

Contrasting arboreal and terrestrial macrolichen and bryophyte communities in old-growth sub-boreal spruce forests of central British Columbia

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ABSTRACT. Macrolichen and bryophyte species diversity, abundance, biomass and nitrogen stocks were compared between arboreal and terrestrial habitats in old-growth sub-boreal spruce forests in central British Columbia, Canada on the two most common soil types in the area, fine- and coarse-textured soils. A total of 118 macrolichen and bryophyte species were identified, including 71 species of macrolichens (44 arboreal and 43 terrestrial) and 47 species of bryophytes, of which only one moss (*Orthotrichum* sp.) was arboreal. Macrolichen functional groups varied in both diversity and abundance between arboreal and terrestrial communities. Cyanolichens were common in both arboreal and terrestrial habitats, but were much more abundant arboreally than terrestrially. This epiphytic biomass was largely attributed to the tripartite cyanolichen species, *Lobaria pulmonaria*, while the most common terrestrial macrolichens were bipartite *Peltigera* cyanolichen species. From a biomass perspective, the epiphyte community was almost entirely lichens while the terrestrial community was predominantly bryophytes. Terrestrial and arboreal macrolichens and bryophytes made a relatively small contribution to total forest above-ground biomass (0.5–1.4% or 1698–3339 kg ha⁻¹), however, a comparison between macrolichen and bryophyte biomass and tree foliar biomass showed lichens and bryophytes to be equivalent to 11.7–20.5% of tree foliar biomass. Macrolichens made a proportionately large contribution when compared to forest foliar nitrogen and contained 6.4–8.1% of forest foliar nitrogen. Nitrogen contents varied greatly between functional

groups, from a maximum of 3.98% N in terrestrial bipartite cyanolichens to a minimum of 0.37% N in *Alectoria* hair lichens. In total, terrestrial and arboreal lichens and bryophytes represented 20–39 kg N ha⁻¹ in this old-growth sub-boreal spruce ecosystem.

KEYWORDS. Macrolichen, bryophyte, diversity, nitrogen, soil texture, sub-boreal spruce forest, British Columbia, Canada.



Lichens and bryophytes represent important components of forest floor and epiphyte communities in many ecosystems, contributing to forest diversity, structure and ecosystem-level processes. Lichens and bryophytes combined occupy a wide range of habitats, colonizing most terrestrial substrates, tree trunks and tree canopies. The diversity and abundance of terrestrial macrolichens and bryophytes and epiphytic lichens have been assessed in various areas of western North America (e.g., Crites & Dale 1998; Goward 1994; Goward & Ahti 1992; Lesica et al. 1991; Neithlich & McCune 1997; Newmaster et al. 2003) including, more recently, the sub-boreal spruce forests of central interior British Columbia (Botting & Fredeen 2006; Campbell & Fredeen 2007). However, few studies have simultaneously compared the community structure and ecosystem contributions of both arboreal and terrestrial lichen and bryophyte species in the same system. This paper documents the combined diversity and abundance of macrolichens and bryophytes in both terrestrial and epiphytic habitats, and examines their relative and total inputs to ecosystem biomass and nitrogen (N).

Lichens and bryophytes can make important contributions to forest nutrient cycling, particularly to N-cycling (Oechel & Van Cleve 1986; Pike 1978; Turetsky 2003). Lichens and bryophytes acquire N and other nutrients through wet or dry deposition (Palmqvist et al. 2002), from canopy throughfall (Knops et al. 1991), from the substrate below (Bates 2000), or in the case of cyanobacterial lichens, from N₂-fixation (Kershaw 1985). The N held in lichens and bryophytes may be released into the ecosystem through periodic leaching (Millbank 1982) and through decomposition (Coxson 1991; Millbank & Olsen 1986; Wilson & Coxson 1999). In the case of N₂-fixing cyanolichens particularly, this constitutes a

supply of otherwise unavailable N to the forest system. Terrestrial lichen N contributions range from 0.04–0.94 kg N ha⁻¹ yr⁻¹ for N₂-fixing lichens in Alaska (Gunther 1989) to 0.1 kg N ha⁻¹ yr⁻¹ for terrestrial *Peltigera* lichens in coniferous forests in Minnesota (Knowles et al. 2006). Epiphytic cyanolichens may provide much more N to conifer forests. Models based on N-fixation rates and standing biomass (550 kg ha⁻¹) for the tripartite cyanolichen *Lobaria oregana* predict annual N-fixation to be between 1.5 and 2.6 kg ha⁻¹ (Antoine 2004). With atmospheric inputs as low as 0.5 kg ha⁻¹ yr⁻¹ and N limitations common in many boreal forest systems (Bhatti et al. 2002; Brockley 2000), even small cyanolichen inputs could impact forest productivity.

Soil texture can affect a wide variety of ecosystem properties such as soil nutrient regime, moisture availability, and tree and vascular plant productivity (Bhatti et al. 2002). In sub-boreal spruce forests, soil texture influences shrub and herbaceous plant species occurrence and forest productivity (Delong 2003) as well as macrolichen and bryophyte communities (Botting & Fredeen 2006; Campbell & Fredeen 2007). These soil-mediated influences may, however, differ between terrestrial and arboreal species (Gauslaa & Holien 1998; Gustafsson & Eriksson 1995).

