

Contrasting the abundance, nitrogen, and carbon of epiphytic macrolichen species between host trees and soil types in a sub-boreal forest

Jocelyn Campbell and Arthur L. Fredeen

Abstract: Differences in lichen diversity and abundance and lichen N and C pools were examined across the two dominant host tree species (*Picea engelmannii* Parry ex Engelm. × *Picea glauca* (Moench) Voss) and *Abies lasiocarpa* (Hook.) Nutt.) and two soil types (fine- and coarse-textured soils) in an old-growth sub-boreal forest in central British Columbia, Canada. Forty-four epiphytic macrolichen species were identified across the study area. Hair lichen species, particularly nonsorediate *Bryoria* species, were more abundant in spruce on coarse-textured soils, while cyanolichens were most commonly observed in subalpine fir on fine-textured soils. Overall macrolichen biomass and C pools were greatest in subalpine fir trees on coarse-textured soils. The tripartite species *Lobaria pulmonaria* (L.) Hoffm. was the dominant macrolichen, particularly over fine-textured soils where its stand level biomass was greater than that of all other species combined. The N pools of *L. pulmonaria* in combination with the less abundant N-rich bipartite cyanolichens amounted to 7.5 ± 1.9 kg N·ha⁻¹ on fine-textured soils. These results indicate that epiphytic cyanolichens may make substantial contributions to ecosystem N despite their relatively insignificant contributions to overall forest biomass and C stocks.

Key words: lichen abundance, sub-boreal forest, soil texture, carbon pool, nitrogen pool, lichen nutrition.

Résumé : Les auteurs ont examiné les différences dans la diversité et l'abondance des lichens, ainsi que dans les pools N et de C, sur deux espèces d'arbres hôtes dominants, le *Picea engelmannii* Parry × *glauca* (Moench) Voss et l'*Abies lasiocarpa* (Hook.) Nutt.), et sur deux types de sols (sols à texture fine et grossière), dans une forêt surannée sub-boréale du centre de la Colombie Canadienne. Ils ont identifié 44 espèces de macrolichens épiphytes sur l'ensemble de l'aire étudiée. Les lichens chevelus, surtout les espèces de *Bryoria* sans sorédies, sont les plus abondants chez l'épinette venant sur des sols à texture grossière, alors qu'on observe les cyanolichens surtout sur les sapins sub-alpins venant sur des sols à texture fine. Dans l'ensemble, la biomasse des macrolichens et les pools de C sont plus importants sur les sapins sub-alpins et sur les sols à texture grossière. L'espèce tripartite, *Lobaria pulmonaria*, est le lichen dominant, surtout sur les sols à texture fine, où l'importance de sa biomasse in situ est plus grande que celle de toutes les autres espèces confondues. Les pools de N du *Lobaria pulmonaria*, (L.) Hoffm. en combinaison avec les cyanolichens bipartites riches en N, moins abondants, représentent $7,5 \pm 1,9$ kg·ha⁻¹, sur les sols à texture fine. Ces résultats indiquent que les cyanolichens épiphytes peuvent apporter une contribution substantielle à l'azote de l'écosystème, en dépit de leurs contributions relativement peu significatives à l'ensemble de la biomasse de la forêt et des pools de C.

Mots-clés : abondance des lichens, forêt sub-boréale, texture du sol, pool de carbone, pool d'azote, nutrition des lichens.

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Introduction

Forest canopies, critical to many important ecosystem functions, may support about 40% of the earth's extant species, of which 10% are predicted to be canopy specialists (Ozanne et al. 2003). A key component of forest canopy diversity in interior, sub-boreal conifer forests is the epiphytic macrolichen community. While many of the lichens of the

sub-boreal forests of central British Columbia are common to the boreal vegetation zone that stretches across the circumpolar north (Ahti 1977), the same is not true of the cyanophytic component. These species are infrequent in the interior forests of British Columbia and are largely restricted to old-growth, rainforest environments (Goward 1994). Cyanolichen species assemblages that were once thought to be endemic to coastal forests are now known to occur in inland rainforest environments (Goward 1994; Campbell and Fredeen 2004; Radies and Coxson 2004; Goward and Spribille 2005) and now in the interior hybrid spruce (*Picea engelmannii* Parry ex Engelm. × *Picea glauca* (Moench) Voss.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests of central British Columbia. The abundance of lichens in inland forests is thought to be a factor of stand age and appropriate moisture regime (Goward and Arsenault 2000a; Goward 2003a). Lichen growth is limited by water availability because physiological activity occurs only when the thallus moisture content is >50% and >150% for chloro-

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J. Campbell^{1,2} and A.L. Fredeen. Faculty of Natural Resources and Environmental Studies, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada.

¹Corresponding author (e-mail: joc_camp@telus.net).

²Present address: Faculty of Forestry, Forest Sciences Centre, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

lichens (Hajek et al. 2001) and cyanolichens (Lange et al. 2004), respectively. While hair lichens are known to require cyclical desiccating and hydrating conditions, cyanolichens tend to be more restricted to moist microhabitats, a pattern due in part to the 200% hydration required for nitrogenase activity (Antoine 2004). However, not all old, moist, interior forest ecosystems provide the same level of habitat even for cyanolichens, and disparate loadings are commonly observed. Possible explanations for these observed differences include soil characteristics (Loppi et al. 1998) and tree species composition (Goward and Arsenault 2001). To date, there has not been an empirical comparison of epiphytic lichen biomass between soil texture types or tree species within interior forest ecosystems. Such a comparison would provide further insight into the continued debate over the ecological factors determining spatial and temporal distributions of these species.

Lichens play an important role in forest nutrient cycling (Knops et al. 1996). This may be particularly true of N_2 -fixing cyanolichens, which have the potential to significantly contribute to the N budget of forest ecosystems (Wollum and Davey 1975; Cleveland et al. 1999). Conservative estimates of the rate of biological N_2 fixation by vascular plants range from 200 kg $N\cdot ha^{-1}\cdot year^{-1}$ for leguminous species (Stewart 1969) to 320 kg $N\cdot ha^{-1}\cdot year^{-1}$ for 20-year-old stands of red alder (*Alnus rubra* Bong.) (Newton et al. 1968). These species are often less abundant in mature sub-boreal spruce forests with atmospheric N inputs as low as 0.5 kg $N\cdot ha^{-1}\cdot year^{-1}$ (Rosen and Lindberg 1980; Hope 2001), and N is thought to be the limiting nutrient (Brockley 2000). Nitrogen-fixing epiphytes, on the other hand, are more abundant in older forests (Goward 1994; Sillett and McCune 1998; Campbell and Fredeen 2004) and have been estimated to fix 3–5 kg $N\cdot ha^{-1}\cdot year^{-1}$ in coastal old-growth forests (Franklin et al. 1981). While no comparable N_2 fixation rates are available for northern interior forests, it may be that cyanolichens are equally important sources of N in these regions.

