Arboreal lichen diversity and abundance at Aleza Lake Research Forest:

Effect of host tree species and soil type.

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Introduction

The Sub-Boreal Spruce Biogeoclimatic zone of British Columbia is broadly transitional between the true boreal forests to the north and the drier Douglas-fir forests to the south. The coniferous forests are part of a major global vegetation zone stretching across the circumpolar north. As a result many of the lichens of the sub-boreal forest are among the most familiar in the world. While the often-extensive range of many sub-boreal species has resulted in numerous distributional observations, much of the documentation has historically focused on lichens of Eurasia. There is little information about the specific diversity and distribution of lichens within the Sub-boreal Spruce zone of British Columbia. This oversight is particularly true of the wetter reaches of the SBS where the zone abuts the mountains and is influenced by orographic precipitation (Ketcheson et al. 1991). With the increased moisture, stand-replacing disturbance events become increasingly rare, resulting in the conditions that foster well-developed 'oceanic' lichen species assemblages. These assemblages have been documented inland only in the cedar hemlock forests of the Rocky Mountains of central British Columbia (Goward 1993, Radies and Coxson 2004, Campbell and Fredeen 2004). Here we present a unique account of an epiphytic lichen flora, which includes oceanic species, in the Sub Boreal Spruce Biogeoclimatic zone of British Columbia, at the Aleza Lake Research Forest (ALRF). In addition, we present information regarding the abundance and, distribution across soil textures and host tree species for each lichen species observed.

That epiphytic lichens increase in diversity and abundance as a forest attains the characteristics of old-growth is documented in both coastal systems (i.e. McCune 1993, Sillett and Neitlich 1996) and in interior forests (Gauslaa and Solhaug 1996, Lesica et al. 1991, Goward 1994, Campbell and Fredeen 2004). Whether soil substrate characteristics or individual tree species contribute to site-level patterns in species occurrence by facilitating or inhibiting lichen communities is not well understood. Research at ALRF begins to show that coarse-textured soils store larger amount of carbon than fine-textured soils, indicating higher productivity on coarse soils (Fredeen et al. 2005). There is, however, little in the literature to indicate how a positive relationship between soil texture and plant productivity in the sub-boreal forest would translate into changes in the epiphyte communities. In this paper, we investigate differences in lichen species composition and abundance between two soil texture types and two host tree species in an

attempt to elucidate optimal conditions for the development of chlorolichen and cyanolichen communities in the wet SBS forest.

Methods and Materials

<u>Study area description</u>

The study was conducted within the Aleza Lake Research Forest (ALRF), located in central interior British Columbia, approximately 60 km east of Prince George. The research forest is in the wet cool variant of the Sub-Boreal Spruce biogeoclimatic zone (SBSwk1). The area is transitional between drier plateau forests to the 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 receives an average of approximately 345 mm of precipitation per year and has an average summer temperature of 14.8°C (ALRF data). The research forest is vegetated primarily by hybrid white spruce (*Picea engelmannii* x *glauca*) and subalpine fir (*Abies* lasiocarpa). Soils on the research forest are formed from glaciolacustrine parent materials. Coarse-textured soils are predominantly Orthic Humo-Ferric Podzols, and fine-textured soils are a mixture of Orthic Gleyed Luvisols and Orthic Luvic Gleysols (Arocena and Sanborn 1999).

Two old-growth (120-240+ years) sites were selected in each of fine (clay)- and coarse (sand) -textured soils. There was a limited selection of old-growth, coarse–textured sites due to an historic harvesting preference for forests on this soil type. Three 10X10m plots were established near what was determined to be the center of the stand. One spruce and fir tree was identified for arboreal lichen assessments within 5m of each plot centre. Trees that supported a lichen loading that was representative of the rest of the plot canopy were selected. Structural safety was the only other criterion for candidate tree selection. Selected trees were rigged, climbed (Perry 1978) and sampled vertically for epiphyte biomass and species diversity (Campbell et al. 1999).

