LICHEN AND BRYOPHYTE DIVERSITY, NITROGEN AND CO_2 EXCHANGE FROM SUB-BOREAL SPRUCE FOREST FLOORS IN CENTRAL BRITISH COLUMBIA

by

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Abstract

The structure, composition and functions of a terrestrial moss, liverwort and lichen community were examined for sub-boreal spruce forests in central British Columbia. The diversity and abundance of bryophytes and lichens were assessed in two ages of forest (old-growth and young second-growth) and two soil texture types (fine and coarse textured). Major differences in species composition were found between forest ages with 30% of species found only in old-growth and 21% found only in second-growth. Different moss and lichen species dominated old-growth and second-growth forest and there was more lichen cover in second-growth. Liverworts were more diverse and abundant in old-growth with 96% of the recorded liverwort cover occurring there. The dominant mosses and lichens had carbon contents of 41 - 48% and nitrogen contents of 0.56 - 3.98%. Instantaneous chamber-based CO_2 exchange measurements (at 430 and 700 μmol mol^{-1} CO_2) were used in conjunction with seasonal microclimate data to model net ecosystem CO_2 exchange (NEC) from old-growth forest floor. Over three months, moss-dominated forest floor had an NCE of -33.8 g C m^{-2} and lichen-dominated logs had an NCE of -42.9 g C m^{-2}. Moss photosynthetic response increased at the elevated CO_2 concentration while lichen photosynthesis was not affected. When summed over the moss, lichen, bare wood and bare litter components of the forest floor for the three month season, old-growth forest floor lost -31.4 g C m^{-2}. This thesis outlines the diversity, nitrogen and carbon contents, and CO_2 exchange characteristics of terrestrial lichens and bryophytes in sub-boreal spruce forests.

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Chapter 1

Introduction

Introduction

Terrestrial bryophytes and lichens are a significant component of the forest floor community in many forest ecosystems. Though often overlooked, the forest floor can include a great diversity of non-vascular species and lichens which play important roles in carbon and nutrient uptake and storage. In the Sub-Boreal Spruce biogeoclimatic zone of central British Columbia, there have been few studies examining the diversity as well as the carbon and nitrogen dynamics of terrestrial mosses, liverworts, and lichens.

Lichens, mosses and liverworts

Lichens and bryophytes (mosses, liverworts, and hornworts), often referred to collectively as cryptogams, exhibit many ecological and physiological similarities. They inhabit a similar range of habitats, from wetlands to rock surfaces to tree canopies, and often coexist (Brodo et al. 2001, Schofield 2002). However, lichens and bryophytes are taxonomically very different with bryophytes being non-vascular plants and lichen being a symbiosis between fungi and either algae and/or cyanobacteria (Green and Lange 1995). There are approximately 1100 species of lichen (Goward et al. 1994), 220 species of liverwort (Schofield 1992), and over 600 species of moss (Schofield 1976) reported to occur in British Columbia.

Lichens are composed of a fungal partner (mycobiont) and a green algal and/or cyanobacterial partner (photobiont) (Ahmadjian 1993). The photobiont supplies the mycobiont with carbohydrates from photosynthesis and, if cyanobacterial, nitrogen from atmospheric N_2-fixation while the mycobiont provides a hospitable habitat, structure and nutrients for the photobiont (Palmqvist 2000). By contrast, mosses and liverworts are leafy or thalloid green non-vascular plants which lack roots and a vascular system. The gametophyte is the dominant stage with a sporophyte (if present) attached to the gametophyte (Schofield 1992).

Both lichens and bryophytes are poikilohydric, meaning that their moisture status depends largely upon the moisture available in their environment (Green and Lange 1995). Lacking roots and stomata and with limited cuticles, exchange of nutrients and water occurs over the entire lichen or bryophyte surface (Palmqvist 2000, Turetsky 2003). Some green algal lichens can take up sufficient moisture from humid air to reactivate photosynthesis while cyanobacterial lichens require additional liquid water (Lange et al. 1986, Lange et al. 2001). Moisture availability often limits the productivity and distribution of lichens and bryophytes (Green and Lange 1995, Palmqvist 2000). In general, bryophytes are more common in wetter environments while lichens dominate in drier environments (Green and Lange 1995).

Lichens and bryophytes play an important role in nutrient uptake and release in forest systems (Oechel and Van Cleve 1986). Both lichen and bryophytes take in nitrogen and other nutrients through wet and dry deposition and from canopy throughfall thus retaining nutrients that might otherwise have been lost to the forest

system (Bates 2000, Palmqvist et al. 2002). Charged cell walls may increase the nutrient uptake efficiency in bryophytes (Sveinbjörnsson and Oechel 1992). Lichen species with cyanobacterial photobionts are capable of atmospheric N_2-fixation and some moss and liverworts form associations with N_2-fixing cyanobacteria (DeLuca et al. 2002, Palmqvist et al. 2002, Turetsky 2003). N_2-fixation from lichen and bryophyte communities can contribute significant quantities of nitrogen to forests and disturbed systems (DeLuca et al. 2002, Knowles 2004). Nutrients and carbon are released as pulses of leachate during rewetting events and during bryophyte and lichen decomposition and supply previously inaccessible nutrients to the ecosystems (Wilson and Coxson 1999, Knowles 2004). Lichens and bryophytes are important components of primary and secondary succession, stabilizing the soil, reducing fluctuations in soil temperature and moisture regimes, and contributing to organic matter build up (Sveinbjörnsson and Oechel 1992, Oechel and Van Cleve 1986). Though they may comprise a small proportion of forest biomass, lichens and bryophytes can play important roles in forest dynamics.

Relationships between forest age, soil texture, and lichen and bryophyte diversity

Forest harvesting is a major anthropogenic disturbance affecting sub-boreal spruce forests in central British Columbia. A recent study suggested that there was between 2.5-47% (depending on sub-zone) of old-growth forest remaining in the sub-boreal spruce biogeoclimatic zone (Burton et al. 1999). Forest harvesting has been cited to have caused the greatest decline in bryophytes worldwide (Christy

1992). In British Columbia, forest harvesting has also been identified as a threat to bryophyte and lichen diversity (Goward 1994, Ryan 1996). The impacts of logging in sub-boreal spruce forests on terrestrial moss, lichen or liverwort diversity have not been assessed. More complete inventories of diversity, including above- and below-ground flora and fauna, are needed in order for biodiversity considerations to be incorporated into management decisions (Burton et al. 1992).

Forest harvesting affects terrestrial bryophyte and lichen communities through changes to substrate and microclimate and through habitat fragmentation. In managed stands, the canopy is more structurally homogeneous, features such as snags are rare (Wells et al. 1998), and the quality and quantity of terrestrial substrates are commonly altered (Lesica et al. 1991, Frisvoll and Presto 1997). Changes to humidity, light, temperature, and nutrient regimes may create microclimate conditions unsuitable for many bryophyte and lichen species (Saunders et al. 1991, Frisvoll and Presto 1997, Renhorn 1997). As well, there are concerns about the ability of some bryophytes and lichens to disperse and recolonize disturbed areas (e.g. Dettki et al. 2000, Sillett et al. 2000, Fenton and Frego 2005).

Several studies in Europe and North America have found moss and liverwort diversity to be greatest in old-growth forests (Söderström 1988, Lesica et al. 1991, Crites and Dale 1998, Rambo and Muir 1998, Newmaster et al. 2003). Liverwort species can be particularly restricted to old-growth conditions and may be dependent upon specific substrates such as coarse woody debris of certain decay classes (Crites and Dale 1998, Rambo and Muir 1998). Epiphytic lichen

communities have been shown to be richer in old-growth forests (Goward 1994, Selva 1994, Renhorn 1997) and in a boreal forest study, different assemblages of terrestrial lichen species were found in old-growth compared with second-growth forest (Crites and Dale 1998).

Forest soil texture affects soil drainage and nutrient status and can affect the productivity and composition of forest communities. The effects of soil type on the composition of vascular plant communities have been documented for sub-boreal spruce forests (e.g. Meidinger and Pojar 1991, OES 1995, DeLong 2003). However, the effects of soil texture type on the diversity and abundance of terrestrial lichens and non-vascular plants in sub-boreal regions of BC has not been well examined.

CO_2 exchange from bryophyte and lichen forest floor communities

Forest ecosystems will be affected by global climate change and elevated atmospheric CO_2 levels due to anthropogenic CO_2 inputs. In the face of these changes, there has been increased interest in quantifying the carbon stocks held in forest ecosystems and the dynamics of these forest carbon pools. The forest floor can play an important role in carbon storage in some forest ecosystems. Mosses store 10-50% of the gross CO_2 uptake of a black spruce forest (Goulden and Crill 1997) and may take up 35% of the forest floor CO_2 efflux (Swanson and Flanagan 2001). The contribution of bryophytes and lichens to net ecosystem CO_2 flux in the sub-boreal spruce forest ecosystem has not been quantified.

Bryophyte and lichen photosynthesis and respiration rates are largely influenced by the surrounding microclimatic conditions (Palmqvist 2000, Turetsky

2003). In particular, moisture, temperature, and light conditions can limit photosynthesis and respiration. The metabolic capacity of lichens and bryophytes is often limited by the amount of time with sufficient moisture content (Palmqvist and Sundberg 2000, Turetsky 2003). In the understory of a forest ecosystem, the light environment tends to be patchy with periodic sunflecks providing high intensity light in an otherwise shaded environment (Chazdon and Pearcy 1991, Pearcy and Pfitsch 1995). For this reason, light levels often limit photosynthesis even when moisture levels are sufficient. Extremely high or low temperatures can also affect photosynthesis (Palmqvist 2000). Soil and wood respiration levels have been found to be largely controlled by temperature and also by moisture levels (e.g. Rayment and Jarvis 2000, Swanson and Flanagan 2001).

It is not known what impact increasing CO_2 concentrations in the atmosphere will have on lichens and bryophytes. Some mosses appear to be CO_2 limited at ambient levels and may increase growth with increasing CO_2 (Green and Lange 1995). The trend for lichens is less clear and ability of lichens to respond to elevated CO_2 may vary with moisture status. High moisture contents can impede CO_2 diffusion into some lichen thalli (Cowan et al. 1992, Green and Lange 1995, Lange et al. 1996). The forest floor may already experience an elevated CO_2 environment due to its proximity to the respiring soil layer below (Sonesson et al. 1992, Tarnawski et al. 1994, Coxson and Wilson 2004). This elevated CO_2 environment may result in higher bryophyte and lichen productivity in light and moisture limited environments at the forest floor (Sonesson et al. 1992).

Objectives

This thesis addresses three primary objectives pertaining to the diversity, carbon and nitrogen contents, and CO_2 exchange of terrestrial bryophytes and lichens in sub-boreal spruce forests.

Objective 1: To quantify and compare the relationships between both forest age and underlying soil texture type and the diversity and abundance of terrestrial moss, liverwort, and lichen species in sub-boreal spruce forests.

Experimental approach:

Eight study sites were established, two in each of old-growth (>200 years) and young second-growth forest (15 years) on fine and coarse textured soils. Diversity information was collected in a series of eight 1 m^2 quadrats at each of the three plots at each study site. All moss, liverwort and lichen species were recorded along with their percent cover and the primary substrate they were growing on. Forest stand, vegetation, and coarse woody debris attributes were characterized for each plot. A series of ANOVAs was used to compare species diversity, species cover, species substrate use, and environmental conditions between sites, forest ages, and soil texture types. Overall bryophyte and lichen community composition patterns were analysed using Nonmetric Multidimensional Scaling ordination (Kruskal 1964, Mather 1976).

Objective 2: To quantify the percent nitrogen and carbon contents of the most common bryophyte and lichen species and to determine the contribution of terrestrial bryophytes and lichens to old-growth and young second-growth sub-boreal spruce forest carbon and nitrogen pools.

Experimental approach:

Biomass samples of representative bryophyte and lichen species were collected from old-growth (7 genera) and young second-growth (6 genera) forest sites on coarse and fine textured soils. The percent nitrogen and carbon content of these species was determined using an NA 1500 Elemental Analyzer. Biomass carbon and nitrogen on the landscape was extrapolated using the percent carbon and nitrogen contents, the biomass data and the percent cover data collected in objective 1. Biomass carbon from the forest floor was compared with the biomass carbon of other components of the forest ecosystem (Fredeen et al. 2005).

Objective 3: To model the net ecosystem CO_2 exchange of moss and lichen dominated forest floor at ambient and elevated CO_2 concentrations and quantify the seasonal forest floor net ecosystem CO_2 exchange of an old-growth sub-boreal spruce forest ecosystem.

Experimental approach:

Between June and October 2003, microclimate information including moss, lichen, soil, and air temperatures, moss and lichen moisture contents, and light

levels were continuously collected from two sites in old-growth forest on fine textured soils. Over the 2004 growing season, chamber-based gas exchange measurements were made at the two sites at a series of permanent collars installed over the moss *Rhytidiadelphus triquetrus* growing on soil, the lichen *Peltigera membranacea* growing on wood, bare soil and bare wood. Using a clear custom chamber and a Li-Cor LI 6400 photosynthesis system, instantaneous net ecosystem CO_2 exchange measurements were made in conjunction with instantaneous microclimate measurements and used to create multiple regression models relating the two. Seasonal net ecosystem CO_2 exchange for the forest floor of an old-growth sub-boreal spruce forest was modeled for 2003 using the continuous seasonal microclimate data and the multiple regression models of 2004.

Organization of the thesis

This thesis has five chapters including this introduction chapter, three main chapters and a concluding chapter. Each of the main chapters describes a different aspect of the terrestrial lichen and bryophyte community of a sub-boreal spruce forest. Chapter 2 entitled, *Contrasting terrestrial moss, lichen and liverwort diversity and abundance between old-growth and young second-growth forest and two soil texture types in central British Columbia,* addresses the species diversity and abundance comparisons outlined in objective 1. Chapter 3, *Carbon and nitrogen contributions from terrestrial bryophytes and lichens for a sub-boreal spruce forest*, looks at carbon and nitrogen content and biomass as set out in objective 2. Chapter 4 entitled, *Net ecosystem CO_2 exchange from the forest floors of old-growth sub-*

boreal spruce forests, examines the measurement and modeling of net ecosystem CO_2 exchange from the forest floor as outlined in objective 3.

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Chapter 2

Contrasting terrestrial moss, lichen and liverwort diversity and abundance between old-growth and young second-growth forest and two soil texture types in central British Columbia

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Abstract

The diversity and abundance of terrestrial lichens, mosses and liverworts were surveyed and compared between two ages of forest (old-growth and young second-growth) on two dominant soil types (fine and coarse textured soils) in sub-boreal spruce forests in central British Columbia. Major differences in species composition were found between forest ages, with 30% of species found only in old-growth forest and 21% found only in young second-growth forest. Liverworts were much more common in old-growth sites with half the liverwort species found exclusively in old-growth, and 90% of the recorded liverwort observations occurring there. Different moss species assemblages dominated old-growth and second-growth sites, with much of second-growth sites covered by *Polytrichum juniperinum*. Young second-growth forest had higher cover of lichen species than old-growth forest. Lichens and bryophytes used different terrestrial substrates in each forest age with higher cover of mosses and lichens occurring on woody substrates in old-growth, irrespective of substrate availability. Nonmetric Multidimensional Scaling ordination clearly separated plots by forest age and also showed soil texture to be a defining variable. Though not statistically significant, there was increased bryophyte diversity on coarse textured soils and increased lichen cover on fine textured soils.

Introduction

Forest harvesting is a major industry in British Columbia and has been identified as a threat to bryophyte and lichen diversity (Goward 1994, Ryan 1996). Forest harvesting in the form of clearcut logging affects terrestrial bryophyte and lichen communities through disturbance, changes in substrate and microclimate, and through habitat fragmentation (Lesica et al. 1991, Fenton et al. 2003). In managed stands, the stand is more structurally homogeneous and even-aged while features such as old trees and snags are rare (Wells et al. 1998). The quality and quantity of terrestrial substrates can be altered, particularly the amount and type of coarse woody debris and the amount of exposed mineral soil (Lesica et al. 1991, Frisvoll and Presto 1997). Microclimate changes including reduced humidity, increased light and temperature, and altered nutrient regimes may create unsuitable conditions for many bryophyte and lichen species (Saunders et al. 1991, Frisvoll and Presto 1997, Renhorn 1997). Habitat fragmentation can reduce the probability of a species dispersing into a disturbed area and the dispersal of propagules is potentially a limiting factor in the reestablishment of bryophyte and lichen species in second-growth forests (Dettki et al. 2000, Sillett et al. 2000, Fenton and Frego 2005).

Logging is widespread in the Sub-Boreal Spruce biogeoclimatic zone (SBS) in central British Columbia. A recent study suggested that some biogeoclimatic sub-zones have 47% old-growth forest remaining, while others have as little as 2.5% remaining (Burton et al. 1999). Neither the effects of extensive forest management on lichen and bryophyte species in sub-boreal spruce forests, nor whether these

effects are uniform across all types of forest stand are well documented. Studies in other areas of North America and Europe have shown bryophyte diversity to be greatest in old-growth forests (Söderström 1988, Lesica et al. 1991, Crites and Dale 1998, Rambo and Muir 1998, Newmaster et al. 2003). Liverwort species appear to be particularly restricted to old-growth conditions and may be dependent upon certain substrates found there, including coarse woody debris of particular decay classes (Söderström 1988, Lesica et al. 1991, Crites and Dale 1998, Newmaster et al. 2003). Epixylic liverwort species diversity may be greatest on intermediate and more decayed logs (Crites and Dale 1998, Rambo and Muir 1998, Rambo 2001). Epiphytic lichen species have shown specificity to old-growth conditions in other areas of Canada and epiphytic lichen communities may become richer over time (Goward 1994, Selva 1994, Campbell and Fredeen 2004). In a mixedwood boreal forest study, terrestrial lichen species were found to show different species assemblages in old-growth forests than in second-growth forests (Crites and Dale 1998). To date, no similar studies have been performed in sub-boreal spruce forests. As well, this study compares old-growth forest with younger second-growth forest (15 years old) than most of the studies cited above (>50 years old) in order to examine the influence of forest harvesting on cryptogam species diversity earlier in forest succession.

Two major soil texture types underlie the Aleza Lake Research Forest (ALRF). While fine textured soils (silty clay loam to silty clay) are the predominant soil type, an overlying veneer of coarse textured soils (silt loam to sandy loam) occurs in parts of the ALRF (Arocena and Sanborn 1999). Soil type affects the

composition of vascular plant communities, resulting in varying species assemblages and different site productivity. Generally, sites on coarse textured soils have better drainage, more productive forests and different herb and shrub species than sites on fine textured soils (Meidinger and Pojar 1991, DeLong 2003). Differences in soil drainage, productivity, and vascular plant composition may affect the poikilohydric, terrestrial bryophyte and lichen species. However, the relationships between soil texture type and bryophyte and lichen species diversity and abundance have not been well examined. Given that forests on coarse textured soils are more productive and have been disproportionately logged, knowledge of lichen and bryophyte diversity on the different soil types would be of interest to forest managers concerned with diversity conservation.

In the sub-boreal spruce forests of British Columbia, little information is currently available on the diversity and distribution of terrestrial lichen and bryophyte species and the threats facing them. Biogeoclimatic references (e.g. Schofield 1988, Meidinger and Pojar 1991) and bryophyte and lichen identification references (e.g. Goward et al. 1994, Schofield 2002) provide some information but a comprehensive survey has not been performed (T. Goward, personal communication, 2002). This study documents the diversity and abundance of terrestrial moss, liverwort and lichen species (cryptogams) in the Aleza Lake Research Forest in central British Columbia and examines the relationships between bryophyte and lichen species diversity and abundance, and both forest age (old-growth versus young second-growth) and underlying soil texture type (coarse versus fine textured soils).

Methods

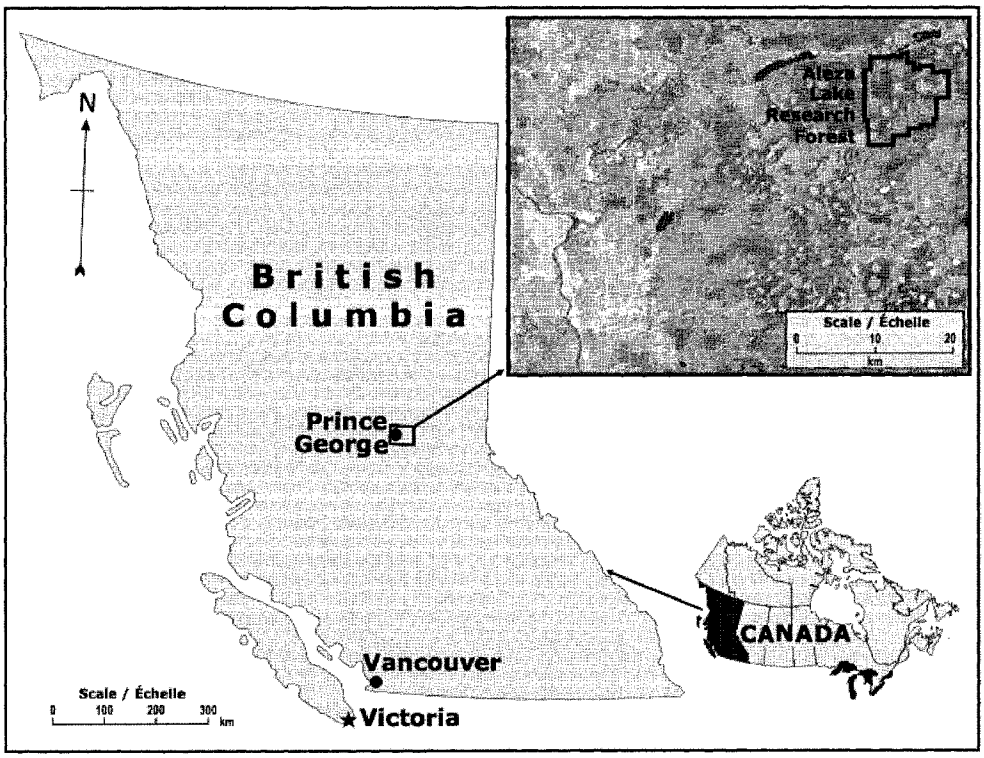
Study area

The study area was located in the Aleza Lake Research Forest (ALRF) in central British Columbia, 60 km northeast of Prince George, BC (122'40"W, 54'11"N) (Figure 2.1). The ALRF is located in the wet cool variant of the Sub-Boreal Spruce (SBSwk1) biogeoclimatic zone (Meidinger and Pojar 1991). Hybrid spruce (*Picea glauca* (Moench) Voss *x engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are the dominant tree species with lesser components of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.) (DeLong 2003). At an elevation of 600-700 m, the climate of the SBSwk1 region is characterized by cool snowy winters and moist cool summers (OES 1995) . The ALRF receives 900 mm of precipitation a year with 65% of that falling as rain and 35% as snow. Average monthly temperatures range from 20 °C in July to -20 °C in January (Murphy 1996).

Soils in the ALRF have a parent material of glaciolacustrine sediments of which the top 50 cm in most areas consists of fine textured soil ranging from silty clay loam to silty clay. Scattered throughout the research forest are areas with an overlying layer of coarse textured soil 1-2 m thick which ranges in texture from silt loam to sandy loam (Arocena and Sanborn 1999).

The planted second-growth stands sampled in this study (subsequently referred to as young second-growth) were clearcut logged and all canopy trees removed in 1989 or 1990. This was the first time these sites had been logged

Figure 2.1 - Location of the Aleza Lake Research Forest study area, north-east of Prince George in central British Columbia.



and all sites were then burned and planted with hybrid spruce seedlings.

Definitions of old-growth for sub-boreal spruce forest range from >140 years of age (MacKinnon and Vold 1998) to more detailed structural criteria including coarse woody debris and basal area characteristics and an age >185 years (Kneeshaw and Burton 1998). Old-growth stands in this study had no history of partial cutting, were >200 years of age and had an uneven aged stand structure.

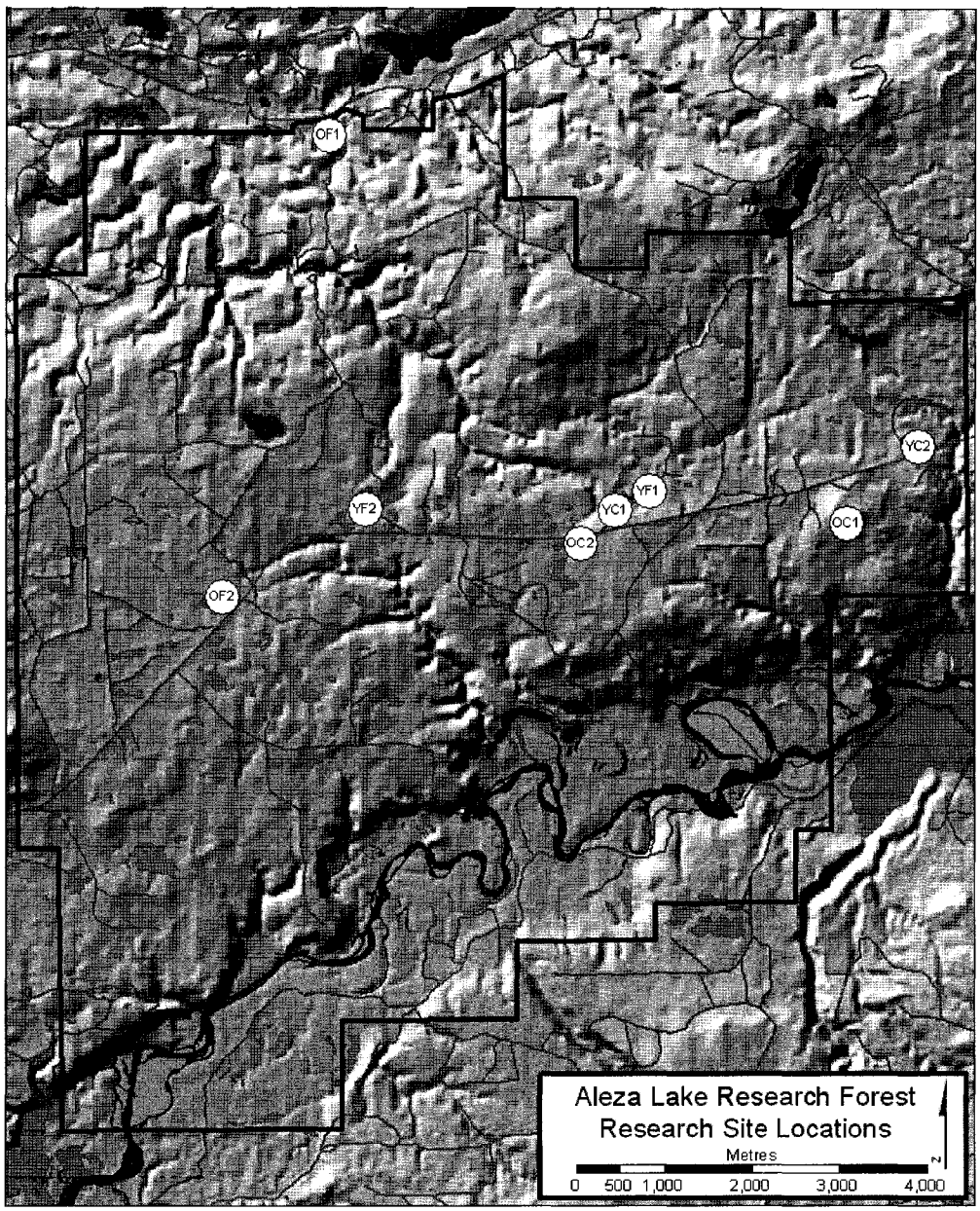
Moss, lichen and liverwort species diversity

Eight study sites were selected for sampling based on stand age and soil texture characteristics (Figure 2.2, Appendix A). Four sites each were located in old-growth forest (>200 years of age) and young second-growth forest (14-15 years of age). Within each forest age, two sites were located on coarse textured soils (BC Ministry of Forests site series 07/08) and two on fine textured soils (site series 01) (DeLong 2003).

At each site, a site centre was located and three plot centres were placed along randomly assigned compass bearings from the site centre, ensuring that no plot was within 50 m of a forest edge or an old road or skid trail (second-growth). At each plot centre, two parallel 20 m transects were established, 10 m apart, bounding half of a 20 x 20 m plot.

Terrestrial lichen, moss and liverwort species diversity and abundance were analyzed in a series of 1 m^2 quadrats. Four quadrats were placed at equal distances along each 20 m transect line. Eight quadrats were sampled per plot for a total of 8 m^2 of forest floor sampled per plot, 24 m^2 per site and a total of 192 m^2

Figure 2.2 – Location of the eight research sites in the Aleza Lake Research Forest study area in central British Columbia. Old-growth (O), young second-growth (Y) forest sites on coarse textured soils (C) and on fine textured soils (F) are indicated.



sampled over all 24 plots (8 sites). At each quadrat, all terrestrial lichen, moss and liverwort species were recorded along with the percent cover of each species. Species were included if they were growing on the ground or on coarse woody debris that was less than 1 m above the ground. Species growing on the base of living trees were not recorded, nor were species which had obviously fallen from trees. For each quadrat, the substrate upon which a species was most frequently growing was recorded. The substrate was classified into four major types which included soil (growing on bare mineral soil or humus), litter (growing on the forest floor litter layer), wood (growing directly on decaying wood) and moss (growing on top of a living moss mat).

Sampling method affects species capture and accuracy of cover measurements. Sampling using many microplots results in the most accurate cover estimates and may be most suitable for areas with dense understory vegetation while belt transects or visual estimation of larger plots may result in higher species capture and may be best for areas with sparse vegetation (McCune and Lesica 1992). This study used many relatively large microplots (1 m^2) which were intended to provide accurate cover estimates but may have missed some rare species.

All terrestrial lichen and bryophyte species were identified to the species level where possible with the exception of two genera. Due to the high degree of gametophyte variability displayed by members of the *Brachythecium* Schimp. genus and a lack of available sporophyte material, members of this genus were not determined to the species level. With the exception of *Plagiomnium insigne* (Mitt.) T. Kopp., all young specimens and other *Plagiomnium* T. Kop. species were

identified only to genus. Nomenclature follows Anderson et al. (1990) for mosses, Stotler (1977) for liverworts, and Hitchcock and Cronquist (1996) for vascular plants. Nomenclature for lichens follows Esslinger (1997) with the exception of *Peltigera* spp. 1 and 2 *fide* Goward. Voucher specimens for lichens and bryophytes reside at the University of Northern British Columbia herbarium.

Ecological and stand characteristics

Forest canopy characteristics were collected for each 20 x 20 m plot. Canopy cover was derived from the average of four spherical densiometer measurements. The diameter at breast height (dbh) of all trees with dbh >10 cm was measured. The largest one or two individuals of each tree species were cored to determine maximum stand age and the height of each was measured. Shrub and herbaceous plant percent cover were assessed in a randomly selected 10 x 10 m sub-plot of the 20 x 20 m plot and the 10 most common species were recorded. Shrubs were considered to be any woody vascular plant species > 0.15 m and < 2 m tall. Herbs were considered to be any non-woody vascular plant species and any shrubs or trees < 0.15 cm tall. Coarse woody debris (CWD) intercepted by 2 perpendicular 20 m transects was assessed by length, diameter, and decay class. Only logs of diameter >10 cm lying or suspended <1.3 m off the ground were included. The CWD decay classes ranged from 1 (least decayed) to 5 (most decayed) using definitions taken from the BC Ministry of Forests (British Columbia Ministry of Forests and Ministry of Environment, Lands and Parks 1998). The CWD volume per hectare was calculated according to Marshall et al. (2000).

Data analysis

The study was laid out as 24 plots in 8 sites with 6 plots located in each combination of forest age and soil texture type. Data analyses were performed using a series of ANOVAs ($\alpha = 0.05$) with main fixed effects of forest age class and soil texture type and with site as a nested effect. To attempt to account for site differences, site was examined as a random variable nested in forest age and soil texture type. ANOVAs were used to examine site, forest age and soil texture effects on cryptogam diversity, cover, and frequency of occurrence. Differences in CWD and forest stand characteristics were also analyzed using ANOVAs.

Four diversity statistics were calculated. Species richness was considered to be the number of species present. The Shannon-Weiner and Simpson's Indices were used to give an indication of the species richness and evenness. The Dominance Index was used to show the proportion of the plot that was dominated by the most common species (Gotelli and Entsminger 2001). An ANOVA was used to examine each of these diversity statistics and the total number of genera of lichen and bryophytes.

Overall bryophyte and lichen community composition patterns were analysed using Nonmetric Multidimensional Scaling (NMS) (Kruskal 1964, Mather 1976) with PC-ORD software (McCune and Mefford 1999). Rare species were retained because the communities contained many rare species and these species were considered important in examining species diversity patterns. Data were log-transformed before ordination to give more weight to rare species and to reduce the effect of several dominant species. The Sörenson distance measure was used with

a random starting configuration, 40 runs of real data, and a stability criterion of 0.0001. NMS was first applied to the full data set to elucidate species patterns between the plots and the associated environmental variables. There were 116 species and 24 plots in the main matrix and 9 environmental variables and 24 plots in the secondary matrix. Old-growth and second-growth sites were then separated and NMS analysis was conducted on each forest age individually. The old-growth main matrix contained 92 species and 12 plots and the second-growth main matrix contained 81 species and 12 plots.