The relative role of substrate features such as underlying soil texture and tree species on the abundance, C stocks, and N pools of lichen functional groups is wholly unknown for interior old-growth forests. Thus, the objective of this study was to compare lichen diversity, biomass (at the species and functional group level), C, and N between soil types and tree species to query the roles of edaphic conditions and host species in epiphytic macrolichen distribution.

Methods and materials

Study area description

The study was conducted in the Aleza Lake Research Forest (ALRF) in central British Columbia, Canada, approximately 60 km east of Prince George (54°11'N, 122°40'W). The ALRF is in the wet cool variant of the Sub-Boreal Spruce biogeoclimatic zone (SBSwk1) (Meidinger and Pojar 1991) and is broadly transitional between drier plateau forests to the south and west and the wet trench and mountain forests of the adjacent Interior Cedar Hemlock (ICH) / Englemann Spruce – Subalpine-fir (ESSF) zones to the east. The ALRF is characterized by cold, snowy winters and cool, moist summers. It receives an average of nearly 900 mm of

precipitation per year, approximately one third as snow, and has a mean summer temperature of 14.8 °C (Murphy 1996). The research forest is approximately 10 000 ha in area and is forested primarily by interior hybrid spruce and subalpine fir with smaller components of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* (Mill.) BSP), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and occasional individuals of western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Soils on the research forest were formed from glaciolacustrine parent materials. Fine-textured soils are the more common texture type and are a mixture of Orthic Gleyed Luvisols and Orthic Luvic Gleysols. The less common coarse-textured soils are predominantly Orthic Humo-Ferric Podzols (Arocena and Sanborn 1999).

Study design

To examine the influence of substrate (soil type and host tree species) on epiphytic lichens, we established a factorial experiment with combinations of two factors: soil type (with coarse- and fine-textured soils, C-T and F-T soils, respectively) and tree species (with the two most common trees, subalpine fir and interior hybrid spruce). By examining both soil type and host tree, we hoped to determine the variation in lichen abundance patterns attributable to each. This factorial design also allowed the testing for potential interactions.

Two old-growth sites (120–240+ years) were selected in each of F-T and C-T soils. Only two old-growth sites could be found on C-T soils owing to an historic harvesting preference on this soil type. Three 10 m × 10 m plots were established near what was determined to be the centre of the stand. The first plot was located 20 m from the site centre along a random compass bearing. The second and third plots were located 20 m from the centre at a random compass bearing of +120 and +240°, respectively. The terrestrial vegetation, nonvascular community, and stand characteristics of each plot are detailed in Botting and Fredeen (2006). One subalpine fir (fir) and one interior hybrid spruce (spruce) were identified for arboreal lichen assessments within 5 m of each plot centre. Trees that were structurally safe and supported a lichen loading that was most representative of that occurring at the site were identified and three study trees of each species were randomly selected from this pool. Selected trees were subsequently rigged, climbed, and sampled vertically for epiphyte biomass and species diversity.

Lichen assessments

Lichen biomass was assessed on every branch of the study trees. Lichens were grouped for assessments using a modified version of the functional groups described by McCune (1993). The four functional groups were *Alectoria* (including *Alectoria sarmentosa* (Ach.) Ach. and lesser amounts of *Usnea* spp. and *Ramalina thrausta* (Ach.) Nyl.), *Bryoria*, foliose chlorolichens, and cyanolichens. Cyanolichen assessments included all species with a cyanobacterial partner, and all references to cyanolichens herein refer to both bipartite species and the tripartite lichen *Lobaria pul-*

monaria (L.) Hoffm. unless specified otherwise. Hair lichens were separated into the two functional groups owing to niche partitioning between *Alectoria* and *Bryoria* as identified by Campbell and Coxson (2001). Biomass estimation techniques are described in Campbell and Coxson (2001) and Benson and Coxson (2002).

Lichen surface area, as a proxy measure for cover, was assessed on one branch selected from each of three distinct height zones in the canopy of each sampled tree. The height zones were based on vertical changes in lichen species composition with the upper canopy characterized by abundant *Bryoria* (Brodo & D. Hawksw.) spp. (particularly nonsorediate species) and the lower canopy by the presence of cyanolichens, most notably *Lobaria pulmonaria*. The middle canopy was delineated by a noticeable absence of both of these defining species groups. The branch that supported an epiphyte community that was most representative of the respective height zone (upper, middle, and lower) was selected and removed for species identification in the laboratory. A 2 cm × 6 cm grid was used to measure the colonisable surface area of the branch and the surface area of each lichen species encountered. The abundance of each species was recorded as the number of square centimetres observed on a given branch. All thalli in the *Alectoria*, foliose chlorolichen, and cyanolichen functional groups were identified and quantified at the species level. All species of *Bryoria* were identified where observed, but the surface area quantification was restricted to broad categories of sorediate or nonsorediate species. Sorediate *Bryoria* species reproduce via soredia and tend to inhabit the lower portions of the canopy, while nonsorediate *Bryoria* reproduce primarily through fragmentation and wind dispersal (Goward 2003b) and make up the bulk of the *Bryoria* loadings observed in the upper canopy in interior forests (Goward 2003a).

Stand-level macrolichen C and N

The nine dominant macrolichen species (*Alectoria sarmentosa*, *Bryoria pseudofuscescens* (Gyeln.) Brodo & D. Hawksw., *Ramalina thrausta*, *Hypogymnia occidentalis* L. Pike, *Parmelia sulcata* (Ach.) Tayl., *Platismatia glauca* (L.) W.L. Culb. & C.F. Culb., *Lobaria pulmonaria*, *Nephroma helveticum* (Ach.), and *Pseudocyphellaria anomala* Brodo & Ahti) were sampled for N and C content. One sample of each species was removed from one subalpine fir and one spruce at each site for a total of eight samples per species. Biomass samples were oven-dried at 55 °C for 3 d, weighed, and ground to a fine powder in a mortar and pestle. The total N and C content was determined by a flash combustion of duplicate 5 mg subsamples (NA 1500 NC elemental analyzer; Fisons Instruments, Italy). To estimate stand-level N and C, N and C contents were multiplied by total tree lichen biomass and again by mean stand density of spruce and fir. The N and C contents were pooled across tree species to obtain totals by soil type. No data were available to compare stem density across soil texture types, and so stand density is based on an average of old-growth sites across the ALRF.

Statistical analysis

Lichen biomass estimates were corrected by comparing the estimates with the measured lichen biomass observed on

sample branches. Simple linear regression equations were calculated and applied according to Campbell and Coxson (2001) for each functional group to correct discrepancies between measured and estimated biomass.

Differences between the biomass of *Alectoria*, *Bryoria*, foliose chlorolichen, and cyanolichen functional groups, the abundance (surface area) of individual lichen species within these groups, and the N and C content were tested across soil and tree species using 2 × 2 full factorial analyses of variance (ANOVAs) with Bonferroni post hoc adjustments. Log transformation of *Bryoria* functional group biomass estimates prior to analysis resulted in normally distributed errors from the ANOVA model. Bipartite cyanolichen biomass is graphically represented, but no statistics were performed because estimates were calculated from total cyanolichen biomass multiplied by the proportion of cover made up by bipartite species. All data are provided as mean ± SE.

