# UNDERSTORY VEGETATION-ENVIRONMENT RELATIONSHIPS OF LICHEN-RICH FORESTS IN NORTH-CENTRAL BRITISH COLUMBIA

by

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# ABSTRACT

I examined the environmental relationships of feathermosses, vascular plants, and mat-forming lichens in lodgepole pine forests. Seventy-two mature forest plots were surveyed using microhabitat-scale sampling for functional group abundance, canopy characteristics, nutrient availability, soil texture, topography, relative humidity and air temperature. Feathermosses positively associate with canopy closure, afternoon shade, nitrogen or base-cation availability, duff thickness, fine soil texture, and water-receiving positions. Lichens positively associate with total irradiance, aluminum:calcium availability, water-shedding positions, and base-cation or nitrogen deficiency. Vascular plants have higher within-group variability, but positively associate with direct irradiance, afternoon shade, canopy heterogeneity, duff thickness, nutrient availability, alkalinity, and fine soil texture. Lichen patches are characterized by lower atmospheric moisture than vascular plant or feathermoss patches, but microclimate is more strongly associated with macroclimate and soil than canopy or understory vegetation. Competition among functional groups probably occurs but is unimportant; environmental filtering and initial floristics are more likely mechanisms of niche partitioning.

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*To my students, for asking me the questions I can't answer, and to my teachers, for cultivating a desire to know.*

# 1. Background and general introduction: The ecology and classification of understory vegetation in lichen-rich forests

> *"We should not consider the [Connell and Slatyer 1977] models of successional change to be mutually exclusive. Nothing inherent in any of them precludes the operation of the others simultaneously or in sequence. Indeed, the question of interest is how they interact." (Krohne 2001, p. 342)*

## 1.1. Ecological interactions in lichen-rich forests

This section summarizes current and historical ecological research on lichen-rich systems, and highlights dominant theories concerning the mechanisms of interaction. Dominant themes include whether understory vegetation composition and abundance is primarily determined through ecological interactions, environmental filtering, or stochastic processes, and whether forest canopy dynamics determine understory successional trajectories. Nomenclature and taxonomic authorities are outlined in Appendix A.

### 1.1.1. Overstory influences

Forest canopies have a significant influence on understory community composition and diversity (Gilliam and Roberts 2003, Hart and Chen 2006, Barbier et al. 2008). The most obvious reason for this is the large physical stature of trees compared to understory species. The trees dominate competition for both light and below-ground resources because they have greater amounts of photosynthetic and root tissue, and have much greater vertical growth than other species.

Trees can also increase the availability of resources, thereby facilitating growth of other plants rather than competing with them. In particular, nutrient availability can be increased in the top soil layers adjacent to trees via deposition of nutrient-laden canopy throughfall precipitation or stemflow runoff (Moore 1980, Økland et al. 1999), and by decomposition of canopy litter (Prescott 2002). Other examples of positive overstory-understory interactions include the increased water availability or reduced evaporation rates that result from thicker organic layers and increased shading (Bonan and Shugart 1989), or by hydraulic lift (soil moisture redistribution) allowing understory vegetation to access water from deeper soil horizons (Liste and White 2008).

Canopy-tree influences that may be even more subtle include attraction of wildlife that can facilitate plant dispersal (Nathan et al. 2008), change soil properties (Stark et al. 2000), or inhibit some understory species via herbivory (den Herder et al. 2003, Boudreau and Payette 2004a and 2004b). Canopy trees also facilitate expansion of soil mycorrhizal communities, which may associate with (and benefit) some non-tree species by altering soil chemistry (Visser 1995).

Because of the difficulty in isolating the contributions of individual processes, discerning the mechanisms of tree influence on understory species has been difficult. Researchers have often been limited to observational studies of associations between tree proximity and certain components of the understory, or certain characteristics of soil resources (Moore 1980, Økland et al. 1999, Goward and Arseneau 2000). Manipulative experiments are often limited to using overstory removal as a treatment, which has been useful in demonstrating the effects of disturbance, but falls short of being able to establish a cause-and-effect pattern of overstory on understory development (Harris 1996, Miége et al. 2001, Bainbridge and Strong 2005, Nelson and Halpern 2005, Dovciak et al. 2006, Kembel et al. 2008). The converse type of experiment, whereby a forest canopy is added to an otherwise disturbed site, is limited by the slow growth of trees, and the difficulty in determining direct or indirect influences on the understory. Furthermore, the combination of multiple facilitative and competitive influences in the field has often resulted in observational studies demonstrating only a net influence of trees on other vegetation, rather than the individual contributions of various facilitative and competitive interactions (Barbier et al.

2008). In addition, observational field studies often show that compositional or distributional patterns are related to multiple correlated environmental variables, such as nutrient availability, canopy density, and dominant canopy species (Salemaa et al. 2008), making interpretation of a true cause and effect somewhat dubious. In other words, the complexity of forested systems limits a mechanistic understanding with traditional ecological tools.

One way of overcoming this problem of complexity in observational studies may be to compare the hypothesized or modelled spatial arrangement of environmental gradients to their observed arrangement in the field (Økland et al. 1999, McIntyre and Fajardo 2009). Rather than assuming that all tree influences are equally applicable in all directions, we may contrive a spatial extent or intensity for each type of influence, informed by the shape of the tree and of the local physical environment, and compare the theoretical patterns to the observed patterns. This approach is almost certainly preferable to more traditional examinations of correlational relationships between dependent and independent variables; however, long-term manipulative experiments will likely continue to be superior for discerning mechanistic explanations of understory composition.

### 1.1.2. Understory interactions

Unfortunately, the large size of canopy trees can lead to the incorrectly arboricentric assumption that canopy trees directly or indirectly control all ecological processes in forested systems. In certain forested systems, the primary ecosystem drivers may be understory vegetation, rather than the canopy (Nilsson and Wardle 2005, Roturier and Bergsten 2006). For such systems, detailed study of understory interactions would be more enlightening from a scientific perspective, and more pragmatic from a management perspective, than study of canopy development.

Some forest-understory species are found in discrete monospecific patches, while others are more evenly dispersed and intermixed with other species, throughout a forest stand. Does this patchiness reflect sharp microsite preferences responsible for important competitive advantages, extremely efficient vegetative spread, or perhaps historical patterns of disturbance? This section will address some of what is currently known about the interactions of understory species with each other and with the physical environment around them.

#### 1.1.2.1. Resource competition

Understory dominance of mat-forming lichens (e.g., *Cladonia rangiferina* (L.) Weber ex. F.H. Wigg.) requires dry, high-light environments, because the resource gradients of light and moisture vary together to determine habitat suitability and survival potential of lichens (Lechowicz and Adams 1974, Maikawa and Kershaw 1976, Johnson 1981, Sulyma and Coxson 2001). This may be explained, in part, by the existence of upper and lower hydration thresholds at which lichens can maintain positive net assimilation; if the lichen mats are in relatively wet locations, net assimilation may become negative as respiration outpaces photosynthesis (MacFarlane and Kershaw 1982, Kershaw 1985). Yet, while a lower threshold of irradiance (Kershaw and MacFarlane 1980), and greater threshold of moisture (MacFarlane and Kershaw 1982) at which these lichens can grow certainly exists, the requirement for exposed, dry conditions may also be the result of lichens being competitively inferior when conditions are otherwise (Oksanen 1986, Crittenden 2000). For dry, northern habitats, lichen growth rate actually increases with precipitation, because increased photosynthetic activity can be sustained for longer periods of time (Cooper et al. 2001). In addition, observations of microsite-specific adaptation to differing light environments within

*Cladonia* populations (Lechowicz and Adams 1973, Legaz et al. 1986), and of other lichen species showing considerable acclimation to both seasonal and experimentally induced changes in light (Kershaw and MacFarlane 1980), suggests that *Cladonia* species should be able to survive canopy closure in the absence of competition. Most vascular plants and feathermosses grow faster than lichens when moisture and temperature are not limiting, such that under dense forest canopies (which reduce the evaporation caused by direct solar radiation), or over thick organic layers (which both insulate the soil and increase water holding capacity), lichens are probably outcompeted for space and light (Yarranton 1975, Brown et al. 2000, Crittenden 2000).

Likewise, feathermosses, such as *Pleurozium schreberi* (Brid.) Mitt., are not necessarily limited by high light conditions, but by their inability to remain hydrated when exposed to direct sunlight for long periods of time, resulting in decreased ability to repair damaged tissues and grow in competition with other species. Given higher ambient moisture conditions (such as those experienced in Pacific Northwestern North America), exposure to greater light levels via clearcutting can actually increase the abundance and growth rate of feathermosses (Nelson and Halpern 2005). In addition, feathermosses are effective competitors in small boreal-forest gaps, where canopy interception of precipitation is low but adjacent trees can still reduce direct irradiance, due to the low zenith angle of the sun in high-latitude regions (Økland et al. 1999, Hart and Chen 2006).

Despite being located in what are usually very dry habitats, understory vascular plants appear to be largely limited by the availability of below-ground resources in boreal forests. Experimental fertilization of lichen or moss-dominated sites often leads to a dramatic increase in vascular plant dominance, both with and without the addition of moisture (Kellner and Mårshagen 1991, Vagts and Kinder 1998, Skrindo and Økland 2002, Olsson and Kellner 2006). The combination of low vascular plant abundance and high lichen or moss abundance in a forest understory has often been used as an indicator of poor fertility (Klinka et al. 1989, Beaudry et al. 1999, Salemaa et al. 2008). In addition, the majority of understory vascular plants that coexist with lichens and feathermosses in boreal forests are either mycorrhizal, such as ericoid shrubs, or leguminous; a strong selective pressure to increase rates of nutrient acquisition via symbiosis seems indicative of potential nutrient limitation in a given habitat.