This study examines macrolichen and bryophyte communities on the two major soil texture types that underlie the Aleza Lake Research Forest in the Sub-Boreal Spruce biogeoclimatic zone (Meidinger & Pojar 1991). There were two primary aims: 1) to assess and compare arboreal and terrestrial habitats with respect to lichen and bryophyte abundance, diversity patterns and functional group prevalence and 2) to examine macrolichen and bryophyte biomass and nitrogen contents to determine

macrolichen and bryophyte contributions to old-growth sub-boreal spruce forest biomass and nitrogen pools.

METHODS

Study area. The study took place in the Aleza Lake Research Forest (ALRF), located 60 km northeast of Prince George in central British Columbia, Canada (54°11'N, 122°40'W). The ALRF is within the wet and cool sub-zone of the Sub-Boreal Spruce biogeoclimatic zone (SBSwk1; Meidinger & Pojar 1991). Forests are dominated by subalpine fir (*Abies lasiocarpa*) and hybrid spruce (*Picea glauca* × *engelmannii*) while Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) make up lesser components of the canopy (DeLong 2003). The ALRF has cool moist summers and cool snowy winters, receiving approximately 900 mm of precipitation annually with 2/3 falling as rain (Murphy 1996). Soils in the region were formed from glaciolacustrine sediments and most areas have fine-textured soils ranging from silty clay loam to silty clay. Scattered throughout the forest are areas with an overlying veneer of coarse-textured soil 0.5–2 m thick, ranging in texture from silt loam to sandy loam (Arocena & Sanborn 1999).

The four study sites were located in an old-growth forest > 200 years of age, with an uneven canopy structure. The canopy was two-tiered with hybrid spruce trees (30.6 ± 4.5 m) emerging over subalpine fir crowns (26.7 ± 2.2 m; Botting & Fredeen 2006). Two of the sites were located on coarse-textured soils and two on fine-textured soils, as determined by soil coring. At each of the four study sites, three plots were located 20 m from the site center along random compass bearings, with one plot located within 50 m of a forest edge. At each plot, terrestrial and arboreal lichen and bryophyte diversity, abundance and biomass were surveyed and forest stand and vascular plant characteristics were inventoried. Field sampling occurred between May and August of 2003. Nomenclature for lichens and mosses follows Esslinger (1997) and Anderson et al. (1990), respectively.

Terrestrial sampling. A full description of terrestrial diversity sampling methods can be found

in Botting and Fredeen (2006). In brief, at each of the 12 plots, two parallel 20 m transects were established 10 m apart, along which macrolichen, moss and liverwort species diversity and abundance were surveyed in 1 × 1 m quadrats placed at five equidistant points on the transect. Each species present in the quadrat was recorded or collected for future identification and its percent cover and the substrate it was growing on were recorded. Eight quadrats were sampled per plot for a total of 8 m² of sampled area per plot and 24 m² of sampled area per site. Sampling methodology affects species capture and the accuracy of cover measurements (McCune & Lesica 1992) and as such, it is likely that the methodology used in this study resulted in reasonably accurate cover estimates but some rare species and rare habitat types may have been missed. To facilitate comparisons between arboreal and terrestrial habitats, species were divided into functional groups: hair chlorolichens, club and shrub chlorolichens, foliose chlorolichens, bipartite cyanolichens, tripartite cyanolichens and terrestrial bryophytes.

Biomass samples were collected for the two most common terrestrial macrolichen species (*Peltigera apthosa* and *P. membranacea*) and for the five dominant moss species (*Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquetrus* and *Rhizomnium nudum*). Samples were collected as 10 × 10 cm or 5 × 5 cm squares removed from the underlying substrate. Biomass samples were considered to include only living material of that species and were manually cleaned to remove all litter and dead material. Three replicate biomass samples were taken from each site for a total of 12 biomass samples per species over the four sites. The samples were oven-dried for 48 hours at 65°C for dry weight determinations. Biomass values for the five moss species for which biomass was collected were used to approximate the biomass of an additional five related common moss species. Biomass values for the two *Peltigera* species for which biomass was collected were used to approximate the biomass of all other *Peltigera* species. Liverworts were not included in biomass sampling due to their small size, low overall percent cover and the difficulty of collecting large enough homogeneous samples. The

moss and *Peltigera* species included in the biomass calculation represented 85–93% of the total lichen and bryophyte forest floor cover.

Arboreal sampling. Detailed information on arboreal data collection methods is available in Campbell and Fredeen (2007). In brief, one hybrid spruce and one subalpine fir tree were selected for assessment within 5 m of each terrestrial assessment plot center for a total of six sample trees per site. Selected arboreal sampling trees supported lichen loadings that were representative of that forest stand and were structurally safe for climbing. Each tree was rigged and climbed and the macrolichen biomass was estimated vertically following Campbell and Coxson (2001) and Benson and Coxson (2002) for the four dominant lichen groups: hair lichens (including dominantly *Alectoria sarmentosa* and *Bryoria* spp. with lesser amounts of *Usnea* spp. and *Ramalina thrausta*), foliose chlorolichens, bipartite cyanolichens and tripartite cyanolichens.

One sample branch was selected using stratified random sampling and removed from each of high, middle and low canopy zones. Biomass estimates were corrected by applying simple linear regression equations calculated according to Campbell and Coxson (2001) by comparing measured lichen on these sample branches with biomass estimates. Macrolichens were identified to species and the lichen surface area was assessed, as a proxy measure for cover, for each taxa encountered on these sample branches. In the case of hair lichens, the surface area measured was that of the volume occupied by the flattened lichen clump.