Results

The canopies of old-growth forests at the ALRF were predominantly populated by spruce and fir with stem densities of these two species ranging from 99 ± 21 to 244 ± 48 stems·ha⁻¹ (>17.5 cm DBH), respectively (M. Karjala, ALRF, Prince George, B.C., unpublished data). Sampled subalpine fir were younger (mean age of 126 years), smaller (mean DBH of 35.6 ± 7.0 cm), and shorter (mean height of 26.7 ± 2.2 m) than spruce, which averaged 134 years of age, 45.0 ± 8.0 cm in DBH and 30.6 ± 3.2 m in height. The difference in the heights of these two species has created a two-tiered canopy structure with spruce as canopy dominants emerging 3–4 m above the fir crowns. Sample trees of both species were, on average, 2.5 m taller on C-T than on F-T soils.

Species abundance

Forty-five species of lichens and mosses were observed in the old-growth spruce–fir canopies at the ALRF. Of these total 45 species, 16 fruticose (hair) lichens, 20 foliose chlorolichens, 7 foliose bipartite cyanolichens, 1 foliose tripartite lichen, and 1 bryophyte were identified (Table 1). This included the first detailed record of the distribution of oceanic or old-growth-dependent species (Goward 1994) within a sub-boreal spruce (SBS) forest in Central British and the first known observation of the maritime species *Usnea chaetophora* Stirt. in an inland environment (Halonen et al. 1998).

Hair lichens

Hair lichens were ubiquitously observed, but with some vertical zonation apparent between species groups; *Alectoria* functional group species (mainly *Alectoria sarmentosa* and *Usnea* spp.; Table 1) were primarily observed in the middle to lower canopy, while the *Bryoria* group, particularly nonsorediate species, dominated the middle to upper canopy. This vertically zoned pattern of hair lichen abundances was similar for both C-T and F-T soils (Fig. 1a).

There was no significant difference in *Alectoria* functional group abundance between soil types or tree species on a tree by tree basis. Furthermore, species-level analysis revealed that only one species of the *Alectoria* functional

Table 1. Cover (mean \pm SE) of hair lichens, foliose chlorolichens, bipartite and tripartite cyanolichens, and bryophytes observed at upper, textured soils at the Aleza Lake Research Forest.

	Coarse-textured, spruce			Coarse-textured, fir
	Upper	Middle	Lower	Upper
Fruticose lichens				
<i>Alectoria sarmentosa</i> (Ach.) Ach.	1.5 \pm 0.3	16.7 \pm 6.8	220.0 \pm 90.7	1.0
<i>Bryoria</i> nonsorediate species	223.4 \pm 60.4	125.2 \pm 51.2	42.0 \pm 22.6	80.2 \pm 17.7
<i>B. capillaris</i> (Ach.) Brodo & D. Hawksw.				
<i>B. fremontii</i> (Tuck.) Brodo & D. Hawksw.				
<i>B. friabilis</i> Brodo & D. Hawksw.				
<i>B. pseudofuscescens</i> (Gyeln.) Brodo & D. Hawksw.				
<i>Bryoria</i> sorediate species	11.8 \pm 5.7	12.5 \pm 4.3	39.8 \pm 20.1	5.2 \pm 2.9
<i>B. glabra</i> (Mot.) Brodo & D. Hawksw.				
<i>B. fremontii</i> (Tuck.) Brodo & D. Hawksw.				
<i>B. fuscescens</i> (Gyeln.) Brodo & D. Hawksw.				
<i>B. lanestris</i> (Ach.) Brodo & D. Hawksw.				
<i>Nodobryoria oregana</i> Tuck. ex Nyl.	0	0	0	0
<i>Ramalina dilacerata</i> (Hoffm.) Hoffm.	0	1.0	0.25	0
<i>R. thrausta</i> (Ach.) Nyl.	3.3 \pm 1.0	29.8 \pm 8.3	40.7 \pm 20.4	7.5 \pm 0.5
<i>Usnea filipendula</i> Stirt.	1.1 \pm 0.5	26.6 \pm 11.0	9.8 \pm 3.8	1.3 \pm 0.8
<i>U. scabrata</i> Nyl.	0	4.5 \pm 1.5	18.5 \pm 1.5	4.5 \pm 1.5
<i>U. chaetophora</i> Stirt.	0	13.0 \pm 1.0	0	0
<i>U. lapponica</i> Vain.	2.0 \pm 1.0	6.0	0	0
<i>U. substeriliz</i> Mot.	0	5.0	0	0
Foliose chlorolichens				
<i>Hypogymnia austerodes</i> (Nyl.) Rae.	1.0	18.8 \pm 3.8	3.0	0
<i>H. bitteri</i> (Lyngé) Ahti.	0	0	1.0	0
<i>H. metaphysodes</i> (Asah.) Rass.	9.9 \pm 5.3	5.9 \pm 1.2	0.6 \pm 0.7	1.4 \pm 0.4
<i>H. occidentalis</i> L. Pike	11.9 \pm 5.4	22.7 \pm 6.9	16.0 \pm 8.1	22.7 \pm 9.0
<i>H. oroborealis</i> Goward	0.8 \pm 0.3	1.0 \pm 0.0	1.3	1.0
<i>H. physodes</i> (L.) Nyl.	11.9 \pm 2.9	23.8 \pm 7.8	13.4 \pm 5.4	9.8 \pm 2.3
<i>H. rugosa</i> (G. Merr.) L. Pike	0	0	0	0
<i>H. tubulosa</i> (Shaerer) Hav.	5.7 \pm 1.7	7.5 \pm 1.2	5.4 \pm 1.1	5.4 \pm 0.7
<i>H. vitatta</i> (Ach.) Parrique	1.0	3.0	8.8 \pm 4.8	0
<i>Melanelia elegantula</i> (Zahlbr.) Essl.	0	0	0	0
<i>M. exasperatula</i> (Nyl.) Essl.	0.7	1.5 \pm 0.5	0.4 \pm 0.1	0.8
<i>M. subelegantula</i> (Essl.) Essl.	0	1.5	0	0
<i>M. subaurifera</i> (Nyl.) Essl.	0	1.8	0	7.0 \pm 5.1
<i>Parmelia hygrophila</i> Goward & Ahti	3.0 \pm 2.0	18.7 \pm 3.7	12.9 \pm 2.5	8.5 \pm 5.3
<i>P. sulcata</i> Tayl.	16.9 \pm 4.9	65.3 \pm 16.4	30.0 \pm 10.9	28.9 \pm 8.2
<i>Parmeliopsis ambigua</i> (Wulfen) Ach.	0	0	0	0.4 \pm 0.1
<i>P. hyperopta</i> (Ach.) Arnold	0.25	0	0	0
<i>Platismatia glauca</i> (L.) Culb. & C.F. Culb.	3.2 \pm 1.7	25.2 \pm 14.9	26.6 \pm 8.1	2.6 \pm 0.8
<i>Tuckermanopsis chlorophylla</i> (Willd.) Hale	1.9 \pm 0.5	6.2 \pm 2.9	2.2 \pm 0.5	1.4 \pm 0.5
<i>T. orbata</i> (Nyl.) M.J. Lai	11.6 \pm 7.3	1.3 \pm 0.2	0.6 \pm 0.2	2.7 \pm 1.3
Bipartite cyanolichens				
<i>Lobaria hallii</i> (Tuck.) Zahlbr.	0.05	9.8 \pm 2.7	4.0 \pm 1.0	0
<i>L. scrobiculata</i> (Scop.) DC.	0	7.7 \pm 3.5	22.0	0
<i>Nephroma helveticum</i> Ach.	0	3.3 \pm 2.8	12.3 \pm 8.9	0
<i>N. isidiosum</i> (Nyl.) Gyeln.	0	2.8 \pm 1.2	8.4 \pm 0.9	0
<i>N. parile</i> (Ach.) Ach.	0	4.3 \pm 1.1	14.6 \pm 7.3	0
<i>Pseudocyphellaria anomala</i> Brodo & Ahti.	0	7.9 \pm 4.6	10.3 \pm 4.5	0
<i>Sticta fuliginosa</i> (Hoffm.) Ach.	0	5.5 \pm 2.5	0	0
Tripartite cyanolichens				
<i>Lobaria pulmonaria</i> (L.) Hoffm.	0	105.8 \pm 79.0	559.2 \pm 189.3	0
Bryophytes				
<i>Orthotrichum</i> spp. Hedw.	0	0	0	0