Indicator species analysis (Dufrêne and Legendre 1997) was used in PC-ORD (McCune and Mefford 1999) to determine whether certain species could be indicators of forest age or soil texture type. Indicator species analysis assigns each species an indicator value based on its abundance in a certain group and its faithfulness to that group (McCune and Grace 2002). The analysis suggests species which favour a forest age or soil texture type, however, these species may not be exclusive to that site type. A Monte Carlo test with 1000 randomisations was used to test for significance.

Results

Species diversity

Overall, 116 terrestrial bryophyte and lichen species were recorded across all sites including 31 mosses, 63 lichens, and 22 liverworts. In total, 92 species were found in old-growth forests and 81 were found in second-growth forests. Thirty five

species (30%) were found only in old-growth forest, 24 (21%) were found only in second-growth forest and 57 (49%) were found in common between forest ages (Table 2.1, Appendix B).

Liverwort species richness was significantly different between forest ages (ANOVA; $p<0.001$), in fact, almost twice as many liverwort species were found in old-growth (19) than in second-growth forest (11) (Table 2.1). Eleven of the liverwort species encountered were found only in old-growth while three were found only in second-growth forest (Table 2.2). There was no significant difference in the number of moss or lichen species recorded between the two forest ages or the two soil types (Table 2.3, Figure 2.3).

A significantly greater number of cryptogam genera occurred in old-growth plots than in second-growth plots (ANOVA; $p=0.010$) (Appendix C). Forty-six genera were encountered in old-growth compared to 35 genera in second-growth. Soil type had no significant effect on diversity at the genus level.

There was a significant effect of forest age on the Shannon Wiener diversity index (ANOVA; $p=0.045$) and on the Simpson's diversity index (ANOVA; $p<0.001$), indicating that cryptogams were more diverse and evenly distributed in old-growth forest than in second-growth (Figure 2.3, Appendix C). The uneven distribution of species in second-growth forest was highlighted by the significantly higher Dominance indices in those sites (ANOVA; $p=0.020$). Between 46% and 80% of second-growth sites were dominated by one species compared to 27% to 36% of the old-growth sites. The dominant species in second-growth forest was *Polytrichum juniperinum* Hedw. and it comprised an average of 63% percent of the

Table 2.1 – Number of moss, lichen and liverwort species observed only in old-growth, only in young second-growth and in both forest ages in sub-boreal spruce forests of central British Columbia.

	Moss species	Lichen species	Liverwort species	Total # species	% of Total
Old-growth specific species	8	16	11	35	30%
Second-growth specific species	4	17	3	24	21%
Species found in both forest ages	19	30	8	57	49%
Total species from all sites	31	63	22	116	100%
Total species found in old-growth	27	46	19	92	
Total species found in second-growth	23	47	11	81	

Table 2.2 – Frequency of observation, mean percent cover, and indicator species status of all terrestrial moss, lichen and liverwort species encountered in old-growth forest and young second-growth forest sites in sub-boreal spruce forest in central British Columbia.

	Old-growth			Second-growth			Indicator
	f	% Cover	SD	f	% Cover	SD	Species [c]
Lichens							
Alectoria spp. Ach.	10	0.010	-	1	0.001	-	O
Bryoria spp. Brodo & D. Hawksw.	1	0.001	-	2	0.002	-	
Cladina arbuscula ssp. *beringiana* (Ahti) N.S. Golwok	-	-	-	10	0.010	-	Y
Cladina rangiferina (L.) Nyl.	3	0.003	3.78×10^{-2}	7	0.008	3.16×10^{-2}	
Cladina spp. Nyl.	1	0.001	-	-	-	-	
Cladonia acuminata (Ach.) Norrlin	-	-	-	1	0.001	-	
Cladonia bacilliformis (Nyl.) Gluck	-	-	-	1	0.001	-	
Cladonia botrytes (K. Hagen) Willd.	4	0.004	-	22	0.023	-	Y
Cladonia cariosa (Ach.) Sprengel	-	-	-	66	0.524	1.20×10^{-2}	Y
Cladonia carneola (Fr.) Fr.	5	0.005	-	25	0.026	-	Y
Cladonia cenotea (Ach.) Schaerer	3	0.003	-	2	0.002	-	
Cladonia cervicornis (Ach.) Flotow.	-	-	-	1	0.001	-	
Cladonia chlorophaea (Florke ex Sommerf.) Sprengel	8	0.008	-	24	0.025	-	Y
Cladonia coniocraea (Florke) Sprengel	1	0.001	-	2	0.002	-	
Cladonia cornuta ssp. *cornuta* (L.) Hoffm.	-	-	-	30	0.109	7.56×10^{-1}	Y
Cladonia crispata var. *crispata* (Ach.) Flotow.	1	0.001	-	7	0.007	-	
Cladonia cfr cyanipes (Sommerf.) Nyl.	-	-	-	1	0.001	-	
Cladonia deformis (L.) Hoffm.	-	-	-	4	0.004	-	
Cladonia digitata (L.) Hoffm.	1	0.001	-	1	0.001	-	
Cladonia ecmocyna Leighton	1	0.001	-	1	0.001	-	
Cladonia fimbriata (L.) Fr.	14	0.015	-	65	0.086	1.63×10^{-3}	Y
Cladonia gracilis ssp. *turbinata* (Ach.) Ahti	3	0.003	-	69	0.275	6.85×10^{-1}	Y
Cladonia norvegica Tonsberg & Ahti	1	0.001	-	-	-	-	
Cladonia ochrochlora Florke	36	0.264	9.22×10^{-3}	61	0.153	5.80×10^{-3}	
Cladonia phyllophora Hoffm.	-	-	-	4	0.004	-	

Table 2.2 continued

	Old-growth			Second-growth			Indicator
	f	% Cover	SD	f	% Cover	SD	Species [c]
Cladonia spp. P. Browne	16	0.046	$5.33x10^{-3}$	48	0.190	$7.15x10^{-3}$	Y
Cladonia sulphurina (Michaux) Fr.	6	0.006	-	34	0.065	$3.71x10^{-3}$	Y
Cladonia umbricola Tonsberg &Ahti	-	-	-	1	0.001	-	
Hypogymnia occidentalis L. Pike	8	0.028	$7.00x10^{-3}$	-	-	-	O
Hypogymnia physodes (L.) Nyl.	8	0.008	-	2	0.002	-	
Hypogymnia spp. (Nyl.) Nyl.	1	0.001	-	1	0.001	-	
Hypogymnia tubulosa (Schaerer) Hav.	3	0.003	-	-	-	-	
Lobaria pulmonaria (L.) Hoffm.	7	0.077	$1.42x10^{-2}$	-	-	-	O
Mycoblastus sanguinarius (L.) Norman	1	0.001	-	-	-	-	
Nephroma bellum (Sprengel) Tuck.	22	0.256	$2.20x10^{-2}$	-	-	-	O
Nephroma helveticum Ach.	1	0.010	-	-	-	-	
Nephroma parile (Ach.) Ach.	13	0.111	$9.25x10^{-3}$	2	0.002	-	O
Parmelia hygrophila Goward & Ahti	1	0.010	-	-	-	-	
Parmelia sulcata Taylor	20	0.071	$9.22x10^{-3}$	2	0.002	-	O
Parmeliopsis ambigua (Wulfen) Nyl.	7	0.017	$3.54x10^{-3}$	3	0.003	-	
Parmeliopsis hyperopta (Ach.) Arnold	4	0.004	-	-	-	-	
Peltigera aphthosa (L.) Willd.	4	0.024	$9.90x10^{-3}$	1	0.001		
Peltigera canina (L.) Willd.	2	0.042	$1.47x10^{-2}$	25	0.425	$2.03x10^{-2}$	Y
Peltigera degenii Gyelnik	1	0.010	-	-	-	-	
Peltigera extenuata (Vainio) Lojka	1	0.001	-	44	1.189	$4.47x10^{-2}$	Y
Peltigera horizontalis (Hudson) Baumg.	13	0.082	$9.65x10^{-3}$	-	-	-	O
Peltigera leucophlebia (Nyl.) Gylenik	2	0.011	$6.63x10^{-3}$	37	0.315	$1.25x10^{-2}$	Y
Peltigera membranacea (Achl.) Nyl.	24	0.323	$1.77x10^{-2}$	16	0.153	$1.03x10^{-2}$	
Peltigera neckeri Hepp. Ex Mull. Arg.	1	0.010	-	5	0.272	$7.02x10^{-2}$	
Peltigera neopolydactyla (Gyelnik) Gyelnik	11	0.325	$3.30x10^{-2}$	6	0.034	$5.14x10^{-3}$	
Peltigera polydactylon (Necker) Hoffm.	-	-	-	1	0.001	-	
Peltigera praetextata (Florke ex Sommerf.) Zopf.	-	-	-	1	0.010	-	
Peltigera rufescens (Weiss) Humb.	-	-	-	5	0.044	$8.22x10^{-3}$	Y
Peltigera spp. *nov. #1*	-	-	-	1	0.010	-	

Table 2.2 continued

	Old-growth			Second-growth			Indicator
	f	% Cover	SD	f	% Cover	SD	Species [c]
Peltigera spp. *nov. #2*	-	-	-	9	0.502	4.16×10^{-2}	
Peltigera spp. Willd.	2	0.002	-	4	0.004	-	
Platismatia glauca (L.) Culb. & C. Culb.	19	0.118	1.02×10^{-2}	-	-	-	O
Pseudocyphellaria anomala Brodo & Ahti	1	0.001	-	-	-	-	
Stereocaulon tomentosum Fr.	-	-	-	1	0.001	-	
Tuckermannopsis chlorophylla Gyelnik	3	0.003	-	-	-	-	
Tuckermannopsis orbata (Nyl.) M.J. Lai	1	0.001	-	-	-	-	
Usnea spp. Dill ex Adams	5	0.005	-	1	0.001	-	
Vulpicida pinastri (Scop.) J.E.Mattsson & M.J.Lai	-	-	-	4	0.004	-	
Lichen total [d]	301 [b]	1.9 [a]		661 [b]	4.5 [a]		
Mosses							
Aulacomnium androgynum (Hedw.) Schwaegr.	-	-	-	38	0.164	5.62×10^{-3}	Y
Aulacomnium palustre (Hedw.) Schwaegr.	-	-	-	1	0.001	-	
Brachythecium spp. Schimp.	82	1.371	1.92×10^{-2}	63	2.333	4.85×10^{-2}	C
Campylium calcareum	-	-	-	1	0.010	-	
Ceratodon purpureus (Hedw.) Brid.	1	0.001	-	76	5.117	8.12×10^{-2}	Y
Dicranum fuscescens Turn.	20	0.191	1.40×10^{-2}	8	0.008	-	O
Dicranum polysetum Sw.	3	0.003	-	19	0.049	4.92×10^{-3}	Y
Dicranum scoparium Hedw.	10	0.020	2.96×10^{-3}	9	0.029	6.60×10^{-3}	
Dicranum spp. Hedw.	8	0.038	7.30×10^{-3}	4	0.004	-	
Dicranum tauricum Sapeh.	35	0.125	7.82×10^{-3}	6	0.006	-	O
Eurhynchium praelongum (Hedw.) Schimp.	5	0.024	5.14×10^{-3}	1	0.001	-	
Eurhynchium pulchellum (Hedw.) Jenn.	5	0.126	2.79×10^{-2}	-	-	-	
Herzogiella seligeri (Brid.) Iwats.	1	0.001	-	-	-	-	
Hylocomium splendens (Hedw.) Schimp.	56	8.100	1.66×10^{-1}	7	0.058	1.93×10^{-2}	O, F
Lescuraea stenophylla (Ren. & Card.) Kindb.	1	0.001	-	-	-	-	
Mnium lycopodioides Schwaegr.	15	0.092	6.17×10^{-3}	1	0.001	-	O
Mnium spinulosum (Voit) Schwaegr.	5	0.065	1.08×10^{-2}	1	0.001	-	

Table 2.2 continued

	Old-growth			Second-growth			Indicator
	f	% Cover	SD	f	% Cover	SD	Species [c]
Orthotrichum speciosum Nees	1	0.001	-	-	-	-	
Plagiomnium insigne (Mitt.) T. Kop.	66	2.733	5.70×10^{-2}	11	0.317	4.64×10^{-2}	O
Plagiomnium spp. T. Kop.	29	0.205	9.40×10^{-3}	10	0.141	1.80×10^{-2}	
Plagiothecium cavifolum (Brid.) Iwats	1	0.001	-	-	-	-	
Plagiothecium denticulatum (Hedw.) Schimp.	1	0.001	-	-	-	-	
Plagiothecium laetum Schimp.	4	0.043	8.09×10^{-3}	-	-	-	
Pleurozium schreberi (Brid.) Mitt.	87	7.344	8.91×10^{-2}	59	0.456	1.50×10^{-2}	O
Pohlia nutans (Hedw.) Lindb.	3	0.023	1.14×10^{-2}	46	0.800	2.46×10^{-2}	Y
Polytrichum juniperinum Hedw.	-	-	-	87	26.017	2.43×10^{-1}	Y
Ptilium crista-castrensis (Hedw.) De Not.	83	7.235	1.08×10^{-1}	39	0.493	3.36×10^{-2}	O
Rhizomnium nudum (Britt. & Williams) T. Kop.	25	1.204	5.02×10^{-2}	2	0.002	-	O
Rhytidiadelphus triquetrus (Hedw.) Warnst.	88	8.595	1.24×10^{-1}	20	0.050	4.80×10^{-3}	O
Sanionia uncinata (Hedw.) Loeske	42	0.689	1.83×10^{-2}	15	0.124	1.35×10^{-2}	O
Tetraphis pellucida Hedw.	3	0.003	-	-	-	-	
Moss total	680 [b]	38.2 [a]		524 [b]	36.2 [a]		
Liverworts							
Anastrophyllum hellerianum (Nees) Schust.	1	0.010	-	-	-	-	
Barbilophozia barbata (Schmid. Ex Schreb.) Loeske	35	0.155	1.10×10^{-2}	5	0.005	-	O
Barbilophozia spp. Loeske	4	0.024	9.90×10^{-3}	2	0.011	6.63×10^{-3}	
Blepharostoma trichophyllum (L.) Dum.	17	0.046	3.68×10^{-3}	-	-	-	O
Cephalozia spp. (Dum.) Dum.	7	0.026	4.58×10^{-3}	-	-	-	O
Cephaloziella rubella (Nees) Warnst.	-	-	-	1	0.010	-	
Cephaloziella spp. (Spruce) Steph.	5	0.107	2.89×10^{-2}	1	0.001	-	C
Geocalyx graveolens (Schrad.) Nees	2	0.002	-	-	-	-	
Harpanthus flotovianus (Nees) Nees	20	0.021	-	2	0.002	-	O, F
Jamesoniella autumnalis (D.C.) Steph.	3	0.032	9.90×10^{-3}	-	-	-	
Jamesoniella spp. (Spruce) Carring.	2	0.031	7.37×10^{-3}	-	-	-	

Table 2.2 continued

	Old-growth			Second-growth			Indicator
	f	% Cover	SD	f	% Cover	SD	**Species** [c]
Jungermannia spp. L.	16	0.066	7.91×10^{-3}	-	-	-	O
Lophocolea heterophylla (Schrad.) Dum.	1	0.001	-	-	-	-	
Lophocolea minor Nees	13	0.144	1.82×10^{-1}	1	0.001	-	O
Lophocolea spp. (Dum.) Dum.	-	-	-	1	0.001	-	
Lophozia longiflora (Nees) Schiffn.	4	0.004	-	-	-	-	
Lophozia spp. (Dum.) Dum.	14	0.209	4.13×10^{-2}	-	-	-	O
Marchantia polymorpha L.	-	-	-	1	0.010	-	
Plagiochila porelloides (Torrey ex Nees) Lindenb.	3	0.003	-	1	0.010	-	
Ptilidium californicum (Aust.) Underw.	22	0.251	1.30×10^{-2}	1	0.001	-	O, F
Ptilidium pulcherrimum (G. Web.) Hampe	2	0.022	1.40×10^{-2}	-	-	-	
Ptilidium spp. Nees	20	0.347	2.87×10^{-2}	4	0.004	-	O, C
Liverwort total [d e]	191[b]	1.5[a]		20[b]	0.06[a]		
Unknown species	23	0.173		18	0.058		
Total		41.8			40.8		

Note: Frequency (f) indicates the number of quadrats in which a species was observed of a total of 96 quadrats sampled in old-growth and second-growth respectively. The % cover is the mean % cover for mosses, lichens and liverworts over 96 quadrats sampled in old-growth and second-growth respectively. Standard deviation (SD) is given for mean % cover except when the coefficient of variance was <1% or where f<3.

[a] Sum of the mean percent cover per quadrat of all species in that group (moss, lichen or liverwort). Indicates the mean percent cover of that group in an average quadrat.
[b] Sum of the frequency of all species in that group (moss, lichen or liverwort) over all quadrats.
[c] Indicator species analysis results for each lichen, moss and liverwort species indicating significant indicators of old-growth (O), young second-growth (Y), coarse textured soils (C) and fine textured soils (F).
[d] Significant effect of forest age on frequency of observation (ANOVA; $\alpha = 0.05$).
[e] Significant effect of forest age on % cover (ANOVA; $\alpha = 0.05$).

Table 2.3 – Species diversity, frequency of observation, and mean percent cover of lichens, liverworts and mosses on coarse textured and fine textured soils in old-growth, in young second-growth and in both forest ages of sub-boreal spruce forest in central British Columbia.

	Coarse textured soil			Fine textured soil		
	# species	f	% cover	# species	f	% cover
Old-growth						
Lichens	36	162	1.8	37	139	2.1
Liverworts[a]	19	71	1.6	13	120	1.4
Mosses	25	327	26.7	18	353	49.8
Total	80	560	30.1	68	612	53.2
Second-growth						
Lichens[b]	33	302	2.9	42	359	6.1
Liverworts[c]	10	14	0.1	4	6	0.0
Moss	23	275	36.6	16	249	35.8
Total	66	604	39.6	62	619	42.0
Both forest ages						
Lichens[b]	52	464	2.3	56	498	4.1
Liverworts[a]	22	85	0.8	13	126	0.7
Moss	30	602	31.6	21	602	42.8
Total	104	1151	34.8	90	1226	47.6

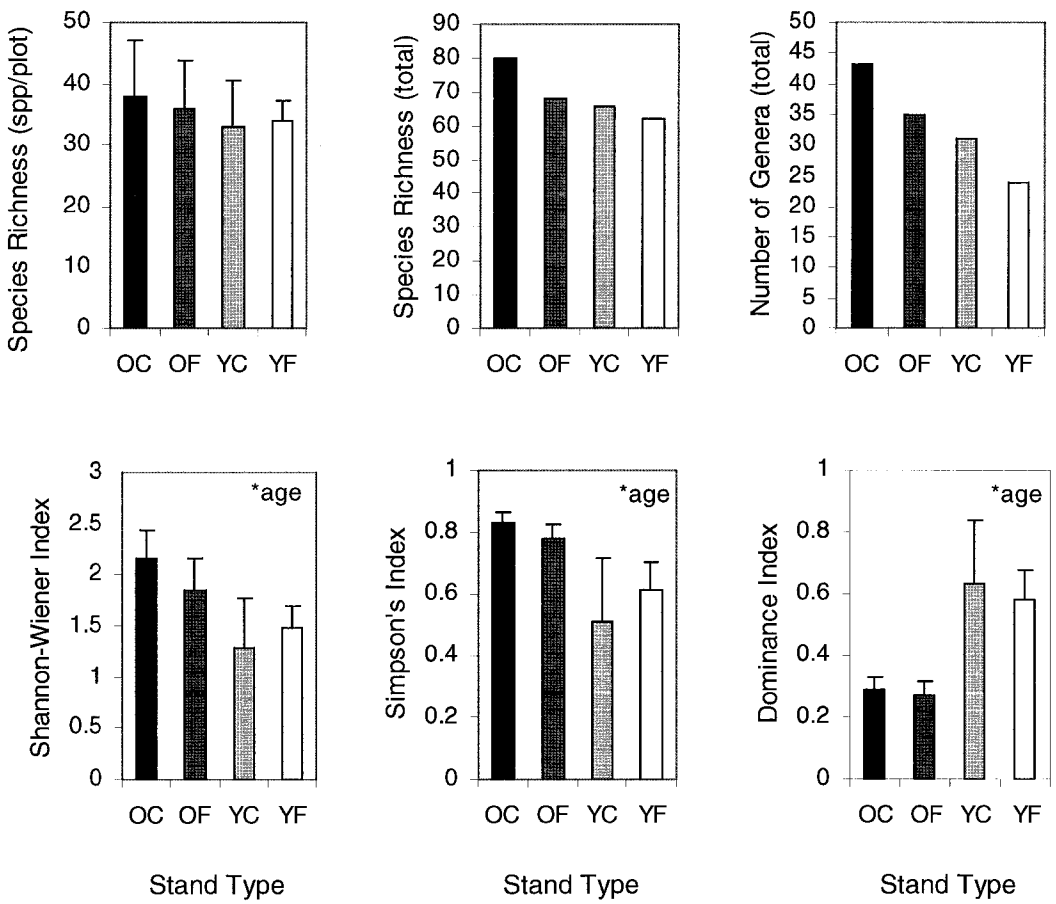
Note: Frequency (f) indicates the number of times lichen, moss or liverwort species were observed in the sampled quadrats. The % cover indicates the mean percent cover of moss, lichen and liverwort species in quadrats in that forest age and soil texture type. The number of quadrats sampled included: old-growth coarse textured soils, 48; fine textured soils, 48; second-growth coarse textured soils, 48; fine textured soils, 48; both forest ages coarse textured soils, 96; fine textured soils, 96.

[a] Significant effect of soil texture type on frequency of occurrence (ANOVA; $\alpha = 0.05$).

[b] Significant effect of soil texture type on % cover (ANOVA; $\alpha = 0.05$).

[c] Significant effect of site on frequency (ANOVA; $\alpha = 0.05$).

Figure 2.3 – Diversity statistics, including species richness per plot, species richness per stand type, number of genera per stand type, Shannon-Wiener Index, Dominance Index, and Simpson's Index, for sites in old-growth (O) and young second-growth (Y) sub-boreal spruce forest growing on coarse textured (C) and fine textured (F) soils.



Note: Species richness per plot, Shannon-Wiener Index, Dominance Index and Simpson's Index are all calculated at the plot level (n=6 plots). Total species richness and total number of genera are calculated as totals for that stand type (OC, OF, YC, YF). Standard deviation is given where applicable (n=6). Significant effects (forest age (age), soil texture, site) are noted with * on each graph (ANOVA; $\alpha = 0.05$).

terrestrial cover of the sites. There was no significant effect of soil texture type on any of the diversity indices.

Terrestrial cover of mosses, lichens and liverworts

Total cryptogam percent cover was similar (about 41%) for old-growth and second-growth sites (Table 2.2). Mosses comprised the greatest proportion of terrestrial cover and the frequency of occurrence and cover of mosses was similar in both forest ages. In contrast, liverworts were significantly more frequent (ANOVA; $p<0.001$) and had higher cover (ANOVA; $p<0.001$) in old-growth forest compared with young second-growth. Old-growth had a 25-fold higher percent cover of liverworts and a 10-fold higher frequency of occurrence of liverworts than second-growth. Lichen cover was significantly influenced by forest age (ANOVA; $p=0.014$) as was lichen frequency (ANOVA; $p=0.015$) with second-growth forest having twice the average percent cover and frequency of occurrence of lichens than old-growth.

Only lichen cover was significantly affected by soil texture (ANOVA; $p=0.043$) and was greater on fine textured soils than on coarse textured soils. Soil type had a significant effect on liverwort frequency (ANOVA; $p=0.023$) with a greater frequency observed for fine textured soils (Table 2.3).

Twenty N_2-fixing lichens belonging to 5 genera (*Lobaria* (Schreber) Hoffm., *Nephroma* Ach., *Peltigera* Willd., *Pseudocyphellaria* Vainio *and Stereocaulon* Hoffm.) were encountered (Table 2.2). Fourteen species from 4 genera of N_2-fixing lichen occurred in old-growth sites compared to 14 species from 3 genera in second-growth sites.

Indicator species

Indicator species analysis determined 27 species were significant indicators of old-growth forest: 10 mosses, 9 liverworts and 8 lichens (Table 2.2, Appendix D). Four species were N_2-fixing lichens, *Lobaria pulmonaria* (L.) Hoffm., *Nephroma bellum* (Sprengel) Tuck., *N. parile* (Ach.) Ach. and *Peltigera horizontalis* (Hudson) Baumg. Nineteen species were significant indicators of second-growth forest including 5 mosses and 14 lichens, of which 9 were *Cladonia* species. Four species were N_2-fixing lichens, *Peltigera canina* L. Willd., *P. leucophlebia* (Nyl.) Gylenik, *P. extenuata* (Vainio) Lojka and *P. rufescens* (Weiss) Humb. Indicator species analysis for soil texture type resulted in 6 indicator species, 3 indicative of fine textured soils and 3 indicative of coarse textured soils (Table 2.2, Appendix D).

Nonmetric multidimensional scaling ordination

Nonmetric Multidimensional Scaling (NMS) ordination of all sites resulted in a one dimensional final solution (Appendix E). This solution had a final stress of 5.028, an instability of 0.00001 after 76 iterations and a significant Monte Carlo test ($p < 0.050$). The single axis described 95% of the variation and showed a very strong separation of plots based on forest age with old-growth and second-growth plots located at opposite ends of the axis. This strong relationship suggests that forest age greatly affected species assemblages.

To elucidate the effect of other environmental variables within the two forest ages, NMS ordinations were conducted on old-growth and second-growth plots separately. The NMS ordination of old-growth plots suggested a three dimensional

solution. The ordination had a final stress value of 5.71, an instability value of 0.00001 after 84 iterations and a Monte Carlo test gave significant p values ($p<0.050$). The first axis explained 30% of the variation, the second axis explained 49% and the third axis explained 14%. The two most explanatory axes are displayed in Figure 2.4. Ordination of the old-growth plots showed plots grouped by soil texture with the exception of one outlier (OC2). Coarse woody debris length ($r^2 = 0.62$) corresponded most strongly with the first axis while soil texture ($r^2 = 0.53$) and herb cover ($r^2 = 0.52$) corresponded most strongly with the second axis.

The NMS ordination for the second-growth plots also suggested a three dimensional solution. The final stress value was 7.34 with an instability of 0.00001 after 94 iterations and a Monte Carlo test gave p values of <0.05 for all three axes. The first axis explained 50% of the variation, the second axis explained 32% and the third axis explained 8%. Figure 2.5 gives a two-dimensional display of the most explanatory ordination axes. Coarse woody debris density ($r^2 = 0.77$) corresponded most strongly with the first axis while soil texture ($r^2 = 0.31$) and average tree height ($r^2 = 0.39$) corresponded most strongly with the second axis. Plots did not group as strongly with soil texture in this forest age.

Stand and coarse woody debris characteristics

Dominant canopy trees in the old-growth forest ranged from 200 to 255 years of age with an average canopy height of 33 m (Table 2.4). Young second-growth forest had a canopy height ranging from 3 m on fine textured soils to 5 m on coarse textured soils. When compared to the young second-growth, old-growth forest had

Figure 2.4 – NMS ordination results for old-growth plots showing the distribution of plots in two dimensions. Axis 1 accounts for 30% of the variation and is most strongly correlated with CWD length (r^2 = 0.62). Axis 2 accounts for 49% of the variation and is most strongly correlated with soil texture type (r^2 = 0.53) and herbaceous plant cover (r^2 = 0.52). Plots on coarse (OC) and fine textured (OF) soils are encompassed by a circle with the exception of an outlier plot OC2.

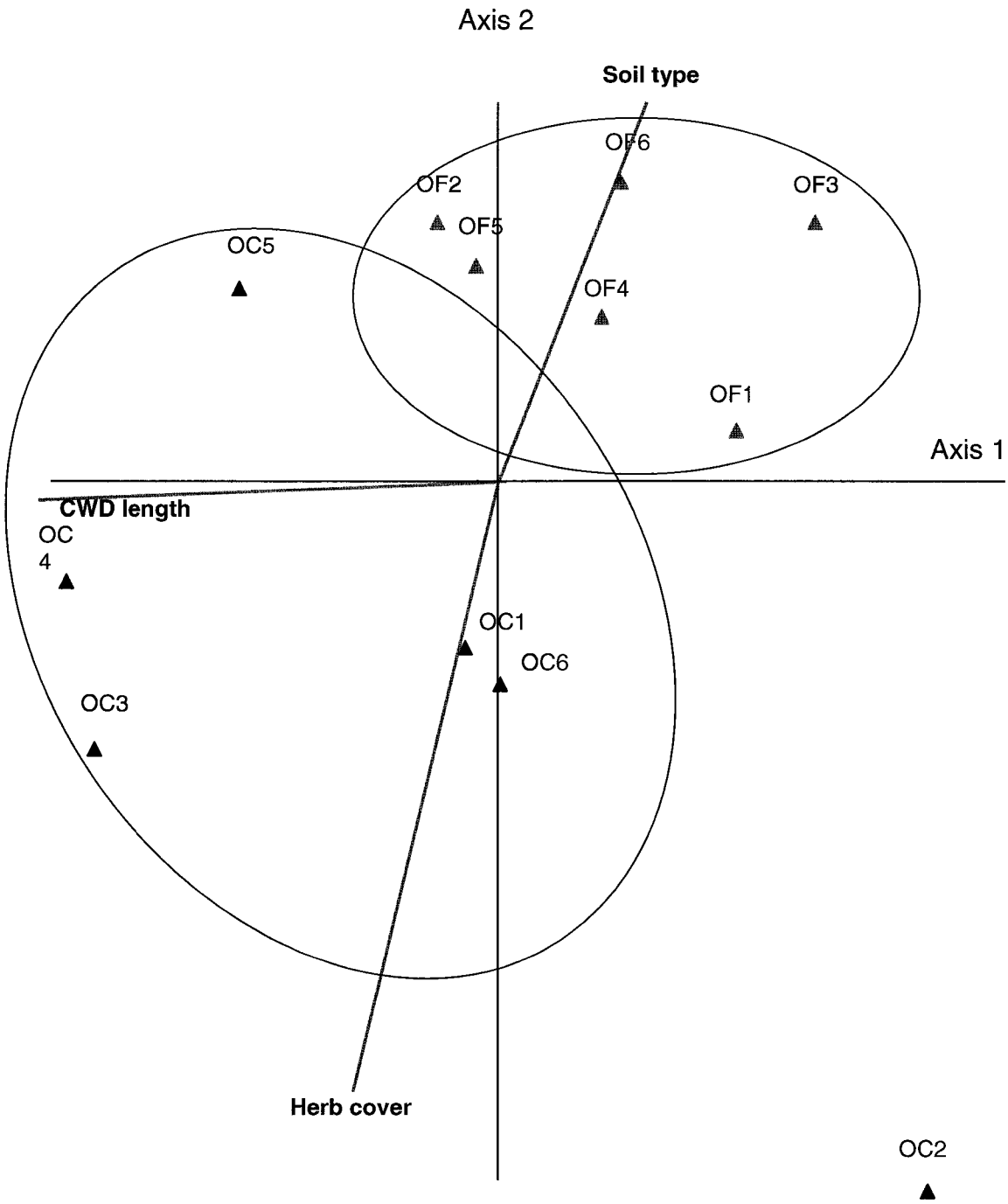


Figure 2.5 – NMS ordination results for young second-growth plots showing the distribution of plots in two dimensions. Axis 1 accounts for 50% of the variation and is most strongly correlated with CWD density ($r^2 = 0.77$). Axis 3 accounts for 32% of the variation and is most strongly correlated with soil texture type ($r^2 = 0.33$) and average tree height ($r^2 = 0.39$). Young second-growth plots are indicated by YC on coarse textured soils and YF on fine textured soils.