Elemental analysis. Terrestrial species collected for elemental analysis included the two most common terrestrial lichens: *Peltigera aphosa* and *P. membranacea*; and the five dominant moss species: *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquetrus* and *Rhizomnium nudum*. These samples were taken according to the same collection methods as the terrestrial biomass samples. Samples of nine arboreal lichen species were collected for element analysis. The three most common species for each functional group were collected. Hair lichens included *Alectoria sarmentosa*, *Bryoria pseudofuscescens* and *Ramalina thrausta*, foliose chlorolichens included *Hypogymnia*

occidentalis, *Parmelia sulcata* and *Platismatia glauca* and cyanolichens included samples of *Lobaria pulmonaria*, *Nephroma helveticum* and *Pseudocyphellaria anomala*. One sample of each arboreal species was collected from a randomly selected hybrid spruce and subalpine fir branch from each of the four sites for a total of eight samples per species.

Samples were oven-dried for 48 hours at 65°C and ground to a fine powder in an electric coffee grinder and a MM200 mixer mill (Retsch Co., Germany). Duplicate sub-samples of 4–5 mg were weighed and each was analyzed with the Dumas combustion method (Kirsten 1983) using a NA 1500 Elemental Analyzer (Fisons Instruments, Italy) to assess the nitrogen and carbon contents by weight for each sample.

Terrestrial biomass and nitrogen values for macrolichen and bryophyte species were scaled up to the site level using percent cover values for each species from eight 1 m² quadrats for each of the three plots per site (24 m² sampled per site) (taken from Botting & Fredeen 2006). As indicated earlier, the species included in biomass and nitrogen calculations represent 85–93% of the total macrolichen and bryophyte forest floor cover. Biomass estimates may therefore be slight underestimations of total non-vascular biomass. The biomass estimates for each site were then extrapolated to a per hectare value and averaged.

Arboreal biomass estimates and lichen-N values were scaled up to the stand level using stem densities recorded in the 20 × 20 terrestrial sampling plots (Botting 2005) and differed from the stem densities of Karjala (unpublished data) as cited in Campbell and Fredeen (2007). Botting (2005) recorded 329 and 467 subalpine fir and 154 and 208 hybrid spruce on coarse- and fine-textured soils, respectively. Biomass estimates are likely still an underestimate as snags and small trees were not included in stem densities or lichen abundance estimates. The contribution of macrolichen and bryophyte biomass relative to tree foliar, shrub and herbaceous plant, and total above-ground forest biomass was calculated using ALRF data from Fredeen et al. (2005), foliar C contents from Lamlon and Savidge (2003), and foliar N contents from Swift and Brockley (1994).

Data analysis. Analysis of variance ($\alpha = 0.05$), with soil texture as a main fixed effect and site as a random effect nested within soil texture, was used to compare forest stand characteristics and coarse woody debris (CWD) characteristics between the two soil texture types. An ANOVA with the main fixed effects of soil texture and habitat type (arboreal or terrestrial) was used to evaluate macrolichen and bryophyte species richness. Differences in Shannon-Wiener diversity indices and percent nitrogen contents between the two soil texture types and two habitat types were also tested against soil texture and habitat type. A one way ANOVA was used to analyze terrestrial lichen and bryophyte biomass, arboreal lichen biomass and biomass nitrogen values across soil texture types.

RESULTS

Species diversity. In total, 71 macrolichen species were identified across all terrestrial and arboreal habitats (Table 1). Terrestrial and arboreal macrolichen species richness were identical with 44 species found in the canopy (Campbell & Fredeen 2007) and 43 species found on the ground (Botting & Fredeen 2006). The fifteen macrolichen species found in common between terrestrial and arboreal habitats included species (e.g., from *Hypogymnia*, *Parmelia*, *Parmeliopsis*, *Platismatia*, *Nephroma* and *Tuckermanopsis*; Table 1) that were most commonly found epiphytically, and when observed in terrestrial habitats were found on intact to moderately decayed coarse woody debris (decay classes 1–3; B.C. Ministry of Forests 1998). In addition, one arboreal moss species (see Campbell & Fredeen 2007) and 27 terrestrial moss and 19 terrestrial liverwort species (see Botting & Fredeen 2006) were identified. Total macrolichen and bryophyte species richness was highest in terrestrial habitats (ANOVA; $p = 0.002$) due to the high diversity of bryophyte species on the ground. No difference in Shannon-Wiener diversity was determined for macrolichen or macrolichen and bryophyte species between either arboreal and terrestrial habitats or the two soil textures though there was a trend towards higher diversity on coarse-textured soils for both arboreal and terrestrial habitats (Table 2).

Macrolichen abundance and diversity within functional groups. Though terrestrial and epiphytic

macrolichen species richness was equivalent, lichen functional group diversity patterns varied (Table 2). For example, terrestrial cyanolichens were more diverse (15 spp.) than arboreal cyanolichens (8 spp.). However, tripartite cyanolichens had low diversity in both habitats (three terrestrial and one arboreal species). Foliose chlorolichens were the most diverse arboreal functional group and had almost twice as many arboreal species (20 spp.; Campbell & Fredeen 2007) as terrestrial species (11 spp.). Club, shrub and hair chlorolichens had similar arboreal (16 spp.; Campbell & Fredeen 2007) and terrestrial (17 spp.) diversity (Table 2). However, morphological niche partitioning was evident as hair lichens occurred almost exclusively in the canopy and, with the exception of two small thalli of the arboreal species *Ramalina dilacerata*, club and shrub chlorolichens were exclusively terrestrial (Table 1).