Note: *Bryoria* was identified at the species level but quantified according to sorediate and nonsorediate species groups. Cover is recorded as the mean

middle, and lower canopy heights in spruce (*Picea glauca* × *Picea engelmannii*) and fir (*Abies lasiocarpa*) growing on coarse- or fine-

Coarse-textured, fir		Fine-textured, spruce			Fine-textured, fir		
Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
23.3±12.3	92.5±24.1	2.5±0.9	29.9±11.8	52.2±18.7	2.5±1.1	15.0±4.7	47.8±16.2
57.5±36.1	22.8±3.5	121.8±65.1	66.6±31.3	16.2±6.2	32.7±26.9	8.5±1.9	2.7±1.3
10.9±3.1	10.8±5.6	5.3±2.8	10.2±4.6	10.5±1.6	1.6±1.5	73.3±4.3	2.8±0.8
0	0	0	2.00	0	0	0	0
0	0	0	0	0	0	0	0
24.2±10.0	35.3±13.8	6.5±3.5	31.5±13.3	78.3±34.8	8.5±0.5	27.2±3.4	28.6±18.3
7.0±2.3	28.3±14.4	0.3	6.0±0.0	5.7±3.2	0.3	0.5	1.0±0.0
0	46.0±27.0	1.5±0.4	4.0±0.0	7.0±1.5	0	0	1.5
0	2.0	0	0	14.0±8.0	0	2.0	3.0
0	2.0	5.0	0	0	0	0	0
0	0	0	0	0	0	0	0
7.3±3.8	0	0	3.9±1.3	4.0±2.0	1.0	1.0	1.1±0.9
0	0	0	0	2.0	0	0	0
9.1±3.1	3.8±0.9	3.2±1.1	3.7±1.3	4.0±1.5	1.9±0.1	5.1±1.6	2.3±0.9
48.2±10.3	12.1±2.0	18.9±4.1	37.6±10.1	12.8±3.9	24.8±7.5	40.3±8.7	29.7±6.6
0.9±0.5	1.4±0.1	0.5	1.1±0.9	0	0	3.0	0
42.7±11.4	6.0±1.0	18.7±4.8	26.3±8.2	7.0±1.7	11.1±3.3	21.1±5.1	13.1±4.2
0	0	0	0	0	2.0	0	0
28.5±6.5	4.0±1.0	4.9±0.3	5.3±1.3	2.6±0.5	2.9±0.4	8.3±3.0	3.8±0.6
8.4±3.3	0	1.0	2.5±0.5	7.0±0.6	0.8±0.3	7.6±3.4	4.3±1.3
0	10.5	0	0	0	0	0	0
0	3.0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
2.7±1.6	1.8±10.8	0	0	0	0	0	0
42.1±11.4	23.6±4.0	1.2±0.4	11.8±3.3	5.1±1.6	2.3±0.8	17.8±3.7	16.8±2.3
104.2±24.4	58.5±7.6	24.9±6.4	46.1±15.8	18.0±4.1	14.9±2.5	42.6±8.1	33.6±7.7
0.6±0.4	0.25	0.3	0	0	0.3±0.0	0.8±0.5	1.0
0	0	0	0	0	0.3	0	0.3
87.7±32.2	124.5±34.6	3.8±1.7	47.8±12.3	49.2±18.1	1.9±0.5	22.6±0.2	34.6±9.6
6.1±1.6	2.9±0.8	4.3±1.0	2.9±0.4	1.7±0.3	3.7±0.7	4.4±0.9	1.9±0.5
5.6±1.8	0.8±0.5	2.8±1.5	0.6±0.2	1.0	1.9±0.7	2.8±0.7	0.6±0.2
5.6±2.5	7.0	0	4.8±3.3	13.3±8.5	0	6.8±5.8	0
13.7±0.7	0.8±0.3	0	10.8±3.2	8.9±3.8	0.3	8.0±2.8	11.4±5.5
2.7±1.2	48.0	0	3.5	34.6±30.3	0	2.0	29.4±14.3
6.8±3.0	10.8±4.6	0	8.7±2.0	10.6±2.7	2.0	2.0±8.1	20.0±7.8
7.5±2.8	17.0	0	16.2±5.4	13.9±4.9	0.3	11.5±4.6	13.2±2.5
9.5±5.5	8.8±6.7	0	15.7±7.8	13.1±3.0	0	13.1±8.1	37.5±22.5
7.3±3.6	0	0	2.1±0.6	2.0±0.0	0	16.8±8.0	3.6±1.0
47.1±37.9	426.7±111.1	0.3	120.0±57.8	1021.01±586.8	0	6.1±2.3	491.6±101.5
0.3±0.0	3.4±2.6	0	0	0	0	0	0

surface area (cm²-branch⁻¹ ± 1 SE) across the six sample branches from each height class in each observational group.

group showed any differences across the sites; *Usnea filipendula* (Stirt.) was found more abundantly on C-T than on F-T soils ($F_{[3,20]} = 8.38$, $p = 0.005$) (Table 1). However, when extrapolated to the stand level, there was greater *Alectoria* biomass in fir than in spruce but only when on the C-T soils ($F_{[3,20]} = 7.99$, $p = 0.01$) (Fig. 2b).