For vascular plants, lichens, and feathermosses in the forest understory, the only initially apparent common resource for which all groups would compete is light. Yet, greater light means both greater photosynthetic potential and greater evaporation of water from the soil surface, so it can be difficult to separate competition for water from competition for light (Tilman 1988). Because of this, much of the ecological research on lichen-rich communities has focused on combining or partitioning resource gradients of light and moisture as related to the forest canopy (Yarranton 1975, Maikawa and Kershaw 1976, Coxson and Marsh 2001, Gilliam and Roberts 2003, Bainbridge and Strong 2005, Kembel and Dale 2006). It is true that the amount of light reaching the ground can significantly influence nutrient and moisture supply through the regulation of soil temperature, and therefore, of microbial respiration and decomposition (Bonan and Shugart 1989, Bonan 1990, Balisky and Burton 1993, Stark et al. 2000, Nilsson and Wardle 2005). But given that soil moisture regime and moisture availability are influenced more by physical properties of the soil and landscape than by canopy conditions, and that soil physical properties are themselves intimately coupled with soil chemistry and nutrient availability (Barber 1995), it is surprising that more research in northern lichen-rich forests has not assessed the relationships between soil properties and vegetation. Despite their lack of a physical mechanisms for extracting nutrients from the soil

(Ellis et al. 2004), lichens and feathermosses are influenced by soil chemical properties both directly (Kershaw 1977, See and Bliss 1980) and indirectly through competition with vascular plants (Yarranton 1975, Crittenden 2000, Williston et al. 2006). The converse is also true: lichens and feathermosses may directly influence soil properties such as moisture regime, temperature, litter decomposition and nutrient availability (Kershaw 1985, Bonan 1990, Stark et al. 2000, Sedia and Ehrenfeld 2005).

#### 1.1.2.2. Interference competition

Understory vegetation can negatively influence other species not only by direct resource competition, but by changing the habitat so it is unfavourable to other species. This is known as interference competition (Krohne 2001), or inhibition (Connell and Slatyer 1977). An obvious example of interference is the physical barrier that mat-forming species create between soil and atmosphere. By physically blocking access to mineral soil, both lichens and mosses can have a negative impact on germination of vascular species from seed (Zamfir 2000). Barriers to the mineral soil are a widespread constraint to the regeneration of trees in northern ecosystems, where seeds may germinate in moss or lichen mats under suitable weather conditions, but germinants frequently die of moisture stress before roots secure access to soil moisture (Nash-Suding and Goldberg 1999, Hille and den Ouden 2004). This phenomenon is obviously of less importance for vascular species that reproduce primarily by underground runners and rhizomes.

The physical barrier presented by feathermosses and mat-forming lichens may prevent the transfer of nutrients and moisture between above- and below-ground sources. Even on days when ambient temperatures are high and solar irradiance is direct, soils under subarctic lichen mats typically remain moist (Kershaw 1985). Both mat-forming lichens and feathermosses have extremely efficient internal recycling of nutrients, such that dead tissues (necromass) and litter that accumulate below the live portion of the thalli are relatively carbon-rich, decompose slowly, and contribute little or nothing to soil nutrient pools (Moore 1980, Crittenden 1991, Turetsky 2003, Sedia and Ehrenfeld 2006, Kytöviita and Crittenden 2007). Furthermore, any nutrients that would normally reach the mineral soil through percolation of rainwater and deposition of canopy litter are captured and (presumably) stored within the mats, largely in water-insoluble forms (Kershaw 1985).

The combination of moisture regulating and nutrient immobilizing properties in lichen and feathermoss mats may also inhibit vascular vegetation growth indirectly through the soil microbial community. Because lower temperatures and anaerobic conditions inhibit microbial activity, the insulative effect of feathermoss and lichen mats may reduce microbial activity in soil. In northern forested systems, where many vascular plants are heavily reliant on mycorrhizal or bacterial associations, reduced microbial activity could translate directly into reduced resource availability and growth rates, thereby ensuring that lichens and feathermosses can compete for space more effectively against otherwise faster growing vascular plants (Sedia and Ehrenfeld 2003).

A slightly different form of interference competition is exhibited by *Vaccinium myrtillus* L. This species produces a number of polyphenolic compounds that are potentially toxic, but rather than influencing competing vegetation through direct toxicity, the influence of these polyphenols is to impede decomposition processes, thereby supporting a constant but slow recycling of nutrients (Northup et al. 1998). By ensuring that nutrient cycling occurs slowly, the slow-growing *V. myrtillus* effectively prevents faster growing species from taking advantage of the microsites it occupies. It is possible that other *Vaccinium* species produce litter similarly laden with polyphenols.

#### 1.1.2.3. Allelopathy

Allelopathic effects are difficult to demonstrate for boreal species through both observational and experimental study. Many authors have shown lichen extracts to be highly toxic to fungi (Land and Lundström 1998, Votintseva and Mukhin 2004, Ruotsalainen et al. 2009), vascular plants (Sedia and Ehrenfeld 2006), and mosses (Thomas et al. 1994) under laboratory conditions, but rarely in the field (Kershaw 1985, Lawrey 1995, Stark et al. 2007). Although the mid- or late-successional status of mat-forming lichens and the abundance of secondary metabolites they produce certainly agrees with a generalized allelopathic strategy (Bazzaz 1979), a true allelopathic influence of mat-forming lichens is unlikely under field conditions. This is because the concentrations of largely hydrophobic allelochemicals leaching into mineral soils from lichen mats rarely reach toxic (or even detectable) levels (Kershaw 1985, Stark et al. 2007, Kytöviita and Stark 2009). Studies have shown the removal of lichen mats to be more detrimental to tree growth than their presence (Bonan and Shugart 1989, Lawrey 1995, Crittenden 2000). It is more likely that instances where lichens have negatively influenced germination or growth are due to physical processes, as discussed above.

A slightly more well-supported case of understory allelopathy is that of *Empetrum nigrum* (syn. *hermaphroditum*) L., a circumpolar boreal and alpine species. *Empetrum nigrum* produces a phenolic compound called betatasin-III, which is released from leaf glands into precipitation and accumulates in soils. The concentration of betatasin-III can eventually build up to toxic levels in forest soils, thereby inhibiting germination of conifer seedlings (Nilsson 1994). This process may have significant ecosystem-level consequences in some places, such that the further development and replacement of canopy trees, and therefore the future structure of the forest, is largely determined by allelopathy (DeLuca et al. 2002, Nilsson and Wardle 2005).

#### 1.1.2.4. Facilitation

Facilitation is an often overlooked process in plant ecology that may nonetheless play a significant role in the successional development of communities (Bruno et al. 2003), particularly in less productive ecosystems such as boreal or montane forests (Cater and Chapin 2000). This may be due, in part, to the difficulty of separating the positive influences from the negative influences of one species on another; the net influence is often all we can measure, and it is often negative. Yet, by careful examination of specific life-stages or habitat types, researchers have been able to separate at least some of the positive from the negative.

Certain species of vascular plants can facilitate the establishment and growth of other vascular and non-vascular species on bare soil. This facilitation may occur via microclimatic regulation, soil enrichment, or redistribution of soil resources (Goldberg and Novoplanksy 1997, Herrnstadt and Kidron 2005, Ingerpuu et al. 2005, Liste and White 2008). For example, *Shepherdia canadensis* (L.) Nutt. is an important contributor to soil and community development in boreal forests, because of its actinorhizal (nitrogen fixing) associations (Rhoades et al. 2008). *Shepherdia canadensis* may also facilitate the establishment of feathermosses, such as *Pleurozium schreberi*, via microclimatic regulation (Figure 1). Although no studies have empirically shown the directionality of this interaction, *S. canadensis* is found much sooner after wildfire than *P. schreberi* (Larson and MacDonald 1998, Cichowski and Williston 2008), indicating that the mechanism is likely to be some sort of microclimatic regulation by the former.

Lichens and feathermosses may also play an important role in habitat enrichment and microclimatic regulation (During and Van Tooren 1990, Frego and Carleton 1995b). This role is particularly well-recognized in xeric habitats such as deserts or tundra, where biological soil crusts (layer consisting of bryophytes, lichens, and bacteria or algae that occupy the soil surface) stabilize and buffer otherwise poor soils (Belnap 1995, Gold and Bliss 1995, Su et al. 2009). In addition to regulating moisture and temperature (and thereby influencing nutrient-cycling), many lichen and moss species associate with nitrogen-fixing cyanobacteria, and therefore contribute to nitrogen enrichment (Brodo et al. 2001, Turetsky 2003, Houle et al. 2006, Knowles et al. 2006). Although the efficient internal recycling and quick reabsorption of leached nutrients exhibited by some lichens and mosses may cast doubt on the biological significance of their contributions (Crittenden 2000, Startsev and Leiffers 2006), even apparently small quantities of leached nutrients may be enough to benefit other plants (Wilson and Coxson 1999).

**Figure 1.** Photographs (by author) showing (possible) facilitation between *Shepherdia canadensis* and *Pleurozium schreberi* in the Omineca Mountains of north-central British Columbia. Note patches of green *Pleurozium* being largely restricted to locations beneath the canopies of *Shepherdia* shrubs.