The canopy was divided into three distinct height zones based on vertical changes in lichen species composition. The upper canopy was characterized by abundant *Bryoria* (particularly non-sorediate species) and the absence of cyanolichens, the middle canopy by the presence of cyanolichens other than *Lobaria pulmonaria,* and the lower canopy by the presence of *L. pulmonaria*, and the general absence of most other cyanolichens. The branch bearing the most epiphyte species in each height zone was selected and removed for species identification in the lab. A 2X6cm grid was used to measure the colonisable surface area of the branch and the surface

area of each lichen species encountered. Species abundances were recorded as a percentage cover of the branch area.

Results

Forty cryptogrammic species (or species assemblages) were observed in the canopy at the Aleza Lake Research Forest. Of these, 9 species and 2 species assemblages (sorediate and non-sorediate *Bryoria*) were fruticose (hair) lichens, 20 were foliose chlorolichens, 8 were foliose cyanolichens and 1 was a bryophyte (Table 1). These species were observed in the canopy within distinct vertical zones. Hair lichens and foliose chlorolichens were present throughout the canopy while foliose cyanolichens were limited to the lower canopy.

Hair Lichens

Hair lichens were generally more abundant over sand than clay and were found more frequently on spruce branches than on fir (Figure 1), only two species (or species groups) showed significant differences across soil and tree species. Non-sorediate *Bryoria* was significantly more abundant in spruce over sand relative to all other sites ($F_{(4, 57)}=2.66$, $p=0.041$, Figure 1a) and *Usnea filipendula* was observed more often over sand than over clay regardless of tree species ($F_{(7,54)}=2.62$, $p=0.021$, Figure 1b).

Foliose chlorolichens

Foliose chlorolichens, as a group, were found on every branch in the study with *Hypogymnia occidentalis, H. physodes, Parmelia sulcata* and *Platismatia glauca* comprising the bulk of the observations. When the functional group is broken down to the species level, some differences across soil and tree species are evident. *Parmelia sulcata* and *Platismatia glauca* were also more prevalent over sand than clay ($F_{(11, 50)}=4.28$, $p<0.000$, Figure 2a) and significantly more abundant in fir than spruce ($F_{(11, 50)}=2.96$, $p=0.004$). *Melanelia* species were entirely absent from clay sites while regularly present over sand. Over sandy soils, *M. exasperatula* and *M. subelegantula* were significantly more abundant in fir than in spruce (Mann Whitney U (18)= 99.00, $p=0.046$; Figure 2b).

Cyanolichens

Cyanolichens were unique in that, unlike all other species groups, they were almost invariably more abundant in fir trees over clay soils than in all other tree/soil combinations. While this effect

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was observed with all species except the tripartite cyanolichen *Lobaria pulmonaria,* significant differences were noted only for *Nephroma isidiosum* ($F_{(1, 673.8)}=7.51$, $p=0.008$), and *Sticta fuliginosa* ($F_{(1, 202.5)}=5.09$, $p=0.027$)*. Lobaria pulmonaria,* which appeared to be equally abundant across all habitat types, was also exceptional with respect to significantly larger abundance observed across all trees in the study. While all other cyanolichens were observed with branch coverage ranging from 0.6 cm^2 (*Sticta fuliginosa* in spruce over clay) to 16.9 cm^2 (*Pseudocyphellaira anomala* in fir over clay), *L. pulmonaria* coverage ranged from 155.3 cm^2 (in fir over sand) to 373.7 cm^2 (in spruce over clay; figure 3).

Discussion

There were 40 cryptogamic species found in the canopy of the spruce and fir dominated old-growth forests at the Aleza Lake Research Forest. Only one byrophyte, *Orthitricum* spp., was observed and only in the lower canopy of fir trees over sandy soils. No conclusions may be drawn from the absence of this group from clay soils and spruce trees as it must, in the context of this study, must be attributed to the rarity of bryophytes in the canopy of interior forests in general.