From a lichen cover and biomass perspective, cyanolichens were the most abundant lichen functional group. They made up 58–74% of terrestrial lichen cover and were the most abundant arboreal functional group on the predominant fine-textured soil type comprising 55% of arboreal biomass (Fig. 1; Campbell & Fredeen 2007). The tripartite cyanolichen species (*Lobaria pulmonaria*) dominated the canopy environment while bipartite cyanolichen species (predominantly *Peltigera membranacea*) made up most of the lichen biomass in terrestrial habitats. Foliose chlorolichens were less abundant than cyanolichens in both habitats, comprising 12–15% of terrestrial lichen cover and 21–33% of arboreal lichen biomass.

Soil texture effects. Differences between soil texture types corresponded with differences in arboreal and terrestrial macrolichen and bryophyte diversity, though these were not statistically significant. On coarse- and fine-textured soils, respectively, there were 37 and 33 arboreal lichen species, 36 and 37 terrestrial lichen species, and 44 and 31 bryophyte species identified (Table 2). Though also not statistically significant in a soil texture comparison, functional groups showed distinct trends in abundance patterns with soil texture. Cyanolichen abundance was greater on fine-textured soils (56% of arboreal biomass; 74% of terrestrial cover) than on coarse-textured soils

Table 1. Identified arboreal and terrestrial macrolichen species in their assigned functional groups (club, shrub and hair chlorolichens, foliose chlorolichens and bipartite and tripartite cyanolichen) from old-growth sub-boreal spruce forest. Note that strands of *Alectoria*, *Bryoria* and *Usnea* spp. were found on terrestrial coarse woody debris substrates but were not identified to species.

Terrestrial Lichen Species	Arboreal Lichen Species
Club, shrub & hair chlorolichens	
<i>Cladina rangiferina</i>	<i>Alectoria sarmentosa</i>
<i>Cladina</i> spp.	<i>Bryoria capillaris</i>
<i>Cladonia botrytes</i>	<i>B. glabra</i>
<i>C. carneola</i>	<i>B. fremontii</i>
<i>C. cenotea</i>	<i>B. friabilis</i>
<i>C. chlorophaea</i>	<i>B. fuscescens</i>
<i>C. coniocraea</i>	<i>B. lanestrus</i>
<i>C. crispata</i> var. <i>crispata</i>	<i>B. pseudofuscescens</i>
<i>C. digitata</i>	<i>Nodobryoria oregana</i>
<i>C. ecmocyna</i>	<i>Ramalina dilacerata</i>
<i>C. fimbriata</i>	<i>R. thrausta</i>
<i>C. gracilis</i> ssp. <i>turbinata</i>	<i>Usnea chaetophora</i>
<i>C. norvegica</i>	<i>U. filipendula</i>
<i>C. ochrochlora</i>	<i>U. lapponica</i>
<i>C. sulphurina</i>	<i>U. scabrata</i>
	<i>U. substerilis</i>
Foliose chlorolichens	
<i>Hypogymnia occidentalis</i>	<i>Hypogymnia austerodes</i>
<i>H. physodes</i>	<i>H. bitteri</i>
<i>H. tubulosa</i>	<i>H. metaphysodes</i>
<i>Mycoblastus sanguinariis</i>	<i>H. occidentalis</i>
<i>Parmelia hygrophila</i>	<i>H. oroborealisis</i>
<i>P. sulcata</i>	<i>H. physodes</i>
<i>Parmeliopsis ambigua</i>	<i>H. rugosa</i>
<i>P. hyperopta</i>	<i>H. tubulosa</i>
<i>Platismatia glauca</i>	<i>H. vittata</i>
<i>Tuckermanopsis chlorophylla</i>	<i>Melanelia elegantula</i>
<i>T. orbata</i>	<i>M. exasperatula</i>
	<i>M. subelegantula</i>
	<i>M. subaurifera</i>
	<i>Parmelia hygrophila</i>
	<i>P. sulcata</i>
	<i>Parmeliopsis ambigua</i>
	<i>P. hyperopta</i>
	<i>Platismatia glauca</i>
	<i>Tuckermanopsis chlorophylla</i>
	<i>T. orbata</i>
Bipartite cyanolichens	
<i>Nephroma bellum</i>	<i>Lobaria hallii</i>
<i>Nephroma helveticum</i>	<i>L. scrobiculata</i>
<i>N. parile</i>	<i>Nephroma helveticum</i>
<i>Peltigera canina</i>	<i>N. isidiosum</i>

Table 1. Continued.

Terrestrial Lichen Species	Arboreal Lichen Species
<i>P. degenii</i>	<i>N. parile</i>
<i>P. extenuata</i>	<i>Pseudocyphellaria anomala</i>
<i>P. horizontalis</i>	<i>Sticta fuliginosa</i>
<i>P. membranacea</i>	
<i>P. neckeri</i>	
<i>P. neopolydactyla</i>	
<i>Peltigera</i> spp. Nov. 1 & 2	
<i>Pseudocyphellaria anomala</i>	
Tripartite cyanolichens	
<i>Lobaria pulmonaria</i>	<i>Lobaria pulmonaria</i>
<i>Peltigera aphthosa</i>	
<i>P. leucophlebia</i>	

(27.5% of arboreal biomass; 58% of terrestrial cover; **Fig. 1**). From a biomass perspective, terrestrial bryophytes (ANOVA; $p < 0.001$) and arboreal lichens (ANOVA; $p < 0.001$) were significantly more abundant on fine-textured than coarse-textured soils while terrestrial lichens showed no difference.