Eight species were identified within the *Bryoria* functional group (Table 1). *Bryoria* species were more abundant in spruce than in fir and on C-T than on F-T soils, with the lowest loadings occurring with the interaction of fir on F-T soils ($F_{[1,20]} = 8.57$, $p = 0.008$) (Fig. 2a). Stand-level *Bryoria* loadings were similarly least abundant in fir on F-T soils ($F_{[3,20]} = 8.50$, $p = 0.008$) (Fig. 2b).

Foliose chlorolichens

Foliose chlorolichens were observed on every branch in the study and did not show any significant differences along a vertical gradient (Fig. 1b). Furthermore, as a group, they did not differ in abundance between sites at the tree level. A noticeable but insignificant ($p = 0.059$) trend toward greater loadings in fir on C-T soils (Fig. 2a) became significant at the stand level ($F_{[3,20]} = 18.73$, $p < 0.001$) (Fig. 2b). *Hypogymnia occidentalis*, *Hypogymnia physodes* (L.) Nyl., *Parmelia sulcata*, and *Platismatia glauca* were present on every branch in the study (Table 1), while other individual species within the functional group showed different distribution patterns across site factors. *Platismatia glauca*, although ubiquitous, was the only foliose chlorolichen for which the interaction of tree species and soil type was significant, with the largest loading in fir on C-T soils ($F_{[3,20]} = 4.28$, $p < 0.001$). Other differences included *Hypogymnia tubulosa* (Shaerer) Hav. and *Parmelia hygrophila* (Goward & Ahti), which were more abundant over fir than over spruce ($F_{[3,20]} = 5.18$, $p = 0.034$ and $F_{[3,20]} = 10.67$, $p = 0.004$, respectively) and over C-T than over F-T soils ($F_{[3,20]} = 7.35$, $p = 0.010$ and $F_{[3,20]} = 6.28$, $p = 0.021$, respectively). *Hypogymnia metaphysodes* (Asah.) Rass. ($F_{[3,20]} = 4.95$, $p = 0.038$) and *Parmelia sulcata* ($F_{[1,20]} = 6.88$, $p = 0.016$) were likewise more abundant over C-T than over F-T soils but showed no differences between tree species. *Melanelia* species were the only member of the foliose chlorolichen group that were not observed at least once within each site type. The four species, while regularly observed in both tree species on C-T soils, were entirely absent on F-T soils (Table 1).

Cyanolichens

Cyanolichens differed from all other species in that they were almost entirely absent from the upper canopy in both C-T and F-T soils (Fig. 1c). Anecdotal observations revealed a partitioning of the lower canopy into zones occupied by bipartite cyanolichens versus the tripartite species *Lobaria pulmonaria*. Bipartite cyanolichen species were proportionally more abundant within the upper regions of the lower canopy, while the tripartite species dominated the lowermost branches. Few bipartite cyanolichen thalli were observed on these lowermost branches.

Lobaria pulmonaria was by far the most abundant cyanolichen species in the study and was several orders of magnitude more prevalent than all other cyanophytic species. For example, maximal areal branch coverage in bipartite cyano-

lichens ranged from 0.75 cm²-branch⁻¹ (*Lobaria scrobiculata* (Scop.) DC. in fir on C-T soil) to 37.5 cm²-branch⁻¹ (*Pseudocyphellaria anomala* in fir on F-T soil), while *L. pulmonaria* had a maximal branch coverage of 1021.0 cm²-branch⁻¹ (in spruce on F-T soil) (Table 1). This was 50-fold higher than the highest loading observed for a bipartite cyanolichen. Tree-level *L. pulmonaria* biomass was statistically similar across all combinations of soil types and tree species (Fig. 2a). However, a trend toward greater biomass on F-T soils coupled with greater fir stem density resulted in higher stand-level tripartite cyanolichen abundance in fir over F-T soils ($F_{[3,20]} = 17.00$, $p < 0.001$) (Fig. 2b). The proportion of branches supporting *L. pulmonaria* thalli was also greater on F-T soils than on C-T soils (64% and 48% of assessed branches, respectively). Differences in the biomass of bipartite cyanolichens were masked by the much more dominant *L. pulmonaria*, but there were tree and soil type differences between the branch cover of *Nephroma isidiosum* (Nyl.) Gyeln. ($F_{[3,20]} = 5.09$, $p = 0.035$) and *Sticta fuliginosa* (Hoffm.) Ach. ($F_{[3,20]} = 5.84$, $p = 0.025$), with both being more abundant in fir on F-T soils than in any other species × soil combination (Table 1).

Relative contribution to epiphyte biomass

The relative contribution of each functional group to the total epiphyte biomass varied with soil type. *Alectoria* was similar across soil types, with 16.4% and 14.9% of total epiphyte biomass on C-T and F-T soils, respectively. The contribution of *Bryoria* to epiphyte biomass on C-T soils (26.1%) was almost twice that on F-T soils (15.2%). Foliose chlorolichens made up 29.5% of the epiphyte biomass on C-T soils and 20.8% on F-T soils. The contribution of chlorolichen species (hair and foliose combined) was thus proportionally greater on C-T soils (72.0%) than on F-T soils (50.9%). The opposite was true for cyanophytic species. Bipartite and tripartite species together comprised 49.1% of the total epiphyte biomass on F-T soils but only 28.0% on C-T soils. Bipartite cyanolichens, while scarce relative to *L. pulmonaria* on both soil types, comprised 10.2% of epiphyte biomass on F-T soils compared with only 2.3% on C-T soils.

Lichen C

All nine lichen species had similar mean C contents (45.0 ± 0.1%). The ecosystem-level standing biomass C stocks thus mirror biomass values. Hair lichens and foliose chlorolichens were the largest in fir over C-T soils, while cyanolichen C stocks were largest in fir over F-T soils (Fig. 2c). Total lichen biomass C stocks were larger in fir than in spruce and over C-T soils than over F-T soils (Table 2).

Lichen N

The most marked variation in N content of the nine macrolichen species was due to the algal partner(s). The average N content of lichens with a cyanobacterial symbiont was significantly higher than for green algal lichens (0.61 ± 0.02% N dry mass). Furthermore, bipartite cyanolichen N (3.52 ± 0.07% N dry mass) was greater than that in the tripartite *Lobaria pulmonaria* (2.35 ± 0.04% N dry mass). The mean N of the three foliose chlorolichen species (0.72 ±

0.02% N dry mass) was statistically similar to that of *Bryoria pseudofuscescens* ($0.71 \pm 0.02\%$ N dry mass) and significantly greater than that of the *Alectoria* functional group ($0.40 \pm 0.01\%$ N dry mass) (Table 3).

Nitrogen content applied to the lichen biomass revealed that lichen N differed across soil type and tree species. Trends in the pool of standing lichen N generally reflected the biomass loadings, with *Alectoria*, *Bryoria*, and foliose chlorolichen functional groups representing larger N stocks on C-T soils than on F-T soils (Fig. 2d). However, owing to the proportionally greater percent N of cyanolichens (Table 3) and the larger cyanolichen biomass on F-T soils, there was a trend toward larger N pools in fir than in spruce and on F-T than on C-T soils (Table 2).