Kershaw (1985) explored many of the microclimatic influences of lichen mats, and concluded that lichen mats generally decreased temperature fluctuation and rates of evaporation at the soil surface, as compared to non-vegetated surfaces. This soil-climate buffering may favour the gradual development of moss or vascular plant components of the system, and has been suggested as the mechanism responsible for increased growth of mycorrhizae and their associated trees in boreal forests (Bonan 1990, Crittenden 2000, Stark et al. 2007, Kytöviita and Stark 2009). Similarly, feathermosses act as a moisture-regulating buffer between the atmosphere and soil, and in doing so may facilitate the dominance of spruce canopies over pine in later stages of forest development in some systems. This is because high variability in moisture content of the moss layer prevents pine seedling roots from reaching the mineral soil before desiccating during dry or hot weather, whereas spruce can reproduce by layering and are therefore protected from desiccation by the moisture regulation of the parent plant (Nilsson and Wardle 2005). This may also be a case of positive feedback, because spruce trees have denser canopies than pine and may be more effective in reducing evapotranspiration at the ground layer, which would benefit feathermosses.

### 1.1.3. Disturbance and succession

#### 1.1.3.1. Fire and logging

Disturbances that immediately affect light and moisture availability, such as clearcut logging, may promote increased lichen dominance at the expense of feathermosses (Nieppola 1992, Sulyma and Coxson 2001, Sulyma 2003), probably because of increased evaporation of soil moisture at ground level, resulting in a reduction in competition from feathermoss. In contrast, even minimal disturbance of the ground layer, by use of heavy machinery or mounding residual timber, may have a significant negative impact on both lichen and feathermoss growth (Miége et al. 2001, Kembel et al. 2008). Increased levels of soil disturbance generally favour development of a vascular plant-dominated community, whereas minimal soil disturbance favours prolonged persistence of mat-forming lichens and/or feathermosses (Sulyma 2003, Hille and Ouden 2004, Uotila et al. 2005, Wang and Kemball 2005). To some extent, this pattern of vascular dominance or relative abundance in early post-disturbance stages appears to hold true after wildfire as well (Oksanen 1986, Haeussler et al. 2002). Although a small number of bryophyte and lichen species are also well adapted to these post-disturbance environments, these are usually acrocarpous mosses and crustose or cup-forming lichens, rather than mat-forming species (Morneau and Payette 1989, Sirois 1995, Coxson and Marsh 2001). The dominance of a vascular functional group appears to be largely driven by soil characteristics, which, after the differences in residual standing dead trees, represent one of the main differences between wildfire and logging (Haeussler et al. 2002, Lindenmayer et al. 2008).

With respect to disturbance of the forest floor and mineral soil, logging practices have a wide range of homogeneously distributed influence, from almost no change to complete mixing of organic and mineral soil, while wildfire tends to leave a patchy distribution of lightly scorched to heavily burned organic layers, often without affecting the underlying mineral soils. In addition, post-fire soils tend to experience an immediate flush of nutrients due to mineralization of litter and coarse woody debris, and increased soil temperatures due to increased solar exposure (Dubreuil and Moore 1982, Bonan 1990). Both logging and fire seem to promote conditions beneficial for the germination of vascular plants. Within a short time after fire, however, nutrient flushes end and canopy trees reach sufficient size to inhibit other vascular species.

This relationship between lichen cover and edaphic factors or potential competition with vascular plants or bryophytes (which are more directly influenced by edaphic factors), also holds true in forests that are only temporarily dominated by pine. In British Columbia's sub-boreal spruce forests, epigeic (growing on soil) lichen abundance and composition differ between young and old forests, with young forests supporting a more diverse and abundant lichen flora. These relationships are likely due to increased moisture in older stands favouring bryophytes over lichens (Botting and Fredeen 2006).

Ultimately, whether disturbance has a net positive or negative effect on abundance of lichens, feathermosses, or vascular plants depends quite heavily on the time-frame of comparison. For example, despite the possible long-term benefits of wildfire for lichen woodland rejuvenation (Uotila et al. 2005), fire can significantly reduce lichen cover over large areas in the short term, after which recovery may be quite slow (Jandt et al. 2008). Large insect outbreaks may have the potential to shift understory species dominance from lichens to dwarf shrubs and bryophytes (Williston et al. 2006). The combination of increased nutrient or water input directly to the soil (through decomposition and precipitation) with a lack of significant nutrient or water sinks (due to the lack of live trees), and a sudden increase in litter deposition creates soil conditions more beneficial to vascular plants than lichens.

#### 1.1.3.2. Herbivory and trampling

Seasonal grazing by *Rangifer tarandus* L. at moderate intensity is the most common type of disturbance to mat-forming lichens in northern regions (Fergusen et al. 2001). Grazing can facilitate lichen dispersal and maintain a lichen community in a sub-climax state almost indefinitely in tundra and alpine ecosystems (Eskilinen and Oksanen 2006, Gough et al. 2008, Vistnes and Nellemann 2008). This is likely the result of both increased dispersal for sub-climax species (whereby caribou are dispersal vectors) and targeted consumption of their preferred forage, the late-successional species *Cladonia stellaris* (Opiz.) Pouzar and Vĕzda, which is more susceptible to trampling damage than others (van der Wal et al. 2001, Boudreau and Payette 2004a, 2004b).

In areas where caribou populations can maintain their natural migratory behaviour, lichen communities may experience irregular periods of moderate-intensity grazing followed by recovery to a climax or near-climax state (Ferguson et al. 2001). When caribou have a limited or fragmented range, their influence on forage lichen abundance and composition is amplified, sometimes to the extent of completely altering the successional trajectory of the system (den Herder et al. 2003, Olofsson 2006). These alterations may be the product of enhanced nutrient mineralization rates caused by the regular addition of herbivore dung, coupled with the negative influence of trampling on mat-forming lichens (Stark et al. 2002). Such high-intensity grazing is thought to occur periodically under natural conditions (Manseau et al. 1996, Arseneault et al. 1997), but has been observed more commonly in areas where logging and human development have reduced caribou winter range in size or quality (Nellemann et al. 2001, Vistnes et al. 2004), where caribou have been introduced to a formerly unoccupied range (Cooper and Wookey 2001), or where herds have been maintained above the natural carrying capacity of the system by human intervention (Vare et al. 1995).

Mat-forming *Cladonia* spp. are damaged as much as or more by trampling in the summer as they are by winter grazing (Pegau 1970, Manseau 1996, Suominen and Olofsson 2000). The trampling mainly occurs during summer months, since lichens are more brittle and do not have a protective snow cover at this time; trampling is therefore often a by-product of grazing on vascular plants (Pegau 1970, Manseau et al. 1996). Yet even in cases of intense disturbance, lichens may begin to regenerate by mycelial expansion soon after, due to the presence of abundant thallus fragments on the substratum (Hammer 1997, Boudreau and Payette 2004). When trampling pressure is sustained over time, communities may shift towards dominance by dwarf-shrubs and grasses (Suominen and Olofsson 2000).

For many species of epigeic lichen, caribou are not necessarily the primary agents of disturbance. Pellerin et al. (2006) found that an increasing density of white-tailed deer (*Odocoileus virginianus* Zimmermann) in heathlands was correlated with decreasing cover and diversity of lichens. Even periodic low-intensity trampling due to recreational or research activities of humans can cause significant reductions in richness and abundance if sustained over time (Arnesen 1999, Torn et al. 2006). Periodic trampling by deer or humans may seem insignificant when compared with disturbances such as fire, but they can nonetheless play an important role in the dynamics of epigeic lichens. Heathlands and tundra appear to be particularly susceptible to this kind of disturbance (Forbes et al. 2001, Pellerin et al. 2006). Yet, when the disturbance occurs infrequently in areas of little plant competition and sufficient moisture, the lichens may be able to recover at reasonably fast rates (Cooper et al. 2001, Torn et al. 2006).

#### 1.1.3.3. Successional stages

Many studies have used a chronosequence approach to document the successional development of lichen-rich forests (Maikawa and Kershaw 1976, Carroll and Bliss 1982, Oksanen 1986, Morneau and Payette 1989, Crites and Dale 1998, Coxson and Marsh 2001, Bainbridge and Strong 2005), while a small number have used long-term observations of stands in varying initial seral stages (Hunt et al. 2003), or employed sedimentary pollen records and dendrochronological methods (Larson and McDonald 1998, Pitkanen and Huttunen 1999). Though none have documented the development of a single stand from initiation to maturity, a general theoretical sequence of successional development has evolved. The initial post-fire (or post-logging, in some cases) stage on pine-lichen sites occurs from about 0 to 15 years after fire, where ruderal (Grime 1977) or r-selected

(MacArthur and Wilson 1967) species abound, quickly utilizing the post-fire flush in nutrient and light availability (Rowe 1983). The young forest stage occurs from about 5 to 50 years after fire, where trees begin to dominate vascular plant competition and cup-forming *Cladonia* spp. become noticeably more abundant in the understory. This dominance of *Cladonia* spp. is attributed to a combination of low nutrient or moisture availability inhibiting vascular competition, due to the intense resource use by pine saplings, and the high dispersal ability of cup-forming *Cladonia* spp. (Ahti 1959, Oksanen 1986, Coxson and Marsh 2001). The mature-forest stage, where the canopy is tall but open enough that mat-forming *Cladonia* spp. are dominant in the understory, usually takes between 30 and 100 years to develop, and may continue until stand replacement in some forests (Oksanen 1986). At this point, the soil organic layer of low-productivity forests has usually not increased enough to contribute significantly to moisture retention, and therefore mat-forming lichens come into dominance. The senescent stage begins between 50 and 250 years after fire, and continues until stand replacement; the canopy begins to limit light in the understory, and when gaps form in the canopy, pine trees are replaced by sub-dominant spruce or fir, while feathermosses dominate the understory. Some authors do not distinguish the first and second stages in this sequence, as the first is relatively short and dominated by generalist species (Coxson and Marsh 2001), but few make reference to non-tree vascular understory species, as they tend to have relatively constant abundance after initial post-fire stages and are not considered ‘dominant’ components of the understory (Johnson 1981).