Terrestrial and arboreal lichen and bryophyte biomass. Terrestrial bryophytes made the largest contribution to total macrolichen and

Table 2. Comparison of terrestrial and arboreal species richness of macrolichen functional groups (hair, club and shrub, and foliose chlorolichens and bipartite and tripartite cyanolichens), total macrolichen and bryophyte species richness and Shannon Index diversity on coarse-textured soils and fine-textured soils.

	Terrestrial		Arboreal	
	Coarse	Fine	Coarse	Fine
Species Richness				
Cyanolichen	11	10	8	8
Club and shrub chlorolichen	10	13	0	0
Foliose chlorolichen	9	10	20	16
Hair chlorolichen	3	2	13	14
Tripartite cyanolichen	2	2	1	1
Bipartite cyanolichen	9	8	7	7
Macrolichen Total	36	37	37	33
Bryophyte	44	31	1	0
Shannon Index				
Macrolichen	2.54	2.48	2.32	2.06
Macrolichen & bryophyte	2.56	2.03	2.32	2.06

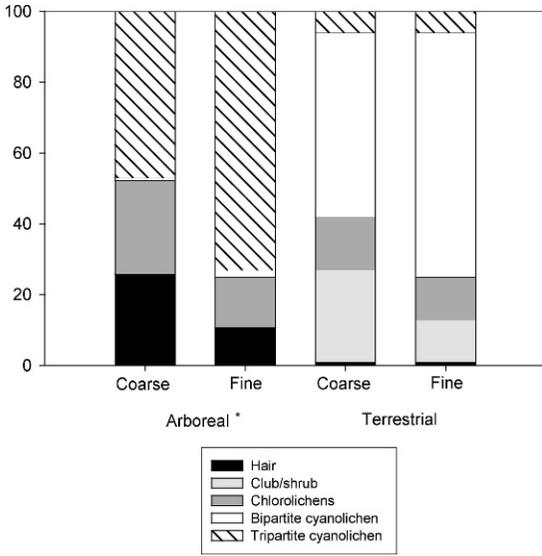


Figure 1. Comparison of the proportion of the cover (terrestrial) or biomass (arboreal) comprised by each lichen functional group (club and shrub chlorolichens, hair chlorolichens, foliose chlorolichens and bipartite and tripartite cyanolichens) in arboreal and terrestrial habitats on coarse-textured (coarse) and fine-textured (fine) soils in old-growth sub-boreal spruce forest. * Arboreal data are extrapolated from Campbell and Fredeen (2007).

bryophyte biomass in sub-boreal spruce forests. Conversely, bryophytes were almost entirely absent from the arboreal habitat. Terrestrial bryophytes were 260% more abundant than arboreal lichens on fine-textured soils while the biomass of terrestrial bryophytes was equivalent to that of arboreal lichens on coarse-textured soils (Fig. 2). Specifically, terrestrial bryophyte biomass varied between $842 \pm 144 \text{ kg ha}^{-1}$ (coarse-textured soils) and $2396 \pm 362 \text{ kg ha}^{-1}$ (fine-textured soils) while total arboreal lichen biomass ranged between $847 \pm 239 \text{ kg ha}^{-1}$ (coarse-textured soils) and $930 \pm 155 \text{ kg ha}^{-1}$ (fine-textured soils). The single epiphytic bryophyte notwithstanding, terrestrial macrolichens had by far the smallest biomass ($10 \pm 2 \text{ kg ha}^{-1}$ on coarse-textured soils, $14 \pm 3 \text{ kg ha}^{-1}$ on fine-textured soils). Total terrestrial and arboreal macrolichen and bryophyte biomass in old-growth sub-boreal forests ranged from 1698 ± 279 to $3339 \pm 394 \text{ kg ha}^{-1}$ on coarse- and fine-textured soils, respectively.

Overall, macrolichens and bryophytes comprised 0.5% (coarse-textured soils) and 1.4% (fine-textured soils) of the total above-ground forest

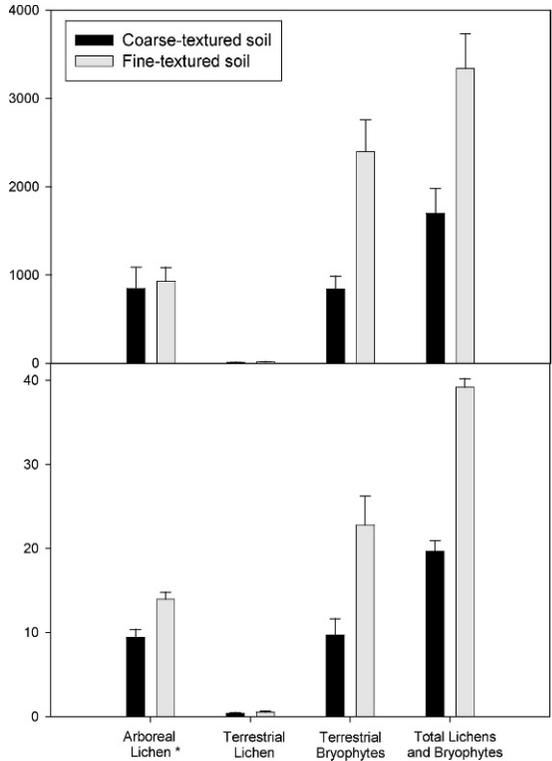


Figure 2. Comparison of the biomass (kg ha^{-1}) (A) and biomass nitrogen (kg N ha^{-1}) (B) of arboreal lichens, terrestrial lichens, terrestrial lichens and bryophytes, and total (terrestrial + arboreal) lichens and bryophytes from coarse-textured (coarse) and fine-textured (fine) soils in sub-boreal spruce forests in central British Columbia. * Arboreal data are extrapolated from Campbell and Fredeen (2007).