By contrast, there were observable differences in the habit of many of the 39 lichen species observed at the ALRF across soil texture and host tree species. There were significant differences in the abundance of hair and foliose chlorolichens across soil types, with both species groups being more abundant over sand than clay soils. Where the two chlorolichen species groups differed was with respect to abundance patterns across host tree species. Hair lichens, specifically *Bryoria* species, were found to be significantly more abundant over spruce than fir trees. The significance of the interaction of soils and tree species with respect to *Bryoria* spp. abundance may be explained by examining the physical characteristics of the spruce-fir canopy. The canopy at ALRF is essentially two-tiered with emergent spruce trees over a largely fir main canopy. Fir trees tend are, on average, 26m tall, while the intermixed spruce trees (over sandy soils) are generally often more than 30m tall. As a result, the habitat in the upper spruce canopy is exposed to higher winds and more intense solar radiation than in the adjacent fir trees. These climatic factors contribute to desiccating conditions for the supported epiphytes. *Bryoria* spp. are understood to require frequent wetting-drying cycles to maintain a balance of the symbionts (Goward 1998, Campbell and Coxson 2001) and as such tend to thrive in upper canopy environments. This is particularly the case with non-sorediate *Bryoria* spp., which reproduce

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through fragmentation and therefore tend to become super abundant in habitats where exposure to wind allows thallus threads to fragment and blow to new habitats (Goward and Campbell, submitted to the Bryologist). It is likely that the significantly larger abundance of non-sorediate *Bryoria* spp. in spruce over sand is attributable to the more favourable environment afforded in these trees relative to the neighbouring fir.

Few significant patterns in the abundance of the foliose chlorolichen species could be identified. While several foliose chlorolichen species (*Melanelia* spp., *Platismatia glauca,* and *Parmelia sulcata)* were observed more frequently in fir trees than spruce over course-textured soils, no patterns emerged with respect to host tree species for the foliose chlorolichen functional group as a whole. These observations indicate that "other lichen" (McCune 1993) or "foliose" (Campbell et al. 1999) functional group may not be a useful species grouping when evaluating distribution patterns within the canopy at ALRF.

Distribution patterns across soil type and host tree species were much more marked for the cyanolichens than for chlorolichen species. Cyanolichens can be separated into two distinct groups; the bipartite cyanolichens that have a cyanobacterium (generally nostoc) as the primary photobiont, and the tripartite cyanolichens where the primary photobiont is a green alga and the cyanobacterial partner is found in discrete cephalodium within the fungal-algal matrix. This distinction is important to make for the epiphyte communities at ALRF because the two groups exhibit very different patterns with respect to soil type and host tree species. The abundance of *Lobaria pulmonaria*, the tripartite cyanolichen, was consistently more than double that of any other cyanolichen regardless of soil type or host tree species. The predominance of *Lobaria pulmonaria* may be attributable to the unique symbiotic arrangement of tripartite cyanolichens. Possession of both the nitrogen fixing capabilities of other cyanolichens, and the tolerance for variable environmental conditions exhibited by chlorolichen species may facilitate establishment in areas where environmental conditions would not support species with a cyanobacterial primary photobiont. This could provide a competitive advantage allowing the species to effectively colonize varied environments. This, coupled with some level of competitive exclusion that invariably would result from the large, leafy and loosely attached morphology of the species, would account for the great abundance of *L. pulmonaria* observed at ALRF regardless of soil type or host species.

The same level of ubiquity was not observed with the bipartite cyanolichens. The presence of these "oceanic" species (Goward 1993) at ALRF was unexpected. They are thought to have originated from coastal forests, and were only recently documented within inland forests (Goward 1993). Even so, the inland range was thought restricted to the Interior Cedar Hemlock biogeoclimatic zone where orographic precipitation creates appropriate climatic conditions (Ketcheson et al. 1991). This report therefore represents a novel documentation of a unique lichen species assemblage.

Within the ALRF, bipartite cyanolichens were found with much greater abundance over clay soils, and more particularly in fir trees within those sites. These species are understood to require liquid water to become photosynthetically active (Budel and Lange 1991, Lange et al. 1985, 1993). Therefore, unlike chlorolichens, which may respond to water vapour, cyanolichens generally inhabit areas of relatively high humidity (Goward 1994, Sillett and Neitlich 1996). These conditions would likely be satisfied in the two-tiered ALRF canopy where the lower canopy branches of fir trees are protected from the atmospheric conditions not only by the upper branches, but also by the emergent spruce trees. In addition, the lower spruce canopy is commonly devoid of large, corticated branches and is therefore probably unable to support the abundant cyanolichen colonization observed in fir trees.