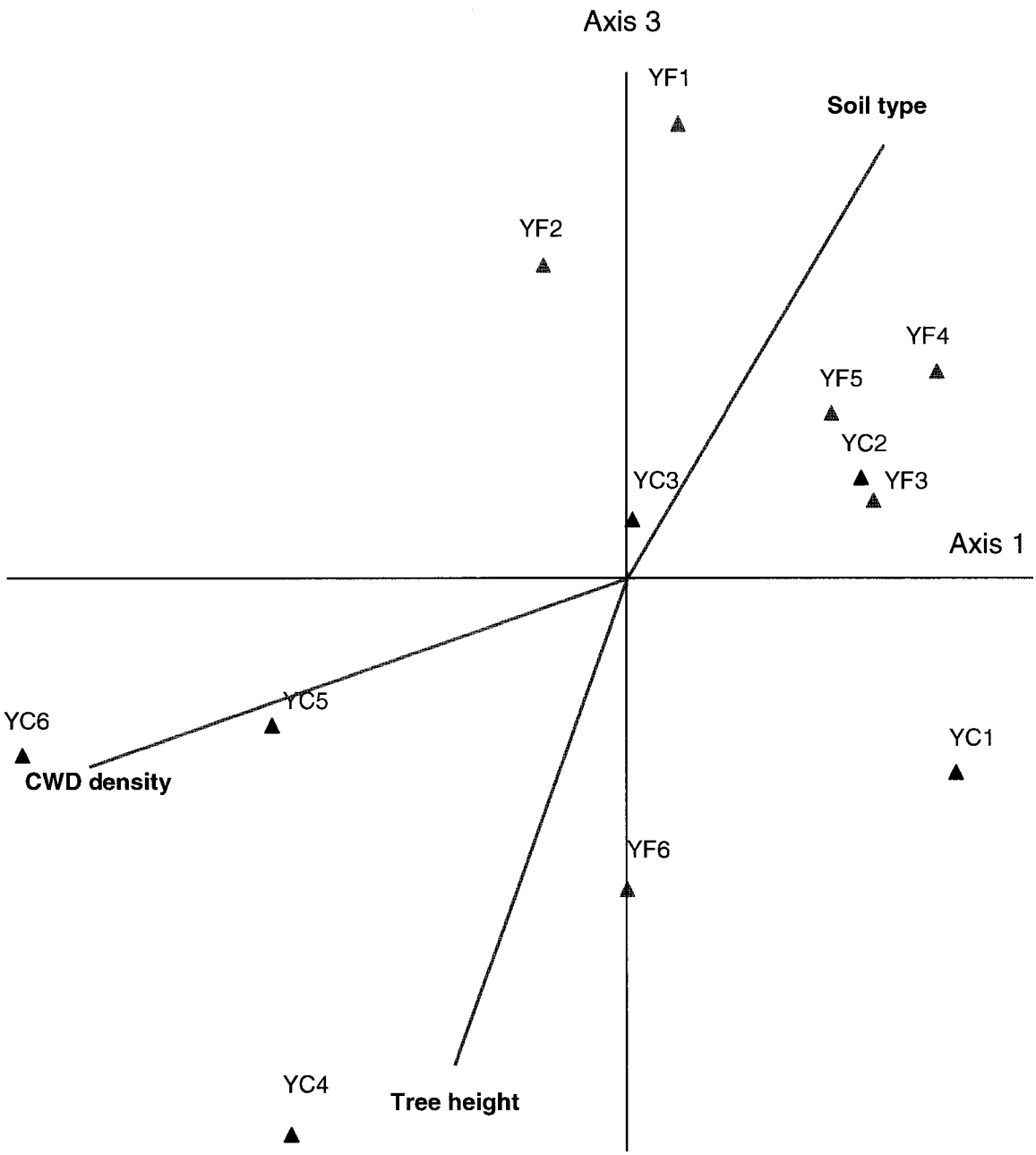


Table 2.4 – Sub-boreal spruce forest stand and coarse woody debris (CWD) characteristics recorded in old-growth forest and young second-growth forest on coarse textured (coarse) and fine textured (fine) soils respectively.

	Old-growth		Second-growth	
	Coarse	**Fine**	**Coarse**	**Fine**
Stand characteristics				
Stand age class	8	8	1	1
Age of oldest canopy tree (yrs)	255	203	15	15
Mean canopy height (m)	33 ± 7	33 ± 3	5	3
Mean DBH trees >10cm (cm)	31 ± 17	24 ± 12	n/a	n/a
Mean shrub cover (%)[a]	71 ± 10	44 ± 7	21 ± 8	30 ± 15
Mean herb cover (%)	55 ± 11	32 ± 9	41 ± 12	56 ± 18
CWD Characteristics				
Mean # pieces CWD (/40m transect)[a]	11 ± 4	15 ± 3	9 ± 2	6 ± 2
Mean length of CWD (m)[a c]	14 ± 9	11 ± 7	5 ± 4	5 ± 4
Mean diameter of CWD (cm)[b c]	26 ± 12	20 ± 9	24 ± 12	18 ± 8
Mean CWD volume (m^3ha^{-1})[a]	279 ± 160	221 ± 56	126 ± 199	46 ± 76
Mean decay class of CWD[c]	3.1 ± 1.2	2.5 ± 1.4	2.7 ± 1.0	3.2 ± 1.0

Note: Means given ± standard deviation (n=6 plots). Stand age classes follow the British Columbia Ministry of Forest age classes where 1 = 1-20 years and 8=141-250 years.
[a] Significant effect of forest age on the characteristic (ANOVA; $\alpha = 0.05$).
[b] Significant effect of soil texture type on the characteristic (ANOVA; $\alpha = 0.05$).
[c] Significant effect of site on the characteristic (ANOVA; $\alpha = 0.05$).

a more heterogeneous stand structure with greater tree canopy cover and a multi-layer canopy. Shrub cover was affected by forest age (ANOVA; p=0.023) and was significantly higher in old-growth. Within old-growth, shrub cover was higher in sites on coarse textured soils than on fine textured soils, though this was only marginally significant (ANOVA; p=0.058). Herbaceous species cover was not significantly different across all sites (Appendix F).

Analysis of CWD data showed significant variation in decay class, diameter, and piece length between forest ages (Table 2.4). Forest age had a significant effect on CWD volume (ANOVA; p=0.020), CWD length (ANOVA; p=0.02), and the number of pieces of CWD present at the plots (ANOVA; 0.003). Old-growth forests contained 50% more pieces of CWD and pieces of CWD were twice as long. Soil texture type had a significant effect on CWD diameter (ANOVA; p=0.044) with higher CWD diameters on coarse soils in both forest ages.

Substrate

Substrate use by moss, lichen, and liverwort species varied with forest age (Table 2.5). In old-growth and second-growth forest, mosses had the highest cover on litter (73%) and soil (93%) substrates respectively. Mosses had more cover on wood in old-growth (26.8%) than in second-growth (4.3%). While there was a greater abundance of wood substrate in old-growth forest relative to second-growth (Table 2.4), there was still more moss cover on wood in old-growth than second-growth when relative wood abundance was accounted for. Liverworts predominantly used wood substrates in old-growth (91%) and used soil (54%) and wood (46%)

Table 2.5 – Relative percent cover of mosses, lichens and liverworts, on available terrestrial substrates (litter layer, wood, bare soil and living moss mat), normalized by stand age or across all sites.

Forest age	Substrate	% Cover normalized by stand age			% Cover normalized over all sites		
		Moss	Lichen	Liverwort	Moss	Lichen	Liverwort
Old-Growth	Litter	73.2	0.5	8.7	37.6	0.1	8.3
	Wood	26.8	99.5	91.2	13.8	29.9	87.6
	Soil	-	-	-	-	-	-
	Moss	0.0	0.0	0.1	0.0	0.0	0.1
Old-growth total		100	100	100	51.4	30.0	96.1
Second-Growth	Litter	2.9	0.1	0.0	1.4	0.0	0.0
	Wood	4.3	18.8	46.4	2.1	13.2	1.7
	Soil	92.7	75.2	53.6	45.1	52.6	2.0
	Moss	0.0	5.9	0.0	0.0	4.2	0.0
Second-growth total		100	100	100	48.6	69.9	3.8
Total					100	100	100

Note: Bare soil substrates did not occur in old-growth sites. Percent cover information is taken from Table 2.2 and then normalized either by stand age or over all sites.

equally in second-growth. Given the low cover of liverworts in second-growth forest, liverwort cover on wood was much higher in old-growth forest even when relative wood abundance was considered. The majority of lichen cover was recorded growing on wood in old-growth sites (99.5%) compared to 75% on soil in second-growth sites. However, the absolute cover of lichen on wood was not higher in old-growth than second-growth sites when relative wood abundance was considered.

Discussion

Influence of forest age

Liverwort species diversity and abundance

Liverwort diversity and abundance were strongly affected by forest age and were much greater in old-growth forests. Eleven of 22 liverwort species were found only in old-growth sites compared with only 3 species found exclusively in second-growth sites. As well, 96% of the overall recorded liverwort cover occurred in old-growth sites. All of the liverwort species observed in second-growth sites had < 5 recorded occurrences and most had only a single observed occurrence. Only the genus *Marchantia* L., which is often found in moist, burned sites (Schofield 2002), had observations restricted to a second-growth site. No liverworts were identified as indicators of second-growth forest while 9 species were identified as potential indicators of old-growth forest. These results are consistent with other studies that have found liverworts to be most diverse and abundant in old-growth forests (e.g. Söderström 1988, Lesica et al. 1991, Crites and Dale 1998, Newmaster et al. 2003).

Greater liverwort diversity and abundance in old-growth forest may occur for several reasons. Firstly, leafy liverworts are commonly drought sensitive and have life forms that make them particularly susceptible to desiccation (During 1992). In fact, liverworts have been observed to reach greatest diversity on moist substrates (Pharo and Beattie 1997). Secondly, many liverwort species are exclusively epixylic (Söderström 1988) and the vast majority of liverworts observed in this study were found growing on woody substrates. As previously noted, less volume and fewer pieces of coarse woody debris were available in the young second-growth sites. Managed forest landscapes with stands harvested at short return intervals may result in a decline in amount and decay classes of CWD due to reduced inputs and the lower maximum ages of such stands (Clark et al. 1998, Ross-Davis and Frego 2002). In this study, it was observed that the wood that was available in second-growth was more desiccated and this more exposed wood may not be of suitable habitat quality for these moisture dependent species. Microclimate conditions at the forest floor in second-growth forest include higher light levels, reduced moisture availability and humidity, and increased soil surface temperatures (Lewis 1998) that when combined with reduced substrates, are likely to create unsuitable conditions for the growth of most liverwort species.

Moss species diversity and abundance

Moss species composed the greatest proportion of the terrestrial cryptogam cover in all sites. This study found that moss diversity and cover were not significantly different between the two forest ages or the two soil texture types;

however, different species were common in old-growth and second-growth sites. Moreover, moss species were found primarily growing on soil in second-growth sites and on litter and wood in old-growth sites. Old-growth sites were dominated by *Plagiomnium* species and feather mosses including *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not. and *Hylocomium splendens* (Hedw.) Schimp. In contrast, second-growth sites were dominated by *Polytrichum juniperinum* (65% of moss cover) and *Ceratodon purpureus* Brid. (14% of moss cover). Indicator species analysis identified these and several other moss species as indicators of second-growth. Moss species such as *P. juniperinum* and *C. purpureus* are colonist species and have characteristics that make them drought tolerant (During 1992, Newmaster and Bell 2002) and therefore well suited to second-growth environments. However, some of the old-growth indicator species, such as *Pleurozium schreberi*, are more common but not restricted to old-growth forest and may not be effective indicators of that forest age.

Lichen species diversity and abundance

Similar numbers of lichen species were identified in young second-growth and old-growth forests. However, species composition and abundance varied between old-growth and second-growth with significantly greater lichen cover in second-growth. This study concurs with other studies that have found lichens to be more abundant in open stands than closed stands (e.g. Pharo and Vitt 2000). Second-growth had higher diversity of *Cladonia* species, concurring with other research that has shown *Cladonia* species to be more numerous and to have

greater diversity in younger forests as compared with older forests (Söderström 1988, Lesica et al. 1991). *Cladonia* species thrive in the drier environment of the open, young stands and can grow on exposed mineral soil (Söderström 1988). In contrast with old-growth, bare soil was common in young second-growth sites that had been burned after logging and lost much of the litter layer. Furthermore, N_2-fixing *Peltigera* species were 3.5-fold more abundant in second-growth than old-growth forest, likely making them an important contributor of nitrogen to these disturbed second-growth ecosystems. *Peltigera* species have been found to contribute significant nitrogen to forest ecosystems through leaching and thallus decomposition (Knowles 2004).

Old-growth sites had a greater number of epixylic lichen species and a greater proportion of lichen occurrences recorded on wood (99%) compared with second-growth (19%). Old-growth indicator species were primarily epixylic or epiphytic species, including *Nephroma bellum* (Sprengel) Tuck., *Platismatia glauca* Taylor and *Hypogymnia occidentalis* L. Pike. This may have been partly due to the relatively higher abundance of woody substrates in old-growth; however, it may also have been due to wood quality differences between forest ages. The greater availability of CWD combined with the microclimate of old-growth stands likely makes for more suitable terrestrial habitat for these epixylic species.

Influence of soil texture

Although differences in species abundance and diversity were anticipated between sites on different soil texture types, this study could not determine a clear

relationship with soil texture in either forest age class. Also, indicator species analysis did not reveal many strong indicators of soil texture type and some of those that were identified may not be ecologically relevant.

In old-growth forest, bryophytes and lichens may not be as strongly affected by differences in underlying soil composition due to the fact that they are commonly found growing on woody substrates or on the litter layer and so are somewhat buffered from the effects of the underlying soil properties. However, though statistical comparison of the totals was not possible, there was a trend towards greater bryophyte diversity on coarse textured soils than on fine textured soils in old-growth forest. Also, NMS ordination of old-growth sites showed soil texture to influence the distribution of bryophyte and lichen species. Vanderpoorten and Engels (2003) found that bryophyte species diversity increased with increasingly sandy forest soils.

In old-growth wet, cool sub-boreal forest, stands on coarse textured soil are more productive (M. Jull, personal communication 2003) and so may have a higher input of woody debris, though in this study only CWD diameter was significantly greater on coarse textured soils. Sites on coarse textured soils had higher shrub cover which may result in more varied microhabitats, may hold more moisture on CWD, or may provide more shade in the summer months. These factors may contribute to slightly higher species diversity on coarse textured soils.

In second-growth, fine textured soils had a significantly higher percent cover of lichens than coarse textured soils, possibly due to the fact that fine textured second-growth sites had a shorter canopy than coarse textured sites. The NMS

analysis of second-growth plots revealed that soil texture was an important explanatory variable though the pattern was not strong. The effects of soil type in the second-growth stands may not be obvious due to the overriding effects of logging on these sites. Clearcut logging would almost certainly cause a greater modification to the overall forest floor environment than differences in underlying soil texture. Further study is needed to resolve the relationship between soil texture and cryptogam species composition.

Succession of bryophytes and lichens after disturbance

Natural succession of lichen and bryophyte communities has been studied in several other systems. Chronosequence studies in boreal forests have noted a transition in terrestrial species composition from colonist moss species, to lichen species, to feather moss mats as the forest reaches canopy closure (Maikawa and Kershaw 1976, Sulyma and Coxson 2001). A study on a postfire chronosequence in a lodgepole pine forest showed a transition from dominant moss cover of *Polytrichum* spp., to lichen species cover, and then finally to feathermoss mats such as *Pleurozium* spp. (Coxson and Marsh 2001). A similar trend may occur in this ecosystem as shrub and tree cover increases. Over time, *Polytrichum juniperinum* and *Cladonia* species in the second-growth forest may give way to the more shade tolerant and old-growth forest dependent moss, lichen and liverwort species. For this transition to occur, microclimate conditions and substrate availability in the second-growth forest must move towards those found in old-growth forests. Given the young age of the second-growth in this study, it is not clear if and when these

conditions will arise. Recent studies in interior cedar hemlock forests of central British Columbia suggest that arboreal lichen assemblages do not recover even after stands are more mature (Campbell and Fredeen 2004) and appear to require old-growth microclimatic and canopy structure conditions (Radies and Coxson 2004). As well, propagules must be available for a species to move into a disturbed area. Increasingly, concerns have been raised as to the inability of many moss, lichen and liverwort species to disperse over long distances as is the case for some old-growth associated lichen species (Dettki et al. 2000, Sillett et al. 2000). With logging continuing across the landscape, the proximity of remaining old-growth forests, and indeed the uncertain future of all old-growth forests, could create dispersal limitations into logged areas. Conservation of small areas of old-growth may aid in protecting propagule sources for recolonization of adjacent areas (Dettki et al. 2000, Newmaster and Bell 2002, Fenton and Frego 2005); however, bryophyte diversity may not be conserved in overly small patches (< 1 ha) due to edge effects on bryophytes extending into the patch (Baldwin and Bradfield 2005).

Even with a propagule source, the length of time required to accomplish the transition from second-growth to old-growth non-vascular floristics is unknown. Will shorter return intervals for harvesting be long enough to allow for the regeneration of the lichen and bryophyte community before the subsequent harvest events? Climate change in northern regions may even preclude regeneration of many species when combined with the multiple effects of forest harvesting disturbance. Retaining a mosaic of forest ages across the landscape may be the only way to ensure that all species have suitable habitat. Schofield (1988) has noted the

importance of maintaining old-growth forest as a benchmark against which to compare the diversity and abundance of bryophytes in successional forests. Additional study of the relationships between soil substrate and forest age and the diversity of the terrestrial lichen and bryophyte community is needed. Until the community dynamics and habitat requirements are better understood, forest managers should retain as much old-growth sub-boreal spruce forest on the landscape as possible.

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Chapter 3

Carbon and nitrogen contributions from terrestrial bryophytes and lichens to a sub-boreal spruce forest

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Abstract

Terrestrial bryophyte and lichen communities can be important components of forest ecosystem carbon and nutrient budgets. The contributions of the dominant terrestrial moss and lichen genera to forest carbon and nitrogen stocks were assessed at sites in old-growth and young second-growth sub-boreal spruce forest on fine and coarse textured soils. Bryophyte and lichen percent nitrogen contents varied among species in both old-growth and young second-growth forest with N_2-fixing lichen species having up to four-fold higher percent nitrogen contents than mosses and non N_2-fixing lichen species. Percent nitrogen ranged from 3.08 - 3.98% for cyanobacterial lichens to 0.56 - 1.51% for mosses and non N_2-fixing lichens. In old-growth forest, percent nitrogen content was higher in bryophytes on coarse textured than fine textured soils. Total biomass carbon and nitrogen contained in bryophytes and lichens were also calculated. Biomass carbon of terrestrial bryophytes and lichens was small when compared with total forest carbon (Fredeen et al. 2005); 0.2 – 0.7% of old-growth forest carbon and 3% of second-growth forest carbon. However, biomass nitrogen may be proportionally more significant due to the potential nitrogen contributions from N_2-fixing lichens and the importance of this nitrogen input to nitrogen-poor woody substrates.

Introduction

Recently, there has been increased interest in the carbon dynamics of forest systems and how carbon is cycled and sequestered within these systems (e.g. Malhi et al. 1999, IPCC 2000), particularly within ratifying nations of the Kyoto Protocol. In order to assess the carbon and nutrient pools contained in a forest ecosystem, an understanding of all components of the system is required. The terrestrial lichen and bryophyte layer is one component of the forest which is often overlooked in studies of forest carbon pools, however, this layer can contain a significant portion of carbon in some forest types. One study in black spruce boreal forest found that the moss layer contained as much carbon as the black spruce forest (Oechel and Van Cleve 1986) while another study indicated that moss photosynthesis contributed 13% of the total forest gross primary production (Swanson and Flanagan 2001). In temperate rainforests in New Zealand, bryophytes contributed less to the forest carbon pool but still constituted 5% of the gross primary production of the forest (DeLucia et al. 2003).

Mosses and lichens are both poikilohydric, meaning they lack roots and instead take up moisture and nutrients across the surface of the moss frond or lichen thallus. As such, their moisture and nutrient status depends largely on their environment (Green and Lange 1995). Bryophytes and lichens, lacking a cuticle and stomata, exchange solutions and gases over the entirety of their frond or thallus surface (Turetsky 2003, Palmqvist 2000). Charged cell walls may increase the nutrient uptake efficiency of bryophytes (Sveinbjörnsson and Oechel 1992). Because bryophytes and lichens cannot control water uptake and loss, moisture is

frequently limiting for metabolic activity (Palmqvist 2000, Turetsky 2003). This also means that both mosses and lichens can acquire nitrogen and other nutrients through wet or dry deposition from the atmosphere (Bates 2000, Palmqvist et al. 2002, Aldous 2002), canopy throughfall (Knops et al. 1991), and soil, litter, or woody substrates (Bates 2000). Wilkinson et al. (2005) even found bryophytes derived nitrogen from salmon carcasses and documented increased nitrogen content in the moss *Rhytidiadelphus loreus* along salmon streams as compared with non-salmon streams. Mosses are very efficient at assimilating nitrogen from atmospheric sources (Turetsky 2003) and may capture 50 - 90% of the nitrogen from simulated rainfall (Weber and Van Cleve 1981, Aldous 2002). In areas with high levels of nitrogenous air pollutants, moss nitrogen content increases dramatically (Pitcairn et al. 1995, Woolgrove and Woodin 1996, Aldus 2002). High levels of nitrogen deposition can be detrimental to moss growth (Van Der Heijden et al. 2000); however, long term exposure to lower levels of elevated nitrogen deposition in the oil sands of Alberta has resulted in increased *Sphagnum* moss production (Vitt et al. 2003).

Unlike mosses, lichens are a symbiotic relationship between a fungal partner (mycobiont) and an algal or cyanobacterial partner (photobiont) (Ahmadjian, 1993). The mycobiont acquires the majority of nutrients from wet and dry deposition while the photobiont acquires the vast majority of the lichen's carbon through photosynthesis and may acquire nitrogen if the photobiont is cyanobacterial (Palmqvist 2000). Lichens may possess green algal and/or cyanobacterial photobionts. In lichens which contain both green algal and cyanobacterial

photobionts (tripartite), green algae are generally the primary photobiont while blue-green algae are the secondary photobiont and are contained in specialized structures called cephalodia (Ahmadjian 1993). Lichen species containing cyanobacteria are capable of fixing atmospheric N_2 (Kershaw 1985) and have been found to contribute significant amounts of nitrogen to forest ecosystems (Knowles 2004). This can be particularly important given that nitrogen commonly limits plant growth and is often a limiting factor in forest productivity and decay processes (Reich et al. 1997, Bhatti et al. 2002). For example, an increase in the rate of leaf litter decay has been reported near N_2-fixing lichens (Knowles 2004) and nitrogen inputs may also contribute to the decomposition of nitrogen-poor woody substrates (Rayner and Boddy 1988).

Recent studies also suggest that some liverwort and moss species, such as the feather moss *Pleurozium schreberi*, are affiliated with cyanobacteria. This association may be responsible for considerable N_2-fixation and input of nitrogen into forests and disturbed ecosystems (Henriksson et al. 1987, DeLuca et al. 2002). The ability of these organisms both to fix N_2 and to absorb nitrogen through deposition can make them important sources of nitrogen in their associated ecosystems (Knops et al. 1991, Turetsky 2003).

Mosses decompose slowly, at rates 1-10% that of the rate of vascular plant matter (Oechel and Van Cleve 1986), due at least in part to their high carbon to nitrogen ratio (Turetsky 2003). Some bryophytes can recycle nitrogen from older tissue into currently growing tissue (Eckstein 2000, Bates 2000, Turetsky 2003) and *Hylocomium splendens* has been shown to have a nitrogen retention time of 3-10

years in the sub-arctic (Eckstein 2000). After two years, *Pleurozium schreberi* and *Hylocomium splendens* growing in a black spruce forest still retained most of their original nitrogen (Weber and Van Cleve 1981). For these reasons, nitrogen and other nutrients obtained from the atmosphere by mosses are often slowly released into the forest ecosystem. Decomposition of N_2-fixing lichen may be higher due to their lower carbon to nitrogen ratio (Longton 1992). However, episodic pulse releases of nutrients, including organic carbon and nitrogen, may occur in bryophytes and lichens after a period of drought. These nutrient releases supply previously inaccessible nutrients to the forest system in a more accessible form (Coxson 1991, Wilson and Coxson 1999, Knowles 2004). Leachate from N_2-fixing *Peltigera* species was nitrogen-enriched by 51% compared with non N_2-fixing lichens (Knowles 2004) and recently fixed nitrogen is particularly prone to leaching from a lichen thallus as it can remain in inorganic form for some time (Boucher and Stone 1992).

This study compared the carbon and nitrogen content of the 6 or 7 most common terrestrial bryophyte and lichen genera growing in old-growth and young second-growth forests on coarse textured and fine textured soils. Lichen and bryophyte biomass carbon and nitrogen were measured and compared across the two forest ages and two soil types.

Methods

Study site

The study took place in the Aleza Lake Research Forest (ALRF) 60 km north-east of Prince George in central British Columbia (122'40"W, 54'11"N) (see Figure 2.1). The ALRF is located in the Sub-Boreal Spruce biogeoclimatic zone and forest is dominated by hybrid spruce (*Picea glauca* (Moench) Voss *x engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (Meidinger and Pojar 1991). Eight study sites were located in two ages of forest and on two dominant soil texture types. Old-growth forests were > 200 years old and young second-growth forests were 15 years old. Soils formed on glaciolacustrine sediments and most areas consist of fine-textured soils ranging from silty clay loam to silty clay. Areas with a veneer of coarse textured soil 1 -2 m thick, ranging in texture from silt loam to sandy loam, are scattered throughout the forest (Arocena and Sanborn 1999). Two sites were sampled from each of the forest age and soil texture combinations (see Figure 2.2, Appendix A). A full description of the Aleza Lake Research Forest and the study sites is given in Chapter 2.

Biomass collection

Terrestrial lichen and bryophyte biomass samples were collected at all eight study sites. Biomass samples were collected for seven genera (5 mosses and 2 lichens) in old-growth forest sites and for six genera (4 mosses and 2 lichens) in second-growth forest sites. Due to more equal species dominance in old-growth, five common moss species were included in old-growth biomass sampling

compared with four in second-growth. In both cases, these 6 or 7 genera made up > 85% of the forest floor percent cover (see below). Three replicate samples of each genus were collected from each site. Biomass samples were collected as 10x10 cm squares, however, samples of 5x5 cm or 2x2 cm were collected for lichens and smaller mosses. The biomass samples were considered to include only living material and samples were carefully cleaned to remove all dead material and litter. Samples were oven dried at 65 °C for 48 hours for dry weight determinations.

The biomass estimates were combined with terrestrial lichen, moss and liverwort percent cover data for each site to obtain an estimate of the biomass of lichen and bryophyte species per square metre. A description of the methodology used to collect percent cover data for bryophytes and lichens is given in Chapter 2.

In old-growth forest sites, the biomass values for the seven genera of moss and lichen were used to give an estimate of biomass for 25 species of those genera which composed between 85% and 93% of the lichen and bryophyte ground cover of the old-growth sites. Similarly, in second-growth forests, the biomass values of the six dominant genera of moss and lichen were used to estimate the biomass of 42 species of these genera which composed between 87% and 98% of the lichen and bryophyte ground cover of the second-growth forest sites. Thus, across all sites, the biomass estimates take into account at least 85% of the actual terrestrial bryophyte and lichen biomass (Appendix G and H). Due to their small size and the difficulty of collecting large enough homogeneous samples, liverwort samples were not collected. Liverworts contributed only between 1.5% (old-growth) and 0.06% (second-growth) to the total terrestrial bryophyte and lichen cover (Chapter 2).

Carbon and nitrogen content

After oven-drying (65°C for 48 hours), each of the lichen and moss biomass samples was ground to a fine powder using first an electric coffee grinder and then a Model MM200 mixer mill (Retsch Co., Haan, Germany). Duplicate sub-samples (approximately 4 g) of each moss and lichen sample were weighed. The sub-samples were then analyzed using the Dumas combustion method (Kirsten 1983) using a NA 1500 Elemental Analyzer (Fisons Instruments SP, Italy) to assess the carbon and nitrogen content by weight for each sample.

Data analysis

Data were analysed using a series of ANOVAs. ANOVAs (α of 0.05) with the main effects of forest age, soil texture type, and site (as a random variable) nested in forest age and soil texture were used to examine differences in carbon and nitrogen biomass between sites, forest ages and soil texture types. ANOVAs (α of 0.05) with the main effects of species, soil texture type, and site (as a random variable) nested in soil texture were used to examine differences in percent carbon and nitrogen content between site, species and soil texture type for each age class.

Results

Nitrogen content and biomass of lichens and bryophytes

In old-growth sites, moss and lichen species percent nitrogen (N) content by weight was significantly different between soil texture types (ANOVA; p=0.002) and

among species (ANOVA; $p<0.001$). Percent N content was higher on coarse textured soils (1.85% N) than fine textured soils (1.71% N) (Table 3.1; Appendix I). However, when moss species and the two *Peltigera* Willd. lichen species were separated, moss species percent N was significantly different between soil types (ANOVA; $p=0.004$) but *Peltigera* species percent N was not (ANOVA; $p=0.200$).

In old-growth, the percent N contents of N_2-fixing *Peltigera* lichen species (3.07 - 3.98%) were as much as four-fold higher than those of moss species (0.91 - 1.51%). A significant difference in N content was seen between the two N_2-fixing *Peltigera* species (ANOVA; $p<0.001$), with the bipartite *Peltigera membranacea* (Ach.) Nyl. (3.74 - 3.98%) having a higher nitrogen content than the tripartite *Peltigera aphthosa* (L.) Willd. (3.07 - 3.08%). When the lichen species were removed from the analysis, there was still a significant difference in percent N among moss species (ANOVA; $p<0.001$) with *Rhizomnium nudum* (Britt. & Williams) T. Kop. having a consistently higher percent N than the other moss species.

Percent N content of mosses and lichens was also significantly different among species in second-growth sites (ANOVA; $p<0.001$) but was not different between soil texture types (ANOVA; $p=0.730$). The one N_2-fixing *Peltigera* species, *Peltigera canina* (L.) Willd., again, had much higher N content than the other non N_2-fixing lichen and moss species in second-growth stands (Table 3.1; Appendix I). Total biomass N was not significantly affected by forest age (ANOVA; $p=0.060$) or by soil texture type (ANOVA; $p=0.200$), though there was a significant site effect (ANOVA; $p<0.001$).

Table 3.1 – Mean percent nitrogen content by weight for moss and lichen species analysed from old-growth and young second-growth sites on fine textured and coarse textured soils in sub-boreal spruce forest (± standard deviation, n = 6 samples per species).

Forest age	Soil texture	Species	% Nitrogen
Old-growth	Coarse	*Hylocomium splendens* (Hedw.) Schrimp.	1.17 ± 0.05
		Peltigera aphthosa (L.) Willd.	3.08 ± 0.22
		Peltigera membranacea (Ach.) Nyl.	3.98 ± 0.23
		Pleurozium schreberi (Brid.) Mitt.	1.02 ± 0.07
		Ptilium crista-castrensis (Hedw.) De Not.	1.03 ± 0.14
		Rhytidiadelphus triquetrus (Hedw.) Warnst.	1.14 ± 0.22
		Rhizomnium nudum (Britt. & Williams) T. Kop.	1.51 ± 0.12
	Coarse mean		1.85 ± 1.12
Old-growth	Fine	*Hylocomium splendens* (Hedw.) Schrimp.	0.95 ± 0.23
		Peltigera aphthosa (L.) Willd.	3.07 ± 0.27
		Peltigera membranacea (Ach.) Nyl.	3.74 ± 0.22
		Pleurozium schreberi (Brid.) Mitt.	0.91 ± 0.08
		Ptilium crista-castrensis (Hedw.) De Not.	0.97 ± 0.33
		Rhytidiadelphus triquetrus (Hedw.) Warnst.	0.95 ± 0.25
		Rhizomnium nudum (Britt. & Williams) T. Kop.	1.38 ± 0.17
	Fine mean		1.71 ± 0.17
Old-growth mean			1.78 ± 1.12
Second-growth	Coarse	*Ceratodon purpureus* (Hedw.) Brid.	1.26 ± 0.46
		Cladonia spp. P. Browne	0.62 ± 0.21
		Peltigera canina (L.) Willd.	3.36 ± 0.30
		Pleurozium schreberi (Brid.) Mitt.	0.79 ± 0.16
		Pohlia nutans (Hedw.) Lindb.	1.36 ± 0.26
		Polytrichum juniperinum Hedw.	1.01 ± 0.06
	Coarse mean		1.40 ± 0.95
Second-growth	Fine	*Ceratodon purpureus* (Hedw.) Brid.	1.30 ± 0.42
		Cladonia spp. P. Browne	0.56 ± 0.15
		Peltigera canina (L.) Willd.	3.46 ± 0.20
		Pleurozium schreberi (Brid.) Mitt.	1.00 ± 0.18
		Pohlia nutans (Hedw.) Lindb.	1.11 ± 0.27
		Polytrichum juniperinum Hedw.	1.09 ± 0.12
	Fine mean		1.42 ± 0.98
Second-growth mean			1.41 ± 0.96
Total mean			1.61 ± 1.06

In old-growth forest, the terrestrial lichen and bryophyte layer contained an average of 1.0 g N m^{-2} on coarse textured soils and 2.3 g N m^{-2} on fine textured soils. In second-growth, the lichen and bryophyte layer contained an average of 3.0 g N m^{-2} on coarse textured soils and 4.3 g N m^{-2} on fine textured soils (Table 3.2).