biomass (Table 3). However, a comparison between macrolichen and bryophyte biomass and the shrub and herbaceous plant biomass revealed that lichen and bryophyte species were equivalent to between 32% (coarse-textured soils) and almost 700% (fine-textured soils) of the combined shrub and herbaceous biomass. Furthermore, combined lichen and bryophyte biomass, recognizing that the majority of the biomass is photosynthetic, was equivalent to 11.7% (coarse-textured soils) and 20.5% (fine-textured soils) of tree foliar biomass (Table 3).

Nitrogen content. Terrestrial bryophytes averaged 1.10% nitrogen (N) content and were the only functional group to show a significant difference in N content between soil texture types (ANOVA; $p=0.004$), with mosses on coarse-textured soils having higher N content (Fig. 3). Mosses also showed significant differences in N content between

Table 3. Terrestrial lichen, terrestrial lichen and moss, arboreal lichen, and total lichen and moss (arboreal + terrestrial) biomass and biomass nitrogen expressed as a percent (%) of tree foliar biomass, shrub + herbaceous plant biomass, above-ground forest biomass and tree foliar biomass nitrogen. Foliar, shrub and herb, and total above-ground forest biomass values were taken from a concurrent study at the Aleza Lake Research Forest (Fredeen et al. 2005) and foliar biomass C and N values were derived by assuming a spruce foliar C content of 50% (Lamton & Savidge 2003) and a spruce foliar N content of 1.06% (Swift & Brockley 1994). Biomass nitrogen estimates were not possible for shrub, herb and total above-ground forest.

	Biomass			Nitrogen
	Foliar	Shrub+herb	Above-ground	Foliar
Coarse-textured soil				
Terrestrial lichen	0.1%	0.2%	0.0%	0.3%
Terrestrial lichen + moss	5.8%	15.7%	0.3%	6.7%
Arboreal lichen	5.8%	15.7%	0.3%	6.1%
Total (arboreal + terrestrial)	11.7%	31.6%	0.5%	12.9%
Fine-textured soil				
Terrestrial lichen	0.1%	2.8%	0.0%	0.3%
Terrestrial lichen + moss	14.8%	480.0%	1.0%	13.1%
Arboreal lichen	5.7%	186.0%	0.4%	7.8%
Total (arboreal + terrestrial)	20.5%	668.8%	1.4%	21.8%

species (ANOVA; $p < 0.001$). Within lichens, N contents varied greatly between functional groups (ANOVA; $p < 0.001$), being highest in bipartite cyanolichen species ($3.54 \pm 0.27\%$ N arboreal Campbell and Fredeen 2007; $3.98 \pm 0.23\%$ N terrestrial) and lowest in hair lichen species (e.g., $0.37 \pm 0.02\%$ N for *Alectoria sarmentosa*; Campbell & Fredeen 2007). Interestingly, a comparison between habitats reveals that both bipartite (ANOVA;

$p = 0.002$) and tripartite (ANOVA; $p < 0.001$) cyanolichens from terrestrial habitats had higher N contents than those from arboreal habitats.

Terrestrial and arboreal lichen and bryophyte nitrogen. As expected, given their higher biomass, terrestrial bryophytes comprised the greatest proportion of total macrolichen and bryophyte biomass N (Fig. 2). Total biomass N contributions were 10.4 ± 2.0 and 23.5 ± 3.3 kg N ha⁻¹ for terrestrial macrolichens and bryophytes and 9.4 ± 1.0 and 14.0 ± 0.8 kg N ha⁻¹ for arboreal macrolichens (Campbell & Fredeen 2007), on coarse- and fine-textured soils, respectively. Overall, lichens and bryophytes represented 19.7 ± 1.3 kg N ha⁻¹ (coarse-textured soils) and 39.2 ± 1.0 kg N ha⁻¹ (fine textured soils) in old-growth sub-boreal spruce forests. These standing N pools were equivalent to 12.9% (coarse-textured soils) and 21.8% (fine-textured soils) of the tree foliar biomass nitrogen (Table 3).

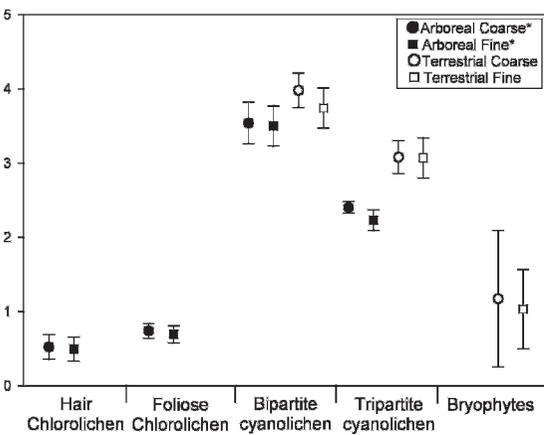


Figure 3. Percent (%) nitrogen content (± standard deviation) of arboreal and terrestrial lichen functional groups (hair lichens, bipartite and tripartite cyanolichens, foliose chlorolichens) and terrestrial bryophytes from coarse-textured (coarse) and fine-textured (fine) soils. * Arboreal data are extrapolated from Campbell and Fredeen (2007).