The C:N ratios (grams dry mass) of the five lichen functional groups also varied with the algal partner (Table 3). The C:N ratios of both tripartite and bipartite cyanolichens were relatively low (19.8 ± 0.4 and 13.3 ± 0.3 , respectively) and varied relatively little within the functional groups. By contrast, the C:N ratio of the *Alectoria* functional group was both high (113.8 ± 3.8) and extremely variable, ranging from 95 to 140. *Bryoria pseudofuscescens* and the foliose chlorolichens had intermediate C:N ratios of 62.6 ± 1.4 and 65.6 ± 2.9 , respectively (Table 3).

Discussion

There were 44 epiphytic lichen species observed at the ALRF. The abundance with which the oceanic component of the epiphyte community was observed in this interior plateau forest was largely unexpected. The factors facilitating these loadings have not yet been fully explored, but this comparison of macrolichen abundance between C-T and F-T soils and between subalpine fir and interior hybrid spruce suggests that edaphic and substrate factors may play a substantial role.

Distribution across soil texture and tree species

Bryoria was the dominant genus within the upper canopy of all trees, but particularly so in spruce trees over C-T soils. Such predominance may be due to the two-tiered forest canopy structure at ALRF where spruce trees are approximately 3–4 m taller than the more numerous fir. The enlarged upper canopy environment is accentuated on C-T soils where spruce trees are taller than their counterparts over F-T soils. The well-ventilated environment created in the upper spruce canopy is an ideal habitat for nonsorediate *Bryoria* species, which are thought to be distributed as a function of wind (Goward 2003b). Nonsorediate species such as *Bryoria pseudofuscescens* and *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw. tend to be intolerant of prolonged wetting and will colonize areas where rainfall events alternate with drought-like conditions (Campbell and Coxson 2001; Goward 2003a). Furthermore, these species primarily reproduce via fragmentation and will be more prevalent in the emergent spruce crowns as a response to improved wind-vectored dispersal (Goward 2003b).

Cyanolichens are likely responding to similar microclimatic factors, but instead tend to colonize areas in which ventilation is at a minimum. Cyanolichens are known to be scarce in the middle and upper canopy of inland forests, an

observation that has been attributed to lower effective moisture in these higher canopy positions (Benson and Coxson 2002). While chlorolichens are capable of achieving net photosynthesis when exposed only to water vapor (Lange and Kilian 1985; Lange et al. 1993) and with only 50% thallus water content (Hajek et al. 2001), cyanolichens are much more restricted. They require direct exposure to liquid water (Budel and Lange 1991) and are incapable of net photosynthesis below 150% thallus water content (Lange et al. 2004). Furthermore, maximal N₂-fixing activity is only achieved at 200% thallus water content (Antoine 2004). More humid conditions that satisfy these hydration requirements are thought to be achieved within the lower canopy where desiccating winds are less frequent and latent heat fluxes are lower. The lower canopy zone of subalpine fir is much more densely branched than spruce, which may have fewer than three branches in the lower 5 m. Fir therefore provides more colonizable substrate than spruce, a feature that likely results in the greater cyanolichen loading observed in subalpine fir.

The disparity in biomass between soil types cannot likewise be explained by colonizable substrate. Nor can broad climatic factors such as rainfall frequency or relative humidity be solely implicated for differences between neighboring stands and so a site-level factor associated with soil-texture is also likely involved. Crittenden et al. (1994) discussed lichen growth as being limited by water availability and the reduction of physiological activity but proposed that the extent of growth achieved during hydrated periods is limited by other factors, specifically nutrient availability. Our observations support the supposition that the chemical environment and the availability of nutrients are responsible for site-scale differences in the distribution of epiphytic lichens in the sub-boreal canopy.

While a direct connection between the epiphytes and the underlying soils is obviously absent, there is mounting evidence to suggest that forest soil chemistry can impact the development of lichen communities (Gauslaa 1985, 1995; Loppi et al. 1998). A comparison between soil types at the ALRF further suggests that soil chemistry may be an important factor. C-T soils at the research forest have a lower base saturation and a reduced cation-exchange capacity compared with F-T soils of the same parent material. They are also more acidic with a soil pH (CaCl₂) ranging from 3.8 to 5.0 (Ahe and BC horizons, respectively) compared with 4.0–7.5 in F-T soils (Ahe and Ckg horizons, respectively) (Arocena and Sanborn 1999). Being distinctly sensitive to acidification (Gilbert 1986; Gauslaa and Holien 1998; Goward and Arsenault 2000b), cyanolichens tend to inhabit substrates with a pH > 5.4 (Farmer et al. 1991; Gauslaa 1995; Wolseley and James 2000). Although no pH data were collected from the host trees in this study, the relatively high abundance of cyanolichens observed over F-T soils may be attributable to the larger clay mineral fraction, the higher CEC, and the greater availability of base cations in F-T soils.

The chemical factors determining the relationship between fine soil texture and cyanolichen occurrence is likely not limited to pH but may also be related to the availability of nutrients in the soil. Differences in species abundances between soil textures were loosely defined by the presence

Fig. 1. Lichen cover in three vertical canopy zones over course-textured soils (●) and fine-textured soils (○). Data are shown for the three dominant macrolichen species for each of (a) hair lichen, (b) foliose chlorolichen, and (c) cyanolichen functional groups at the Aleza Lake Research Forest.