Carbon content and biomass of lichens and bryophytes

In old-growth sites, percent carbon (C) content of lichen and bryophyte species by weight did not differ significantly between soil types (ANOVA; p=0.063) though in all but one species, percent C was higher on coarse textured sites (Table 3.3; Appendix I). Percent C was significantly different among species (ANOVA; p=0.002) with some moss species, such as *Rhizomnium nudum* (44.8%), having lower percent C than others, such as *Pleurozium schreberi* (Brid.) Mitt. (46.8%) and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. (46.5%). The two *Peltigera* species sampled in old-growth also differed in C content with *Peltigera aphthosa* having a higher percent C (47.7%) than *Peltigera membranacea* (45.2%). In contrast, percent C content did not differ significantly between soil types (ANOVA; p=0.260) or among species (ANOVA; p=0.390) in young second-growth stands (Table 3.3; Appendix I).

In old-growth sites, the terrestrial lichen and bryophyte species contained on average 39.1 g C m^{-2} on coarse textured soils and 110.4 g C m^{-2} on fine textured soils. In young second-growth sites, terrestrial lichen and bryophyte species accounted for, on average, 135.5 g C m^{-2} on coarse textured soils and 157.3 g C m^{-2} on fine textured soils (Table 3.4). Due to a high degree of variation among sites,

Table 3.2 – Mean biomass nitrogen (g m^{-2}) in terrestrial mosses and lichens old-growth and young-second growth sites on fine textured and coarse textured soils in sub-boreal spruce forest (± standard deviation, n=6 plots).

Forest age	Soil texture	Nitrogen (g m^{-2})
Old-growth	Coarse	1.0 ± 0.5
Old-growth	Fine	2.3 ± 0.4
Old-growth average		1.7 ± 0.8
Second-growth	Coarse	3.0 ± 1.7
Second-growth	Fine	4.3 ± 1.4
Second-growth average		3.6 ± 1.6

Table 3.3 – Mean percent carbon content by weight for moss and lichen species analysed from old-growth and young second-growth sites on fine textured and coarse textured soils in sub-boreal spruce forest (± standard deviation, n=6 samples per species).

Forest age	Soil texture	Species	% Carbon
Old-growth	Coarse	*Hylocomium splendens* (Hedw.) Schrimp.	46.47 ± 0.48
		Peltigera aphthosa (L.) Willd.	48.32 ± 0.18
		Peltigera membranacea (Ach.) Nyl.	45.64 ± 0.20
		Pleurozium schreberi (Brid.) Mitt.	47.23 ± 0.58
		Ptilium crista-castrensis (Hedw.) De Not.	45.49 ± 0.70
		Rhytidiadelphus triquetrus (Hedw.) Warnst.	46.68 ± 0.82
		Rhizomnium nudum (Britt. & Williams) T. Kop.	44.85 ± 1.12
	Coarse mean		46.38 ± 1.26
Old-growth	Fine	*Hylocomium splendens* (Hedw.) Schrimp.	46.24 ± 0.59
		Peltigera aphthosa (L.) Willd.	47.14 ± 0.46
		Peltigera membranacea (Ach.) Nyl.	44.83 ± 0.48
		Pleurozium schreberi (Brid.) Mitt.	46.49 ± 0.37
		Ptilium crista-castrensis (Hedw.) De Not.	45.85 ± 0.50
		Rhytidiadelphus triquetrus (Hedw.) Warnst.	46.32 ± 0.51
		Rhizomnium nudum (Britt. & Williams) T. Kop.	44.72 ± 0.61
	Fine mean		45.94 ± 0.95
Old-growth mean			46.16 ± 1.13
Second-growth	Coarse	*Ceratodon purpureus* (Hedw.) Brid.	46.49 ± 3.47
		Cladonia spp. P. Browne	44.85 ± 0.21
		Peltigera canina (L.) Willd.	45.32 ± 0.72
		Pleurozium schreberi (Brid.) Mitt.	46.85 ± 1.47
		Pohlia nutans (Hedw.) Lindb.	43.67 ± 4.50
		Polytrichum juniperinum Hedw.	45.69 ± 2.13
	Coarse mean		45.48 ± 2.61
Second-growth	Fine	*Ceratodon purpureus* (Hedw.) Brid.	39.46 ± 10.47
		Cladonia spp. P. Browne	45.26 ± 0.92
		Peltigera canina (L.) Willd.	45.75 ± 0.45
		Pleurozium schreberi (Brid.) Mitt.	45.78 ± 1.02
		Pohlia nutans (Hedw.) Lindb.	40.50 ± 10.64
		Polytrichum juniperinum Hedw.	46.68 ± 2.17
	Fine mean		43.90 ± 6.40
Second-growth mean			44.69 ± 4.92
Total mean			45.48 ± 3.51

Table 3.4 – Average biomass carbon (g m^{-2}) of terrestrial mosses and lichens in old-growth and young-second growth sites on fine textured and coarse textured soils in a sub-boreal spruce forest (± standard deviation, n=6 plots).

Forest age	Soil texture	Carbon (g m^{-2})
Old-growth	Coarse	39 ± 22
Old-growth	Fine	110 ± 22
Old-growth average		75 ± 43
Second-growth	Coarse	136 ± 73
Second-growth	Fine	157 ± 58
Second-growth average		136 ± 64

there was no significant difference in biomass C of the terrestrial moss and lichen layer between old-growth and young second-growth sites (ANOVA; $p=0.110$) or between soil texture types (ANOVA; $p=0.270$). Site was statistically significant (ANOVA; $p<0.001$). Though not significant statistically, young second-growth stands had higher biomass C than old-growth stands (Appendix I).

Discussion

Nitrogen

The percent N contents of the bryophyte and lichen species in this study were similar to those found in other studies. Percent N contents of 0.79-1.02% for *Pleurozium schreberi* and 1.01-1.09% for *Polytrichum juniperinum* Hedw. found in this study were only slightly lower than those reported by Hunt et al. (2005) for a jack pine forest (0.99% *Pleurozium schreberi*, 1.38% *Polytrichum juniperinum*). The lower N content in the non N_2-fixing *Cladonia* Browne species in this study (0.56-0.62%) was also recorded for *Cladina* species in that system (0.44%) (Hunt et al. 2005). In Alaskan forests, N contents for *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* were 0.83% and 0.76%, respectively, while on a warmer, more productive site in the Yukon, N contents ranged from 1.9 to 2.4 % (Weber and Van Cleve 1981). These values bracket the 1.1% N content of *H. splendens* and 1.0% N content of *P. schreberi* found in this study. Some variation in N content between studies may be due to seasonal variation in N content with metabolic activity, often resulting in higher N during the winter and lower N contents during the

growing season (Hovenden 2000).

Peltigera lichen species had higher N contents than moss species and *Cladonia* lichen species due to their ability to fix N_2. All *Peltigera* species contain a cyanobacterial photobiont capable of fixing N_2, however, in *P. membranacea* and *P. canina,* the primary photobiont is the cyanobacterium *Nostoc* while in *P. aphthosa,* the primary photobiont is the green algae *Cocomyxa* with the cyanobacterium *Nostoc* as the secondary photobiont (Brodo et al. 2001). The higher observed N contents in *P. membranacea* and *P. canina* are consistent with a cyanobacteria being the primary photobiont. Palmqvist et al. (2002) surveyed 75 lichen species and found that lichens with cyanobacteria as the primary photobiont had the greatest N concentration followed by tripartite lichens and then lichens having only green algal photobionts. They found a similar range of N contents for lichen in boreal forests (green algal lichens, 1.1%; tripartite lichens, 2.2%; cyanobacterial lichens, 3.7%) to those we observed for the sub-boreal forest floor. As well, the N contents they found for *Peltigera* species in boreal and arctic systems (*P. aphthosa,* 2.2-3.3%; *P. canina,* 3.6-4.6%; *P. membranacea,* 2.4-3.1%) were similar to those encountered in this study (*P. aphthosa,* 3.1%; *P. canina,* 3.4%; *P. membranacea,* 3.9%). Kershaw (1985) gives thallus percent N contents for a range of lichens with cyanobacterial photobionts spanning from 2.2% to 6.4% and gives values of 3.3-3.5% for two *Peltigera* species.

Peltigera species percent cover was much higher on second-growth forest floor (2.96%) than in old-growth forest floor (0.83%) (see Chapter 2). These results indicate the potential for greater N_2-fixation by *Peltigera* species in second-growth

sites, possibly resulting in higher N inputs into this disturbed system. These increased N inputs may be important in enriching soils in second-growth sites which have been depleted due to disturbance, have lost epiphytic N_2-fixing lichens, and have reduced organic soil matter because of post-harvest broadcast burning. Higher light levels in second-growth versus old-growth understory could further enhance N_2-fixation by cyanobacterial lichens in the second-growth stands (Kershaw 1985).

N_2-fixation can be particularly important in secondary succession when total N is low (Berglund 2004). Foster et al. (1995) found that full tree harvesting of a jack pine forest would remove 50% of the forest carbon and 300 kg ha^{-1} of nitrogen. As well, in sites like the Aleza Lake Research Forest where most nitrogen, sulphur, and phosphorus are concentrated in the organic horizons (Arocena and Sanborn 1999), treatments such as burning that remove the surficial organic matter may deplete total forest nutrient pools (Ballard and Carter 1985). Bhatti et al. (2002) note that N losses from disturbance such as forest harvesting must be offset by N inputs in order for the forest to be productive. In the forests of northern Minnesota, it was estimated that the input of N leached from N_2-fixing *Peltigera* species was > 0.2 g N ha^{-1} yr^{-1} while most of the input of N resulted from decaying thalli, 100 g N ha^{-1} yr^{-1} (Knowles 2004). Combined, they represented a small proportion of the nitrogen requirements of the forest but were still an important exogenous source of N and helped to counter the effects of N loss due to harvesting, erosion, and leaching (Knowles 2004). In boreal and tundra ecosystems, N_2-fixation by terrestrial lichens and mosses with cyanobacterial associations is estimated to result in inputs of 50 -

400 mg N m^{-2} yr^{-1} (cited in Longton 1992). Knowles (2004) also found that *Peltigera* species increased soil N contents in a sphere up to 150 cm around each lichen thallus and that there were increased rates of leaf litter decay near *Peltigera* thalli.

N_2-fixation by *Peltigera* and other cyanobacterial lichens may also play an important role in old-growth forests. Nitrogen levels are often low in wood and limit log decomposition (Rayner and Boddy 1988). Given that in old-growth stands in this study, *Peltigera* species were generally growing on woody substrates (see Chapter 2), N inputs by *Peltigera* species may be promoting wood decomposition in old-growth stands. Also, old-growth forests have been found to contain significant biomasses of arboreal cyanobacterial lichens which are absent in regenerating stands (Benson and Coxson 2002). In interior cedar hemlock forests in British Columbia, Benson and Coxson (2002) found arboreal cyanolichen biomasses of 1 332 kg ha^{-1} in old-growth forest that was absent in regenerating forest. Further study would be required to determine the extent that N_2-fixation by lichens is enriching both old-growth and second-growth stands.

In mid to late successional boreal forests, a cyanobacterial symbiosis with the feather moss *Pleurozium schreberi* resulted in substantial N inputs (1.7 kg N ha^{-1} yr^{-1}) through N_2-fixation (DeLuca et al. 2002). Other moss and liverwort species, such as the genus *Ceratodon*, have also been found to form cyanobacteria associations (Henriksson et al. 1987, Rai et al. 2000). The extent to which N_2-fixing cyanobacteria may be associated with moss species, such as *Pleurozium schreberi,* in sub-boreal forests is not known. In this study, *Rhizomnium nudum* had significantly lower % C and higher % N values than the other moss species,

potentially indicating the presence of an N_2-fixing association. *Ceratodon purpureus* also had a high % N. Additional examination would be needed to confirm the existence of bryophyte-cyanobacterial associations in these sub-boreal forests.

In white spruce boreal forest, Oechel and Van Cleve (1986) found that the moss layer contained 13 kg N ha^{-1}, a similar amount to the 17 kg N ha^{-1} (1.7 g N m^{-2}) held in the moss and lichen layer of old-growth sub-boreal spruce forests in this study. They found that the N contained in the moss layer was almost the same as the N held in the white spruce itself (16 kg N ha^{-1}). The biomass N held in the bryophyte and lichen layer of the sub-boreal spruce forests in this study can be compared with the foliar biomass N contained in the foliage of the trees (Fredeen et al. 2005). Assuming a spruce foliar C content of 50% (Lamlon and Savidge 2003) and a spruce foliar N content of 1.06% (Swift and Brockley 1994), the foliar biomass N of trees in old-growth stands were 155 kg N ha^{-1} on coarse textured soils and 179 kg N ha^{-1} on fine textured soils. Thus, the lichen and bryophyte layer of the forest floor contributed 6% of the total tree foliar and cryptogam biomass N on coarse textured soils and 12% on fine textured soils. In second-growth stands, the biomass N from tree foliage was smaller, therefore, lichen and bryophyte biomass N contributed between 28% and 67% of the total tree and cryptogam biomass N. Thus, though bryophytes and lichens represented a small proportion of the biomass C of the sub-boreal spruce forests in this study, it is likely that they contributed a more significant proportion of the biomass N in this ecosystem.

This study found bryophyte N contents to be significantly greater on coarse textured soils than fine textured soils in old-growth stands while lichens showed no

difference in N content with soil texture type. At the Aleza Lake Research Forest, the coarse textured soils consist of silt loams to sandy loams and are imperfect to well drained while the fine textured soils are silt clays to clays and are imperfect to poorly drained (Arocena and Sanborn 1999, Fredeen et al. 2005). Stands on coarse textured soil have a greater volume of trees and are more productive forests (M. Jull personal communication 2003, Fredeen et al. 2005). The better drainage of the coarse textured soils may lead to faster decomposition of organic matter and higher nutrient availability in the soils. Increased clay content resulting in poorer drainage and reduced aeration often leads to reduced decomposition, decreased N mineralization, and reduced available N (Bhatti et al. 2002). Given that N is usually limiting in forest ecosystems, reduced N can result in lower forest productivity and less carbon storage (Bhatti et al. 2002). Furthermore, in this study, sites on coarse textured soils had a greater abundance of plant species indicative of increased N availability, such as *Oplopanax horridus* (Sm.) Miquel, *Rubus parviflorus* Nutt. and *Streptopus roseus* Michx. (see Appendix F) (Klinka et al. 1989). Weber and Van Cleve (1981) found higher N contents in mosses on black spruce permafrost-free sites with better nutritional status compared with permafrost sites with poorer nutritional status. Other sites with warmer temperatures and better drainage had even greater total N concentrations and faster microbial decomposition (Weber and Van Cleve 1981). Økland et al. (1999) found that elemental concentrations in the moss *Hylocomium splendens* varied with soil nutrient conditions between sites in spruce forest. It is possible then that the increased N contents of bryophytes on coarse textured soils in this study are due to N enrichment from a more productive

underlying soil layer as a result of greater litter inputs from a more productive forest stand and enhanced decomposition from better drained soils. The fact that *Peltigera* lichens were not affected by soil type may be due to the fact that they were primarily growing on wood and would not likely have been as affected by N enrichment in the soil. It may also be that these N_2-fixing species are not as dependent on external sources of N as mosses are. Further study would be needed to verify linkages between nitrogen and soil type.

Carbon

This study found that the contribution of live green terrestrial bryophytes and lichens to the old-growth sub-boreal spruce forest C pool was 39 g C m^{-2} (390 kg C ha^{-1}) on coarse textured soils and 110 g C m^{-2} (1100 kg C ha^{-1}) on fine textured soils. This is of similar magnitude to the 960 kg C ha^{-1} contained in the live green bryophytes in a densely treed black spruce bog in Ontario (Dyck and Shay 1999) and the 720 kg C ha^{-1} of moss in a boreal black spruce forest in Saskatchewan (Uchida et al. 1998). A concurrent study at the Aleza Lake Research Forest found forest C contributions for the herb, shrub, tree and total living biomass of old-growth sites to be 100, 5 300, 155 000, and 195 000 kg C ha^{-1} for coarse textured soils and 200, 300, 119 000, and 149 000 kg C ha^{-1} for fine textured soils (Fredeen et al. 2005). Thus, the moss and lichen forest floor contributed 0.2% and 0.7% to total old-growth forest C pool on coarse and fine textured soils, respectively. For old-growth stands, the bryophyte and lichen layer contained a small proportion of the total forest C biomass, but an amount that exceeded that found in the herbaceous

plant layer on coarse textured soils and herbaceous and shrub layers combined on fine textured soils. A study of mosses in an old-growth Douglas-fir forest had a total biomass of 1075 kg ha-1 and contributed only 0.7% of the above ground biomass (Binkley and Graham 1981). Hunt et al. (2005) also found that the understory vegetation of jack pine forests comprised a small proportion of the total above ground biomass (0.4-2.6%), though it contributed a greater proportion of the above ground nutrient pool. This may also be the case in these sub-boreal spruce forests.

In second-growth stands, the moss and lichen layer constituted a greater proportion of the overall forest C pool. In second-growth, C contributions for bryophytes and lichens, herbs, shrubs, trees, and total pool were 1 360, 3500, 6500, 20 000, and 42 000 kg C ha^{-1} for coarse textured soils and 1 570, 300, 700, 9 000, and 49 000 kg C ha^{-1} for fine textured soils, respectively. Thus, the terrestrial moss and lichen layer contributed 3% of the overall second-growth forest C pool on both coarse and fine textured soils and contained more biomass than both the herb and shrub layers combined on fine textured soils.

A study of two moss species in Alaska by Weber and Van Cleve (1981) found similar, though slightly lower, percent C contents to those found in this study. They recorded a C content of 40.8% for *Hylocomium splendens* and 40.9% for *Pleurozium schreberi* compared with 46.4% for *H. splendens* and 46.9% for *P. schreberi* found in this study. A study of lichen in Alaska found percent C contents in a tripartite lichen, *Peltigera aphthosa,* to be 44.3% and in a cyanobacterial lichen, *P. malacea*, to be 45.5% (Hahn et al. 1993). This study found similar percent C contents for the cyanobacterial *P. membranacea* but higher percent C contents for *P. aphthosa*.

Due to their poikilohydric nature, lichens and bryophytes undergo frequent periodic cycles of desiccation and rehydration (Turetsky 2003). After drying and rewetting cycles, bryophytes may contribute a pulse of nitrogen, phosphorus and soluble carbon to the forest floor through leaching (Carleton and Read 1991, Wilson and Coxson 1999). In a sub-alpine spruce-fir forest in Alberta, Wilson and Coxson (1999) found that the feather moss mat may release a pulse of up to 15 kg ha^{-1} of soluble C during a rain event. Carleton and Read (1991) found that carbon, nitrogen and phosphate leachates from the moss *Pleurozium schreberi* were transferred to mycorrhizal mycelia and then to infected conifer roots. Thus even when bryophytes and lichens contribute little to forest C biomass, they are still contributing to the C and nutrient dynamics of the forest ecosystem.

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Chapter 4

Net ecosystem CO_2 exchange from the forest floors of old-growth sub-boreal spruce forests

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Abstract

This study used instantaneous chamber-based CO_2 exchange measurements (2004) in conjunction with seasonal microclimate data (2003) to model growing season net ecosystem CO_2 exchange (NEC) for terrestrial bryophyte and lichen communities in a sub-boreal forest in central British Columbia, Canada. Multiple regression models using microclimate variables described between 35 and 53% of the variation in moss or lichen dominated forest floor NEC at ambient CO_2 concentrations in the light and dark. Moss or lichen moisture content, moss or lichen temperature, and light level were all important variables in describing NEC variation from moss and lichen dominated forest floor patches while soil temperature was the most important variable explaining NEC from bare soil and wood. Moss dominated forest floor, predominantly composed of *Rhytidiadelphus triquetrus*, showed relatively constant NEC rates in the light across the three month period while lichen (*Peltigera membranacea*) dominated logs showed more negative NEC rates in July and August and less negative NEC rates in September. Over the three month growing season of 2003, moss dominated forest floor had a total NEC of -33.8 g C m^{-2} and lichen dominated wood had a total NEC of -42.9 g C m^{-2}. When NEC from the moss, lichen, bare wood and bare litter components of the forest floor

community is summed over the three month period, the old-growth sub-boreal spruce forest floor had an NEC of -31.6 g C m^{-2}, representing a loss of this amount of carbon over this interval. The moss dominated forest floor seemed to be limited by ambient CO_2 concentrations of 430 µmol mol^{-1} and exhibited increased photosynthesis when the CO_2 concentration was increased to 700 µmol mol^{-1}. The lichen on wood substrate did not show an increase in photosynthesis at the higher CO_2 concentration.

Introduction

In light of climate change, there is increased need to quantify carbon pools and fluxes and there has been a recent focus on the importance of understanding the carbon dynamics of forest ecosystems (Malhi et al. 1999) in order to assess the ways in which climate variables influence the carbon balance of forest ecosystems. One forest ecosystem component that is not always included in carbon budget models is the forest floor community. However, CO_2 flux from the terrestrial bryophyte and lichen layer can contribute significantly to the overall forest CO_2 flux (Goulden and Crill 1997, Morén and Lindroth 2000, Swanson and Flanagan 2001). In the boreal forest, mosses may take up 35% of the forest floor CO_2 efflux (Swanson and Flanagan 2001) and can store 10-50% of the gross CO_2 uptake of the black spruce forest (Goulden and Crill 1997). In northern peat bogs, *Sphagnum* mosses are the primary mechanism for carbon sequestration (O'Neil 2000). Therefore, a better understanding of the CO_2 exchange from the forest floor can

contribute significantly to an understanding of forest carbon cycling.

In mosses and lichens, photosynthesis and respiration are controlled largely by microclimate conditions (Palmqvist 2000). Due to their poikilohydric nature, the growth of non-vascular plant species and lichens is often limited by environmental water availability (Hahn et al. 1993, Sundberg et al. 1997, Palmqvist and Sundberg 2000). With sufficient moisture, light and temperature are often limiting factors (Hahn et al. 1993, Palmqvist 2000, Swanson and Flanagan 2001, Heijmans et al. 2004). Light levels in the forest understory are generally patchy due to the variable canopy overhead, with short sunflecks providing periods of elevated light in the shaded understory (Pearcy and Pfitsch 1995, Canham et al. 1999). Sunflecks can provide a high proportion of the total light intensity, up to 50% of the light reaching the forest floor of temperate forests (Chazdon and Pearcy 1991). Temperature is often less important than moisture or light but high temperatures can decrease carbon gain in lichens (Palmqvist 2000). Respiration from the underlying soil and woody substrates of the forest floor is largely affected by temperature and by moisture availability (e.g. Bowden et al. 1998, Russell and Voroney 1998, Drewitt et al. 2002, Dilustro et al. 2005).

Seasonal net ecosystem CO_2 exchange (NEC) estimates for the forest floor have commonly been obtained using chamber-based measurements, either continuously operating automated chamber systems (e.g. Goulden and Crill 1997) or manually operated instantaneous flux measurements (e.g. Swanson and Flanagan 2001). Given the dependence of the forest floor community NEC on climate and microclimate variables, continuous seasonal microclimate values are required for

temporal scaling up of instantaneous NEC measurements.

In a world experiencing increasing atmospheric CO_2 concentrations, mosses and lichens on the forest floor are already growing in a localized elevated CO_2 environment due to their proximity to the respiring soil layer below (Sonesson et al. 1992, Tarnawski et al. 1994, Green and Lange 1995, Coxson and Wilson 2004). In a sub-alpine spruce forest, Coxson and Wilson (2004) found average CO_2 levels of 700 μmol mol^{-1} in the middle of moss mats and 430 μmol mol^{-1} at the mat surface. This elevated CO_2 environment may be affecting bryophyte photosynthesis and may be increasing productivity. Some moss species appear to be CO_2 limited at ambient levels and do not become CO_2 saturated until 2000 μmol mol^{-1} (Green and Lange 1995). There is less consensus on the effect that elevated CO_2 has on lichen species, partly due to the varying responses of some lichens to elevated CO_2 and the dependence upon moisture content (Green and Lange 1995, Lange et al. 1996). For example, in some lichens, CO_2 diffusion can be impeded by water films (Cowan et al. 1992).

This study aimed to assess the contribution of bryophyte and lichen forest floor communities to the overall ecosystem carbon balance of sub-boreal forests. Chamber gas exchange techniques were used to take instantaneous net ecosystem CO_2 exchange (NEC) measurements across the growing season for moss or lichen dominated forest floor and for bare soil and wood substrates. Instantaneous measurements of microclimate made in conjunction with the instantaneous NEC measurements (2004) were used to generate multiple regression models that could then be applied to continuous seasonal microclimate measurements (2003) to model

NEC for an entire season. This study also examined the response of lichen and moss dominated forest floor NEC to an elevated CO_2 concentration (700 µmol mol^{-1}) in relation to the ambient CO_2 concentration of the forest floor (430 µmol mol^{-1}).

Methods

Study area

The study was located in the Aleza Lake Research Forest in central British Columbia, 60 km northeast of Prince George, BC (122'40"W, 54'11"N) (see Fig. 2.1). The Aleza Lake Research Forest has been managed as a research forest almost continuously since 1924 and is currently co-managed by the University of Northern British Columbia and the University of British Columbia. The Aleza Lake Research Forest is located in the Sub-Boreal Spruce biogeoclimatic zone in the cool wet variant SBSwk1 (Meidinger and Pojar 1991). The dominant tree species are hybrid spruce (*Picea glauca* (Moench) Voss *x engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.) make up a lesser proportion of the canopy (DeLong 2003). At an elevation of 600-700 m, the research forest climate is characterized by cool snowy winters and moist cool summers (OES 1995). The Aleza Lake Research Forest receives 900 mm of precipitation a year with 65% of that falling as rain and 35% falling as snow. Average monthly temperatures range from about 20 °C in July to -20 °C in

January (Murphy 1996). Soils in the region consist primarily of fine-textured, clay dominated glaciolacustrine soils with scattered pockets of overlying coarse-textured soils (Arocena and Sanborn 1999).

Two forest stands were examined in this study, both of which were located in old-growth sub-boreal spruce forest growing on fine textured soil. Both old-growth stands were older than 200 years of age and had many of the structural characteristics of an old-growth sub-boreal spruce forest (Kneeshaw and Burton 1998). Soils were cored and soil texture type was verified over the sites. The study sites will be referred to as site A and site B in this chapter though both of these sites have been described in more detail in Chapter 2 and are equivalent to sites OF1 and OF2, respectively (Figure 2.2, Appendix A).

In the study sites, mosses, liverworts and lichens constituted on average 53% of the forest floor cover (Chapter 2). Mosses composed the majority of this cover and the most common moss species included *Pleurozium schreberi* (Brid.) Mitt., *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *Ptilium crista-castrensis* (Hedw.) and *Hylocomium splendens* (Hedw.) B.S.G. The most common lichens were of the genus *Peltigera* Willd. This study examined the moss *Rhytidiadelphus triquetrus* growing on soil and the lichen *Peltigera membranacea* (Ach.) Nyl. growing on coarse woody debris. *Rhytidiadelphus triquetrus* is an upright moss typically found growing in loose mats often on the soil litter layer (Schofield 1992). *Peltigera membranacea* is a foliose lichen with a cyanobacteria as the primary photobiont and is often found growing on decaying wood (Brodo et al. 2001). Coarse woody debris substrates studied were all of a moderate decay class, decay class 3-4 using

definitions taken from the British Columbia Ministry of Forests (where 1 is less decayed and 5 is most decayed) (Ministry of Forests and Ministry of Environment 1998).

Seasonal microclimate measurements

During the 2003 growing season, microclimate stations were set up at each of the two study sites from 26 June to 22 October 2003. The data loggers were checked and downloaded every two weeks throughout this season. At site A, light measurements from three quantum sensors (Li-Cor Inc., Lincoln, NE, USA) randomly placed throughout the site were recorded every five minutes using a 21X data logger (Campbell Scientific, Logan, UT, USA). At both sites, soil, moss frond, and lichen thallus temperatures were recorded every five minutes using CR10X data loggers (Campbell Scientific). Soil temperature was recorded using a copper constantan thermocouple (0.27 x 0.46 mm) (Omega Engineering Inc., Indianapolis, IN, USA) inserted 10 cm into the ground. The temperatures of two lichen thalli and two moss fronds were measured using fine wire copper constantan thermocouples (Omega Engineering Inc.) placed into the middle of a moss mat or through a lichen thallus. Air temperature was recorded by the internal thermocouple of the data loggers.

At both sites, the moisture contents of three lichen thalli and three moss fronds were measured using the impedance method as described by Coxson (1991). Electrical impedance measurements were taken between pairs of non-serrated microclips (also known as alligator clips) attached to the outer edge of a

lichen thallus or the main stem of a moss frond, at a distance of 5 mm apart. The microclips were 1 mm wide and were attached at a depth of 5 mm for a contact surface area of 5 mm^2. The microclips were covered with plastic clip covers to prevent interference with current flow due to the clips touching each other or the ground. An AC half bridge with excitation voltage of 2500 mV was applied to the microclips from the CR10X data logger (Campbell Scientific) and impedance measured in ohms. In the lab, the impedance measurements were calibrated to the actual percent water content of the lichen or moss. Measurements were conducted on single moss fronds and similar sized pieces of lichen thalli, at a temperature of 21 °C. The lichen/moss was first soaked in water for several hours then removed and patted dry to remove any water adhering to the surface. The lichen/moss was fitted with two microclips and impedance measurements were taken every 5 – 15 minutes followed by weight determination. This continued until the lichen/moss reached a lower moisture level than could be measured with the impedance method. The lichen/moss was then oven dried at 60 °C for 48 hours and weighed to obtain dry weight. Percent moisture was calculated as: (wet weight – dry weight)/dry weight * 100. These measurements were repeated 3 times for each set of moisture clips that had been used in the field for a total of 18 replicates each for moss and lichen. The percent moisture and the impendence values were plotted and fit with curves (Fig. 4.1) and used to estimate moss frond or lichen thallus moisture content over the growing season.

Corrections to microclimate data

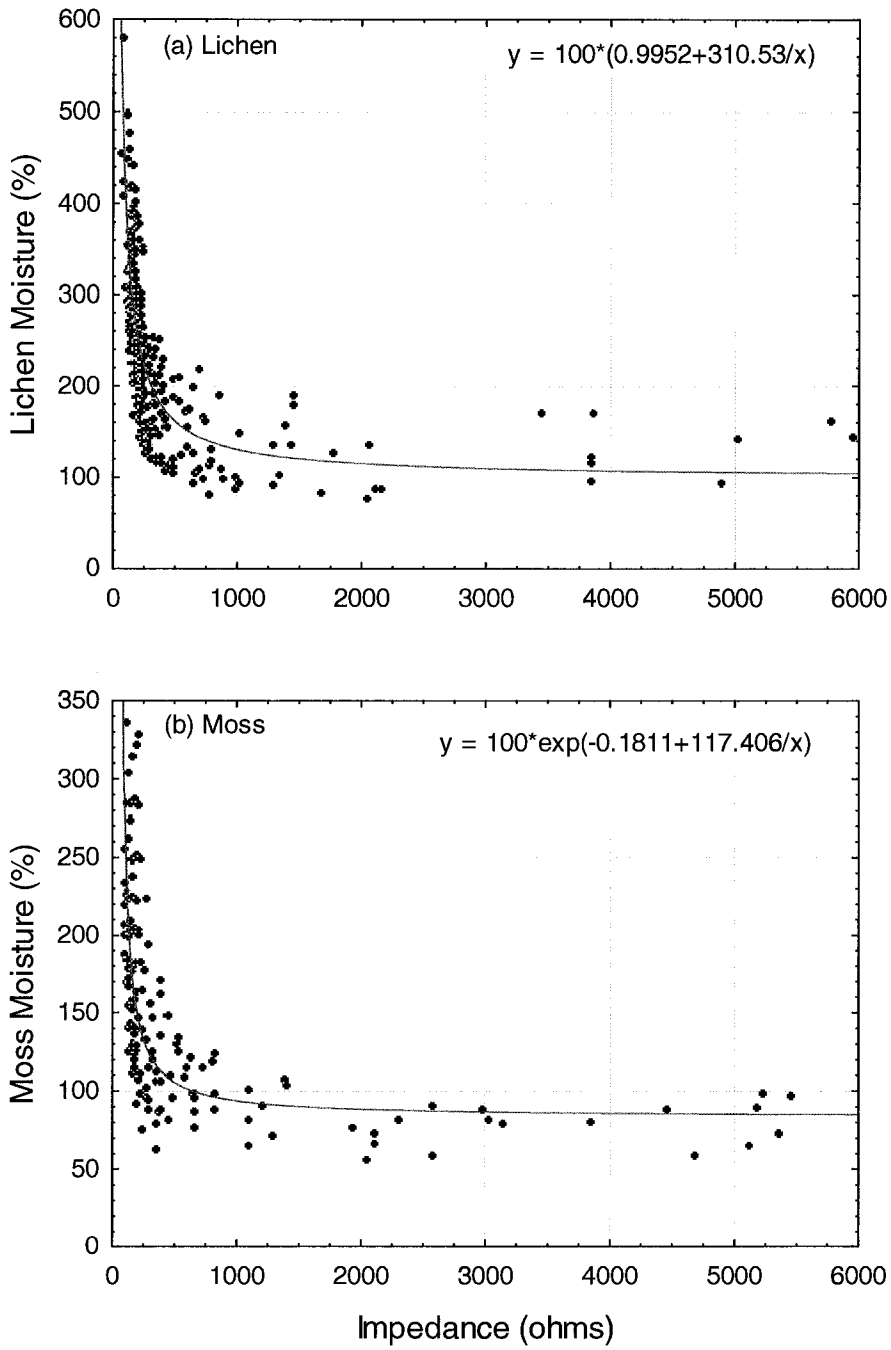
Power and equipment failures resulted in some data gaps in the 2003 microclimate measurements. Gaps in moisture and temperature data from one microclimate station were filled using data from the corresponding period from the other station since they were only 6 km apart and experienced similar climatic conditions. As there were quantum sensors at only one station, gaps in the quantum sensor data could not be filled in this way. Small data gaps in the quantum sensor data were filled using an average of light values from the days on either side of the gap. One larger gap was filled by first assessing the approximate light level of each day from a climate station in the research forest and then filling the gap with data from days of corresponding light levels on either side of the gap.