The overlap occurring between many of the stages is because the exact timeline can change significantly from one region to the next. Some forests may never reach the last stage, and remain in a state of lichen dominance for longer than 250 years, or until stand replacement (Jasinski and Payette 2005, Girard et al. 2009), while others are already in the last stage within several decades (Carroll and Bliss 1982, Hunt et al. 2003).

#### 1.1.3.4. Climate Change

Many recent investigations of lichens and climate change have focused on northern and alpine environments, as climate-modelling scenarios show that these regions will undergo the most significant changes (Ellis et al. 2007). Several authors have suggested that climate change may increase the fertility of soils in polar and alpine ecosystems, because warmer temperatures and increased moisture will increase soil microbial activity, organic matter decomposition, and nitrogen fixation (Emmett et al. 2004, Wasley et al. 2006). Others have demonstrated experimentally that increased soil fertility leads to increased cover of competitively superior vascular plants and decreased lichen cover (Cornelissen et al. 2001, Fremstad et al. 2005), while still others have shown that increased temperature and precipitation lead to increased dominance of vascular plants, especially grasses, in tundra ecosystems (Hollister et al. 2005, Wahren et al. 2005, Walker et al. 2006). Though long-term community responses to artificial warming have been somewhat variable among study sites (Hollister et al. 2005), the consistency of lichen impoverishment among them is remarkable. It is abundantly clear that the environmental changes caused by global warming could lead to significant declines in terrestrial lichen abundance and diversity throughout the global north.

Heathland communities of boreal, arctic, and alpine systems may appear to be exceptions to this effect of warming-induced lichen impoverishment. In some cases, lichen abundance appears to remain within the natural range of variation (Jägerbrand et al. 2006), or be entirely unaffected by warming (Jónsdóttir et al. 2005), though such responses are likely limited to sites with a single dominant species that forms a continuous ground layer (such as feathermoss heathlands. In one instance, lichen communities on mossy hummocks actually expanded as the hummocks became less hospitable to dwarf-shrubs and the mosses themselves due to warming (Malmer et al. 2005). Long-term monitoring and fine-scale analysis of these habitats is required to determine if such exceptions will persist, or if accompanying rises in decay rates may lead to compaction and subsequent expansion of the graminoids that dominate wetter areas in moss heaths at the expense of lichens.

## 1.2. Vegetation classification and the use of functional groups

Assembling groups of species into functional or taxonomic guilds has a long history in plant ecology, and results from the perceived benefit of system simplification. Organizing species into groups can be beneficial for logistical reasons, including theoretical generalization and modelling of environmental or evolutionary relationships (Grime 1977, Grime et al. 1990, Hadar et al. 1999), reduction of field-identification error in cryptic species (Lang et al. 2009), and reduction of zero-inflation in sample data (Lang et al. 2009). The use of species functional groups can also be advantageous for biological reasons, such as the existence of some form of symbioses or complementary process among species that requires them to occur together (Ettema and Wardle 2002, Barbier et al. 2008), or because there is significant functional redundancy among species that are present (Walker 1992, Naeem and Li 1997, Hadar et al. 1999). However, the use of functional groups may also lead to reduced power to detect significant trends or environmental relationships (Olsson and Kellner 2006).

In ecological studies of lichen-rich northern forests, it is a common practice to treat terrestrial lichens (mostly *Cladonia* spp.) and mosses as distinct functional groups when examining environment relationships (Pharo and Vitt 2000, Bainbridge and Strong 2005, Lang et al. 2009). Others have used finer division of moss and lichen groups, such as generic-level separation of lichens and growth-form separation of mosses, on the basis of their association with successional stages (Coxson and Marsh 2001). Vascular plants are occasionally used as a third group (Lang et al. 2009, Sedia and Ehrenfeld 2005, Walker et al. 2006), but are more often divided into graminoids, forbs or herbs, dwarf shrubs (Ericaceae), and shrubs (Pharo and Vitt 2000, Baingridge and Strong 2005, Olsson and Kellner 2006, Lang et al. 2009). In general, amalgamation of species into broader taxonomic groups tends to increase the significance of vegetation-environment relationships. Lang et al. (2009) recommended a minimum level of separation for cryptogams that include the taxa: lichens, liverworts, *Sphagna*, and mosses, but did not make recommendations for vascular plant functional groups.

In practice, the choice of how to use functional groups in ecological research has as much to do with the species composition of the study area as it does with the taxonomic or functional relevancy of those groups. A boreal montane ecosystem on xeric soils would be unlikely to support many species of graminoid, *Sphagna*, or vascular cryptogams (Coxson and Marsh 2001), thereby justifying omission of these groups or their amalgamation with others. Indeed, the lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.) forests of north-central BC are largely dominated by mat-forming lichens, feathermosses, or dwarf shrubs, all of which are valid functional groups (Lang et al. 2009). Herbaceous species are less common, but should theoretically have far more in common with dwarf shrubs than either lichens or mosses, and may therefore be combined with dwarf shrubs to provide increased detection frequency. If the intent of a study is to differentiate among the habitat associations of these three groups, the distinctiveness of their growth forms, physiology, and successional relationships should allow each group to show cohesive patterns of environmental association.

## 1.3. Summary and outline of following chapters

Forests are visually, and often functionally, dominated by trees. Consequently, ecologists tend to focus on the associations between stand age or successional stage and understory composition in lichen-rich forests, but few have done so using continuous, rather than categorical analyses of environmental variables. Furthermore, this arboricentric focus has meant that ecosystem managers emphasize biotic influences from the forest canopy as the primary determinants of understory composition. This assumption is only partly true, since other studies have shown forest understories and abiotic factors to exert considerable control over ecosystem processes.

Also related to the assumption that canopy trees dominate interactions in lichen-rich systems is the scale at which study takes place; most researchers have studied these systems at the stand scale. Because competitive interactions are thought to largely take place at the scale of individual plants or genets (cushions of genetically identical lichen or moss individuals), examination of habitat characteristics at this same scale may prove more useful in delineating habitat associations. At the patch scale, it also becomes apparent that understory vascular plants may be worthy of designation as a functional group with similar standing as mat-forming lichens or feathermosses, particularly in the context of competitive interactions.

Chapters 2 and 3 of this thesis examine the environmental associations of mat-forming lichens, feathermosses, and vascular plants, using both continuous and categorical analyses, with equivalent treatment of biotic, abiotic, and soil chemical variables. Specifically, chapter 2 focuses on the patch-scale, while chapter 3 does on the plot scale. By doing so, I address the knowledge gaps of whether the understory interactions of lichen-rich forests are primarily associated with aspects of the forest canopy or of some other coinciding variables, whether vascular plants warrant inclusion as a third understory functional group, and what scale is most useful or appropriate to examine these phenomena. In addition, the microhabitat focus should provide information on potential mechanisms of environmental influence, and comparison of the consistency of functional group associations with each other will provide information on the potential type and importance of functional group interactions.

Because the relevancy of scale at which an investigation is conducted depends not only on the spatial dispersion of dependent variables (i.e., understory vegetation composition or species abundance), but also on the dispersion of independent variables, it is useful to determine whether there is autocorrelation present in any of the measured variables. In addition to testing assumptions of independence that are required for certain statistical procedures, examination of spatial relationships may assist researchers in interpreting whether detected patterns are the result of intrinsic or extrinsic factors. Spatial investigations may also allow researchers to improve future sampling strategies, such that sample plots are well spaced and do not represent redundant information. Chapter four examines how environmental dissimilarity in measured variables relates to geographic distance at multiple spatial scales, and comments on the efficacy of sampling strategies and measurement tools.

The growth rate of lichens and mosses is dependent on the length of time for which carbon gain from photosynthesis is greater than carbon loss from respiration. Generally speaking, neither photosynthesis nor respiration can take place when lichens and mosses are dried out. However, it is widely held that mat-forming lichens have a far greater tolerance of prolonged dehydration than do feathermosses, because this is reflected in their habitat preferences. If lichen and feathermoss presence is the result of environmental filtering, rather than stochastic processes, it follows that patches dominated by feathermoss or lichen should correspond to low and high moisture stress conditions, respectively; vascular plants should be less susceptible to conditions of moisture stress because they can access water stored in the soil, may therefore show intermediate moisture stress. Chapter five describes and compares the microclimatic associations of these three understory functional groups, and compares the strength of association between macroclimate and microclimate to the strength of association between forest canopy or soil properties and microclimate.

Given that lichen-rich forests are important for conservation of biodiversity and threatened species, as well as being indicators of overall ecosystem health, it is useful to extend the results of this study towards management and conservation. Chapter six provides a synthesis and discussion of the preceding chapters, makes several management recommendations, and suggests avenues for future research.