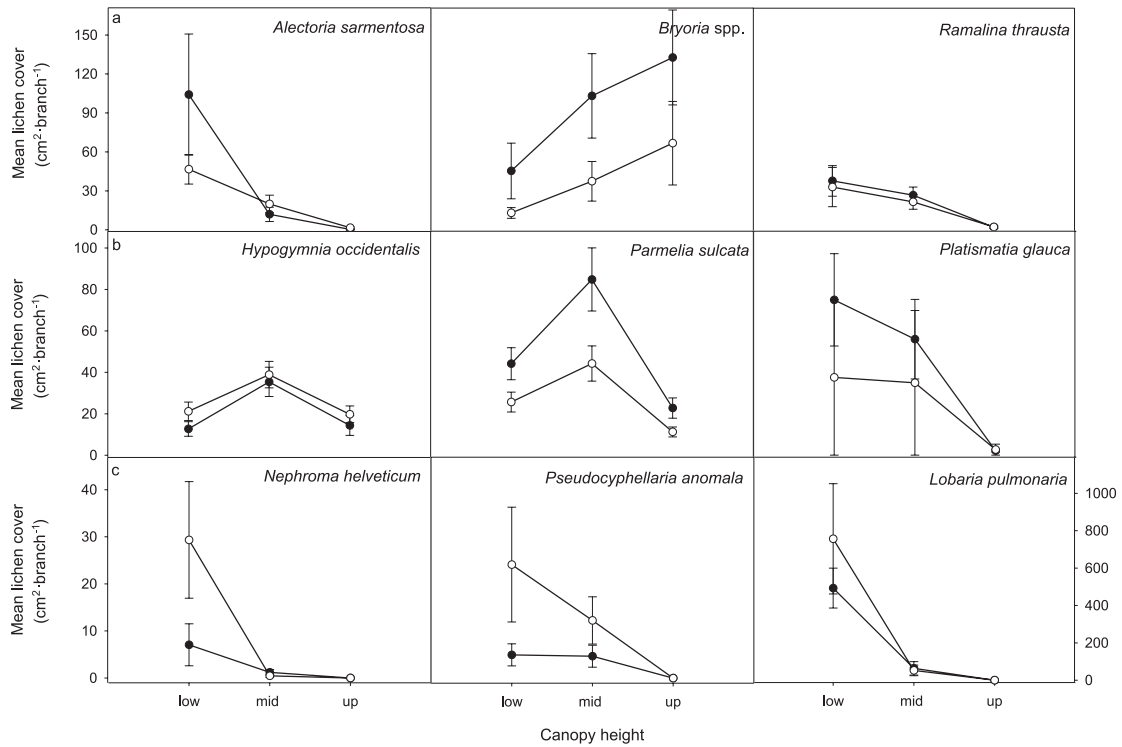


Fig. 2. Lichen biomass at the (a) tree level and (b) stand level, (c) lichen C at the stand level, and (d) lichen N at the stand level for each combination of soil type and host tree species. Biomass is represented for the *Alectoria* (including dominantly *Alectoria sarmentosa* and lesser amounts of *Usnea* species and *Ramalina thrausta*), *Bryoria*, and foliose chlorolichen (label: chlorolichens) functional groups. Lichens with cyanophytic partners are separated into bipartite species (label: cyanolichens) and the tripartite species *Lobaria pulmonaria*. Values labelled with different letters are significantly different (ANOVA, $p < 0.05$). Letters are omitted where no differences exist.

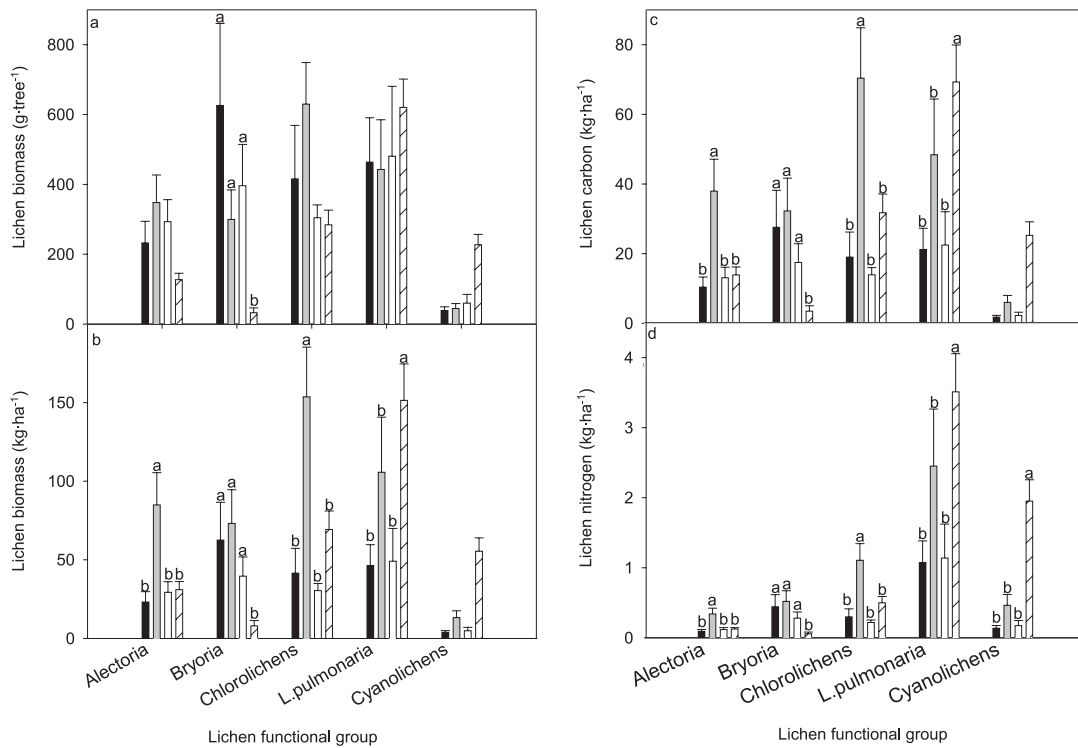


Table 2. Comparison of mean \pm SD total lichen biomass, mean \pm SD total lichen C, mean \pm SD lichen N by species group, and mean \pm SD total lichen N across two soil-texture types (coarse-textured (C-T) and fine-textured (F-T)) and across a factorial of two host trees (spruce and fir) \times two soil texture types.

	C-T	F-T	C-T, spruce	C-T, fir	F-T, spruce	F-T, fir
Biomass and lichen C						
Total biomass (kg-ha ⁻¹) *	603.0 \pm 168.4	472.5 \pm 82.4	175.4 \pm 72.0a	427.6 \pm 152.2b	153.7 \pm 52.0a	318.8 \pm 64.0b
Total C (kg-ha ⁻¹) *	272.6 \pm 76.1	214.9 \pm 37.6	79.0 \pm 32.1a	193.6 \pm 69.0b	69.4 \pm 23.6a	145.5 \pm 29.3b
Lichen N						
<i>Alectoria</i> (g-tree ⁻¹) †	1.2 \pm 0.2	0.8 \pm 0.2	0.9 \pm 0.3a	1.4 \pm 0.3a	1.2 \pm 0.3a	0.5 \pm 0.1b
<i>Bryoria</i> (g-tree ⁻¹) ‡	3.3 \pm 0.9	1.5 \pm 0.6	4.4 \pm 1.7a	2.1 \pm 0.6a	2.8 \pm 0.8a	0.2 \pm 0.1b
Foliose chlorolichens (g-tree ⁻¹) §	3.8 \pm 0.7a	2.1 \pm 0.2b	3.0 \pm 1.1	4.5 \pm 0.9	2.2 \pm 0.3	2.0 \pm 0.3
Bipartite cyanolichens (g-tree ⁻¹)	1.6 \pm 0.4	4.9 \pm 1.1	1.4 \pm 0.4b	1.9 \pm 0.6b	1.7 \pm 0.7b	8.0 \pm 1.0a
<i>Lobaria pulmonaria</i> (g-tree ⁻¹)	10.4 \pm 2.08	12.9 \pm 2.5	10.8 \pm 2.9	10.1 \pm 3.2	11.4 \pm 4.8	14.4 \pm 1.9
Total N (g-tree ⁻¹)	20.3 \pm 2.3	22.2 \pm 2.9	20.5 \pm 2.4	20.0 \pm 4.1	19.3 \pm 5.0	25.2 \pm 2.8
Total N (kg-ha ⁻¹) ¶	6.6 \pm 2.4	7.5 \pm 1.9	2.0 \pm 0.5a	4.7 \pm 2.4b	1.9 \pm 1.2a	5.6 \pm 1.6b

Note: Means with dissimilar letters indicate significant differences ($\alpha = 0.05$).