CO_2 concentrations

Coxson and Wilson (2004) found mean CO_2 levels of 430 µmol mol^{-1} at the surface of a forest floor moss mat and 700 µmol mol^{-1} mid moss mat in sub-alpine spruce fir forests in Alberta. Based on these results, a CO_2 concentration 430 µmol mol^{-1} was taken to represent ambient CO_2 at the forest floor and a CO_2 concentration of 700 µmol mol^{-1} was taken to represent elevated CO_2. Also, many elevated CO_2 experiments in the past have used 700 µmol mol^{-1} as an elevated CO_2 treatment.

On several occasions during May and early June 2004, CO_2 concentrations in the moss mats at the forest floor surface were measured with the LI6400 Portable Photosynthesis System (Li-Cor Inc.) using 2 m of flexible Excelon Bev-A-Line tubing

Figure 4.1 – Calibration curve and equation for the relationship between impedance measurements and % moisture content by weight for the lichen *Peltigera membranacea* (a) and the moss *Rhytidiadelphus triquetrus* (b).



(Thermoplastic Processes Inc., Stirling, NJ, USA) with pin prick holes along the length. A low flow rate was used to minimize the sampling of ambient air above the forest floor layer. The CO_2 concentration in the middle of the living moss mat layer averaged 439 µmol mol^{-1} and reached a maximum concentration of 520 µmol mol^{-1}. The concentration at the surface of the moss mat was 387 µmol mol^{-1}.

Bryophyte and lichen collars

Twenty plastic PVC collars (diameter 10 cm; depth 5 cm) were installed in pairs at intervals over each of the two forest sites for a total of 40 collars. The collars were installed one week prior to the commencement of measurements to minimise disturbance effects on flux measurements. Pairs of collars were sunk 3 cm into the soil or wood substrate with the first collar located in either a homogenous area of the moss *Rhytidiadelphus triquetrus* growing on soil or over a large lichen thallus, *Peltigera membranacea*, growing on decaying wood. The second collar was installed on adjacent litter or wood from which the mosses and lichens had been removed down to bare wood or litter. Any small vascular plants occurring inside the collars were carefully removed at the time of collar installation. On average, lichens covered 78% of the ring area while mosses covered 95% of the ring areas. Measurements were not scaled percent cover because NEC was shown not to vary by ring area covered.

Instantaneous net ecosystem CO_2 exchange measurements

Instantaneous net ecosystem CO_2 exchange (NEC) measurements were

made between 17 May 2004 and 27 September 2004, generally between 9:00 a.m. and 5:00 p.m. Instantaneous NEC measurements were made using an open flow LI6400 Portable Photosynthesis System (Li-Cor Inc.). A custom chamber was constructed using 3 mm thick plexi-glass lined with Teflon tape and the Li6400-19 custom chamber kit (Li-Cor Inc.) (Appendix L). The cylindrical chamber was 10 cm (diameter) by 17 cm (height) for a chamber volume of 1135 cm^3 and a basal chamber surface area of 78.5 cm^2. The bottom of the chamber had an overlapping lip which fit snugly down over the PVC collars. A fan inside the sensor head circulated air from the chamber into the IRGA located in the sensor head. Flow rate was set at 500 µmol s^{-1} and the fan was set on high. No internal chamber fan was required because of the relatively small chamber volume (LI6400 Application Note #3, Li-Cor Inc.). Relative humidity inside the chamber was constrained to a maximum of 80% and normally never went below 45%.

Pairs of collars were visited on average 5.4 times each for a total of 107 visits to the twenty pairs of collars over the three month season. During each visit, measurements were taken at the lichen or moss collar in the light and with the chamber darkened, at the two CO_2 concentrations (430 and 700 µmol mol^{-1}), and at the bare wood or soil collar in the light at the two CO_2 concentrations. After the chamber was attached to a collar, and prior to each measurement, an equilibration period of 4 to 5 minutes was permitted for the chamber to come within 95% of the CO_2 concentration set point (LI6400 Application Note #3, Li-Cor Inc.). In the case of lichen or moss collars, measurements were first taken at a CO_2 concentration of 430 µmol mol^{-1} in the light and then with the chamber covered by a dark cloth. With the

chamber still covered, measurements were taken with CO_2 at 700 μmol mol^{-1}. The cloth was removed and measurements were taken in the light at 700 μmol mol^{-1}. The chamber was then moved to the adjacent bare wood or bare litter collars and measurements were taken in the light with CO_2 concentrations of 430 μmol mol^{-1} and 700 μmol mol^{-1}, respectively. For all measurements, NEC values were allowed to stabilize before three points were logged at 10 second intervals and averaged.

For moss dominated forest floor, instantaneous NEC (μmol m^{-2} s^{-1}) is defined, in the light, as the sum of moss photosynthesis and moss, soil, heterotrophic and root respiration and, in the dark, as the sum of moss, soil, heterotrophic and root respiration. For lichen dominated wood, instantaneous NEC (μmol m^{-2} s^{-1}) is defined, in the light, as the sum of lichen photosynthesis and lichen, wood, heterotrophic, and root respiration and, in the dark, as the sum of lichen, wood, heterotrophic, and root respiration. In this study, negative NEC values indicate a loss of CO_2 to the atmosphere or net ecosystem respiration and positive NEC values indicate uptake of CO_2 from the atmosphere or net ecosystem photosynthesis.

At the time of each NEC measurement, moss frond or lichen thallus temperature was measured using a fine wire chromega constantan thermocouple (Omega Engineering Inc.) inside the chamber, coupled to the Li-Cor LI6400 sensor head. External air temperature was measured by the LI6400. Photon flux density (PFD) was measured using an external quantum sensor (LI9901-013, Li-Cor Inc.) mounted on the LI6400 sensor head. At the start of each series of measurements at a collar, moss frond or lichen thallus moisture measurements were taken on a comparable specimen growing adjacent to the measured collar using the impedance

measurement technique discussed above and recorded on a CR10X data logger (Campbell Scientific). As soil temperature was not collected along with the 2004 data, air temperature was used to estimate soil temperature using a relationship (r^2 = 0.78) between air and soil temperature derived from the 2003 seasonal microclimate data. Throughout the field season, efforts were made to take flux measurements under a full range of moisture, light, and temperature conditions.

Modeling of seasonal NEC

Multiple linear regressions were used to model instantaneous NEC by simultaneous measures of PFD, temperature, and moisture. These regression relationships then permitted the prediction of seasonal NEC from the continuous seasonal microclimate data of 2003.

Input regression variables included moss frond and lichen thallus temperature, soil temperature, moss frond and lichen thallus percent moisture, PFD and time of year. The PFD variable was log transformed to provide a linear relationship with NEC and to improve normality. No other microclimate variable was transformed before analysis. Regression equations were not site specific as CO_2 exchange measurements from sites A and B were pooled before analysis to increase sample size.

Regression equations were created for the moss and lichen collars at CO_2 concentrations of 430 and 700 μmol mol^{-1}, in the light and dark, for a total of four regression equations each for moss and lichen. Regression equations for bare wood and bare litter were created for CO_2 concentrations of 430 and 700 μmol mol^{-1}

for a total of two regression equations each for bare wood and bare soil. An α level of 0.10 was chosen as a threshold for inclusion of a microclimate variable in a regression equation. All regression models were significant at the α=0.05 level.

Before the regression equations could be applied to the 2003 seasonal microclimate data, the data had to be first divided into light and dark periods. A threshold light level of PFD = 5 μmol m^{-2} s^{-1} was determined to be a suitable light level below which most mosses and lichens would be respiring and below their respective light compensation points. Light compensation points have been reported as being 12 - 20 μmol m^{-2} s^{-1} for a blue green algal *Peltigera* (Lange et al. 1996) and 5 - 10 μmol m^{-2} s^{-1} for two foliose lichen species (Sundberg et al. 1997). Sonesson et al. (1991) found a light compensation point of 30 μmol m^{-2} s^{-1} for the moss *Hylocomium splendens*. In this thesis, NEC in the light is denoted as NEC_L and NEC in the dark is denoted as NEC_D

Results

Instantaneous NEC regression models

All of the regression models for NEC were significant at α=0.05. At a CO_2 concentration of 430 μmol mol^{-1}, the lichen regression equations had R^2 values of 0.48 (light) and 0.47 (dark) while the moss regression equations had R^2 values of 0.53 (light) and 0.35 (dark) (Table 4.1). The moss dark regression equation included only moisture and was a poorer fit to the data. The regression equation for litter (R^2 = 0.38) was greater than that for wood (R^2 = 0.14). Moss, bare wood and bare litter

Table 4.1 – Multiple regression equations for the estimation of net ecosystem CO_2 exchange (NEC) (µmol m^{-2} s^{-1}) for lichen dominated wood (*Peltigera membranacea)*, moss dominated forest floor (*Rhytidiadelphus triquetrus*), bare litter, and bare wood substrates in the light and dark (at CO_2 concentrations of 430 and 700 µmol mol^{-1}) in a sub-boreal spruce forest.

	n	Regression Equation	R^2	F	p
CO_2 = 430					
Lichen (light)	51	NEC_L = 1.35logA - 0.06B + 0.14C - 1.86	0.48	14.18	<0.001
Lichen (dark)	47	NEC_D = -0.038B - 0.11C + 0.22	0.47	19.47	<0.001
Moss (light)	54	NEC_L = 1.41logA - 0.04B + 0.06C - 1.43	0.53	19.47	<0.001
Moss (dark)	53	NEC_D = -0.10C - 0.517	0.35	27.32	<0.001
Litter (light & dark)	54	NEC = -0.089D - 0.11C + 0.91	0.38	15.41	<0.001
Wood (light & dark)	47	NEC = -0.0397D + 0.182	0.14	7.10	0.011
CO_2 = 700					
Lichen (light)	51	NEC_L = 1.54logA - 0.05B + 0.13C - 2.24	0.32	7.38	<0.001
Lichen (dark)	51	NEC_D = -0.02B - 0.09C - 0.17	0.23	7.17	0.002
Moss (light)	53	NEC_L = 2.22logA - 0.09B - 1.46	0.67	51.60	<0.001
Moss (dark)	53	NEC_D = -0.11C - 0.46	0.38	31.82	<0.001
Litter (light & dark)	52	NEC = -0.0758D - 0.104C + 0.758	0.34	12.42	<0.001
Wood (light & dark)	51	NEC = -0.0487D + 0.286	0.14	7.67	0.008

Note: Variables include - A = PFD (µmol m^{-2} s^{-1}), B = Moss frond or lichen thallus temperature (°C), C = Moss frond or lichen thallus moisture (proportion), and D = Soil temperature (°C). The significance value for inclusion of variables in the regression equations was p=0.1. NEC in the light is denoted NEC_L and is defined as periods of time with a PFD value of greater than 5 µmol m^{-2} s^{-1} while NEC in the dark is denoted NEC_D and is defined as all periods with lesser PFD values.

all had similar R^2 at 430 µmol mol^{-1} and 700 µmol mol^{-1} while lichen had a higher R^2 at 430 µmol mol^{-1} than 700 µmol mol^{-1}.

Influence of microclimate on instantaneous NEC

As indicated by the regression models, moisture, light and temperature all affected moss and lichen dominated forest floor NEC rates over the season. The PFD was highest in July and August (average 45 µmol m^{-2} s^{-1}) and decreased through September (average 30 µmol m^{-2} s^{-1}) (Table 4.2, Appendix J). Moss frond and lichen thallus moisture levels were lowest in July and August and increased steadily through September (Table 4.2). Mosses and lichens were dry about 50% and 30 – 50% of the time, respectively, in July and August but were only dry 8% (mosses) to 16% (lichens) of the time in September (Appendix K). Moss frond and lichen thallus temperatures were slightly higher in August than July and decreased by an average of 3 °C in September (Table 4.2). Moss and lichen temperatures were consistently higher during periods in which the fronds or thallus were dry than when they were wet (Appendix K).

Some general observations were made on the instantaneous NEC data prior to creating the multiple regression models. For example, in mosses growing on soil, low moisture values generally resulted in negative NEC while at high moisture levels positive NEC was curtailed primarily by low light levels (PFD <25 µmol m^{-2} s^{-1}). The maximum observed moisture content for mosses was 800%. Positive NEC values were not observed in this study until PFD exceeded 24 µmol m^{-2} s^{-1}. However, even at high light levels, photosynthesis was restricted by low moisture values. The effect

Table 4.2 – Average microclimate conditions at two sites (site A and B) in a sub-boreal spruce forest, measured at the forest floor for the moss *Rhytidiadelphus triquetrus* and the lichen *Peltigera membranacea* in the light and in the dark over a three month season in 2003.

	27June-26July		27July-25Aug		26Aug-24Sept	
	Site A	Site B	Site A	Site B	Site A	Site B
Total						
Light						
Avg. moss temp. (°C) [a]	16.3	15.7	16.9	16.5	11.6	11.3
Avg. lichen temp. (°C)	15.6	15.7	16.4	16.3	11.3	11.3
Avg. soil temp. (°C) [b]	12.1	12.4	11.9	12.6	10.4	9.7
Avg. PFD (μmol m^{-2} s^{-1}) [c]	45.6	45.6	45.3	45.3	30.9	30.9
Avg. moss moisture (%)[d]	155	149	124	180	245	230
Avg. lichen moisture (%)	168	254	136	153	213	238
Dark						
Avg. moss temp. (°C)	12.3	11.7	12.1	11.7	8.7	8.4
Avg. lichen temp. (°C)	12.3	11.7	12.0	11.7	8.5	8.5
Avg. soil temp. (°C)	11.3	11.4	12.0	12.3	10.6	9.9
Avg. PFD (μmol m^{-2} s^{-1})	0.7	0.7	0.7	0.7	0.6	0.6
Avg. moss moisture (%)	138	141	119	161	230	218
Avg. lichen moisture (%)	168	249	138	156	214	237

Note: Light is defined as periods of time with a PFD value of greater than 5 μmol m^{-2} s^{-1} while dark is defined as all periods with lesser PFD values.

[a] Average moss/lichen temperature refers to the moss frond or lichen thallus temperature.

[b] Soil temperature refers to the temperature at 10 cm depth in the soil.

[c] PFD is the photosynthetic flux density.

[d] Moss/lichen temperature refers to the moss frond or lichen thallus percent moisture content.

of temperature on moss or lichen NEC was less important than that of either moisture or temperature of the frond. There was a trend towards less positive NEC at high temperatures, however, this was also when low frond moisture was commonly observed (Appendix K). In lichens growing on wood, positive NEC values were observed at thallus moisture levels over 110% and the maximum thallus moisture content was 525%. Again, at high thallus moisture levels, positive NEC was limited by low light levels (PFD <20 μmol m^{-2} s^{-1} at low temperatures to < 40 μmol m^{-2} s^{-1} at high temperatures). At high temperatures, higher light levels were required for positive NEC.

Both wood and litter showed a trend towards increased respiration at higher temperatures and exhibited the lowest NEC values at the lowest recorded temperatures. Over the season, soil temperatures ranged from an average of 12 °C for July and August to 10 °C in September, 2003 (Table 4.2). The relationship between respiration and moisture was not as clear in wood and litter substrates. However, lichen and moss moisture contents may have been poorer correlates of wood and soil moisture.

Comparison of modeled and measured instantaneous NEC at ambient CO_2

Modeled NEC values for moss or lichen dominated forest floors were similar to measured NEC values with respect to minimum values but underestimated maximum and mean values (Table 4.3). Measured NEC values from moss dominated forest floor ranged from +3.6 μmol m^{-2} s^{-1} to -1.6 μmol m^{-2} s^{-1} while modeled moss NEC values ranged from +2.2 to -1.5. For lichen dominated wood,

measured lichen NEC values ranged from +4.4 μmol m^{-2} s^{-1} to -1.9 μmol m^{-2} s^{-1} and modeled lichen NEC ranged between +1.8 μmol m^{-2} s^{-1} and -2.1 μmol m^{-2} s^{-1}. Maximum measured lichen NEC values were greater than modeled NEC values, however, the high maximum measured NEC value (+4.4 μmol m^{-2} s^{-1}) from site A was twice as high as the next highest measured NEC value and was recorded during optimum temperature, moisture and light conditions. Both moss and lichen had maximum modeled NEC rates in July, minimums in August, and intermediate rates in September.

Comparisons of the measured and modeled NEC rates showed a good fit to the 1:1 line for lichen in the light and dark and for moss in the light (Fig. 4.2). Moss in the dark showed a poorer fit due to the dependence of that regression model solely on moss moisture content which was constrained by maximum and minimum measurable moisture contents (Fig. 4.2).

Bare wood and litter had similar NEC values and comparable maximum and minimum measured and modeled NEC values (Table 4.4). The lowest measured NEC value from bare litter was -1.6 μmol m^{-2} s^{-1} while the minimum modeled litter NEC value was -1.4 μmol m^{-2} s^{-1}. For bare wood, the lowest NEC value measured was -1.9 μmol m^{-2} s^{-1} while the minimum modeled NEC was less negative at -0.7 μmol m^{-2} s^{-1}.

Climate data from a permanent climate station at the research forest indicated that the climate was similar between the 2003 and 2004 seasons (1 June to 1 October). Average daily temperatures over the period varied by 0.5 °C between years (12.6 °C in 2003, 13.1 °C 2004). Rainfall varied slightly between the two years

Table 4.3 – Comparison of the maximum, mean and minimum instantaneous net ecosystem CO_2 exchange (NEC) rates (µmol m^{-2} s^{-1}) of moss and lichen modeled with the multiple regression equations (and seasonal microclimate data from the 2003) and the maximum, mean and minimum NEC rates measured over the 2004 growing season.

		Modeled NEC 2003 Season									**Measured NEC** 2004 Season		
		27June-26July			**27July-25Aug**			**26Aug-24Sept**			**21May-27Sept**		
		Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.
CO_2 430 µmol mol^{-1}													
Moss Light	Max	2.17	2.15	2.16	1.72	2.19	1.96	1.81	1.83	1.82	3.57	2.69	3.13
	Mean	-0.02	0.00	-0.01	-0.09	-0.04	-0.06	0.03	0.04	0.04	0.60	-0.20	0.2
	Min	-1.37	-1.33	-1.35	-1.46	-1.42	-1.44	-1.22	-1.22	-1.22	-1.07	-1.60	-1.34
Moss Dark	Max	-0.60	-0.60	-0.60	-0.60	-0.60	-0.6	-0.60	-0.60	-0.6	-0.12	-0.06	-0.09
	Mean	-0.66	-0.66	-0.66	-0.64	-0.68	-0.66	-0.75	-0.74	-0.74	-0.81	-0.97	-0.88
	Min	-0.85	-0.93	-0.89	-0.84	-1.94	-1.39	-0.99	-0.93	-0.96	-1.70	-2.73	-2.22
Lichen Light	Max	1.61	1.82	1.72	1.08	1.31	1.20	1.28	1.45	1.36	4.36	2.07	3.22
	Mean	-0.55	-0.43	-0.49	-0.67	-0.64	-0.6	-0.44	-0.40	-0.42	0.01	-0.08	-0.04
	Min	-2.00	-2.00	-2.00	-2.12	-2.10	-2.11	-1.87	-1.87	-1.87	-1.92	-0.81	-1.36
Lichen Dark	Max	-0.16	-0.10	-0.13	0.00	-0.03	-0.2	0.02	-0.02	-0.02	-0.27	-0.30	-0.28
	Mean	-0.43	-0.50	-0.46	-0.39	-0.40	-0.40	-0.34	-0.36	-0.35	-1.00	-0.91	-0.96
	Min	-0.81	-1.04	-0.92	-0.84	-0.71	-0.78	-0.73	-0.73	-0.73	-1.99	-1.69	-1.84
CO_2 700 µmol mol^{-1}													
Moss Light	Max	3.76	3.76	3.76	3.11	3.11	3.11	3.28	3.30	3.29	4.77	3.15	3.96
	Mean	0.34	0.39	0.36	0.25	0.28	0.26	0.41	0.44	0.42	0.81	-0.12	0.34
	Min	-1.85	-1.77	-1.71	-2.02	-1.94	-1.98	-1.55	-1.55	-1.55	-1.06	-1.51	-1.28

Table 4.3 continued

		Modeled NEC 2003 Season									Measured NEC 2004 Season		
		27June-26July			27July-25Aug			26Aug-24Sept			21May-27Sept		
		Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.
Moss Dark	Max	-0.55	-0.55	-0.55	-0.55	-0.55	-0.55	-0.55	-0.55	-0.55	-0.09	-0.10	-0.10
	Mean	-0.61	-0.61	-0.61	-0.59	-0.64	-0.62	-0.71	-0.70	-0.70	-0.76	-0.94	-0.85
	Min	-0.81	-0.89	-0.85	-0.80	-1.96	-1.38	-0.96	-0.90	-0.93	-1.61	-2.72	-2.16
Lichen Light	Max	1.75	1.94	1.84	1.16	1.42	1.29	1.34	1.50	1.42	5.27	1.46	3.36
	Mean	-0.64	-0.53	-0.58	-0.75	-0.72	-0.74	-0.58	-0.54	-0.56	0.04	-0.14	-0.05
	Min	-2.19	-2.19	-2.19	-2.31	-2.29	-2.30	-2.08	-2.08	-2.08	-1.98	-0.90	-1.44
Lichen Dark	Max	-0.41	-0.38	-0.40	-0.34	-0.34	-0.34	-0.33	-0.33	-0.33	-0.21	-0.14	-1.18
	Mean	-0.58	-0.64	-0.61	-0.55	-0.56	-0.56	-0.54	-0.56	-0.55	-0.97	-0.85	-0.91
	Min	-0.83	-1.03	-0.93	-0.78	-0.79	-0.78	-0.78	-0.78	-0.78	-2.46	-1.61	-1.04

Note: NEC values are given for the moss *Rhytidiadelphus triquetrus,* the lichen *Peltigera membranacea.* Light is defined as periods of time with PFD values of greater than 5 µmol m^{-2} s^{-1} while dark is all periods with lesser PFD values. Measurements were taken in the light and dark with CO_2 concentrations of 430 and 700 µmol mol^{-1}.

Table 4.4 – Comparison of the maximum, mean and minimum instantaneous net ecosystem CO_2 exchange (NEC) rates (µmol m^{-2} s^{-1}) of bare wood and bare litter modeled from the multiple regression equations (and seasonal microclimate data from the 2003) and the maximum, mean and minimum NEC rates recorded during the 2004 season.

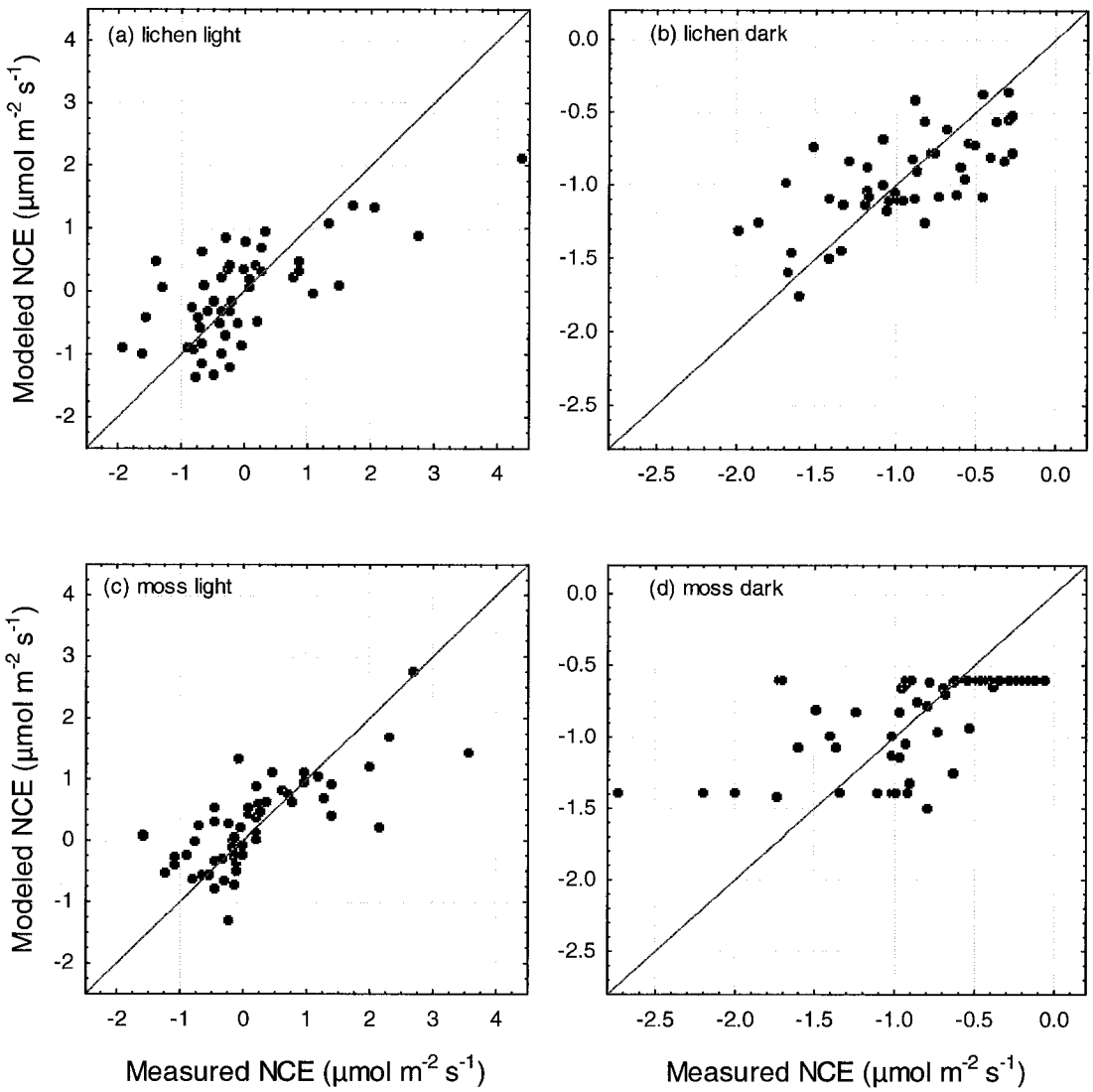
		Modeled NEC 2003 Season									**Measured NEC** 2004 Season		
		27June-26July			**27July-25Aug**			**26Aug-24Sept**			**21May-27Sept**		
		Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.
CO_2 430 µmol mol^{-1}													
Litter Light	Max	-0.03	0.02	0.00	0.01	0.08	0.40	0.01	-0.01	0.00	-0.16	-0.19	-0.18
	Mean	-0.33	-0.34	-0.34	-0.28	-0.41	-0.34	-0.29	-0.27	-0.28	-0.49	-0.69	-0.59
	Min	-0.69	-0.98	-0.84	-0.78	-1.36	-1.07	-0.65	-0.51	-0.58	-1.00	-1.57	-1.28
Litter Dark	Max	-0.03	0.02	0.00	-0.02	0.08	0.30	0.01	-0.01	0.00			
	Mean	-0.25	-0.26	-0.26	-0.29	-0.36	-0.32	-0.29	-0.28	-0.28			
	Min	-0.60	-0.69	-0.64	-0.74	-1.95	-1.34	-0.66	-0.56	-0.61			
Wood Light	Max	-0.15	-0.14	-0.14	-0.17	-0.14	-0.16	-0.10	-0.10	-0.10	-0.07	-0.13	-0.10
	Mean	-0.30	-0.31	-0.30	-0.29	-0.32	-0.39	-0.23	-0.23	-0.23	-0.55	-0.39	-0.47
	Min	-0.49	-0.62	-0.56	-0.47	-0.74	-0.60	-0.35	-0.35	-0.35	-1.89	-0.95	-1.42
Wood Dark	Max	-0.15	-0.14	-0.14	-0.19	-0.15	-0.17	-0.13	-0.13	-.013			
	Mean	-0.27	-0.26	-0.26	-0.29	-0.30	-0.30	-0.24	-0.24	-0.24			
	Min	-0.45	-0.49	-0.47	-0.44	-0.55	-0.50	-0.35	-0.35	-0.35			
CO_2 700 µmol mol^{-1}													
Litter Light	Max	-0.05	-0.01	-0.03	-0.02	0.05	0.02	-0.02	-0.04	-0.03	-0.21	-0.23	-0.22
	Mean	-0.32	-0.32	-0.32	-0.27	-0.39	-0.33	-0.28	-0.27	-0.28	-0.44	-0.65	-0.54
	Min	-0.61	-0.86	-0.74	-0.71	-1.27	-0.96	-0.61	-0.48	-0.54	-0.90	-1.35	-1.12

Table 4.4 continued

		Modeled NEC 2003 Season									Measured NEC 2004 Season		
		27June-26July			27July-25Aug			26Aug-24Sept			21May-27Sept		
		Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.	Site A	Site B	Avg.
Litter Dark	Max	-0.05	-0.01	-0.03	-0.05	0.04	-0.00	-0.03	-0.04	-0.04			
	Mean	-0.24	-0.25	-0.24	-0.28	-0.34	-0.31	-0.29	-0.27	-0.28			
	Min	-0.54	-0.62	-0.58	-0.68	-1.80	-1.24	-0.61	-0.51	-0.56			
Wood Light	Max	-0.12	-0.11	-0.12	-0.14	-0.11	-0.12	-0.06	-0.06	-0.06	-0.06	-0.16	-0.11
	Mean	-0.30	-0.31	-0.30	-0.29	-0.33	-0.31	-0.22	-0.22	-0.22	-0.54	-0.38	-0.46
	Min	-0.54	-0.70	-0.62	-0.51	-0.84	-0.68	-0.36	-0.36	-0.36	-1.58	-0.93	-1.26
Wood Dark	Max	-0.13	-0.11	-0.12	-0.16	-0.12	-0.14	-0.10	-0.10	-0.10			
	Mean	-0.26	-0.26	-0.26	-0.30	-0.31	-0.30	-0.23	-0.23	-0.23			
	Min	-0.49	-0.54	-0.52	-0.47	-0.61	-0.54	-0.37	-0.37	-0.37			

Note: Light is defined as periods with a PFD value of greater than 5 µmol m^{-2} s^{-1} while dark is all periods with lesser PFD values. Measurements were taken in the light and dark with CO_2 concentrations of 430 and 700 µmol mol^{-1}.

Figure 4.2 – Comparison of the modeled net ecosystem CO_2 exchange (NEC) (µmol m^{-2} s^{-1}) measurements and the modeled NEC measurements for the lichen *Peltigera membranacea* and the moss *Rhytidiadelphus triquetrus* in the light and in the dark at a CO_2 concentration of 430 µmol mol^{-1}. The lines indicate the 1:1 relationship. Correlation coefficients were (a) 0.69, (b) 0.69, (c) 0.73 and (d) 0.59.



with a greater number of small rainfall events in 2004 compared with fewer, larger rainfall events in 2003 and a 20% lower total rainfall over the 2003 season (263 mm in 2003, 327 mm in 2004). Total growing season daily solar radiation varied by <2% across years (1 June to 1 August; 1319 Mj m^{-2} 2003, 1336 Mj m^{-2} 2004).

Monthly and seasonal NEC at ambient CO_2

At a CO_2 concentration of 430 µmol mol^{-1}, lichens growing on wood had more negative seasonal NEC values than mosses on soil (Table 4.5). Mosses had seasonal NEC rates of -34.2 and -33.5 g C m^{-2}, over the three month growing season while lichens had NEC rates of -43.7 and -42.2 g C m^{-2}, over the same period, for sites A and B, respectively. Mosses and lichens differed dramatically in their light NEC (NEC_L) and dark NEC (NEC_D) values. Moss NEC_L was consistently much less negative than moss NEC_D. Over the growing season, moss NEC_L was close to zero (-1.13 to +0.05 g C m^{-2}; Table 4.5), indicating that moss photosynthesis was on average balancing below ground and moss respiration in the light. Lichen light and dark NEC values were both negative and of similar magnitudes, with NEC_L being slightly more negative than NEC_D. Only during the third month was lichen NEC_L less negative than NEC_D.