# 2. Microhabitat associations of understory functional groups in lichen-rich, lodgepole pine forests

## 2.1. Abstract

Although many researchers have studied the succession and environmental relationships of lichen-rich forests at scales relevant to forest and wildlife management, few have done so at the scale of individual understory patches, and none have done so while adequately accounting for environmental variability in all three primary resource gradients that influence vegetation (light, moisture, and nutrients). I conducted an investigation of understory vegetation at the scale of individual functional group patches, to highlight the environmental associations of three broad understory functional groups (terrestrial mat-forming lichens, feathermosses, and vascular plants). Analysis of variance, multiple regression, and multiple regression on principal components were used as complimentary techniques to compare the relative strength of associations. Transmitted irradiance (direct and diffuse), base-cation deficiency, aluminum availability, and several other variables related to low canopy cover were positively associated with lichen dominance or abundance. Vascular plants tended to be positively associated with base-cation availability, sulphur and phosphorus availability, fine soil texture, thicker organic layers, and high direct irradiance. Most measures of canopy closure were positively related to feathermoss abundance and dominance, as were ammonium and calcium availability, while several metals were negatively associated with feathermoss dominance. These results suggest that, although canopy characteristics are clearly associated with understory composition, canopy trees should not necessarily be treated as the only drivers of understory development; soil properties, both chemical and physical, still may play a role in determining understory composition.

## 2.2. Introduction

Mat-forming lichens (mostly *Cladonia* spp.), feathermosses, and vascular plants represent three taxonomically and functionally unique groups that dominate extensive areas of coniferous forest understories in high-altitude or high-latitude regions (see Appendix A for nomenclature and taxonomy). Often referred to as lichen woodlands, or lichen-rich forests, due to their relatively open-canopied structure and high abundance of lichens and mosses in the understory, these forests tend to be dry and dominated by pine (*Pinus* spp.), spruce (*Picea* spp.), or fir (*Abies* spp.). The lichen component of these systems is of particular conservation concern due to its importance as forage for threatened woodland caribou (*Rangifer tarandus caribou*), and its own sensitivity to disturbance (Pegau 1970, Cichowski 1993, Manseau et al. 1996, Jandt et al. 2008). At a local level, the understory of these forests is organized into relatively discrete patches of lichen, feathermoss, or vascular plants (Figure 2).

There have been two traditional approaches used in explaining these patterns of vegetation dominance in lichen-rich forest understory communities. The first is to examine environmental variables that affect habitat suitability and growth rates of lichens and feathermosses; variables such as canopy closure, leaf area index, stand age, and organic layer depth often show strong positive relationships with feathermoss dominance and negative relationships with lichen dominance (Oksanen 1986, Coxson and Marsh 2001, DeLuca et al. 2002, Hunt et al. 2003, Bainbridge and Strong 2005, Uotila et al. 2005). The second approach is to explain the presence of one understory group by the absence of another; mat-forming lichens are generally regarded as poor competitors, and are often overgrown by the competitively superior feathermosses as woodlands age (Frego and Carleton 1995a, Pharo and Vitt 2000, Williston et al. 2006). Yet, neither approach by itself is completely satisfying from an empiricist's perspective.

**Figure 2.** Photograph of Site 29 (by author), showing the patchy understory structure in a typical lichen-rich forest of north-central B.C.

Despite widespread belief that competition with increasingly abundant feathermoss causes lichen decline during woodland succession (Yarranton 1975, Crittenden 2000, Sulyma and Coxson 2001), this has been difficult to demonstrate through observational study because measures of abundance or dominance of the two groups are never statistically independent in a one-time set of samples. In a system where much of the available ground-cover space is occupied by either lichens or feathermosses, the abundance of the two will inevitably be negatively correlated. Demonstrating this statistically may indicate the potential type of interaction among species groups, but concluding that an interaction is indeed occurring is premature. The small number of studies that recorded competitive interactions over time were the result of experimental manipulation or unusually distinct changes in the environment (i.e., canopy removal, reciprocal transplants or drought), and are not necessarily indicative of natural ecosystem processes (Ipatov and Tarkhova 1983, Sedia and Ehrenfeld 2003, Sulyma 2003). Whether the replacement of lichens by feathermosses in forest chronosequences is mediated through changing environmental conditions becoming more favourable to one group over the other as stands age, or whether this is due to the groups having intrinsically different competitive abilities and dispersal potential is unknown. Despite the lack of mechanistic evidence, most researchers have concluded it is changes to the understory environment that causes feathermosses to become more dominant in older stands, and that this occurs primarily through the process of canopy closure (Figure 3).

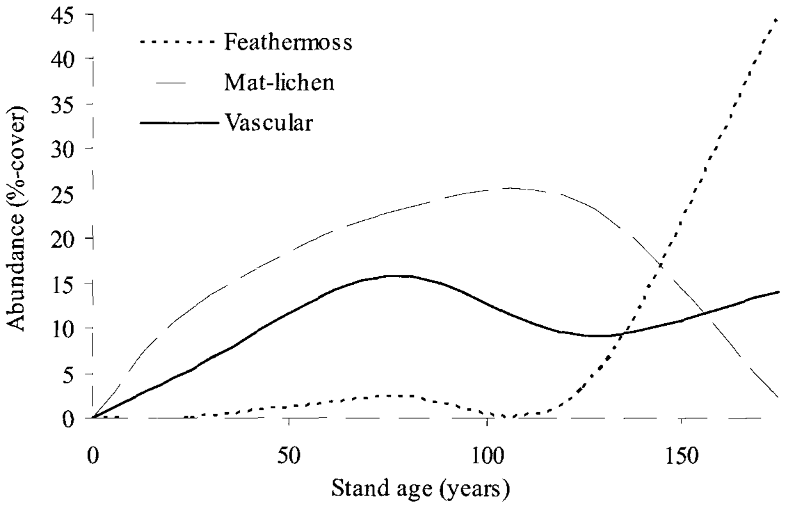

**Figure 3.** Abundance of understory functional groups by stand age in lodgepole pine woodlands of Northern British Columbia (adapted from Coxson and Marsh 2001).

Although many studies show strong support for an influence of the forest canopy on understory development, the relationship has rarely been demonstrated using continuous data. Those researchers who conclude that the canopy drives understory development often cite the mechanisms of moisture and light regulation, which are correlated with the age of the stand (Lechowicz and Adams 1974, Oksanen and Ahti 1982, Kershaw 1977, Hunt et al. 2003, Simon 2005, Uotila et al. 2005, Kotelko et al. 2008); this agrees with the 'relay floristics' (RF) model of succession (Egler 1954). Those who detect little or no canopy influence may conclude that the understory community is primarily structured by the slow expansion of species that are initially present due to stochastic dispersal events or disturbance refugia (Fortin et al. 1999, Kembel and Dale 2006, Pharo and Vitt 2000, Frego and Carleton 1995b). Dominance of stochastic processes agrees with the 'initial floristic composition' (IFC) model of succession (Egler 1954), and suggests that the low productivity that is characteristic of lichen-rich forests limits true competitive interactions (Goldberg and Novoplansky 1997). It is also common for researchers to implicate a combination of environment, disturbance, and species interactions as controlling factors (Brulisauer et al. 1996, Girard et al. 2009).

Two more extreme explanations are that understory development is significantly related to – but independent of – the canopy, such that the two components develop in tandem based entirely on abiotic edaphic or climatic conditions (Barbier et al. 2008), or that the communities are structured entirely by stochastic cycles of disturbance and recolonization, such that coexistence is dependent on variation in dispersal and competitive ability (Frego and Carleton 1995b). Alternatively, a community may appear to be environmentally structured if competition takes place on a longer temporal scale than we can observe in an experimental setting, because the magnitude of competitive asymmetry (and therefore the amount of time required to observe it) is influenced by environmental variability (Grime et al. 1990, Shipley and Keddy 1994).

This problem is not limited to the study of lichen-rich forests, but is a central question in plant community ecology: are communities structured by random processes or environmental interactions (Fargione et al. 2003)? The most common answer is: 'a little bit of both', but that the detection of a prevailing influence is dependent on the scale at which we measure it (Karst et al. 2005, Kembel and Dale 2006, Lang et al. 2009). Fine-scale environmental filtering of species can be particularly difficult to investigate, as both environmental conditions and species presence can be highly spatially influenced (Fortin et al. 1999, Karst et al. 2005). Yet because competition occurs at a fine scale (i.e., between individuals), investigations that focus on fine scales, or at least on scales that are similar to the size of the study organism, should be the method of choice when investigating the processes behind patterns of species distributions in the context of interspecific competition (Burton 1993, Økland and Bakkestuen 2004). Furthermore, some environmental gradients, particularly those involving soil chemical and biological properties (Bengston et al. 2007, Smithwick et al. 2005), are only detectable at fine scales, and are likely to be overlooked if the scale of investigation is too large.

A fine-scale ecological approach has rarely been applied to the study of lichen-rich forests. This may be partly because such studies usually focus on management of forests or caribou (*Rangifer tarandus* L.), a species that relies almost entirely on mat-forming lichens for winter forage (Cichowski 1993, Jandt et al. 2008). But it may also be a product of convention, based on the prevailing belief that the forest overstory is the primary driver of understory development (Gilliam and Roberts 2003). Both suggest that the forest stand scale is the most ecologically (and socioeconomically) relevant one. Indeed, studies that have shown forest canopy conditions to influence understory composition often select their study sites to control for similar edaphic or climatic conditions, and measure variables using stand-scale approaches, such that an influence of canopy conditions (or successional stage) is more likely to be the primary gradient detected (Ahti and Hepburn 1967, Johnson 1981, Coxson and Marsh 2001, Bainbridge and Strong 2005, Simon 2005, Barbier et al. 2008). Yet, the patchy distribution of understory species suggests that fine-scale environmental patterns are of significance in their development (Rouse and Kershaw 1973, Leichowicz and Adams 1974, Nieppola 1992, Fortin et al. 1999, Økland et al. 1999, Sulyma and Coxson 2001, Kembel and Dale 2006). Furthermore, the recognition that competition with other understory components may be a determinant of patch occupancy for lichens (Crittenden 2000, Sulyma and Coxson 2001), that overstory properties are related both to underlying edaphic and climatic properties as well as to disturbance regime (Nieppola 1992, Hunt et al. 2003, Girard et al. 2009), and that the understory development itself can influence canopy development (Bonan and Shugart 1989, Bonan 1990, Crittenden 2000, Sedia and Ehrenfeld 2003, Nilsson and Wardle 2005, Hart and Chen 2006), suggests that underlying soil and climatic properties could also influence habitat suitability for mat-forming lichens. Indeed, the difficulty in separating such environmental influences as canopy shading, precipitation interception, and litter deposition from edaphic, topographic, and climatic factors in observational studies (Salemaa et al. 2008) has probably acted as a deterrent of more extensive study.