DISCUSSION

Macrolichens were equally diverse on the ground and in the canopies of the sub-boreal spruce forest at the Aleza Lake Research Forest. The 15 lichen species that were found to overlap between the arboreal and terrestrial habitats grew on coarse woody debris which was often poorly to moderately decayed. As decay progressed, there was a transition

to solely terrestrial lichens and bryophytes. Terrestrial macrolichens were almost exclusively found growing on CWD (Botting & Fredeen 2006). Bryophytes had high diversity on the ground but only one moss genus was recorded in the canopy, at low frequency and abundance. This was expected as epiphytic mosses are not common in sub-boreal spruce forests (Schofield 1988) and epiphytic bryophyte species are generally found in areas with higher humidity and moisture than epiphytic lichens (Frahm 2003).

The combined terrestrial and arboreal diversity of 71 macrolichen species was only slightly less than the shrub and herbaceous plant diversity of 75–80 species identified in a survey of corresponding site types at the Aleza Lake Research Forest (Oikos 1995). Given that only macrolichen species were evaluated in our study, and that only coniferous trees were assessed, it is probable that total lichen diversity surpasses vascular plant diversity in these sub-boreal spruce forests. When the bryophyte diversity of 47 species was included, the diversity of macrolichens and bryophytes was considerably higher than that of vascular plants. These results are similar to those found in forests in Montana where epiphytic and terrestrial cryptogam diversity also exceeded vascular plant diversity (McCune & Antos 1981). Difficulties in identifying lichen and bryophyte species and in accessing canopy habitats mean that these populations are often not included in forest surveys, obviously leaving a large segment of forest diversity unexplored.

From a biomass perspective, lichens were the predominant functional group in the canopy while bryophytes dominated terrestrial habitats. These old-growth sub-boreal spruce forests exhibit conditions intermediate between the high terrestrial bryophyte biomass often observed in boreal forests (e.g., Oechel & Van Cleve 1986) and the high epiphytic lichen and bryophyte biomass observed in temperate rainforests (e.g., Benson & Coxson 2002; McCune 1993; Pike et al. 1977). The sub-boreal spruce forests in this study contained an overall macrolichen and bryophyte biomass of 1700–3300 kg ha⁻¹ of which 28–50% was arboreal lichen biomass and the majority of the remainder was terrestrial bryophyte biomass. These biomass estimates are only slightly lower than the 3500 kg ha⁻¹ of lichen and bryophyte biomass found

in *Abies lasiocarpa* forests in Washington (Rhoades 1981). Lichens and bryophytes in this study accounted for 0.54–1.4% of the total above-ground forest biomass. However, given that the majority of macrolichen and bryophyte biomass is photosynthetic, a comparison between lichen and bryophyte biomass and tree foliar biomass is more telling. This showed lichens and bryophytes to be equivalent to 11.7–20.5% of tree foliar biomass.

Cyanolichens comprised substantial proportions of lichen biomass in both terrestrial and arboreal habitats, though overall, their abundance was much greater in the canopy. Interestingly, a tripartite cyanolichen species (*Lobaria pulmonaria*) dominated arboreal habitats (Campbell & Fredeen 2007) while bipartite cyanolichen species (*Peltigera* spp.) were most common in terrestrial habitats. This pattern may be influenced by moisture as bipartite cyanolichens require more moisture to become photosynthetically active than green algal lichens (Honegger 1991), many of which are able to rehydrate sufficiently from humid air to resume photosynthesis (Lange et al. 1986, 1993). Tripartite cyanolichen species, containing green algal and cyanobacterial photobionts, may have more flexible moisture requirements, giving them greater success in the generally drier arboreal habitat.

While not statistically different, there were trends towards greater abundance of arboreal and terrestrial cyanolichens and terrestrial bryophytes on fine-textured soils and greater abundance of club, shrub and hair chlorolichens (Campbell & Fredeen 2007) on coarse-textured soils. Though both arboreal and terrestrial functional groups appear to be influenced by soil type they are likely responding to different abiotic factors including light, moisture, substrate and nutrient availability. Forests on the fine-textured soils may be more humid due to poorer soil drainage, possibly favoring both cyanolichens and terrestrial bryophytes. Arboreal cyanolichens have been found to be more abundant in wetter forests (Lehmkuhl 2004; Sillett & Neitlich 1996) and *Peltigera* species also often favor wetter sites (Honegger 1991) while hair lichens, particularly *Bryoria* species, are more prevalent in well-ventilated habitats where conditions facilitate the cyclic wetting and drying that is thought to be required for survival

(Goward 2003; Goward & Campbell 2005). There may have been an indirect effect of soil texture on light levels at the forest floor due the significantly more abundant shrubs and herbaceous plants on coarse-textured sites (Botting & Fredeen 2006; Fredeen et al. 2005) resulting in lower light conditions for terrestrial species. As well, CWD pieces were significantly larger on coarse textured stands (Botting & Fredeen 2006), potentially providing more terrestrial habitat. Nutrient differences between these two soil texture types as noted by Arocena and Sanborn (1999) could also affect species composition. All these factors are correlated and are likely acting in concert (McCune 1993) to determine differences in lichen and bryophyte functional group abundance between soil types.