Bare litter and wood had similar total seasonal NEC values with litter being slightly more negative (Table 4.5). Litter had total growing season NEC totals of -27.1 and -30.0 g C m^{-2} while wood had growing season NEC totals of -25.2 and -25.8 g C m^{-2}, for sites A and B respectively. Both showed a trend towards more negative NEC_L values early in the season, when there were more hours of daylight,

Table 4.5 - Modeled net ecosystem CO_2 exchange (NEC) (g C m^{-2} $month^{-1}$ or $season^{-1}$) of moss and lichen dominated forest floor, bare soil or bare wood at the two study sites (site A and B) for each of the three months individually and combined over the 2003 three month growing season in a sub-boreal spruce forest.

	27June-26July		27July-25Aug		26Aug-24Sept		Seasonal NEC_L and NEC_D		Total Seasonal NEC (NEC_L + NEC_D)	
	Site A	Site B	Site A	Site B	Site A	Site B	Site A	Site B	Site A	Site B
CO_2 430 µmol mol^{-1}										
Moss Light	-0.25	0.08	-1.33	-0.57	0.45	0.54	-1.13	0.05		
Moss Dark	-9.49	-9.53	-10.00	-10.68	-13.58	-13.36	-33.07	-33.57	-34.20	-33.52
Lichen Light	-9.19	-7.23	-10.32	-9.85	-5.78	-5.29	-25.29	-22.37		
Lichen Dark	-6.24	-7.16	-6.10	-6.21	-6.06	-6.50	-18.40	-19.87	-43.69	-42.24
Litter Light	-5.59	-5.75	-4.39	-6.38	-3.76	-3.54	-13.74	-15.67		
Litter Dark	-3.55	-3.69	-4.56	-5.62	-5.28	-5.02	-13.39	-14.33	-27.13	-30.00
Wood Light	-4.95	-5.12	-4.47	-4.93	-3.01	-3.01	-12.43	-13.06		
Wood Dark	-3.82	-3.72	-4.61	-4.76	-4.32	-4.31	-12.75	-12.79	-25.18	-25.85
CO_2 700 µmol mol^{-1}										
Moss Light	5.68	6.45	3.83	4.29	5.41	5.81	14.92	16.55		
Moss Dark	-8.80	-8.84	-9.23	-9.94	-12.79	-12.56	-30.82	-31.34	-15.90	-14.79
Lichen Light	-10.65	-8.86	-11.63	-11.20	-7.54	-7.09	-29.82	-27.15		
Lichen Dark	-8.34	-9.23	-8.53	-8.71	-9.76	-10.14	-26.63	-28.08	-56.45	-55.23
Litter Light	-5.29	-5.43	-4.20	-5.96	-3.72	-3.51	-13.21	-14.90		
Litter Dark	-3.46	-3.59	-4.33	-5.30	-5.19	-4.94	-12.98	-13.83	-26.19	-28.73
Wood Light	-5.04	-5.25	-4.48	-5.09	-2.88	-2.88	-12.40	-13.22		
Wood Dark	-3.79	-3.67	-4.67	-4.87	-4.19	-4.18	-12.65	-12.72	-25.05	-25.94

Note: NEC values are given for the moss *Rhytidiadelphus triquetrus* the lichen *Peltigera membranacea* and for bare wood and bare litter substrates. Measurements were taken at CO_2 concentrations of 430 and 700 μmol mol^{-1}. NEC_L represents a sum of NEC over the three months in light and NEC_D represents a sum of NEC over the three months in the dark. Total seasonal NEC represents a sum of NEC_L and NEC_D. Light is defined as periods of time with PFD values of greater than 5 μmol m^{-2} s^{-1} while dark is defined as all periods with lesser PFD values. Negative NEC values indicate carbon release into the atmosphere.

and less negative NEC_L values later in the season. Wood, particularly, had relatively constant NEC values for the first two months (27 June to 25 August) and became less negative during the third month.

Seasonal forest floor NEC totals

From Chapter 2, the average percent cover of bryophytes and lichens in old-growth sub-boreal spruce forest on fine textured soils was 53% (2% lichen cover, 51% moss and liverwort cover) (Table 2.3). Coarse woody debris had 12% cover, out of which the 2% lichen cover was subtracted for a remaining 10% bare wood cover. The final 38% of the area was composed of bare litter. It was assumed that all mosses were growing on litter and all lichens on wood, which likely resulted in a slight over-estimation of bare wood cover and an under-estimation of bare litter cover. Tree basal areas comprised 0.5% of the area and for the purposes of this calculation were omitted. When these percent cover estimates were multiplied by their respective NEC values (Table 4.5) and summed over the moss, lichen, bare wood and bare litter components of the forest floor community, the old-growth sub-boreal spruce forest floor lost -31.6 g C m^{-2} over the three month period (Table 4.6).

Moss or lichen contributions to the forest floor CO_2 exchange, independent of the soil or wood, were estimated (Table 4.7) using seasonal instantaneous measured mean NEC values (Table 4.3) or modeled mean NEC values (Table 4.3). Mean daytime net photosynthesis was calculated as [mean growing season moss or lichen NEC_L – mean growing season litter or wood NEC] while mean night time respiration was calculated as [mean growing season moss or lichen NEC_D - mean

Table 4.6 – The percent of the forest floor made up by the bryophyte, lichen, wood and litter components, their average net ecosystem CO_2 exchange (NEC) (g C m^{-2}) over a 3 month growing season, their proportional NEC and the total NEC for old-growth forest floor of a sub-boreal spruce forest, British Columbia.

	% Area	**Average NEC** (g C m^{-2})	**Proportional NEC** (g C m^{-2})
Bryophytes	51%	33.8	-17.2
Lichens	2%	43.0	-0.9
Bare wood	10%	25.5	-2.6
Bare litter	38%	28.6	-10.9
Total	100%		-31.6

Table 4.7 – Measured and modeled instantaneous NEC means for moss and lichen dominated forest floor in the light (NEC_L) and dark (NEC_D) and for soil and wood in the light ($soil_L$ or $wood_L$) and dark ($soil_D$ or $wood_D$). Measured and modeled derived seasonal means for the moss and lichen components, independent of the soil and wood substrates, for mean net daytime photosynthesis (PS), mean net night time respiration (Resp.), mean gross photosynthesis (PS), and net carbon gain. Measured values are given in µmol m^{-2} s^{-1} and modeled values are given in µmol m^{-2} s^{-1} and g C m^{-2} $season^{-1}$ for moss and lichen at CO_2 concentrations of 430 µmol mol^{-1} (430) and 700 µmol mol^{-1} (700).

	Measured or modeled forest floor instantaneous means[a]				Derived moss or lichen seasonal means			
	NEC_L	NEC_D	$Soil_L$ or $Wood_L$[b]	$Soil_D$ or $Wood_D$[b]	Net daytime PS	Net night time Resp.	Gross PS	Net carbon gain
Measured Instantaneous NEC (µmol m^{-2} s^{-1})								
Moss (430)	0.20	-0.88	-0.59	n/a	0.79	-0.29	1.08	0.50
Lichen (430)	-0.04	-0.96	-0.47	n/a	0.43	-0.49	0.92	-0.06
Moss (700)	0.34	-0.85	-0.54	n/a	0.88	-0.31	1.19	0.57
Lichen (700)	-0.05	-0.91	-0.46	n/a	0.41	-0.45	0.86	-0.05
Modeled Instantaneous NEC (µmol m^{-2} s^{-1})								
Moss (430)	-0.01	-0.69	-0.32	-0.30	0.31	-0.38	0.68	-0.08
Lichen (430)	-0.50	-0.40	-0.31	-0.27	-0.19	-0.13	-0.10	-0.32
Moss (700)	0.35	-0.64	-0.31	-0.28	0.63	-0.36	0.99	0.27
Lichen (700)	-0.63	-0.57	-0.28	-0.26	-0.37	-0.31	-0.06	-0.68
Modeled Seasonal NEC (g C m^{-2} $season^{-1}$)								
Moss (430)	-0.54	-33.32	-14.71	-13.86	14.17	-18.61	32.78	-4.44
Lichen (430)	-23.83	-19.14	-12.74	-12.77	-11.09	-6.37	-4.69	-17.46
Moss (700)	15.74	-31.08	-14.06	-13.40	29.80	-17.86	46.82	12.12
Lichen (700)	-28.48	-27.36	-12.81	-12.68	-15.67	-14.68	-1.12	-30.35

Note:
Mean daytime net moss or lichen photosynthesis = [mean growing season moss or lichen NEC_L – mean growing season litter or wood NEC]
Mean night time net moss or lichen respiration = [mean growing season moss or lichen NEC_D - mean growing season litter or wood NEC]
Mean moss or lichen gross photosynthesis = [mean growing season moss or lichen NEC_L – mean growing season moss or lichen NEC_D]
Net moss or lichen carbon gain = [mean daytime net photosynthesis + mean net night time respiration]

[a] Values are taken from Tables 4.3 and 4.4
[b] Litter for moss, wood for lichen.

growing season litter or wood NEC]. Mean gross photosynthesis was calculated as [mean growing season moss or lichen NEC_L – mean growing season moss or lichen NEC_D]. Averaged over the three months, approximately 49% of the hours in a day were light and 51% were dark, as previously defined. Therefore, net carbon gain by moss fronds or lichen thalli was approximated as [mean daytime net photosynthesis + mean night-time respiration].

At a CO_2 concentration of 430 μmol mol^{-1}, mosses had a measured mean daytime net photosynthetic rate of +0.79 μmol m^{-2} s^{-1}, a measured mean night time net respiration of -0.29 μmol m^{-2} s^{-1} and a measured mean gross photosynthesis of 1.08 μmol m^{-2} s^{-1} (Table 4.7). Modeled values were +0.31 μmol m^{-2} s^{-1} for moss mean daytime net photosynthetic rate, -0.38 μmol m^{-2} s^{-1} for mean night time net respiration and +0.68 μmol m^{-2} s^{-1} for mean gross photosynthesis.

Lichens at a CO_2 concentration of 430 μmol mol^{-1} had a measured mean daytime net photosynthesis of +0.43 μmol m^{-2} s^{-1} and a measured mean night time respiration of -0.49 μmol m^{-2} s^{-1} (Table 4.7). Measured mean gross photosynthesis for lichens was 0.92 μmol m^{-2} s^{-1}. Lichens had a modeled mean daytime net photosynthesis of -0.19 μmol m^{-2} s^{-1}, a modeled mean night time net respiration of -0.13 μmol m^{-2} s^{-1} and a modeled mean gross respiration -0.10 μmol m^{-2} s^{-1}.

From a seasonal perspective, modeled values of seasonal totals of NEC (Table 4.5) were also used to estimate moss or lichen contributions to forest floor CO_2 exchange (Table 4.7). Over the season, gross photosynthesis for mosses was 32.79 g C m^{-2} and for lichens was -4.69 g C m^{-2}. Seasonal modeled net carbon gain was negative for mosses (-4.44 g C m^{-2}) and lichens (-17.46 g C m^{-2}).

Effect of elevated CO_2 concentration

Increasing the ambient CO_2 concentration from 430 µmol mol^{-1} to 700 µmol mol^{-1} had a positive effect on moss photosynthesis. Over the three month growing season, moss NEC ranged from an average -33.8 g C m^{-2} at 430 µmol mol^{-1} to an average of -15.3 g C m^{-2} at 700 µmol mol^{-1} (Table 4.5). Moss seasonal NEC_D was almost constant between the two CO_2 concentrations while moss seasonal NEC_L varied from -0.5 g C m^{-2} at 430 µmol mol^{-1} to +14.7 g C m^{-2} at 700 µmol mol^{-1}. The elevated CO_2 concentration allowed for an increase in *Rhytidiadelphus triquetrus* photosynthesis during the light but, as expected, had no impact on dark respiration. In contrast, lichen photosynthesis was not obviously affected by the higher CO_2 concentration (Table 4.5). In fact, total seasonal NEC and the seasonal NEC_L and NEC_D values were all slightly less positive at the higher CO_2 concentration.

Discussion

Model fit

The regression models based on moisture, light and temperature describe about 50% of the variation in CO_2 flux from lichen and moss dominated forest floor. Some of the additional variability in the moss and lichen regression models may be due to limitations in the sensitivity of the moss frond/lichen thallus moisture calibration exponential relationships. The moisture measurement methodology is less responsive to changes in moisture at the wet end of the moisture scale and is limited by its ability to detect moisture variation beyond a threshold at the dry end of

the moisture scale.

Additional variation in the regression models may be due to the heterogeneity of the sites and the underlying substrates. Drewitt et al. (2002) noted substantial differences in flux values, even over small areas, between collars in a Douglas-fir forest and Rayment and Jarvis (2000) similarly found considerable spatial heterogeneity in soil fluxes. Local variation in organic matter turnover and roots also influences below ground CO_2 flux (Pypker and Fredeen 2003, Heijmans et al. 2004). There may have been heterogeneity in the woody substrates due to differences in species composition because, though most were spruce, it was not always possible to determine the species composition of logs. Respiration rates have been found to vary significantly between some log species (Marra and Edmonds 1994).

Though the regression models were significant, the litter and wood models explained only 15-35% of the variation. The litter regression models contained both the soil temperature and moss moisture variables. Soil temperature and moisture have generally been found to be the most important factors controlling soil respiration (Bowden et al. 1998, Russell and Voroney 1998, Drewitt et al. 2002, Pypker and Fredeen 2003). However, the litter regression model would likely have been improved by having an actual measure of soil moisture rather than substituting moss frond moisture. The wood regression model had the lowest R^2 value likely due to the fact that the variables available for the wood model were the least suitable and the model contained only the soil temperature variable. Soil temperature may not have given an accurate depiction of temperature variation in a woody substrate. Using lichen thallus moisture to approximate wood moisture may

also not have been accurate as lichen moisture levels are likely much more variable over the season than wood moisture levels. Marra and Edmonds (1994) found that logs retained significantly more moisture over the summer and had less seasonal variation in moisture than either the forest floor or the soil. Wood moisture levels have been shown to influence wood respiration in other systems (Marra and Edmonds 1994, Progar et al. 2000). Had wood temperature or moisture been available, there may have been an improved model fit.

Monthly and seasonal NEC from moss and lichen dominated forest floor

Moss dominated forest floor showed constant photosynthetic activity over the season. For all three months, moss NEC_L was close to zero, indicating that there was a balance between moss photosynthesis and moss and belowground respiration in the light. As expected, moss NEC_D got progressively more negative across the three months as night length increased.

Lichen dominated woody substrates showed low NEC values during the first two months (27 June – 26 August) and showed less negative NEC values in the fall measurement period (26 August to 24 September). September was the only one of the three months in which lichen NEC_L was less negative than NEC_D. This change is even more pronounced by the fact that the fall is the period when there are the fewest hours of light and the most hours of dark. This may indicate that either of two possible events occurred during this period. It may be that lichen photosynthesis increased or respiration decreased in the fall as discussed below. The bare wood data also shows less negative NEC during September so it may also be that the

woody substrate had reduced respiration during this period. With the data available, it was not possible to rule out any of these explanations.

Given the above NEC patterns over the season, it may be that mosses and lichens exhibit differences in photosynthetically active periods over the growing season. The moss, *Rhytidiadelphus triquetrus*, seemed to be consistently photosynthetically active all through the summer and fall. Conversely, it may be that the lichen, *Peltigera membranacea*, was most photosynthetically active in the fall when moisture levels were highest and perhaps also in the spring (i.e. before these measurements began) when light levels were higher and trees and shrubs had not yet leafed out. *Peltigera membranacea* is epixylic and therefore may be more affected by wood moisture contents which are likely higher in the spring from snow melt and higher precipitation levels, drier over the summer season, and higher in fall when both evaporative demand is decreased and moisture is increased again (Marra and Edmonds 1994). During the summer months, moisture availability likely reduced the amount of time lichens spent photosynthesising. Heijmans et al. (2004) found a similar trend where *Sphagnum* moss was photosynthetically active through the summer season while lichen and the moss *Hylocomium splendens* lost CO_2 in the middle of the growing season and increased CO_2 uptake again at the end of the growing season as moisture content increased.

Morphological differences between the moss and the lichen species may result in additional variation in photosynthetic patterns. The moss *Rhytidiadelphus triquetrus* grows vertically in dense mats while the lichen *Peltigera membranacea* is a foliose lichen and grows horizontally on logs. This resulted in more biomass of

moss per ring area and may have led to more photosynthetic output per ring area. Morphological differences may also have affected the wetting and drying patterns of these two species. A greater number of wetting and drying cycles can be observed for lichens in the seasonal moisture graphs for these two species (Appendix J), though over the three month season, both species are wet for similar lengths of time (Appendix K). Light interception by lichens may have been affected by the orientation of the log on which they were growing, though most lichens that were chosen were growing horizontally. As well, lichens generally have greater respiration than plants due to the high proportion of the thallus composed of respiring fungal hyphae (Sundberg et al. 1997).

Microclimate influences on instantaneous NEC

Photosynthesis in both moss and lichen dominated forest floors was limited to periods of adequate frond or thallus moisture and then further to periods of sufficient light and temperature. This was particularly the case for lichens with the maximum measured lichen NEC_L measurement (4.3 µmol m^{-2} s^{-1}) occurring during a time of very high moisture content (800%), high PFD (1300 µmol m^{-2} s^{-1}) and high temperature (26 °C). These conditions did not occur frequently. That the photosynthesis of mosses and lichens is limited by adequate light and by sufficient moisture levels due to their poikilohydric nature has been observed in many studies (Hahn et al. 1993, Sundberg et al. 1997, Palmqvist and Sundberg 2000). As well, DeLucia et al. (2003) found that irradiance decreased steeply with depth in the moss layer, with a decrease in irradiance of 53% in the first centimetre and a decrease

down to 5% irradiance at 4 cm, indicating that only the top layer of the moss mat is likely to be photosynthetically active. In this study, the productivity of the moss and lichen forest floors is constrained by both moisture and light conditions experienced during the growing season.

Seasonal forest floor NEC

The modeled growing season NEC for the forest floor community [moss + lichen + litter + wood] was -31.6 g C m^{-2}. This is a lower CO_2 flux than those found by studies in other forest types. For example, over a 5 month season Swanson and Flanagan (2001) found a net exchange of -255 g C m^{-2} for the forest floor of a boreal black spruce forest and Marra and Edmonds (1994) found soil CO_2 efflux values of -48 g C m^{-2} per month and wood CO_2 efflux values of -33 g C m^{-2} per month in a temperate rainforest. The lower NEC values observed in this study may be due to these sites being upland sites in a relatively dry climate and so having drier site conditions than either black spruce forests or temperate rainforests. As well, the old-growth stands in this study are likely near equilibrium with slower growth than may be expected in younger, more dynamic stands. The coverage of moss and lichen is lower in these stands (53%) than has been observed in black spruce forests with almost complete moss cover (Swanson and Flanagan 2001).

Instantaneous NEC values ranged from -2.7 to +3.6 μmol m^{-2} s^{-1} for moss dominated forest floor and -2.0 to +4.4 μmol m^{-2} s^{-1} for lichen dominated forest floor. These values are similar to those of Swanson and Flanagan (2001) who observed net CO_2 exchange from feather mosses to range from -5 to +1 μmol m^{-2} s^{-1}. Forest

floor respiration values found in this study (-2.7 to -0.1 μmol m^{-2} s^{-1}) were at the lower end of the range of soil only respiration values (-6 to -2 μmol m^{-2} s^{-1}) observed by Pypker and Fredeen (2003) for a mature forest in the Aleza Lake Research Forest. The flux values observed in our study were similar to those observed by Goulden and Crill (1997) in feather moss dominated boreal black spruce forests where night time CO_2 efflux from the forest floor ranged between -2.5 and -1.0 μmol m^{-2} s^{-1}.

Independent of the soil layer below, mosses had a measured mean gross photosynthesis of +1.08 μmol m^{-2} s^{-1} and a modeled mean gross photosynthesis value of +0.68 μmol m^{-2} s^{-1}. Goulden and Crill (1997) observed gross photosynthesis to range from 0.5 to 1.0 μmol m^{-2} s^{-1} for boreal feather mosses, similar to our results. Other studies have reported maximum photosynthetic rates of 1.9 μmol m^{-2} s^{-1} for the feather moss *Pleurozium schreberi* in a boreal forest (Whitehead and Gower 2001) and 1.9 μmol m^{-2} s^{-1} for moss mats taken from the forest floor of a temperate rainforest in New Zealand (DeLucia et al. 2003).

Lichens had a measured mean gross photosynthesis value of +0.92 μmol m^{-2} s^{-1} and a modeled mean gross photosynthesis of -0.10 μmol m^{-2} s^{-1}. Over the three months, both measured (-0.06 μmol m^{-2} s^{-1}) and modeled (-0.32 μmol m^{-2} s^{-1}) net carbon gain for lichens imply that over this period, the lichens lost carbon. Given the relatively high measured gross photosynthesis and low net carbon gain, higher respiration rates in lichens appear to affect overall carbon gain. This may be expected given that only the algal fraction of the lichen is photosynthetic. It was suggested earlier that perhaps the lichen is most photosynthetically active in spring

and fall and so additional sampling would be needed to gain a more complete picture of lichen net carbon gain over the year. As well, the contribution of *Peltigera* species to forest floor carbon gain, though small in absolute and relative terms, could have greater implications for N_2-fixation, particularly as would relate to the decomposition of nitrogen-poor logs.

In both moss and lichen, modeled values were more negative than measured values of net daytime photosynthesis, gross photosynthesis and moss and lichen net carbon gain. For example, measured net carbon gain for mosses over the season was approximately +0.50 μmol m^{-2} s^{-1}, suggesting mosses had a net gain of carbon over the three month period, while modeled net carbon gain for mosses was -0.08 μmol m^{-2} s^{-1} and seasonal modeled net carbon gain was -4.44 g C m^{-2} suggesting a small loss of carbon. These lower modeled values may have occurred due to the moss and lichen models underestimating maximum photosynthetic rates as seen in the lower maximum modeled instantaneous NEC rates in Table 4.3. This would lead to a lower estimate of gross photosynthesis and net carbon gain over the season. The lichen model, in particular, underestimated the modeled maximum photosynthesis and resulted in a lower estimate of modeled mean photosynthesis. It is also possible that the measured moss and lichen instantaneous NEC values overestimate photosynthesis due to the fact that the instantaneous measured values were all taken under relatively favourable climatic conditions and during the middle part of the day. As well, the low growth rates of bryophytes and lichens in the low light understory environment mean that net carbon gain is close zero to and it may in fact be very difficult to accurately measure these small values with this approach.

It was not possible to make gross photosynthesis measurements on a finer temporal scale due to an apparent hysteresis and possible artifactual discrepancy between concurrent instantaneous measurements of moss/lichen forest floor NEC values and corresponding bare wood/litter NEC values. In the case of the bare litter, removal of the moss layer may have resulted in a more variable temperature and moisture regime because of the lost insulation layer (Oechel and Van Cleve 1986) also acting as a barrier to evaporative soil water losses (Swanson and Flanagan 2001). During small rain events, this bare litter would have received more water than the moss covered litter, however, during the summer months, the bare litter would also have dried out faster. Bare wood may have been similarly affected by the temperature and moisture buffering capacity of the covering lichens and, additionally, the lichens may have had an important effect on the nitrogen content of the wood and may be an important source of nitrogen for log decomposition (Rayner and Boddy 1988). Knowles (2004) found that *Peltigera* species contributed significantly to the nitrogen content of the forest floor and that leaf litter decomposition was enhanced around *Peltigera* thalli. The fact that the total seasonal NEC value for lichen dominated wood was substantially more negative than the total seasonal NEC for bare wood may also be due to reduced wood decomposition in the absence of a nitrogen source. Possibly, bare litter and woody substrates should have been covered with moss and lichen 'plugs', respectively, during the periods between measurements to minimise microclimatic hysteresis and/or nutrient changes in the substrate.

The contributions of forest floor bryophytes and lichens to forest CO_2 uptake

have been estimated for systems in which forest floor mosses constitute a significant proportion of forest photosynthesis and those in which forest floor mosses constitute a smaller proportion of photosynthesis. One study of a boreal black spruce forest indicated that moss photosynthesis reduced forest floor CO_2 fluxes by 35% and contributed 13% of the forest gross primary productivity (Swanson and Flanagan 2001) while another study suggested that moss photosynthesis reduced the CO_2 efflux from the forest floor by 16% annually in a mixed boreal spruce and pine forest in Sweden (Morén and Lindroth 2000 as cited in DeLucia et al. 2003). In a temperate rainforest in New Zealand, forest floor bryophytes took up 10% of the forest floor CO2 respiration and constituted 5% of forest gross primary productivity (DeLucia et al. 2003). Though gross primary productivity could not be calculated in this study, the average biomass carbon from the terrestrial moss and lichen layer for these old-growth forest stands overlying fine textured soils was 110.4 ± 22.4 g C m^{-2} (see Chapter 3, Table 3.4). This constituted only 0.7% of the total old-growth forest biomass carbon (Fredeen et al. 2005). Given the small proportion of the biomass which the moss and lichen forest floor constitutes, it is unlikely that these species are contributing largely to forest primary productivity.

Effect of elevated CO_2 concentration

The preliminary analysis in this study found that an elevated CO_2 environment occurs in the moss layer at the forest floor. The average CO_2 level in the moss mats (439 µmol mol^{-1}) was higher than both the CO_2 concentration at the surface of the moss mats (387µmol mol^{-1}) and the global average CO_2 concentration

of 377 µmol mol^{-1} (Keeling and Whorf 2005). These CO_2 concentrations are similar to those found in a temperate rainforest in New Zealand in which the CO_2 concentration was 466 µmol mol^{-1} in the top layer of the moss mat and 376 µmol mol^{-1} at 10 cm above the mosses (DeLucia et al. 2003). Sonesson et al. (1992) also found average CO_2 concentrations between 400-450 µmol mol^{-1} in *Hylocomium splendens* moss mats in the sub-arctic. However, this study did not find the highly elevated CO_2 environments shown to occur in moss mats in some other areas (Tarnawski et al. 1994, Coxson and Wilson 2004). Additional study would be required to gain a more complete picture of the CO_2 environment in sub-boreal moss mats.

In this study, the moss *Rhytidiadelphus triquetrus* seemed to be CO_2 limited at ambient forest floor levels (430 µmol mol^{-1}) and photosynthesis was considerably enhanced by increasing the CO_2 concentration to 700 µmol mol^{-1}. Average measured moss gross photosynthesis at a CO_2 level of 700 µmol mol^{-1} was 1.19 µmol m^{-2} s^{-1}, representing a 10% increase in photosynthesis over that observed at 430 µmol mol^{-1} (1.08 µmol m^{-2} s^{-1}) and a 14% increase in measured net carbon gain. Modeled gross photosynthesis values increased from 0.68 µmol m^{-2} s^{-1} at 430 µmol m^{-2} s^{-1} to 0.99 µmol m^{-2} s^{-1} at 700 µmol m^{-2} s^{-1}, a 45% increase in gross photosynthesis. Both of these estimates represent an increase in photosynthesis for mosses at elevated CO_2. These values are similar to those found by Van Der Heijden et al. (2000) who observed a 17% increase in *Sphagnum* dry mass production over 6 months with an elevated CO_2 concentration of 700 µmol mol^{-1}. Other studies have indicated even greater increases in photosynthesis and a 3-4

fold increase in photosynthesis was observed in the moss *Hylocomium splendens* between 350 and 1000 μmol mol^{-1} (Sonesson et al. 1992). Sonesson et al. (1992) suggest these higher CO_2 levels are needed in order for moss growing in the light and moisture limited environment on the forest floor to maintain positive fluxes.

In this study, photosynthesis in the lichen *Peltigera membranacea* was not positively influenced by increased CO_2 concentration. Mean gross lichen photosynthesis at 700 μmol mol^{-1} was 0.86 μmol m^{-2} s^{-1} compared with 0.92 μmol m^{-2} s^{-1} at 430 μmol mol^{-1}, representing a decrease in photosynthesis at the higher CO_2 concentration. Modeled estimates show an even greater decrease in gross photosynthesis at elevated CO_2. The literature shows there to be variation in the reported CO_2 dependencies of lichens that are likely due to differences in methodologies and variability in the hydration dependence of different lichens (Green and Lange 1995, Lange et al. 1996). The CO_2 saturation point for lichens depends upon diffusion resistance of CO_2 at different moisture contents in many lichen species. For example, at very high water contents a cyanobacterial *Peltigera* species had maximum photosynthesis at a CO_2 concentration of 810 μmol mol^{-1} but at optimal hydration was not very sensitive to increases above 350 μmol mol^{-1} (Lange et al. 1996). Lange et al. (1996) suggest that increasing atmospheric CO_2 concentrations may increase lichen productivity during periods of high moisture saturation. The fact that the lichens in this study were moisture limited during much of the three month study period may have meant that increased CO_2 concentration had little effect on photosynthesis. It may also be that the equilibration periods allowed before measurements were not long enough to allow for CO_2 equilibration in

the thallus. Additional study with more controlled moisture and temperature conditions would be required to fully understand the dependence of photosynthesis on CO_2 concentration in *P. membranacea*.

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Chapter 5

Conclusion

This thesis examined three different but related aspects of terrestrial moss, liverwort and lichen ecology in a sub-boreal spruce forest ecosystem. Bryophyte and lichen diversity and abundance were quantified and compared between old-growth and young second-growth stands and two soil texture types. The carbon and nitrogen content and biomass of terrestrial bryophytes and lichens were quantified in each of these sites. Finally, the net ecosystem CO_2 exchange from bryophyte and lichen dominated forest floor was measured in old-growth forest on fine textured soil and modeled over a growing season.

In total, 116 species of moss, liverwort and lichen were identified in all study sites (see Chapter 2). Of those, 92 species were found in old-growth forest and 81 species were found in young second-growth forest. Moss, liverwort and lichen diversity and abundance were affected differently by forest age. Moss species richness was similar between the two forest ages, however, second-growth sites were largely dominated by one moss species with other species present only in small quantities. Lichen species were more abundant in second-growth sites and, though species diversity did not differ between forest ages, there were different species assemblages present in each forest age. Lichen species dependent on woody substrates and lichen species commonly found as epiphytes were much less common in second-growth sites while *Cladonia* species and some *Peltigera* species

were more common in second-growth sites. Liverworts were the most affected by forest age and were almost exclusively restricted to old-growth forest sites. About 96% of the recorded cover of liverworts occurred in old-growth forest. There were significant differences in forest canopy cover, shrub cover and coarse woody debris volume between second-growth and old-growth stands that likely resulted in changes in microclimate and microhabitats. However, the time required for a sub-boreal spruce clearcut to regain sufficient old-growth characteristics to support additional bryophyte and lichen species, particularly liverwort species, cannot be determined by this study. Additional study of intermediate ages of forest would be instructive in determining how long such a transition would take. This may become particularly important in sub-boreal areas where forest harvesting is increasing. There are also questions surrounding the ability of bryophyte and lichen species to disperse back into a disturbed habitat once it becomes habitable. Study of the dispersal abilities of bryophytes and lichens in these systems would be of interest.

Bryophytes and lichens were also affected by substrate differences between forest ages. Moss and lichens used different substrates in second-growth compared with old-growth with use of woody substrates being much more common in old-growth sites and use of bare mineral soil being more common in second-growth sites. Liverworts almost exclusively used woody substrates. The lack of suitable woody substrates may be one reason for differences in diversity and species composition, particularly in liverworts, between the forest ages. Coarse woody debris (CWD) analysis indicated that there was a reduced quantity of CWD in second-growth stands and observational data indicated that there were differences

in wood characteristics between forest ages, including drier wood and greater amounts of charred wood in the young second-growth stands. This study did not examine different post harvest site preparations, such as burning, and their effect on structural features like CWD. Additional study of the characteristics of woody substrates in different forest ages would contribute to an understanding of the effect of forest age on CWD. As well, additional study verifying the specificity of various species to different substrates would be of interest in evaluating the effect of forest age on lichen and bryophyte species.

This study suggested some differences in species diversity and abundance between the two soil texture types, particularly in old-growth sites. Results were not statistically significant, however, there was a trend towards higher species diversity on coarse textured soils but increased species cover on fine textured soils. The coarse textured sites have more productive forests, increased shrub cover and may have higher nitrogen availability, possibly resulting in different, more heterogeneous microsites or site conditions that lead to higher bryophyte and lichen diversity. It may be that increased light reaching the forest floor of fine textured sites, due to less canopy and shrub cover, and increased moisture, due to poorer drainage, resulted in greater biomass of cryptogam species on fine textured soils. There were no substantial differences in lichen or bryophyte species diversity or cover between soil types in second-growth sites, likely due to the disturbed nature of the second-growth sites. The imposed disturbance regime and the effects of broadcast burning of the area likely were more significant than the effects of the underlying soil type. Additional study on the effects of soil texture seems needed to refine an

understanding of the effects of soil characteristics on lichens and bryophytes.