More striking than differences across host tree species, was the difference in bipartite cyanolichen diversity across soil types. There were more bipartite cyanolichen thalli observed on branches from clay sites than sand sites irrespective of host tree species. This observation may provide support for the theory that these species are responding to zones of localized nutrient enrichment (Goward and Arsenault 2000). The contribution of soil substrate characteristics to epiphyte species occurrences is not well understood. Loppi et al (1999) showed a strong correlation between the elemental composition of the forest soil and that of the epiphytic lichens above. This may be explained by a 'nutrient conduit' effect whereby nutrients are drawn from the soil and dripped onto branches supporting epiphytic lichens (Goward and Arsenault 2000). This "nutrient conduit" may be dependent on soil texture as different soil types have disparate abilities to retain nutrients. Fine-textured (clay-rich) soils have a greater cation-exchange capacity than coarse-textured (sandy) soils, and might be expected to enrich vegetation in these cations (Kimmins 1997, Bracy and Weil 2004). Our observations of greater cyanolichen diversity over clay soils may be consistent with Goward and Arsenault's observations (2000), but it is clear that

further research is required to elucidate the causal environmental factors, the pathway, and the epiphytic response to any such process of nutrient enrichment.

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Figure 1. The abundance of common (A) and infrequently observed (B) hair chlorolichen species at the Aleza Lake Research Forest. The average branch cover (cm^2) is given for each tree species/soil type combination.
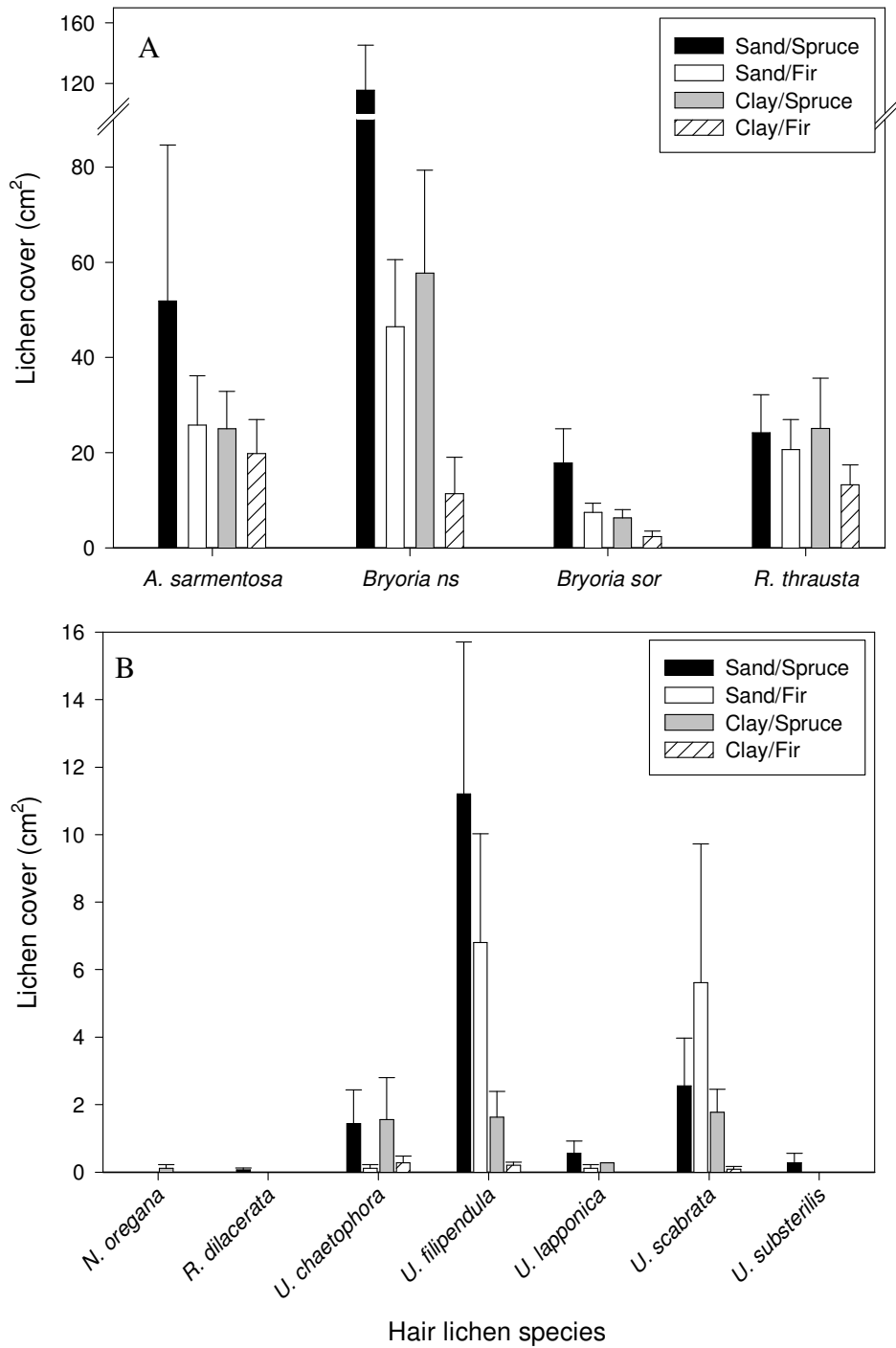
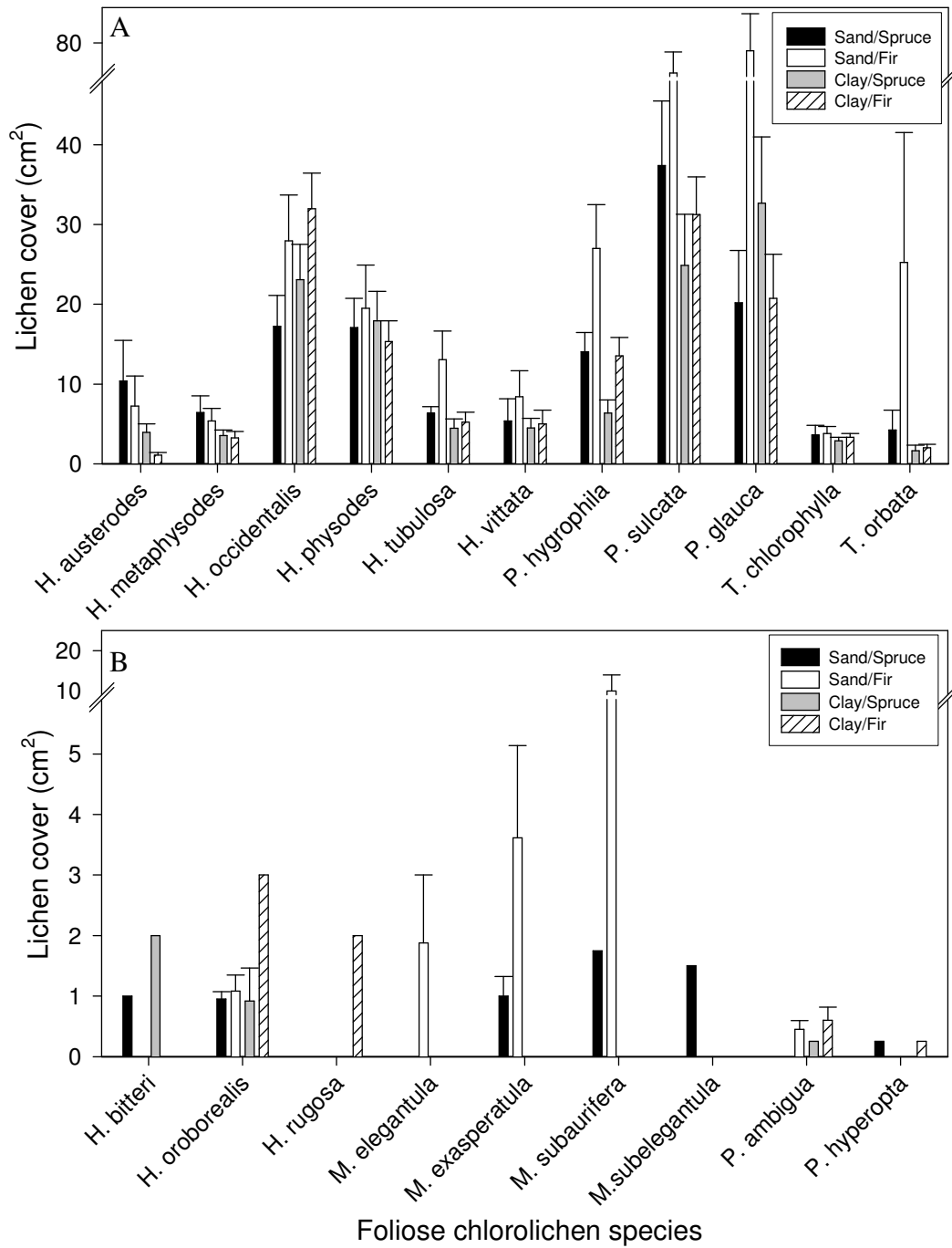Figure 2. The abundance of common (A) and infrequently observed (B) foliose chlorolichen species at the Aleza Lake Research Forest. The average branch cover (cm^2) is given for each tree species/soil type combination.
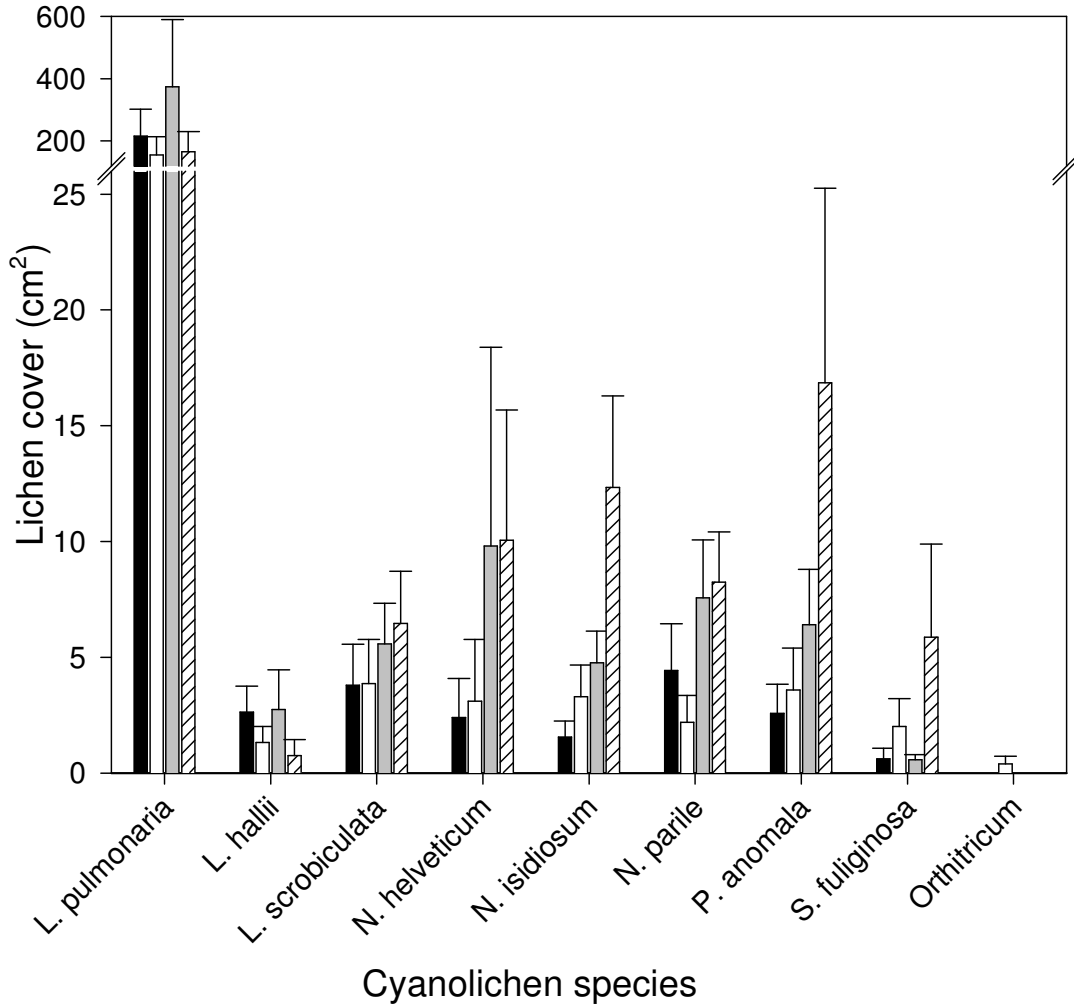
Figure 3. The abundance of foliose cyanolichen species at the Aleza Lake Research Forest. The average branch cover (cm^2) is given for each tree species/soil type combination.