As expected, N contents varied greatly between functional groups, from a minimum of 0.37% N in *Alectoria sarmentosa* (Campbell & Fredeen 2007) to a maximum of 3.98% N in terrestrial bipartite cyanolichens. These results concur with cryptogamic N contents previously reported and the relatively high N contents observed for the cyanolichen functional groups are comparable to previous results. Palmqvist et al. (2002) surveyed 75 lichen species and found lichens with cyanobacteria as the primary photobiont to have the greatest N concentration, followed by tripartite lichens, and then green algal lichens. The ranges of N contents observed in lichens in that boreal forest (chlorolichens 1.1%; tripartite lichens 2.2%; bipartite lichens 3.7%) were comparable to those reported here. Holub and Lajtha (2003) found *Lobaria pulmonaria* to be 2.1% N, similar to the 2.3% N observed in this study.

Bryophyte percent N values were within the range of values found for *Hylocomium splendens* (0.83–1.9%) and *Pleurozium schreberi* (0.74–2.4%) from Alaskan forests (Weber & Van Cleve 1981). Interestingly, there was a difference in the N content of both bipartite and tripartite cyanolichens across habitat types with terrestrial cyanolichens having a higher N content than those from arboreal habitats. However, as the same species were not compared from each habitat, it was not clear whether these differences were due to habitat or species differences. Palmqvist et al. (2002) found similar relative N patterns where

terrestrial bipartite and tripartite *Peltigera* species had higher N contents than the arboreal tripartite *Lobaria pulmonaria*. However, in their study, a terrestrial tripartite *Nephroma* species had lower N content than *Lobaria pulmonaria* indicating that further work is required to determine if terrestrial cyanolichen species accumulate N to greater amounts than their arboreal counterparts. Bryophytes were the only functional group to show disparate N contents across soil types with significantly higher N content in bryophytes on coarse-textured soils. The higher N contents of bryophytes on coarse-textured soils may have been related to higher total N levels in the LF layer (Arocena & Sanborn 1999) as recent evidence suggests that bryophytes may access such pools directly (Ayres et al. 2006). Though Holub and Lajtha (2004) have shown that N can transfer from decomposing lichens to the surrounding moss, the difference in bryophyte N content across soil types cannot be attributed to an N supply from epiphytic or terrestrial cyanolichens as differences in lichen N between site types were not significant. It may be that the greater N contents observed on coarse-textured soils is due to a concentration of available N. That is, total available N may be similar across site types, but is more concentrated in bryophytes on coarse-textured soils due to the smaller bryophyte biomass observed at these sites. The N rich thalli of cyanolichens and the relatively heavy biomass of *Lobaria pulmonaria* in particular (Campbell & Fredeen 2007) meant that although lichens and bryophytes comprised a relatively small proportion of above-ground forest biomass, they provided a proportionally higher contribution to biomass N. Terrestrial lichens also made greater contributions to N, comprising only 0.1% of foliar biomass but 0.3% of foliar biomass N. Similarly, other studies have found that understory vegetation and cryptogams made a greater contribution to nutrient pools, including N, than to above-ground biomass (Hunt et al. 2005; Pike 1978). Terrestrial bryophytes represented 10–25 kg N ha⁻¹; a value comparable to the 13 kg N ha⁻¹ contained in the moss layer in white-spruce boreal forest (Oechel & Van Cleve 1986). However, this presentation of combined epiphytic and terrestrial macrolichens and bryophytes provides a novel insight into the total N contribution of non-vascular species as well the

relative input from each habitat type. In total, terrestrial and arboreal lichens and bryophytes represented 19.7–39.2 kg N ha⁻¹ in this old-growth sub-boreal spruce ecosystem. While this is within the range previously observed for epiphytic lichens in a coastal conifer forest (1.7–27 kg N ha⁻¹; Pike 1978), the large amount of standing N apparently present over fine-textured soils indicates the importance of macrolichen and bryophyte N pools. These pools, particularly from cyanolichen sources, may represent a crucial source of N to old-growth forest systems that are commonly N-deficient (Brockley 2000). Although the N pools are small even compared with terrestrial bryophytes, it is important to consider that unlike vascular and bryophyte N, some proportion of cyanolichen N would not be available to that ecosystem were it not for the N₂-fixing activity of these lichens. These N inputs are made available to the forest system via arboreal lichen leachate (Coxson 1991; Millbank & Olsen 1986) and decomposition (Holub & Lajtha 2004). Terrestrial N₂-fixation by the dominant *Peltigera* species may also be important in promoting decomposition of wood where N may be limiting (Rayner & Boddy 1988) and the elevated soil N observed near *Peltigera* species has been found to increase litter decay rates around the thalli (Knowles et al. 2006). Though not assessed in this study, N₂-fixation by cyanobacterial symbionts with bryophyte species may result in additional N inputs as boreal forest feather moss associations have been found to result in substantial N inputs through N₂-fixation (DeLuca et al. 2002).

In the sub-boreal spruce forests of central British Columbia, macrolichens and bryophytes contribute substantially to forest diversity and combined are more diverse than the vascular plants in these forests. Lichens dominate the arboreal community while bryophytes comprise the majority of terrestrial biomass. The differences in functional group abundance and diversity observed between arboreal and terrestrial habitats are of interest, particularly the pattern of tripartite cyanolichen dominance of the canopy and bipartite dominance of the terrestrial cyanolichen community. In addition, it is clear that the combined arboreal and terrestrial macrolichen and bryophyte communities have the potential to contribute significant amounts of fixed N into the

sub-boreal forests sub-boreal forest ecosystem. Quantification of the rate of N₂-fixation and release of N compounds is needed if their true functional significance in such ecosystems is to be determined.

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