Analysis of the carbon and nitrogen contents of several representative lichen and bryophyte species indicated that bryophytes have higher nitrogen contents on coarse textured soils (see Chapter 3). As indicated above, coarse textured soils are better drained and have more productive forest stands, possibly resulting in faster decomposition and increased soil nitrogen availability. This may have contributed to the higher nitrogen contents in lichens and bryophytes. There were also species related differences in nitrogen content, with the N_2-fixing *Peltigera* species having significantly higher nitrogen contents than the mosses and other non N_2-fixing lichen species. As expected, bipartite cyanobacterial *Peltigera* species had higher nitrogen contents than tripartite *Peltigera* species. Given the greater cover of *Peltigera* species in the second-growth sites, it seems likely that lichens are supplying nitrogen to these disturbed second-growth sites. Additional study quantifying the contribution of nitrogen being introduced into these systems by lichen species would be of interest, as well as an examination of the existence of nitrogen inputs from cyanobacterial associations with mosses and liverworts.

In old-growth forest, moss and lichen biomass amounted to 39 g C m^{-2} on coarse textured soils and 110 g C m^{-2} on fine textured soils. This biomass represented 0.2% (coarse textured soils) and 0.7% (fine textured soils) of the total forest carbon biomass in old-growth sub-boreal spruce forests. In second-growth forests, moss and lichen biomass amounted to 136 g C m^{-2} on coarse textured soils and 157 g C m^{-2} on fine textured soils and represented 3% of the total forest carbon pool on both coarse and fine textured soils. Thus, bryophyte and lichen species

contribute a relatively small proportion of the forest biomass and carbon in sub-boreal spruce forests, though proportionally more in regenerating second-growth forests where their contribution of nitrogen and nutrients may also be important.

Instantaneous chamber-based CO_2 exchange measurements in conjunction with seasonal microclimate data were used to model growing season net ecosystem CO_2 exchange (NEC) of the terrestrial bryophyte and lichen community in old-growth forest on fine textured soils (see Chapter 4). Multiple regression models using microclimate variables were able to describe between 35-53% of the variation in moss and lichen dominated forest floor NEC at ambient CO_2 concentrations. Moisture, temperature and light levels all had significant effects on the CO_2 exchange of lichens and bryophytes. Moisture and light levels had the greatest impact with low levels of either moisture or light limiting photosynthesis. Temperature moderated the effect of the other two variables and often varied simultaneously with moisture.

Measured instantaneous NEC values ranged from +3.6 to -2.7 μmol m^{-2} s^{-1} for moss dominated forest floor and +4.4 to -2.0 μmol m^{-2} s^{-1} for lichen dominated forest floor. Gross photosynthesis was approximated using the instantaneous flux values and was found to range between +1.08 μmol m^{-2} s^{-1} (measured) and +0.68 μmol m^{-2} s^{-1} (modeled) for mosses and +0.92 μmol m^{-2} s^{-1} (measured) and -0.10 μmol m^{-2} s^{-1} (modeled) for lichens. Variation between the measured and modeled values may have been due to the model underestimating the maximal photosynthesis values and due to the measured values being recorded under optimal microclimate conditions.

Over the three month season, the moss *Rhytidiadelphus triquetrus* growing on soil substrate showed consistent NEC values with average NEC_L (in the light) of -0.54 g C m^{-2} and average NEC_D (in the dark) of -33.32 g C m^{-2}. Total seasonal NEC for moss dominated forest floor was -33.8 g C m^{-2}. The lichen *Peltigera membranacea* growing on wood showed more negative NEC during July and August and less negative NEC in September. Over the three month season, lichen had an average NEC_L of -21.84 g C m^{-2}, average NEC_D of -21.12 g C m^{-2} and a total seasonal NEC of -42.9 g C m^{-2}. When summed over the moss, lichen, bare wood, and bare litter components of the forest floor ecosystem for the three month period, the old-growth sub-boreal spruce forest floor lost -31.6 g C m^{-2}.

This study found an elevated CO_2 environment to occur in the moss layer of the forest floor with an average CO_2 level of 439 µmol mol^{-1} in the moss mat and 387µmol mol^{-1} at the surface of the moss mat. The moss *Rhytidiadelphus triquetrus* seemed to be CO_2 limited at 'ambient' forest floor CO_2 levels (430 µmol mol^{-1}) and photosynthesis was considerably enhanced (>10%) by increasing the CO_2 concentration to 700 µmol mol^{-1}. In contrast, photosynthesis in the lichen *Peltigera membranacea* was not positively influenced by increased CO_2 concentration. It seems that rising atmospheric CO_2 concentrations may affect the productivity of these two species differently. Additional, longer term studies under more controlled microclimate conditions would be required to confirm the effect of elevated CO_2 on moss and lichen species in the sub-boreal spruce forest.

This study has provided new information on the impact of forest harvesting on terrestrial lichen, moss and liverwort species diversity and abundance. It has

provided a better understanding of the role of lichens and bryophytes CO_2 exchange in at the forest floor of sub-boreal spruce forests and the contribution of these species to forest biomass carbon and nitrogen. This study is only a first step in gaining a better appreciation of the diversity and importance of terrestrial lichens, mosses and liverworts to the sub-boreal spruce forest ecosystem.

Appendix A

UTM coordinates for the eight study sites in the Aleza Lake Research Forest used in this study.

Table A.1 – UTM coordinates for the eight study sites in the Aleza Lake Research Forest used in this study.

Site #	Forest Age	Soil Texture	UTM
OC1	Old-growth	Coarse	10U 0565517 5991119
OC2	Old-growth	Coarse	10U 0562476 5990875
OF1	Old-growth	Fine	10U 0559594 5995525
OF2	Old-growth	Fine	10U 0558383 5990268
YC1	Second-growth	Coarse	10U 0562874 5991257
YC2	Second-growth	Coarse	10U 0566323 5991982
YF1	Second-growth	Fine	10U 0563263 5991475
YF2	Second-growth	Fine	10U 0560020 5991267

Note: In Chapter 4, site A is the same as OF1 and site B is the same as OF2.

Appendix B

Moss, liverwort and lichen species recorded growing only in old-growth sites and those recorded growing only in young second-growth sites.

Table B. 1 – Moss, lichen and liverwort species recorded only in old-growth forest sites and only in young second-growth forest sites respectively.

Old-growth specific species	Second-growth specific species
Lichens	**Lichens**
Cladina spp. P. Browne	*Cladina arbuscula* ssp. *beringiana* (Ahti) N.S.Golubk.
Cladonia norvegica Tonsberg & Holien	*Cladonia acuminata* (Ach.) Norrlin
Hypogymnia occidentalis L.Pike	*Cladonia bacilliformis* (Nyl.) Gluck.
Hypogymnia tubulosa (Schaerer) Hav.	*Cladonia cariosa* (Ach.) Sprengel
Lobaria pulmonaria (L.) Hoffm.	*Cladonia cervicornus* (Ach.) Flotow
Mycoblastus sanguinarius (L.) Norman	*Cladonia cfr cyanipes* (Sommerf.) Nyl.
Nephroma bellum (Sprengel) Tuck.	*Cladonia cornuta* ssp. *cornuta* (L.) Hoffm.
Nephroma helveticum Ach.	*Cladonia deformis* (L.) Hoffm.
Parmelia hygrophila Goward & Ahti	*Cladonia phyllophora* Hoffm.
Parmeliopsis hyperopta (Ach.) Arnold	*Cladonia umbricola* Tonsberg & Ahti
Peltigera degenii Gyelnik	*Peltigera polydactylon* (Necker) Hoffm.
Peltigera horizontalis (Hudson) Baumg.	*Peltigera praetextata* (Florke Sommerf.) Zopf
Platismatia glauca (L.) Culb. & C. Culb.	*Peltigera rufescens* (Weiss) Humb.
Pseudocyphellaria anomala Brodo & Ahti	*Peltigera* spp. *nov. #1*
Tuckermannopsis chlorophylla Gyelnik	*Peltigera* spp. *nov. #2*
Tuckermannopsis orbata (Nyl.) M.J. Lai	*Stereocaulon tomentosum* Fr.
	Vulpicida pinastri (Scop.) J.E.Mattsson&M.J.Lai
Mosses	**Mosses**
Eurhynchium pulchellum (Hedw.) Schwaegr	*Aulacomnium androgynum* (Hedw.) Schwaegr.
Herzogiella seligeri (Brid.) Iwats	*Aulacomnium palustre* (Hedw.) Schwaegr.
Lescuraea stenophylla (Ren.&Card.) Kindb.	*Campylium calcareum*
Orthotrichum speciosum Nees	*Ceratodon purpureus* (Hedw.) Brid.
Plagiothecium cavifolium (Brid.) Iwats	*Polytrichum juniperinum* Hedw.
Plagiothecium denticulatum (Hedw.) Schimp	
Plagiothecium laetum Schimp.	
Tetraphis pellucida Hedw.	
Liverworts	**Liverworts**
Anastrophyllum hellerianum (Nees) Schust.	*Cephaloziella rubella* (Nees) Warnst.
Blepharostoma trichophyllum (L.) Dum.	*Lophocolea* spp. (Dum.) Dum.
Cephalozia spp. (Dum.) Dum.	*Marchantia polymorpha* L.
Geocalyx graveolens (Schrad.) Nees	
Jamisoniella autumnalis (D.C.) Steph.	
Jamisoniella spp. (Spruce) Carring	
Jungermannia spp. L.	
Lophocolea heterophylla (Schrad.) Dum.	
Lophozia longiflora	
Lophozia spp. (Dum.) Dum.	
Ptilidium pulcherrimum (G.Web.) Hampe	

Appendix C

ANOVA results for bryophyte and lichen diversity tests, coarse woody debris data and bryophyte and lichen biomass.

Table C.1 – ANOVA p statistics for the diversity indexes (species richness, diversity of genera, Shannon Index, Dominance Index and Pie Index).

	Site	Age	Soil
Species Richness	0.117	0.414	0.824
Number of Genera	0.483	**<0.001**	0.349
Shannon Index	**0.003**	**0.045**	0.794
Dominance Index	**<0.001**	**0.020**	0.961
Simpson's Index	**<0.001**	**0.043**	0.832

Note: Bold numbers indicate a significant effect of site, forest age or soil texture on the diversity index.

Table C.2 – ANOVA p value results for coarse woody debris characteristics including: volume of CWD per plot, density of CWD per plot, diameter of CWD pieces, decay class of CWD, number of pieces of CWD, and length of CWD pieces.

	Site	Age	Soil
Volume of CWD		**0.018**	0.051
Decay of CWD	**0.001**	0.493	0.503
Diameter of CWD	**0.012**	0.463	**0.044**
# Pieces of CWD	0.108	**0.026**	0.665
Length of CWD	0.018	0.003	0.202

Note: Bold numbers indicate a significant effect of site, forest age or soil texture on the CWD characteristic.

Table C.3 – ANOVA p values for biomass results including total lichen and bryophyte biomass, moss biomass, lichen biomass, bryophyte and lichen biomass in old-growth sites, and bryophyte and lichen biomass in second-growth sites.

	Site	Age	Soil
Total Biomass	**<0.001**	0.102	0.247
Moss Biomass	**<0.001**	0.131	0.270
Lichen Biomass	0.344	**<0.001**	0.067
Old-growth Biomass	**0.035**		0.080
Second-growth Biomass	**0.001**		0.778

Note: Bold numbers indicate a significant effect of site, forest age or soil type.

Appendix D

Indicator species analysis results giving moss, liverwort and lichen species that are indicators of forest age and indicators of soil texture.

Table D.1 - Indicator species analysis results showing moss, liverwort and lichen species that are significant indicators of old-growth and young second-growth forest types. Indicator values of 100 indicate a species that is a perfect indicator of that forest age (n=24, α <0.05).

Species	Forest Age Indication	Indicator Value	Mean	St. Dev.	p value
Mosses					
Aulacomnium androgynum (Hedw.) Schwaegr.	young	100	36	9.22	0.001
Ceratodon purpureus (Hedw.) Brid.	young	100	37.8	9.33	0.001
Dicranum fuscescens Turn.	old	79.8	46.1	11.86	0.011
Dicranum polysetum Sw.	young	78.3	41.2	10.88	0.004
Dicranum tauricum Sapeh.	old	87.3	43.8	10.29	0.001
Hylocomium splendens (Hedw.)Schimp.	old	91	47.8	10.05	0.002
Mnium lycopodioides Schwaegr.	old	57.7	28.4	9.87	0.019
Plagiomnium insigne (Mitt.) T. Kop.	old	91.1	46.1	8.67	0.001
Pleurozium schreberi (Brid.) Mitt.	old	94.2	59.6	7.18	0.001
Pohlia nutans (Hedw.) Lindb.	young	81	37	10.29	0.001
Polytrichum juniperinum Hedw.	young	100	34.8	8.33	0.001
Ptilium crista-castrensis (Hedw.) DeNot	old	93.6	59.8	9.01	0.001
Rhizomnium nudum (Britt.&Williams) T.Kop.	old	49.9	27.8	9.72	0.029
Rhytidiadelphus triquetrus (Hedw.) Warnst	old	99.4	57.7	9.22	0.001
Sanionia uncinata (Hedw.) Loeske	old	77.7	50.5	8.96	0.009
Liverworts					
Barbilophozia barbata (Schmid) Loeske	old	64.5	32.3	9.36	0.003
Blepharostoma trichophyllum Loeske	old	91.7	34.5	9.84	0.001
Cephalozia spp. (Dum.) Dum.	old	58.3	25.7	9.41	0.008
Harpanthus flotovianus (Nees) Nees	old	45.5	26.6	8.31	0.036
Jungermannia spp. L.	old	58.3	25.9	9.66	0.005
Lophocolea minor Nees	old	49.6	25.1	9.17	0.020
Lophozia spp. (Dum.) Dum.	old	75	36.1	10.84	0.001
Ptilidium californicum (Aust.) Underw.	old	58.1	26.9	8.71	0.01
Ptilidium spp. Nees	old	65.9	36.2	10.39	0.008
Lichens					
Alectoria spp. Ach.	old	60.6	28.7	8.33	0.009
Cladina arbuscula ssp. *beringiana* Brodo & D. Hawksw.	young	58.3	24.1	7.9	0.006
Cladonia botrytis (K.Hagen) Willd.	young	84.6	40.8	7.58	0.001
Cladonia cariosa (Ach.)Sprengel	young	100	35.6	9.34	0.001
Cladonia carneola (Fr.) Fr.	young	76.4	41.3	8.21	0.003
Cladonia chlorophaea (Florke ex Sommerf) Sprengel	young	75	48.2	6.93	0.002
Cladonia cornuta ssp. *cornuta* (L.) Hoffm.	young	83.3	32.8	9.82	0.001
Cladonia fimbriata (L.) Fr.	young	85.6	53.3	7.54	0.001

Table D1 continued

Species	Forest Age Indication	Indicator Value	Mean	St. Dev.	p value
Cladonia gracilis var. *turbinata* (Ach.) Ahti	young	98.9	40.5	9.71	0.001
Cladonia spp. P. Browne	young	80.5	55.3	8.83	0.013
Cladonia sulphurina (Michaux) Fr.	young	83.6	46.1	9.96	0.004
Hypogymnia occidentalis L.Pike	old	58.3	28.2	9.17	0.007
Lobaria pulmonaria (L.) Hoffm.	old	41.7	19.9	8.26	0.047
Nephroma bellum (Sprengel) Tuck.	old	75	30.5	9.99	0.001
Nephroma parile (Ach.) Ach.	old	57.3	26.9	8.73	0.008
Parmelia sulcata Taylor	old	81	41.2	11.24	0.003
Peltigera canina (L.) Willd.	young	83.5	39.2	9.64	0.001
Peltigera extenuate (Vainio) Lojka	young	99.9	39	10.07	0.001
Peltigera horizontalis (Hudson) Baumg.	old	66.7	28.1	9.45	0.003
Peltigera leucophlebia (Nyl.) Gyelnik	young	88.4	40	10.57	0.001
Peltigera rufescens (Weiss) Humb.	young	41.7	19.6	7.41	0.028
Platismatia glauca (L.) Culb. & C. Culb.	old	83.3	33.3	10.29	0.001

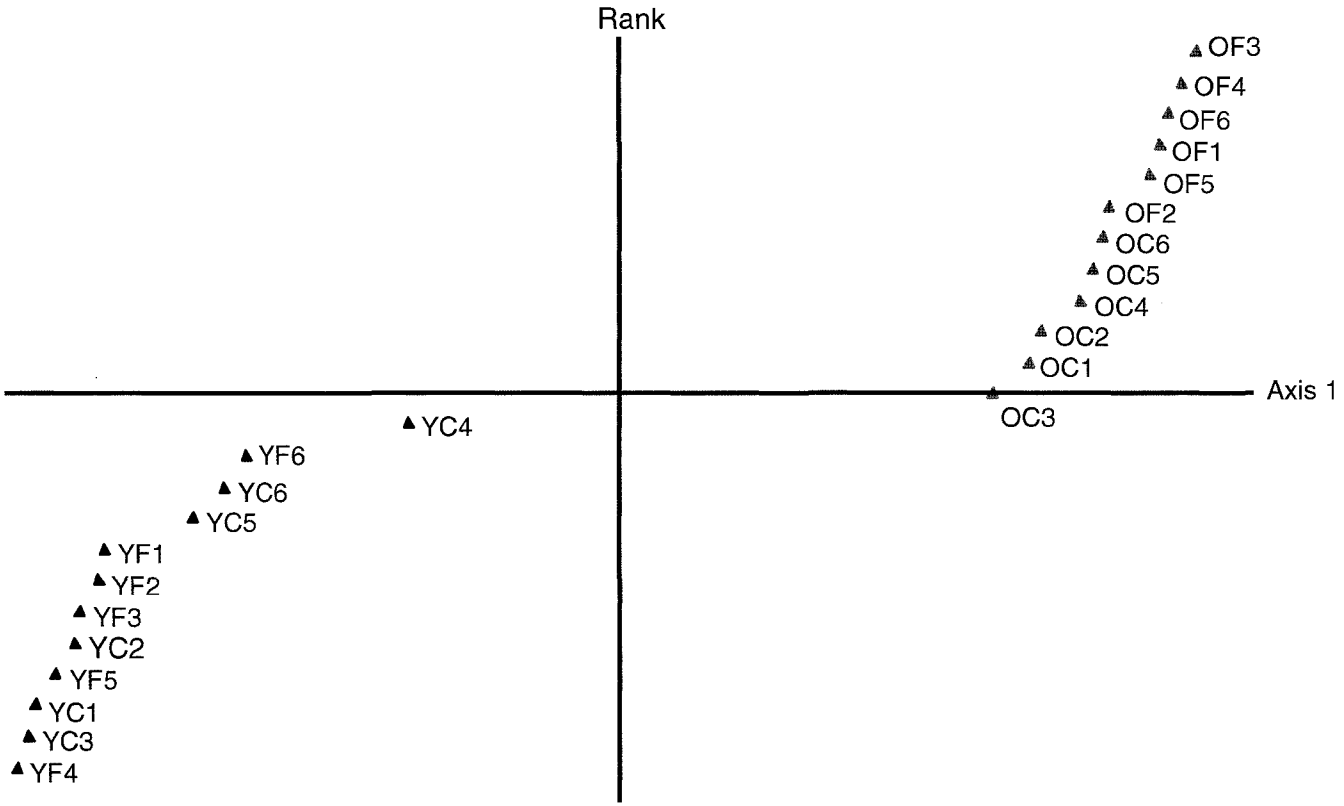
Table D.2 – Indicator species analysis results showing moss, liverwort and lichen species that are significant indicators of coarse textured and fine textured soil types. Indicator values of 100 indicates a species that is a perfect indicator of that soil type (n=24, α <0.05).

Species	Soil Texture Indication	Indicator Value	Mean	St. Dev.	p value
Mosses					
Brachythecium spp. Schimp.	coarse	74	59.5	6.8	0.029
Hylocomium splendens (Hedw.) Schimp.	fine	79.6	47.6	9.94	0.005
Liverworts					
Cephaloziella spp. (Spruce) Steph.	coarse	50	23.1	9.11	0.015
Harpanthus flotovianus (Nees) Nees	fine	45.5	26.6	8.03	0.033
Ptilidium californicum (Aust.) Underw.	fine	49.6	27.3	8.96	0.025
Ptilidium spp. Nees	coarse	56	35.5	10.39	0.05

Appendix E

Nonmetric multidimensional scaling ordination of all study sites (old-growth and second-growth) showing the distribution of sites along one axis. The one axis described 95% of the variation and corresponded strongly to forest age.

Figure E.1 – Non-metric multidimensional scaling (NMS) ordination of all study sites (old-growth and young second-growth on coarse and fine textured soils). The one axis described 95% of the variation and corresponded strongly to forest age. Sites are indicated as old-growth (O), young second-growth (Y), on coarse (C) and on fine textured soil (F).



Appendix F

Percent cover of the dominant shrub and herbaceous plant species recorded in old-growth and second-growth study sites on coarse and fine textured soils in sub-boreal spruce forest in the Aleza Lake Research Forest. Percent cover is an average for the species over the 6 plots of each site type.

Table F.1 – Dominant shrub and herbaceous plant species recorded in old-growth and second-growth study sites on coarse and fine textured soils. Percent cover is an average for the species over the 6 plots of each site type.

Shrub Species	% Cover	Herb Species	% Cover
Old-growth on coarse textured soil			
Oplopanax horridus (Smith) Miq.	23.2	*Streptopus roseus* Michx.	11.0
Rubus parviflorus Nutt.	11.8	*Gymnocarpium dryopteris* (L.) Newm.	8.2
Vaccinium ovalifolium Smith	9.2	*Tiarella trifoliate* L.	6.0
Acer glabrum Torr.	4.8	*Disporum hookeri* (Torr.) Nicholson	2.8
Vaccinium membranaceum Dougl.	2.8	*Aralia nudicaulis* L.	2.2
Ribes lacustre (Pers.) Poir	2.0	*Athyrium filix-femina* (L.) Roth.	2.2
Lonicera involucrate (Rich.) Banks	1.5	*Cornus canadensis* L.	1.8
Alnus crispa ssp. *sinuata* (Regel) Rydb.	1.3	*Rubus pedatus* J.E. Smith	1.5
Viburnum edule (Michx.) Raf.	0.7	*Pteridium aquilinum* (L.) Kuhn.	1.2
Picea glauca x engelmannii (Moench) Voss	0.3	*Clintonia uniflora* (Schult.) Kunth.	0.7
Spiraea betulifolia Pall.	0.3	*Smilacina racemosa* (L.) Desf.	0.5
Sambucus racemosam L.	0.2	*Mitella nuda* L.	0.3
Old-growth on fine textured soil			
Vaccinium ovalifolium Smith	12.2	*Cornus canadensis L.*	5.7
Vaccinium membranaceum Dougl.	8.8	*Rubus pedatus* J.E. Smith	4.8
Abies lasiocarpa (Hook.) Nutt.	4.8	*Streptopus roseus* Michx.	4.5
Lonicera involucrata (Rich.) Banks	2.7	*Gymnocarpium dryopteris* (L.) Newm.	4.3
Sorbus scopulina Greene	2.3	*Tiarella trifoliate* L.	3.2
Alnus crispa ssp. *Sinuate* (Regel) Rydb.	2.0	*Aralia nudicaulis* L.	2.2
Ribes lacustre (Pers.) Poir	1.3	*Lycopodium* spp. L.	2.0
Rubus parviflorus Nutt.	1.0	*Smilacina racemosa* (L.) Desf.	0.3
Rosa acicularis Lindl.	0.7	*Petasites palmatus* (Ait.) Cronq.	0.2
Spiraea betulifolia Pall.	0.7		
Corylus cornuta Marsh.	0.7		
Viburnum edule (Michx.) Raf.	0.7		
Second-growth on coarse textured soil			
Rubus parviflorus Nutt.	10.2	*Epilobium angustifolium* L.	14.3
Picea glauca x engelmanii (Moench) Voss	2.2	*Hieracium umbellatum* L.	5.7
Lonicera involucrata (Rich.) Banks	2.0	*Cornus canadensis* L.	5.3
Salix spp. L.	1.0	*Aralia nudicaulis* L.	0.3
Corylus cornuta Marsh.	0.8	*Hieracium aurantiacum* L.	4.2
Rosa acicularis Lindl.	0.5	*Maianthemum canadense* Web.	2.3
Populus tremuloides Michx.	0.5	*Smilacina racemosa* (L.) Desf.	0.8
Vaccinium ovalifolium Smith	0.3	*Anaphalis margaritacea* (L.) B.&H.	0.7
Viburnum edule (Michx.) Raf.	0.3	*Taraxacum officinale* Weber	0.7

Table F1 continued

Shrub Species	% Cover	Herb Species	% Cover
Amelanchier alnifolia Nutt.	0.3	*Veratrum viride* Ait.	0.7
Rubus pubescens Raf.	0.2	Grass spp.	0.7
Ribes lacustre (Pers.) Poir	0.2	*Athyrium filix-femina* (L.) Roth.	0.2
Sambucus racemosa L.	0.2		
Sorbus scopulina Greene	0.2		
Spiraea douglasii Hook.	0.2		
Second-growth on fine textured soil			
Picea glauca x engelmannii (Moench) Voss	9.5	*Hieracium aurantiacum* L.	20.0
Spiraea douglasii Hook.	3.7	*Hieracium umbellatum* L.	9.2
Salix spp. L.	3.2	*Epilobium angustifolium* L.	8.0
Lonicera involucrata (Rich.) Banks	2.2	*Cornus canadensis* L.	3.0
Rosa acicularis Lindl.	2.0	*Petasites palmatus* (Ait.) Cronq.	2.2
Corylus cornuta Marsh.	1.8	*Taraxacum officinale* Weber	2.2
Populus tremuloides Michx.	1.8	*Maianthemum canadense* Web.	1.7
Amelanchier alnifolia Nutt.	0.8	Grass spp.	0.8
Ribes lacustre (Pers.) Poir	0.5	*Achillea millefolium* L.	0.5
Rubus parviflorus Nutt.	0.5	*Aralia nudicaulis* L.	0.5
Populus balsamifera ssp. *trichocarpa* L.	0.2	*Equisetum arvense* L.	0.2
		Equisetum sylvaticum L.	0.2

Appendix G

Moss and lichen species collected for biomass determination from old-growth and second-growth sites, the area of biomass samples collected, and the average dry weight biomass for each species.

Table G.1 – Moss and lichen species collected for biomass determination from old-growth and second-growth sites, the area of biomass samples collected, and the average dry weight biomass for each species.

Old-growth Species	Sample Size (cm^2)	Average Biomass (kg ha^{-1})	Second-growth Species	Sample Size (cm^2)	Average Biomass (kg ha^{-1})
Moss			**Moss**		
Hylocomnium splendens (Hedw.)Schrimp	100	4956 ± 1186	***Ceratodon purpureus*** (Hedw.) Brid.	4	6083 ± 1145
Pleurozium schreberi (Brid.) Mitt.	100	2743 ± 463	***Pleurozium schreberi*** (Brid.) Mitt.	25	3325 ± 774
Brachythecium spp. Schimp.			*Brachythecium* spp Schimp.		
Ptilium crista-castrensis (Hedw.) DeNot.	100	4016 ± 890	***Pohlia nutans*** (Hedw.) Lindb.	4	9500 ± 7183
Rhizomnium nudum (Britt&Williams) T.Kop.	100	1408 ± 831	***Polytricum juniperinum*** Hedw.	100	9747 ± 1515
Plagomnium insigne (Mitt.) T. Kop.					
Plagomnium spp. T. Kop.			**Lichen**		
Mnium lycopodioides Schwaegr.			***Cladonia* spp.** Nyl.	4	4917 ± 1964
M. spinulosum (Voit) Schwaegr.			*C. acuminata* (Ach.) Norrlin		
Rhytidiadelphus triquetrus (Hedw.) Warnst	100	5110 ± 1773	*C. bacilliformis* (Nyl.) Gluck		
			C. botrytes (K. Hagen) Willd.		
Lichen			*C. cariosa* (Ach.) Sprengel		
Peltigera leucophlebia (Nyl.) Gyelnik	25	1138 ± 31	*C. carneola* (Fr.) Fr.		
P. aphthosa (L.) Willd.			*C. cenotea* (Ach.) Schaerer		
Peltigera membranacea (Ach.) Nyl.	25	1437 ± 256	*C. cervicornis* (Ach.) Flotow.		
			C. chlorophaea (Florke ex Sommerf.) Sprengel		
P. canina (L.) Willd.					
P. degenii Gyelnik			*C. coniocraea* (Florke) Sprengel		
P. extenuata (Vainio) Lojka			*C. cornuta* ssp. *cornuta* (L.) Hoffm.		
P. horizontalis (Hudson) Baumg.			*C. crispata* var. *crispata* (Ach.) Flotow.		
P. neckeri Hepp. ex Mull. Arg.			*C. cfr cyanipes* (Sommerf.) Nyl.		
P. neopolydactyla (Gyelnik) Gyelnik			*C. deformis* (L.) Hoffm.		
Peltigera spp. Willd.			*C. digitata* (L.) Hoffm.		
			C. ecmocyna Leighton		
			C. fimbriata (L.) Fr.		
			C. gracillis ssp. *turbinata* (Ach.) Ahti		

Table G1 continued

Old-growth Species	Sample Size (cm^2)	Average Biomass ($kg\ ha^{-1}$)	Second-growth Species	Sample Size (cm^2)	Average Biomass ($kg\ ha^{-1}$)
			Lichen		
			C. norvegica Tonsberg & Ahti		
			C. ochrochlora Florke		
			C. phyllophora Hoffm.		
			C. sulphurina (Michaux.) Fr.		
			C. umbricola Tonsberg & Ahti		
			Peltigera canina (L.) Willd.	25	2653 ± 843
			P. aphthosa (L.) Willd.		
			P. extenuata (Vainio) Lojka		
			P. leucophlebia (Nyl.) Gyelnik		
			P. membranacea (Ach.) Nyl.		
			P. neckeri Hepp. Ex Mull. Arg.		
			P. neopolydactyla (Gyelnik) Gyelnik		
			P. polydactylon (Necker) Hoffm.		
			P. praetextata (Florke ex Sommerf.) Zopf.		
			P. rufescens (Weiss) Humb.		
			Peltigera spp. *nov. #1*		
			Peltigera spp. *nov. #2*		

Note: Biomass samples were collected for species shown in bold and used to approximate biomass for the species following them. At each of the 12 sites of each forest age, 3 replicates of each species were collected (n = 36).

Appendix H

Biomass (g m^{-2}) of moss and lichen species from old-growth sites and young second-growth sites on coarse textured (coarse) and fine textured (fine) soils in sub-boreal spruce forest.

Table H.1 – Biomass (g m^{-2}) of moss and lichen species from old-growth sites and young second-growth sites on coarse textured (coarse) and fine textured (fine) soils in sub-boreal spruce forest.

	Old-growth		Second-growth	
	Coarse	**Fine**	**Coarse**	**Fine**
Moss biomass	84 ± 47	240 ± 50	285 ± 159	329 ± 119
Lichen biomass	1.0 ± 1.0	1.4 ± 1.7	10.9 ± 3.7	19.9 ± 7.1
Total biomass	85 ± 48	241 ± 48	296 ± 159	349 ± 121

Note: Biomass values ± standard deviation (n=6 plots). Liverwort biomass was not collected.

Appendix I

ANOVA results for lichen and bryophyte biomass carbon and biomass nitrogen, lichen and bryophyte % carbon and % nitrogen contents, and for *Peltigera* and moss species % nitrogen contents.

Table I.1 – ANOVA results for lichen and bryophyte biomass carbon and biomass nitrogen.

	Site	Age	Soil
Biomass carbon	**0.037**		0.080
Biomass nitrogen	**<0.001**	0.070	0.204

Note: Bold numbers indicate a significant effect of site, forest age, or soil texture type on the biomass carbon or nitrogen.

Table I.2 – ANOVA results for lichen and bryophyte percent (%) carbon and nitrogen in old-growth and young second-growth study sites.

	Species	Soil
Old-growth % carbon	**0.002**	0.063
Second-growth % carbon	0.387	0.265
Old-growth % nitrogen	**<0.001**	**0.002**
Second-growth % nitrogen	**<0.001**	0.732

Note: Bold numbers indicate a significant effect of species or soil texture type on % carbon or % nitrogen.

Table I.3 – ANOVA results for % nitrogen in old-growth study sites separated into *Peltigera* lichen species and moss species.

	Species	Soil
Peltigera % nitrogen	**<0.001**	0.199
Moss % nitrogen	**<0.001**	**0.004**

Note: Bold numbers indicate a significant effect of species or soil texture type on % nitrogen.

Appendix J

Continuously recorded seasonal microclimate measurements from stations at site A and B including moss frond and lichen thallus temperature, air temperature, soil temperature, photosynthetic flux density, moss frond and lichen thallus moisture regimes from June – October 2003.