Table 1. Fruticose lichens, foliose chlorolichens and foliose cyanolichens observed at low, middle and high canopy heights in spruce and fir trees over sand and clay soils at the Aleza Lake research forest. *Bryoria* was identified to broad sorediate and non-sorediate species groups. Abundance is recorded as the mean surface area (cm2) across the 6 trees in each experimental group.

	Sand/Picea			Sand/Abies			Clay/Picea			Clay/Abies		
	up	mid	low	up	mid	low	up	mid	low	up	mid	low
Fruticose Lichens												
Alectoria sarmentosa	1.50±0.34	16.67±6.78	220.00±90.72	1.00	23.25±12.30	92.50±24.05	2.50±0.87	29.92±11.82	52.22±18.65	2.50±1.06	15.00±4.74	47.75±16.18
Bryoria non-sorediate	223.40±60.38	125.20±51.18	42.00±22.64	80.20±17.67	57.50±36.08	22.75±3.45	121.8±65.08	66.60±31.25	16.17±6.23	32.70±26.85	8.50±1.85	2.67±1.33
Bryoria sorediate	11.75±5.71	12.50±4.26	39.8±20.13	5.20±2.87	10.92±3.12	10.75±5.59	5.25±2.75	10.20±4.62	10.50±1.56	1.56±1.48	73.31±4.30	2.75±0.80
Nodobryoria oregana	0	0	0	0	0	0	0	0	2.00	0	0	0
Ramalina dilacerata	0	1.00	0.25	0	0	0	0	0	0	0	0	0
R. thrausta	3.25±1.03	29.83±8.34	40.67±20.39	7.50±0.50	24.21±10.01	35.33±13.85	6.50±3.50	31.50±13.33	78.25±34.76	8.50±0.50	27.20±3.41	28.58±18.31
Usnea filipendula	1.08±0.51	26.58±11.03	9.75±3.82	1.25±0.75	7.00±2.28	28.33±14.45	0.25	6.00±0.00	5.67±3.18	0.25	0.50	1.00±0.00
U. scabrata	0	4.50±1.50	18.50±1.50	4.50±1.50	0	46.00±27.00	1.50±0.50	4.00±0.00	7.00±1.53	0	0	1.50
U. chaetophora	0	13.00±1.00	0	0	0	2.00	0	0	14.00±8.00	0	2.00	3.00
U. lapponica	2.00±1.00	6.00	0	0	0	2.00	5.00	0	0	0	0	0
U. substerilis	0	5.00	0	0	0	0	0	0	0	0	0	0
Foliose chlorolichens												
Hypogymnia austerodes	1.00	18.75±3.75	3.00	0	7.25±3.75	0	0	3.88±1.34	4.00±2.00	1.00	1.00	1.13±0.88
H. bitteri	0	0	1.00	0	0	0	0	0	2.00	0	0	0
H. metaphysodes	9.94±5.26	5.90±1.23	0.63±0.38	1.38±0.43	9.08±3.08	3.75±0.92	3.19±1.11	3.69±1.31	4.00±1.50	1.87±0.13	5.08±1.56	2.33±0.88
H. occidentalis	11.85±5.39	22.71±6.91	16.00±8.11	22.70±9.01	48.17±10.30	12.08±1.99	18.92±4.11	37.58±10.13	12.75±3.89	24.80±7.51	40.25±8.67	29.71±6.57
H. oroborealis	0.75±0.25	1.00±0.00	1.25	1.00	0.92±0.55	1.38±0.13	0.50	1.13±0.88	0	0	3.00	0
H. physodes	11.90±2.85	23.79±7.83	13.44±5.38	9.79±2.30	42.71±11.36	6.00±0.97	18.71±4.84	26.25±8.15	6.95±1.67	11.10±3.25	21.13±5.08	13.08±4.15
H. rugosa	0	0	0	0	0	0	0	0	0	2.00	0	0
H. tubulosa	5.70±1.69	7.54±1.25	5.38±1.07	5.40±0.68	28.50±6.51	3.96±0.99	4.90±0.29	5.25±1.28	2.63±0.47	2.87±0.42	8.25±2.98	3.79±0.62
H. vitatta	1.00	3.00	8.75±4.75	0	8.42±3.25	0	1.00	2.50±0.50	7.00±0.58	0.75±0.25	7.63±3.44	4.33±1.30
Melanelia elegantula	0	0	0	0	0	10.50	0	0	0	0	0	0
M. exasperatula	0.75	1.50±0.5	0.38±0.13	0.75	0	3.00	0	0	0	0	0	0
M. subelegantula	0	1.50	0	0	0	0	0	0	0	0	0	0
M. subaurifera	0	1.75	0	7.00±5.05	2.65±1.59	1.83±0.83	0	0	0	0	0	0
Parmelia hygrophila	3.00±2.00	18.67±3.66	12.90±2.53	8.50±5.30	42.10±11.44	23.63±4.02	1.20±0.44	11.83±3.34	5.13±1.62	2.25±0.78	17.79±3.67	16.79±2.29
P. sulcata	16.92±4.92	65.33±16.40	30.00±10.94	28.92±8.16	104.17±24.39	58.50±7.63	24.86±6.42	46.08±15.76	18.00±4.08	14.85±2.51	42.58±8.11	33.58±7.71
Parmeliopsis ambigua	0	*0*	0	0.38±0.13	0.63±0.38	0.25	0.25	0	0	0.25±0.00	0.75±0.50	1.00
P. hyperopta	0.25	*0*	0	0	0	0	0	0	0	0	0.25	0.25
Platismatia glauca	3.19±1.65	25.17±14.91	26.58±8.11	2.55±0.75	87.71±32.19	124.50±34.62	3.79±1.74	47.75±12.30	49.20±18.10	1.85±0.47	22.63±0.22	34.63±9.55
T. chlorophylla	1.94±0.54	6.17±2.93	2.21±0.47	1.42±0.51	6.10±1.63	2.90±0.82	4.30±1.04	2.92±0.44	1.67±0.30	3.70±0.70	4.38±0.91	1.88±0.53
T. orbata	11.56±7.26	1.30±0.22	0.56±0.24	2.67±1.30	5.60±1.80	0.81±0.48	2.75±1.47	0.60±0.22	1.00	1.90±0.66	2.79±0.73	0.58±0.17
Foliose cyanolichens												