Although forest canopies may act as a proxy for environmental variables, exclusion of edaphic features from studies of understory vegetation may lead to erroneous interpretations of causal or unidirectional relationships, or at least limit their generalizability (Barbier et al. 2008). A stand-level focus may also bias the investigation towards recognizing understory species assemblages that form apparently continuous cover at that same scale, namely feathermosses and mat-forming lichens. The role of understory vascular plants in particular has been downplayed (Ahti and Oksanen 1990), despite evidence that they can be significant competitors of lichens and feathermosses (Crittenden 2000, DeLuca et al. 2002), they can alter overstory development or nutrient cycling (DeLuca et al. 2002, Nilsson and Wardle 2005), they can alter ground-level irradiance (Messier et al. 1998), and that they can respond more rapidly than either lichens or mosses to changes in the environmental conditions (Vagts and Kinder 1999, Walker et al. 2005, Olsson and Kellner 2006, Wasley et al. 2006, Williston et al. 2006).

A central goal in studying natural ecosystems is to understand why they change under varying environmental conditions, often with the assumption that we will be able to predict the effects of future anthropogenically-induced changes, such as global warming, or manage them to maximize a particular resource or value, such as caribou forage. Addressing this requires investigation at multiple scales, with as many relevant components (species) of the system as can be measured and examination of environmental variables that could affect any one of them. This study begins to bridge the gap between stand- and microsite-scale investigations of understory composition in lichen-rich forests, and re-examine concepts of environmental filtering of understory vegetation. More specifically, I investigate the relative strength of associations between functional group abundance or dominance and forest overstory or edaphic conditions in lodgepole pine forests of northern British Columbia.

### 2.2.1. Hypotheses

The small-scale patterns observed in pine-lichen-rich forests suggest at least partial niche separation of functional groups. The hypothesized niches of these functional groups are expressed in terms of three resource gradients in Figure 4; generally, I expected that: (1) feathermosses will favour moist sites irrespective of nutrient and light availability, but will be replaced by vascular plants in the richest sites, and will be replaced by lichens in the most exposed or best-drained sites, due to the increased evaporative pressures; (2) vascular plants will favour sites with greater nutrient availability, because moisture availability will likely change the vascular plant composition, but with sufficient nutrient availability (particularly the macronutrients nitrogen and phosphorus, which are commonly held to be limiting in northern systems; Bonan 1990, De Luca et al. 2002, Smithwick et al. 2005, Salemaa et al. 2008, Smithwick et al. 2009) the vascular plant functional group will be dominant irrespective of moisture or light availability; and (3) lichens will favour sites that disfavour other functional groups, because low nutrient availability will limit vascular plants, and low moisture will limit feathermosses, allowing mat-forming lichens to become dominant because of their high nutrient use efficiency and desiccation tolerance. The presence of high light in itself is not a necessary or sufficient indicator of lichen habitat.

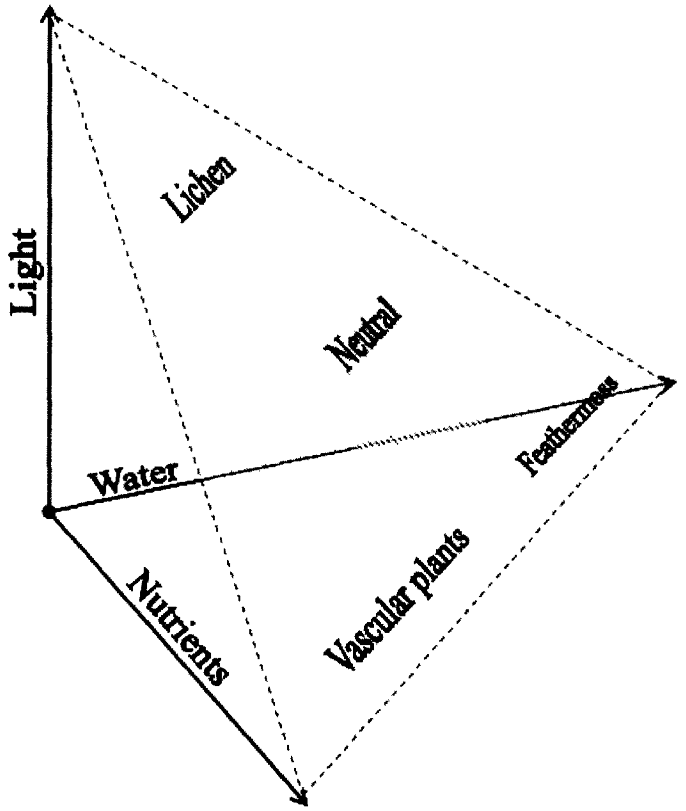

**Figure 4.** Conceptual diagram of potential niche space, based on primary resource gradients for lichens, vascular plants, and feathermosses. The three axes (solid lines) represent three primary resource gradients, while the triangular plane (dotted surface) represents niche space. When habitat characteristics are equally favourable for two or more groups (i.e., neutral niche space, represented by the striped portion of triangular plane), stochastic processes will determine patch occupancy, and dominance will not be related to habitat characteristics. Otherwise, habitat characteristics will favour one group over another.

## 2.3. Methods

### 2.3.1. Study area

The study area covers from 124.68° to 125.67° W longitude and from 55.65° to 56.41° N latitude, in the Omineca Mountains of northern British Columbia (Figure 5). All sites are located in the Stikine variant of the dry-cool Boreal White and Black Spruce biogeoclimatic subzone (BWBSdk1, Delong 2004), range from approximately 800 - 1000 m in elevation, have a mean annual precipitation of 511 - 622 mm, and have a mean annual temperature ranging from -0.1 to 1.3° C (from Climate BC v 3.21, Wang et al. 2006). Soils are generally nutrient-poor, with xeric or subxeric moisture regimes, and of glacial-fluvial or colluvial origins that are extremely coarse-textured (Plouffe 1997a, 1997b, Delong 2004). Where the stoniness is low enough, soils would likely be classified as Dystric Brunisols under the Canadian System of Soil Classification (SCWG 1998), but are merely skeletal amid large numbers of cobbles and boulders in some locations.

Forest fires occur frequently (see results section for average stand age), resulting in canopies dominated by lodgepole pine (*Pinus contorta* Dougl. *ex* Loud. var. *latifolia* Engelm. *ex* S. Wats.) with occasional subdominant hybrid white spruce (*Picea engelmanii* Parry *ex* Engelm. × *glauca* (Moench) Voss), black spruce (*Picea mariana* (P. Mill.) B.S.P.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), or trembling aspen (*Populus tremuloides* Michx.). The shrub layer is sparsely populated by *Shepherdia canadensis* (L.) Nutt., and ground cover includes *Vaccinium* L. spp., *Pleurozium schreberi* (Brid.) Mitt., or *Cladonia* Hill ex P. Browne spp. and *Stereocaulon* Hoffm. spp. (Delong 2004). Commercial logging has been operating in the area for several decades, but it is unlikely that the stands examined have been subject to logging in the recent past, as no cut stumps were encountered.