Figure J.1 – Maximum, minimum and mean daily temperature values for moss fronds (*Rhytidiadelphus triquetrus*), measured by 4 fine wire thermocouples at sites A and B of the Aleza Lake Research Forest in central British Columbia, 2003.

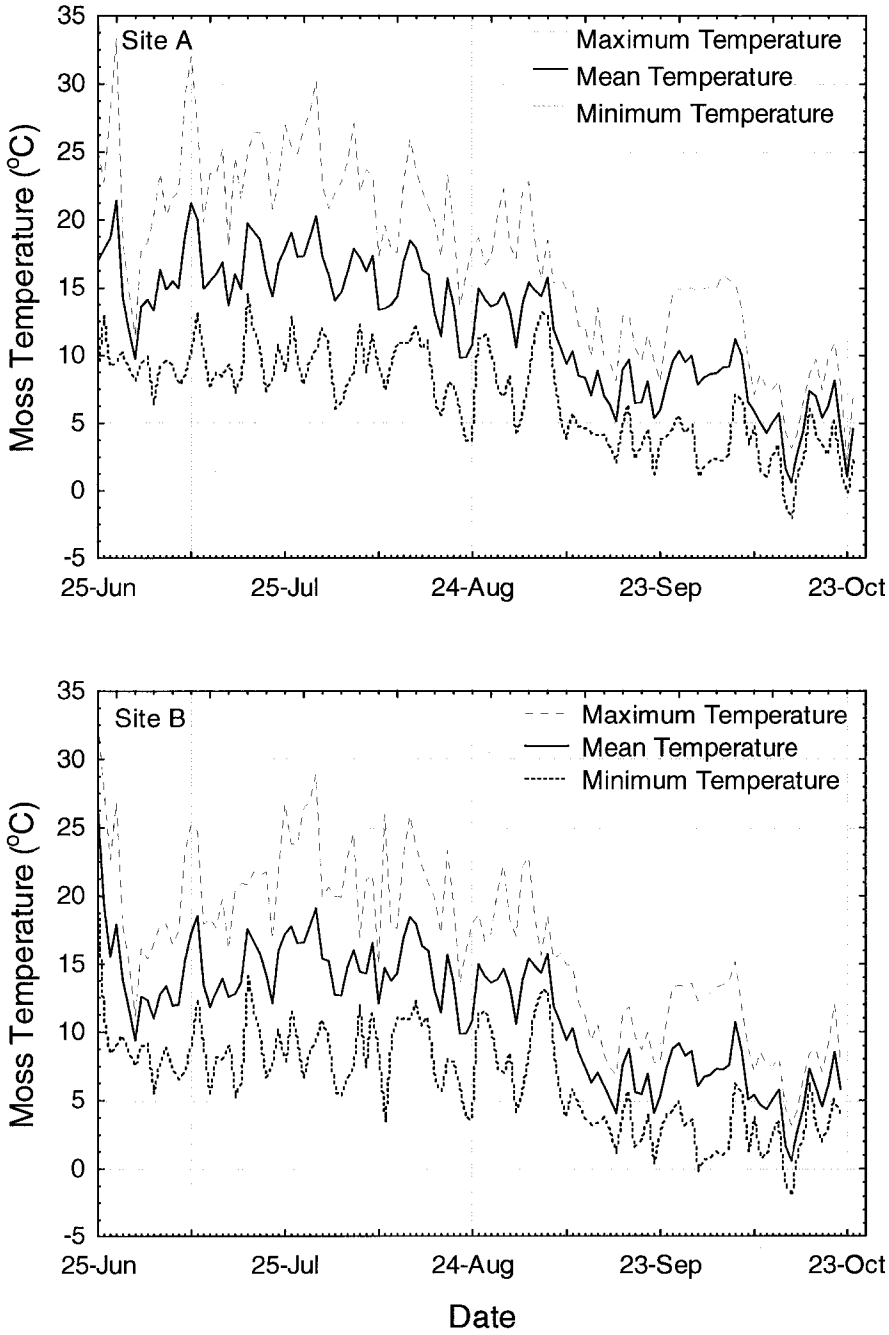


Figure J.2 – Maximum, minimum and mean daily temperature values for lichen thalli (*Peltigera membranacea*), measured by fine wire 4 thermocouples at sites A and B of the Aleza Lake Research Forest in central British Columbia, 2003.

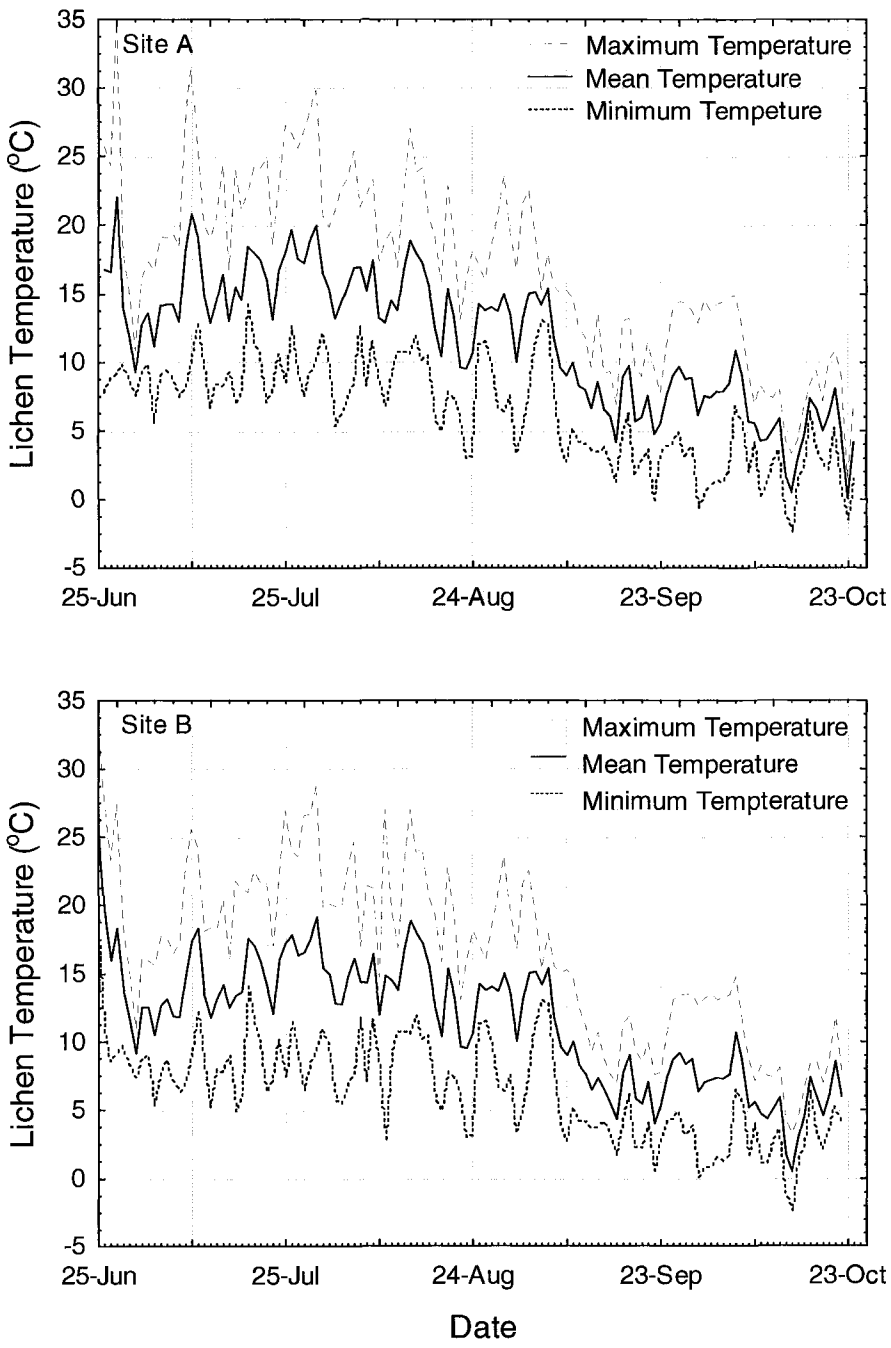


Figure J.3 – Maximum, minimum and mean daily air temperature values measured at the microclimate stations at sites A and B of the Aleza Lake Research Forest in central British Columbia, 2003.

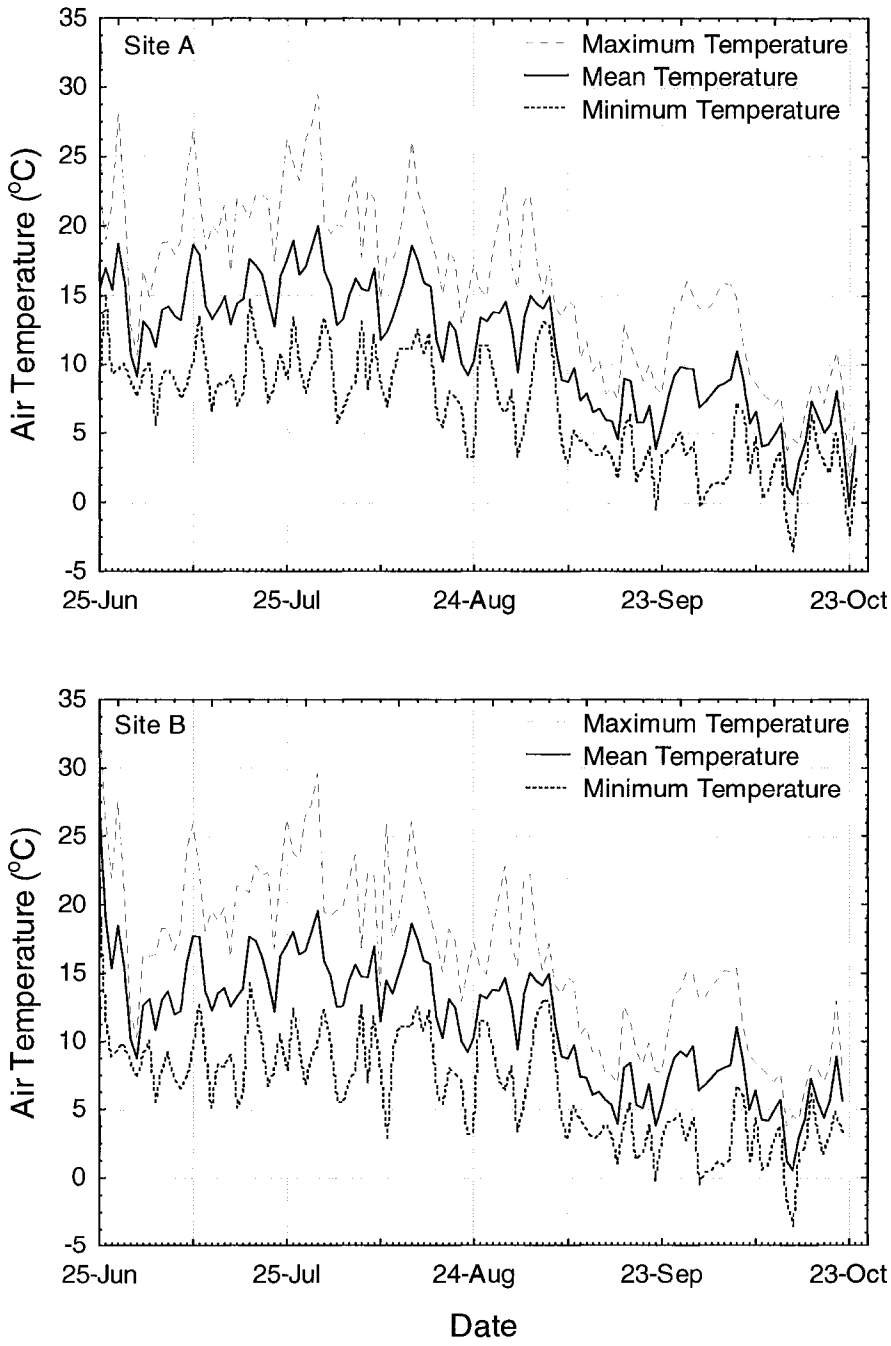


Figure J.4 – Maximum, minimum and mean daily soil temperature values measured by a thermocouple (10 cm depth) at sites A and B of the Aleza Lake Research Forest in central British Columbia, 2003.

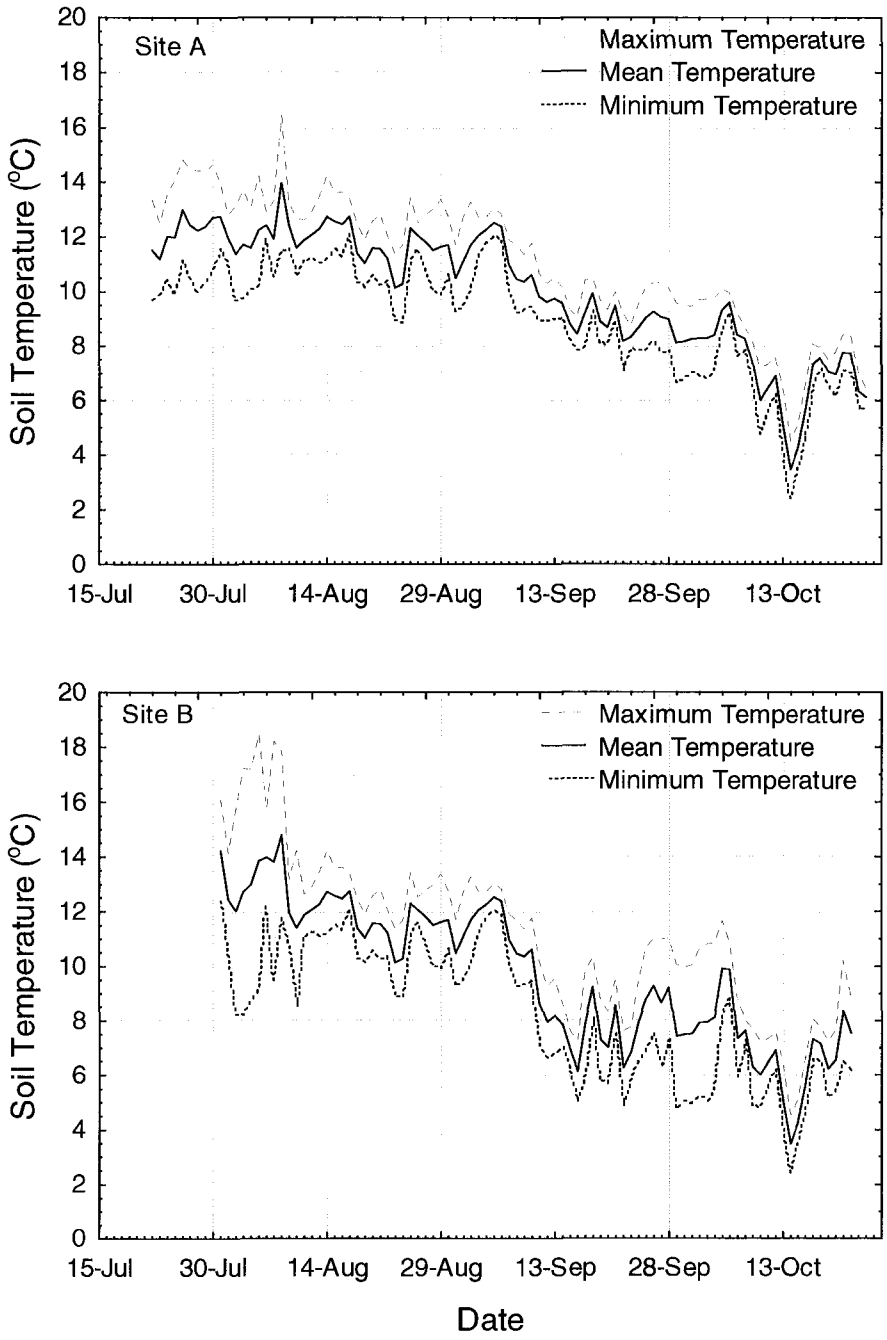


Figure J.5 – Mean seasonal photosynthetic flux density (PFD) (400-770 nm) patterns measured every 5 minutes at 3 quantum sensors at site A at the Aleza Lake Research Forest in central British Columbia, 2003.

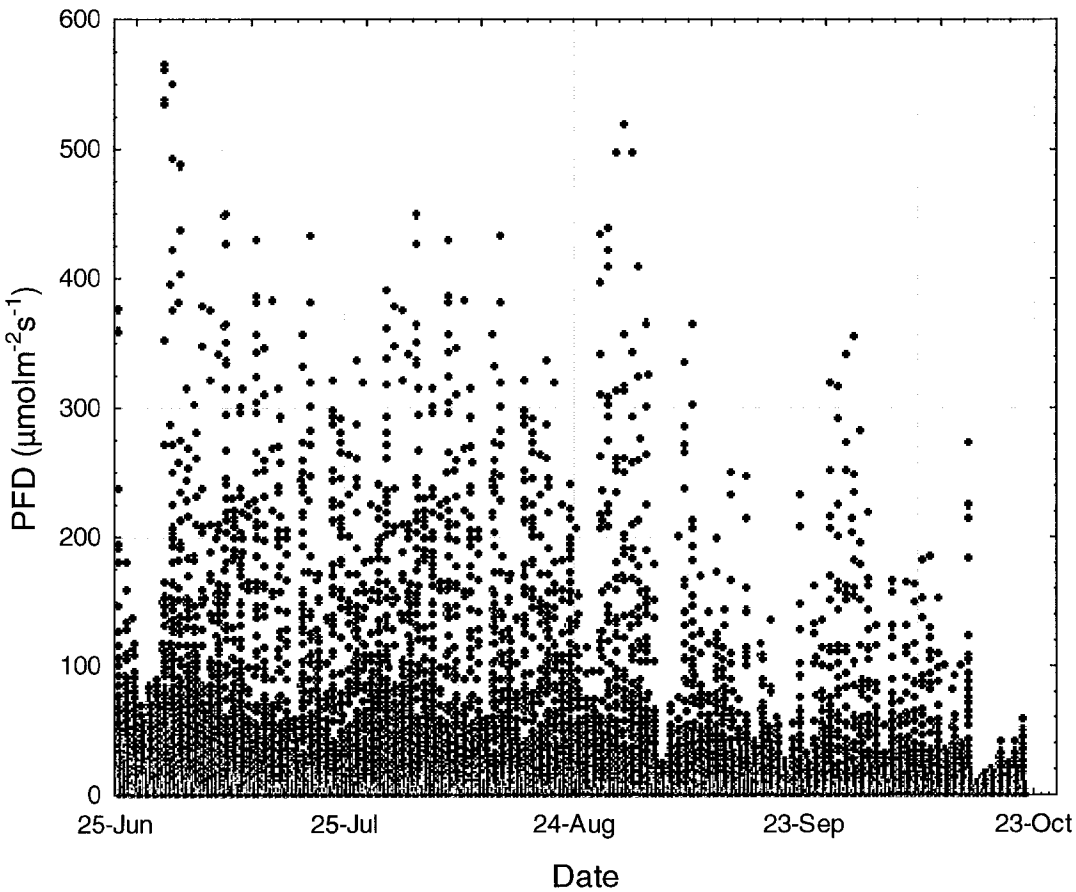


Figure J.6 – Mean seasonal percent moisture content of moss fronds (*Rhytidiadelphus triquetrus*) measured every 5 minutes at the microclimate stations at sites A and B of the Aleza Lake Research Forest, 2003 (n=3).

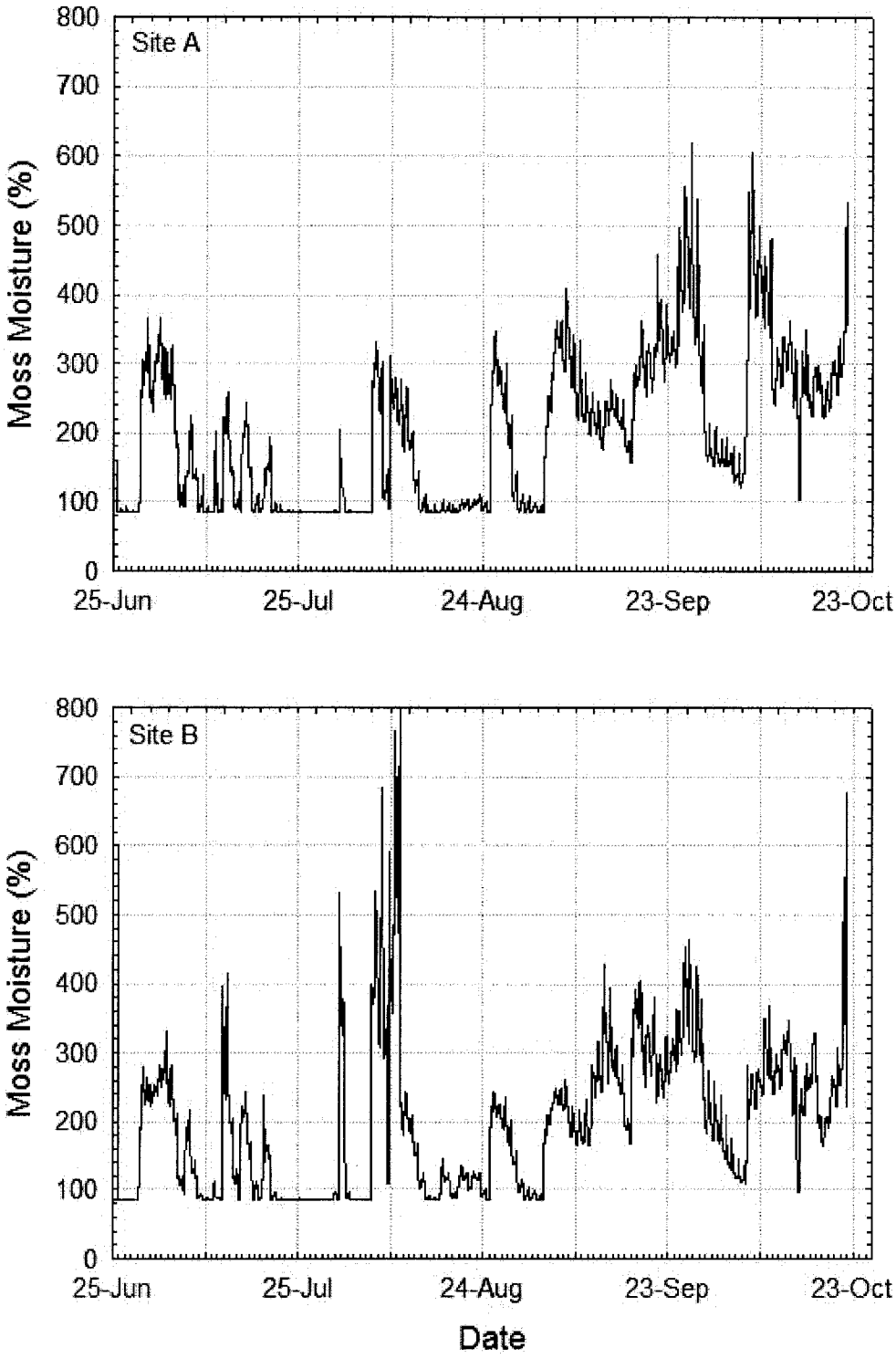
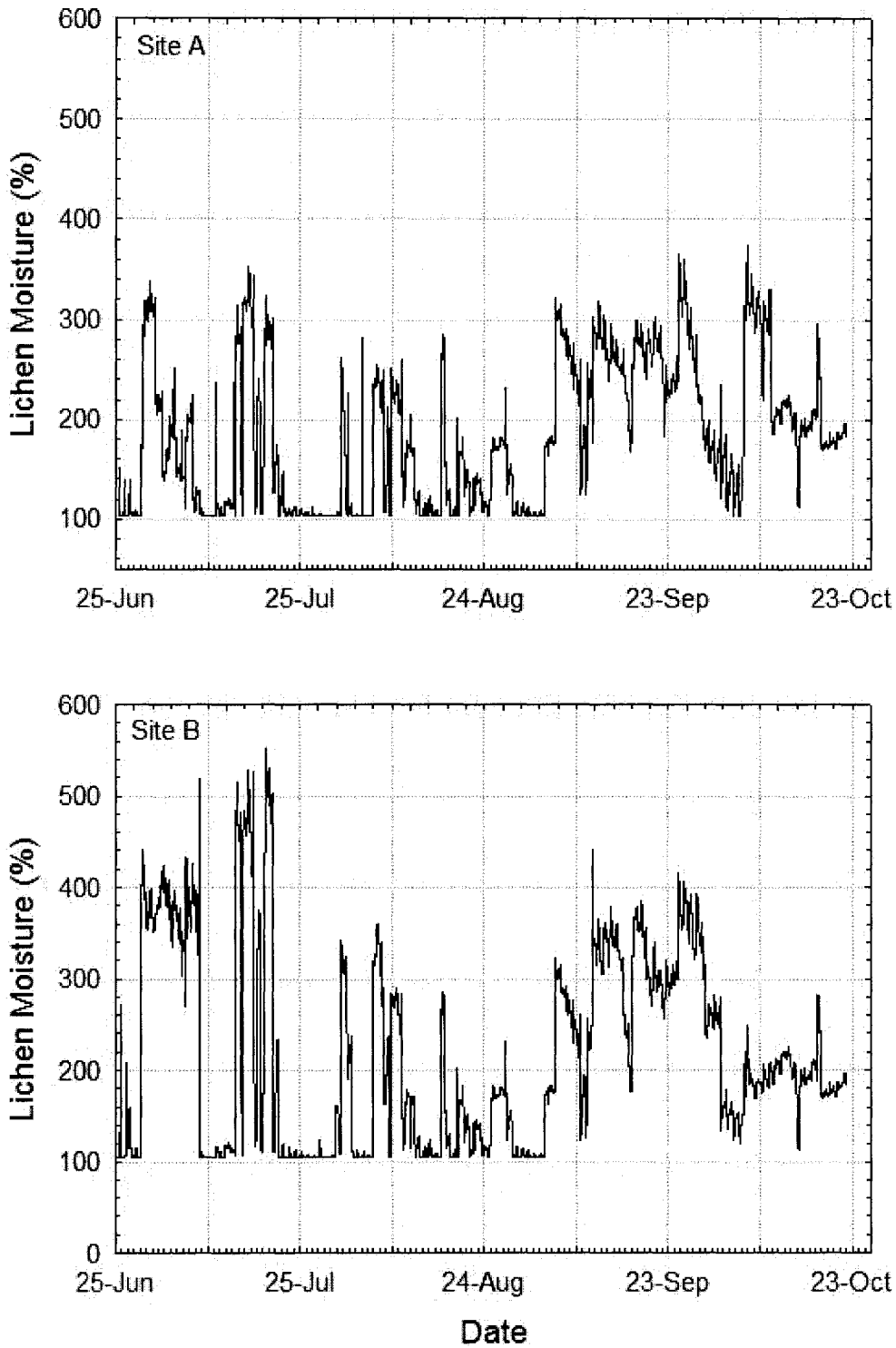


Figure J.7 – Mean seasonal percent moisture content of lichen thalli (*Peltigera membranacea*), measured every 5 minutes at the microclimate stations at sites A and B of the Aleza Lake Research Forest in B.C., 2003 (n=3).



Appendix K

Mean microclimate conditions measured at sites A and B for moss and lichen in the light and dark during periods when the moss frond or lichen thallus was moist or dry, over the three month measurement period.

Table K.1 – Mean microclimate conditions measured at sites A and B for the moss *Rhytidiadelphus triquetrus* in the light and dark during periods when the moss frond was moist or dry over the three month measurement period.

	27June-26July		27July-25Aug		26Aug-24Sept	
	Site A	Site B	Site A	Site B	Site A	Site B
Moist						
Light						
Avg. moss temp. (°C) [a]	14.4	13.8	14.5	14.6	11.0	10.8
Avg. soil temp. (°C) [b]	11.4	11.4	11.6	11.9	10.2	9.6
Avg. PFD (µmol m^{-2} s^{-1}) [c]	50	50	44	44	29	30
Avg. moss moisture (%) [d]	204	193	170	246	261	242
Percent of light moist (%) [e]	58	59	46	58	91	93
Dark						
Avg. moss temp. (°C)	11.2	10.4	11.1	11.1	8.4	8.2
Avg. soil temp. (°C)	10.6	10.6	11.9	12.0	10.5	9.8
Avg. PFD (µmol m^{-2} s^{-1})	0.8	0.7	0.6	0.6	0.6	0.5
Avg. moss moisture (%)	178	182	157	211	243	228
Percent of dark moist (%)	58	58	48	61	92	93
Dry						
Light						
Avg. moss temp. (°C)	18.9	18.6	18.8	19.2	18.2	17.7
Avg. soil temp. (°C)	13.0	14.1	12.1	13.6	12.0	11.8
Avg. PFD (µmol m^{-2} s^{-1})	40	40	46	48	48	45
Avg. moss moisture (%)[d]	85	85	85	85	85	86
Percent of light dry (%)	42	41	54	42	9	7
Dark						
Avg. moss temp. (°C)	13.9	13.6	13.1	12.7	12.4	11.8
Avg. soil temp. (°C)	12.1	12.3	12.1	12.6	12.0	11.8
Avg. PFD (µmol m^{-2} s^{-1})	0.6	0.6	0.7	0.7	0.8	0.9
Avg. moss moisture (%)	85	86	85	86	87	87
Percent of dark dry (%)	42	42	52	39	8	7

Note: Light was defined as periods of time with a PFD value of greater than 5 µmol m^{-2} s^{-1} while dark was defined as all periods with lesser PFD values. Moist was defined as periods when moss frond moisture was greater than 90%.

[a] Average moss/lichen temperature refers to the moss frond or lichen thallus temperature.

[b] Soil temperature refers to the temperature at 10 cm depth in the soil.

[c] PFD is the photosynthetic flux density.

[d] Moss/lichen temperature refers to the moss frond or lichen thallus percent moisture content.

[e] Percent of light moist is the average percent of time during the light period during which the moss frond was moist. Percent of dark moist is the percent of time during the dark period during which the moss frond was moist.

Table K.2 – Mean microclimate conditions measured at sites A and B for the lichen *Peltigera membranacea* in the light and dark during periods when the lichen thallus was moist or dry over the three month measurement period.

	27June-26July		27July-25Aug		26Aug-24Sept	
	Site A	Site B	Site A	Site B	Site A	Site B
Moist						
Light						
Avg. lichen temp. (°C) [a]	14.0	14.1	13.7	13.9	10.2	10.1
Avg. soil temp. (°C) [b]	11.5	11.8	11.6	11.9	10.2	9.4
Avg. PFD (µmol m^{-2} s^{-1}) [c]	48	46	40	40	26	26
Avg. lichen moisture (%) [d]	202	318	171	197	236	266
Percent of light moist (%) [e]	65	70	47	52	82	82
Dark						
Avg. lichen temp. (°C)	11.5	10.8	10.9	11.0	8.1	8.1
Avg. soil temp. (°C)	10.9	10.7	11.9	12.1	10.5	9.6
Avg. PFD (µmol m^{-2} s^{-1})	0.7	0.7	0.6	0.6	0.5	0.5
Avg. lichen moisture (%)	200	316	169	194	232	260
Percent of dark moist (%)	67	68	52	58	86	86
Dry						
Light						
Avg. lichen temp. (°C)	18.6	19.2	18.7	18.9	16.5	16.5
Avg. soil temp. (°C)	13.0	13.5	12.1	13.4	11.3	11.3
Avg. PFD (µmol m^{-2} s^{-1})	42	44	50	50	53	53
Avg. lichen moisture (%)	104	104	104	104	104	104
Percent of light dry (%)	35	30	53	48	18	18
Dark						
Avg. lichen temp. (°C)	13.8	13.7	13.1	12.5	10.8	10.8
Avg. soil temp. (°C)	12.0	11.9	12.2	12.5	11.7	11.7
Avg. PFD (µmol m^{-2} s^{-1})	0.6	0.6	0.7	0.7	0.7	105
Avg. lichen moisture (%)	105	105	105	105	105	0.7
Percent of dark dry (%)	33	32	48	42	14	14

Note: Light is defined as periods of time with a PFD value of greater than 5 µmol m^{-2} s^{-1} while dark is defined as all periods with lesser PFD values. Moist is defined as periods when lichen thallus moisture was greater than 110%.

[a] Average moss/lichen temperature refers to the moss frond or lichen thallus temperature.

[b] Soil temperature refers to the temperature at 10 cm depth in the soil.

[c] PFD is the photosynthetic flux density.

[d] Moss/lichen temperature refers to the moss frond or lichen thallus percent moisture content.

[e] Percent of light moist is the average percent of time during the light period during which the lichen thallus was moist. Percent of dark moist is the percent of time during the dark period during which the lichen thallus was moist.

Appendix L

The Li-Cor LI6400 and the custom built clear chamber equipment set-up at ring sites.

Figure L.1 – Photographs of the custom built clear chamber and the LI6400 equipment set-up.