Lobaria hallii	0.50	9.75±2.74	4.00±1.00	0	5.58±2.53	7.00	0	4.75±3.25	13.33±8.51	0	6.75±5.75	0
L. pulmonaria	0	105.80±78.96	559.21±189.26	0	47.05±37.93	426.70±111.05	0.25	119.95±57.79	1021.00±586.80	0	6.05±2.26	11.42±101.49
L. scrobiculata	0	7.71±3.54	22.00	0	13.65±0.65	0.75±0.25	0	10.79±3.24	8.94±3.75	0.25	7.96±2.84	11.42±5.47
Nephroma helveticum	0	3.25±2.75	12.25±8.92	0	2.67±1.20	48.00	0	3.50	34.60±30.26	0	2.00	29.38±14.33
N. isidiosum	0	2.81±1.21	8.38±0.88	0	6.75±2.96	10.83±4.62	0	8.70±1.95	10.56±2.67	2.00	2.00±8.11	20.00±7.80
N. parile	0	4.30±1.07	14.56±7.26	0	7.50±2.75	17.00	0	16.15±5.41	13.88±4.87	0.25	11.50±4.63	13.21±2.47
Pseudocyphellaria anomala	0	7.88±4.63	10.25±4.50	0	9.50±5.53	8.75±6.71	0	15.69±7.76	13.13±3.00	0	13.08±8.13	37.50±22.53
Sticta fuliginosa	0	5.50±2.50	0	0	7.25±3.59	0	0	2.08±0.58	2.00±0.00	0	16.80±7.99	3.63±1.02
Bryophytes												
Orthitricum spp.	0	0	0	0	0.25±0.00	3.38±2.63	0	0	0	0	0	0