* $F_{[3,20]} = 11.30, p < 0.001$.

† $F_{[1,20]} = 5.52, p = 0.029$.

‡ $F_{[1,20]} = 8.57, p = 0.008$.

§ $F_{[1,20]} = 5.12, p = 0.035$.

^{||} $F_{[1,20]} = 15.41, p < 0.001$.

¶ $F_{[3,20]} = 8.99, p < 0.001$.

Table 3. Comparison of mean \pm SD percent N content and mean \pm SD C:N for nine macrolichen species grouped according to the photobiont (green algae or cyanobacteria) ($n = 8$).

Species	Photobiont	N (%)	C:N
Fruticose lichens			
<i>Alectoria sarmentosa</i>	Green	0.37 \pm 0.02	121.2 \pm 6.1
<i>Bryoria pseudofuscescens</i>	Green	0.71 \pm 0.02	62.6 \pm 1.4
<i>Ramalina thrausta</i>	Green	0.42 \pm 0.01	107.3 \pm 2.9
Foliose chlorolichens			
<i>Hypogymnia physodes</i>	Green	0.75 \pm 0.01	60.1 \pm 1.4
<i>Parmelia sulcata</i>	Green	0.81 \pm 0.02	59.1 \pm 1.3
<i>Platismatia glauca</i>	Green	0.59 \pm 0.03	77.6 \pm 3.8
Cyanolichens			
<i>Lobaria pulmonaria</i>	Green plus cyanobacteria	2.35 \pm 0.04	19.8 \pm 0.4
<i>Nephroma helveticum</i>	Cyanobacteria	3.70 \pm 0.05	12.7 \pm 0.2
<i>Pseudocyphellaria anomala</i>	Cyanobacteria	3.40 \pm 0.07	13.9 \pm 0.4

of a cyanobacterial symbiont; bipartite and tripartite cyanolichens were most abundant over F-T soils, while the opposite was true for chlorolichens. Cyanobacterial photobionts require larger nutrient supplies than their green algal counterparts (Allen and Arnon 1955) and increases in cyanolichen growth rates have been demonstrated with the addition of P (Kurina and Vitousek 1999) and N (Gauslaa et al. 2006). Furthermore, nitrogenase activity is stimulated by the availability of Mg and Ca (Liengen and Olsen 1997), and phosphate (Liengen 1999; Weiss et al. 2005). Cyanolichens may therefore have greater success on nutrient-enriched substrates (Gauslaa 1985; Goward and Arsenault 2000b) where the nutrient supply is sufficient for the energetically expensive processes of supplying fixed C as well as fixed N. Our work showed greater overall cyanolichen biomass and a greater proportion of total biomass attributed to cyanolichens over F-T soils. These results could be related to the

higher available P, Ca, and Mg in F-T soils than C-T soils at the ALRF (Arocena and Sanborn 1999).

The distribution of chlorolichens may similarly be determined by nutrient supply. Many chlorophytic species tend to be both oligotrophic and acidophilic in nature (Gauslaa 1995). The latter is particularly true of *Melanelia* species, which are more abundant with increased acidification of bark substrates (James and Rose 1974). *Melanelia elegantula* (Zahlbr.) Essl., for example, is described as being found predominantly on acidic bark of pH 3.8–4.6 (James and Rose 1974; Tønsberg et al. 1996). The fact that *Melanelia* species were found on sample branches exclusively from C-T soils and that most foliose chlorolichens trended toward greater biomass on C-T than on F-T soils adds further support to a proposed relationship between epiphytic lichen distribution soil chemistry. Further study is now underway to explore the degree to which chemical site factors influence

the colonization and growth of epiphytic lichens within sub-boreal forests.

Epiphytic lichen contributions to ecosystem biomass, C, and N

Total standing biomass for epiphytic lichens in old-growth forests at the ALRF ranged from 472 (F-T soils) to 603 (F-T soils) kg ha⁻¹. These were somewhat lower than the 837 kg ha⁻¹ reported by Edwards et al. (1960) for a Douglas-fir/Engelmann spruce/subalpine fir forest in Wells Gray Park, British Columbia, and less than half the 1332 kg ha⁻¹ found in wetter interior western redcedar/western hemlock forests to the east (Benson and Coxson 2002).

Comparison of epiphytic C stocks at the ALRF reveals that C-T soils supported higher macrolichen biomass (0.273×10^6 g C·ha⁻¹) than F-T soils (0.215×10^6 g C·ha⁻¹) (Table 2). These were similar in trend to ecosystem-level C where C-T soils support greater total forest C stocks (423×10^6 g C·ha⁻¹) than F-T soils (324×10^6 g C·ha⁻¹) (Fredeen et al. 2005). Lichen epiphyte C stocks, however, were very small, representing 0.064%–0.066% of total forest ecosystem C on C-T and F-T soils, respectively. An arguably more valid assessment of lichen function is a comparison of epiphyte with host tree foliage biomass or C. Epiphytic lichens represented 3.7% and 2.7% of (photosynthetic) host tree foliage biomass or C on C-T and F-T soils, respectively. These ratios are approximately half the lichen to foliage ratio (6%) observed for coastal Douglas-fir forests in Oregon (Pike 1978), but this particular comparison would yield an even greater contrast if bryophytes were considered because of their near complete absence in sub-boreal forest canopies.

Stand-level macrolichen N was greater on F-T soils, a result largely attributable to the N contributed by cyanolichens, which were proportionally more abundant on F-T than on C-T soils. The comparatively heavy biomass and relatively high N content (%) of *Lobaria pulmonaria* combined with the less abundant but N-rich bipartite cyanolichens amounted to 7.5 ± 1.9 kg N·ha⁻¹ on F-T soil. While this provides no indication of the rate of N₂ fixation by these species, studies have shown that *Lobaria oregana* (Tuck.) Müll. Arg., a closely related tripartite cyanolichen, may fix between 2.5 (Pike 1978) and 16.5 kg N₂·ha⁻¹·year⁻¹ (Antoine 2004) in coastal Douglas-fir forests, albeit with a standing biomass of at least 900 kg·ha⁻¹ (Pike et al. 1977 as summarized in Knops et al. 1996). If we assume that standing N pools are a general indicator of N₂-fixing capacity, it becomes apparent that cyanolichens, especially the biomass dominant *Lobaria pulmonaria*, are crucial components of the N cycle. This is perhaps particularly the case in the interior of British Columbia where N deficiencies are common (Brockley 2000) and atmospheric N inputs are likely as low as 0.5 kg N·ha⁻¹·year⁻¹ (Hope 2001). It is clear that the contribution of epiphytic cyanolichens to ecosystem function through N₂ fixation may be substantial despite contributing little to overall forest biomass or C stocks.

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