times \text{distance}$; $r^2_{adj} = 0.453$; $P < 0.001$. Chlorophyll *a/b*-ratio = $2.2245 + 0.00481 \times \text{distance}$; $r^2_{adj} = 0.198$; $P = 0.003$. Effective PSII yield for *L. oregana* = $0.0402 + 0.000606 \times \text{distance}$; $r^2_{adj} = 0.445$; $P = 0.003$; for *L. pulmonaria* = $0.111 + 0.00359 \times \text{distance}$; $r^2_{adj} = 0.115$; $P = 0.063$; *L. retigera* = $0.0592 + 0.0003 \times \text{distance}$; $r^2_{adj} = 0.096$; $P = 0.082$. Maximal photosystem II efficiency for *L. oregana* = $0.612 + 0.0001 \times \text{distance}$; $r^2_{adj} = 0.201$; $P = 0.047$; for *L. pulmonaria* = $0.669 + 0.00685 \times \text{distance}$; $r^2_{adj} = 0.265$; $P = 0.007$; *L. retigera* = $0.469 + 0.000609 \times \text{distance}$; $r^2_{adj} = 0.157$; $P = 0.034$.

Table 1. Mean values (± 1 standard error) of measured variables in the three studied species (*Lobaria pulmonaria*, *L. oregana*, and *L. retigera*) across all transect distances and forest patches

Parameter	<i>Lobaria</i> <i>pulmonaria</i>	<i>Lobaria</i> <i>oregana</i>	<i>Lobaria</i> <i>retigera</i>
Thallus area, cm ²	28.20 $\pm$ 2.41 ^{AB}	36.60 $\pm$ 4.26 ^A	20.49 $\pm$ 2.41 ^B
Specific thallus mass, mg DM cm ⁻²	10.37 $\pm$ 0.36 ^A	8.53 $\pm$ 0.63 ^B	9.47 $\pm$ 0.33 ^{AB}
Chlorophyll <i>a</i> , mmol m ⁻²	0.0892 $\pm$ 0.0103	0.0914 $\pm$ 0.0182	0.0824 $\pm$ 0.0103
Chlorophyll <i>a/b</i>	2.36 $\pm$ 0.09	2.58 $\pm$ 0.12	-
Effective PSII yield (Φ_{PSII})	0.129 $\pm$ 0.008 ^A	0.083 $\pm$ 0.014 ^B	0.073 $\pm$ 0.008 ^B
Maximal photosystem II efficiency (F_V/F_M)	0.704 $\pm$ 0.014 ^A	0.689 $\pm$ 0.025 ^B	0.495 $\pm$ 0.014 ^C

Species with significantly different means according to All Pairwise Multiple Comparison Procedures (Holm-Sidak method) have different superscript letters.

Table 2. Linear regression analyses for effective PSII yield (Φ_{PSII}), maximal photosystem II efficiency (F_V/F_M), specific thallus mass (STM), chlorophyll *a*, chlorophyll *a/b*-ratio with increasing distance from the edge (continuous predictor) and species (*Lobaria pulmonaria*, *L. oregana*, and *L. retigera*) and forest patch as categorical predictors. Analysed data are given in Fig. 1.

Parameter	Effective PSII yield (Φ_{PSII})			F_V/F_M		STM		Chlorophyll <i>a</i>		Chlorophyll <i>a/b</i>		
	$r^2_{\text{adj}}=0.483$			$r^2_{\text{adj}}=0.730$		$r^2_{\text{adj}}=0.222$		$r^2_{\text{adj}}=0.485$		$r^2_{\text{adj}}=0.337$		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Regression	6	10.49	<0.001	28.49	<0.001	4.21	0.001	10.56	<0.001	4	3.84	0.011
Distance (D)	1	9.89	0.003	8.52	<0.001	1.99	0.164	18.34	<0.001	1	8.63	0.006
Species (S)	2	10.28	<0.001	31.57	<0.001	1.83	0.170	0.26	0.772	1	0.07	0.797
D x S	2	0.80	0.455	0.42	0.660	0.36	0.700	1.27	0.289	1	1.19	0.282
Forest patch (random)	1	2.52	0.118	0.81	0.373	9.49	0.003	5.03	0.029	1	0.23	0.633
Error	55									34		
Total	61									38		

The chlorophyll *a/b*-ratio was only analysed for the two cephalolichens

Fig. 1