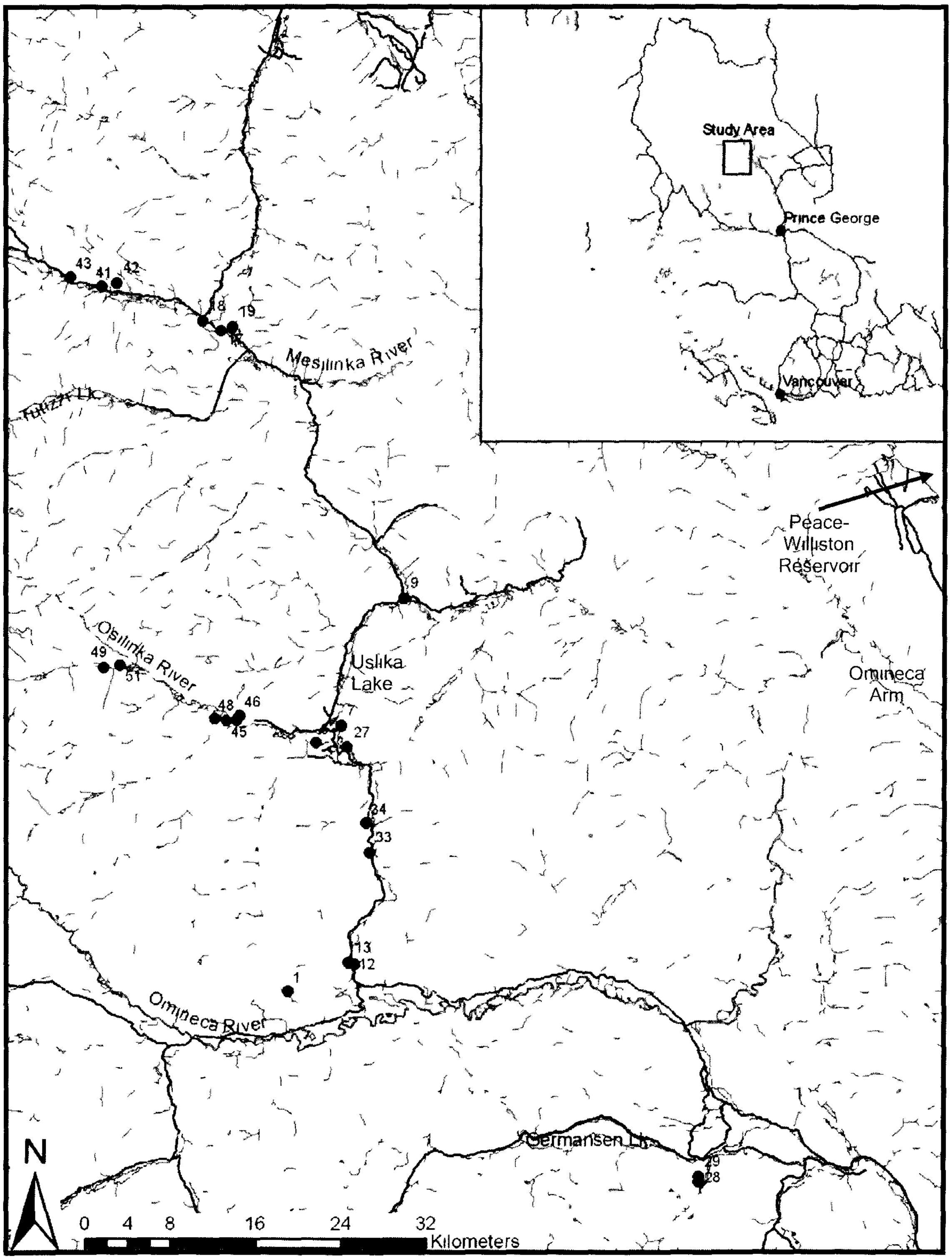

**Figure 5.** Map of study area, numbered points represent sample sites, black lines represent forest service roads, and medium gray lines represent rivers or creeks Map courtesy of R Sulyma and Wildlife Infometrics Inc

### 2.3.2. Plot layout and sampling procedures

I selected 24 forest polygons, based on accessibility, from a suite of 60 that were being used for research on caribou activity in known winter ranges. The sixty possible polygons were pine-dominated caribou winter ranges (at least 400 ha in size), which were determined from caribou telemetry data coupled with forest inventory polygons (B.C. MoFR 2007, McNay et al. 2009). These selection criteria ensured that sites were of a 'lichen-rich pine forest' type; specific surficial geology of forest polygons was unknown at the time of site selection. The approximate centroid of a polygon served as a starting point from which three systematically arranged circular plots were surveyed for vegetation and soil characteristics (Figure 6). For the duration of this report, a series of three plots in triangular formation, within the same forest polygon, are collectively referred to as a 'site'.

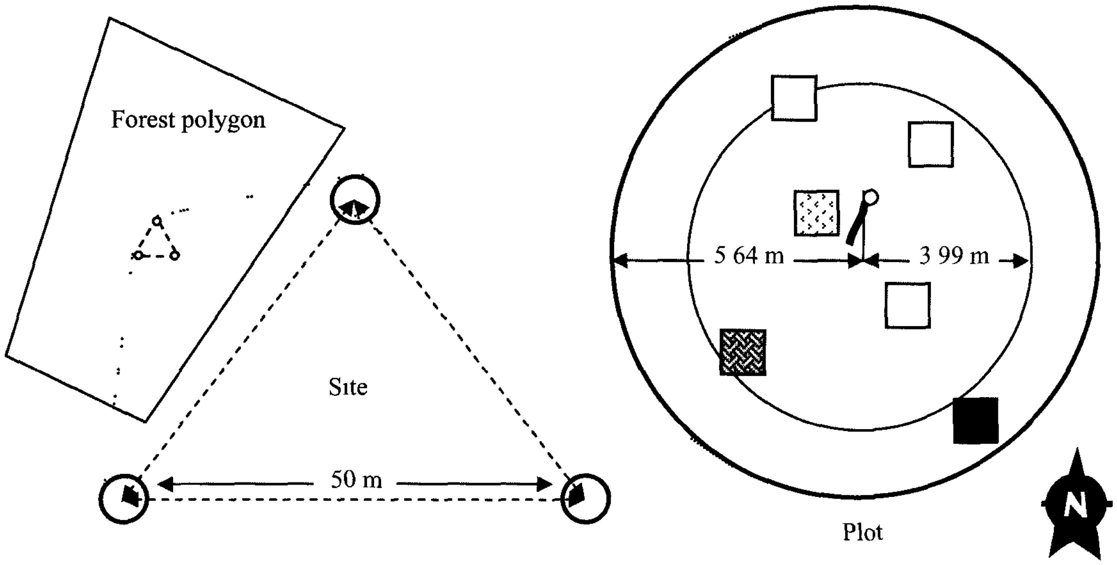

**Figure 6:** Diagrammatic representation of site and plot layout; empty squares represent random quadrats while patterned squares represent functional group quadrats

Using a handheld global positioning system receiver, surveyors (author and assistants) established the first of three sample plots on the polygon centroid itself. The second plot was centered on a point fifty metres from the first in one of the sub-cardinal directions (NW, SW, SE, NE), alternating the direction in clockwise sequence from one plot to the next. We then turned 120 degrees to the right of the bearing used to establish the second plot, and centered the third plot on the 50 m point of this line, thereby completing an equilateral triangle with a plot at each corner and sides of 50 m. Fifty-m spacing is sufficient to reduce the effects of tree-caused autocorrelation among plots (Kuuluvainen et al. 1998) while maximizing stand survey efficiency within a site. The centre of each sample plot was marked by inserting a steel 'pig-tail' pin into the ground.

Each sample plot actually consisted of two circles, one nested inside the other. The smaller of the two circles (3.99 m radius, or 50 $m^2$) was a regeneration survey plot for trees <7.5 cm in diameter at breast height (henceforth DBH, or the diameter of the stem measured 1.3 m from base), while the larger of the two circles (5.64 m radius, or 100 $m^2$) was a large-tree (>7.5 cm in DBH) survey plot. We identified all trees at the species level, and for large trees additionally recorded wildlife tree classification (following B.C. MoFR 2007), crown depth (distance from top to bottom of crown for each tree), DBH, and tree height; tree height was measured with a hypsometer (Haglöf Vertex IV; resolution = 0.1 m). Within large tree plots, we extracted increment cores from at least two live canopy trees, in addition to any trees with noticeable fire scars, to determine stand age and estimate the time since last disturbance. We took two digital photographs of the surrounding forest from the center of each plot, one facing northwards and one facing southwards, to provide a permanent visual reference. In the regeneration plots, we tallied the number of seedlings and saplings, and estimated the percent-cover of shrubs in three height classes (<10 cm, 10 cm - 130 cm, and >130 cm) by species.

Upon arrival at the plot, one surveyor selected locations for six small vegetation quadrats and marked them with 'pig-tail' pins to ensure that other surveyors could avoid trampling the soil and vegetation within quadrats. These quadrats were located within the large-tree plot, square in shape, oriented with the sides facing cardinal directions, and 0.25 $m^2$ in size (Figure 6). This size of quadrat is small enough that functional group dominance and species percent-cover estimates should be consistent and accurate, and that nutrient availability assessments should be representative of the entire quadrat (McCune and Lesica 1992, Rosentreter and Eldridge 2002, Western Ag Innovations Inc. 2008). In addition, the size of small vegetation quadrats coincided with what are considered genetically uniform patches of feathermoss or lichen (Ahti 1961, Cronberg et al. 2006).

The first three quadrats were used to characterize the patterns of vegetation dominance at the plot scale, with finer taxonomic resolution than could be efficiently used at the plot scale; these quadrats are henceforth referred to as ‘random quadrats’. We used random number tables to determine random quadrat locations, based on x-y coordinates within the large plot, using the southwest corner of a square grid overlaying the plot as an origin. Microtopographic position, distance to the nearest tree, and the percent cover of vegetation, litter, and bare ground were recorded at each random quadrat.

The last three quadrats in each plot were used to evaluate the environmental characteristics associated with functional group dominance and abundance. These quadrats will be henceforth referred to as ‘functional-group quadrats’, or ‘FG quadrats’; to further avoid unnecessarily verbose modifiers, discussion of analyses and results from data collected at FG quadrats will simply refer to the functional group identity (lichen, feathermoss, vascular plant). Because soils can be highly variable at fine spatial scales (Farley and Fitter 1999), and the number of soil analyses that could be performed was limited by logistic and financial considerations, the most effective way to document the presence of underlying gradients was to emphasize the extremes of those gradients. Each of these last three quadrats was, therefore, placed on the most completely dominated patches of mat-forming lichen, feathermoss, and vascular plants within the large tree plot. Where possible, functional group patches that appeared to be in a state of persistent dominance were selected over those that appeared transitional. For example, if the most abundant plants in a particular patch looked unhealthy, or were being overgrown by a species from another functional group, the quadrat was located elsewhere. Selecting the most clearly dominated patch for a particular functional group quadrat was rarely difficult, but when surveyors were uncertain a hierarchical decision tree (Appendix B) was used to guide the selection process.

During initial visits (mid-to late July 2008), surveyors recorded the percent cover of all species (<10 cm tall) that could be identified in both types of quadrats. The slope inclination, slope aspect, and meso- and micro-topographic position were also recorded. Surveyors inserted Plant Root Simulator™ (PRS, Western Ag Innovations Inc. 2008) probes vertically into the quadrat center to obtain measurements of nutrient availability (for $NH_4^+$, $NO_3^-$, K, S, Ca, Mg, Al, P, Fe, Mn, Cu, Zn, B, and Pb); probes were left for six weeks between July 15th and September 15th, 2008. PRS™ probes consist of cation or anion-exchange resin membranes encased by a plastic spike, which passively absorb available nutrients with minimal soil disturbance (Western Ag Innovations Inc. 2008). When the soil was too unyielding or rocky for hand-insertion, surveyors created a narrow ‘pilot hole’ with a steel knife, and a light-weight hammer was used to tap the probes into place.

Surveyors took two photographs at each FG quadrat: 1) ground-cover vegetation, using a 12 MP digital camera from approximately 1.3 m looking directly downwards, and 2) the forest canopy, using a hemispherical (fish-eye) lens with a 6 MP digital camera mounted on a bubble-levelled platform, from approximately 10-15 cm above the ground. Hemispherical canopy photos were later used to calculate leaf area index (LAI), transmitted direct irradiance, transmitted diffuse irradiance and total transmitted irradiance (hereafter simply direct, diffuse, or total irradiance, respectively), using GLA software (Frazer et al. 1999), which classifies individual pixels in an image as either "sky" or "non-sky", and uses additional geographic information to calculate multiple measures of light transmission.

To examine the spatially explicit associations between trees and understory vegetation we recorded the species identity, diameter at breast height (DBH), wildlife-tree class, and distance and direction of the nearest three trees (DBH >7.5 cm and height >1.3 m) to each quadrat. Shrubs or saplings (more than 1.3 m tall, up to 7.5 cm in DBH) were counted instead when no trees were available at less than six metres in distance. Finding more than three drip-zone trees or shrubs at similar distances was rare, but when it did occur we gave preference to the largest ones, as they would have a disproportionately large influence. The indices these data were used to derive are elaborated on in the next section and in Appendix C.

Those ground-cover species that could not be identified (several lichens and mosses) in the field were collected for laboratory identification during the second round of field surveys and at least one specimen of each laboratory-identified species was kept for herbarium preservation. Each specimen was verified by an expert (T. Goward or C. Bjork, of Enlichened Consulting Ltd.) and archived at the University of Northern British Columbia (UNBC) herbarium.

After all other field measurements were complete, we excavated the center of each functional group quadrat to a depth of approximately 20 cm into the mineral soil (this was usually the deepest pit that could be dug within the quadrat), ensuring as little disturbance as possible to the edges. The thickness of litter, fermentation, and humus (LFH) layers, and of identifiable mineral horizons were recorded on site, and mineral soil samples of approximately two L in volume were taken from each pit and transported back to the laboratory at UNBC for texture analysis.

In the laboratory each soil sample was dried for at least two weeks, followed by hand and sieve separation into three classes: coarse fragments larger than 7.5 cm in diameter, coarse gravel between 0.9 cm and 7.5 cm in diameter, and finer components less than 0.9 cm in diameter. A 250-g subsample was taken of finer components to further separate the fine gravel (2 mm - 9 mm), from the sand (0.05 mm - 2 mm), and the silt and clay (<0.05 mm). Each 250.0 g subsample was mechanically shaken through a two-layer closed sieve with a 2 mm screen and a 0.05 mm screen for five and a half minutes. Each class was weighed to the nearest 0.5 g, and raw weights were transformed into percentages from one of five soil particle size classes: 1) coarse fragments (>75 mm); 2) gravel (2 mm - 75 mm); 3) fines (grain size <2 mm); 4) sand (0.05 -2 mm); and 5) silt and clay (grain size <0.05 mm). Organic materials such as needle litter, charcoal, and cellulosic materials were generally only present in the organic (LFH) layers and thus avoided by collecting samples of only the mineral horizons.

A further subsample was taken of the fine fraction for pH analysis. Specifically, 10.0 g of fines (<2.0 mm) were taken from the 250.0 g subsample and mixed with 20 mL of deionized water (pH 5.41 ± 0.01) to make a suspension. In a glass beaker, the suspension was mixed and allowed to settle, then tested using a pH meter and combination electrode.

After brushing PRS™ probes free of soil in the field, surveyors sealed them individually in plastic bags and transported them back to the laboratory at UNBC. I then washed all probes with de-ionized water, and sent them back to Western Ag Innovations Inc. for further analysis. Western Ag Innovations Inc. (2008) analyzes the probes by elution for one hour with 0.5 N HCl / 2 M KCl, followed by automated colourimetric analysis for ammonium ($NH_4^+$) and nitrate ($NO_3^-$), and inductively-coupled plasma spectrophotometry, atomic absorption spectrometry, and flame emission spectrometry for levels of phosphorous , potassium, sulphur, calcium, magnesium, aluminum, iron, manganese, copper, zinc, boron, and lead.

### 2.3.3. Canopy closure indices

I chose four indices of canopy closure to represent the spatially and directionally explicit intensity of canopy influence on ground cover vegetation. Although only one out of these four (leaf area index) has been previously used by other researchers, they are all based on geometric abstractions of measurements from the three nearest trees to each FG quadrat, and therefore must represent some form of canopy closure over a given patch. The indices are estimated Leaf Area Index (LAI), SouthWest facing Canopy Cover (SWCC), Crown Radius Drip Zone (CRDZ), and Wind-Influenced Drip Zone (WInDZ). The two latter methods both relied on data from measurement of the nearest three trees to each quadrat, while the former methods relied on direct measurements of the forest canopy.

I used Gap Light Analyzer software (GLA v. 2.0 1999, Frazer et al. 1999) to calculate the effective leaf area index (LAI) from canopy photos, using the portion of the image that corresponded to zenith angles 0° through 60°. Gap Light Analyzer calculates LAI based on the theoretical relationship between gap-fraction and LAI (Frazer et al. 1999). Although hemispherical photographs are considered superior to many other methods for assessing canopy attributes (Gagney and Block 1994, Euglund et al. 2000), some authors have suggested that using them to estimate LAI may be misleading, particularly in coniferous forests, because they include woody material (stem and branches) and the formulae used rarely take into account the non-random dispersion (clumping) of leaves in the canopy, potentially leading to high error rates (Gower et al. 1999, Bréda 2003). However, GLA software has been shown to give reasonably accurate estimation of the 'effective leaf area index' (Frazer et al. 2000), allowing results from this study to be more comparable to similar studies (e.g., Sulyma 2001).

I devised crown-radius-drip zone (CRDZ) as a simple linear measure of the overlap between crown radius projection and a FG quadrat. Once a quadrat is entirely within the crown radius projection (i.e., score $\approx 0.6$), CRDZ becomes a measure of proximity to the bole of the tree. For each of the three nearest trees I subtracted the quadrat-to-tree distance from the estimated crown radius of that tree, which was determined using allometric models for crown radius published by Bechtold (2004); being completely outside of the crown radius projection yielded a score of zero (i.e., negative scores were counted as zero). Crown radius drip-zone was then calculated as the sum of the three overlap distances.

Surveyors measured the percent-canopy cover for the four central squares of a convex spherical densiometer, taken at 0.3 m above the ground when facing southwest (southwest canopy closure, or SWCC). This was intended to give a slight bias to trees that were on the southwest side of the quadrat, due to the supposition that the prevailing winds would be similar to those in the Prince George area. Despite this not being the case (the winds are predominantly from the West in the study area), the SWCC was retained as a potentially useful indicator of afternoon shade.

I devised wind-influenced drip-zone, or WInDZ, as an index of canopy influence at ground level that varied based on the size of the tree and the tendency for that influence to be asymmetrical as a result of prevailing wind speed and direction. Wind-influenced drip-zone essentially provides a two-dimensional area of canopy influence intensity representing potential throughfall precipitation (or perhaps precipitation interception) by calculating the distance that a drop of water would travel, based on the height and decay class of a tree, a constant acceleration due to gravity, and estimates of the average summer windspeed at a given site. It was then scaled by the frequency of that windspeed for the direction in which the quadrat was located from the tree (see Appendix C for elaboration). The final index was the sum of these calculations for each of the three closest trees or shrubs to a given quadrat.

### 2.3.4. Statistical Analyses

#### 2.3.4.1. Functional group dominance and environment

I summarized the frequency of detection for individual species graphically for FG quadrats, and in tabular form by quadrat type (random or FG). Environmental variables (Table 1) were summarized in graphical form using quadrat-level averages with associated standard errors, for all three FG quadrat types. I assessed environmental variables for normality, and where necessary, log or power-transformed them. I used factorial (fixed effects) analysis of variance (ANOVA) to determine whether environmental variables differed significantly among the three vegetative functional groups. Although my hypotheses pertained only to differences among functional groups, both observations in the field and preliminary examination of data suggested that variability in environmental variables was greater among sites than among functional groups. Consequently, it was necessary to account for the influence of 'site' to avoid obscuring the differences among functional groups: I used type-one sum of squares to account for this hierarchical distribution of variance, with 'site' as the first fixed effect and 'functional group identity' (lichen, feathermoss, or vascular plant) as a second. Post-hoc Tukey's tests were used to assess between-functional group differences, with $\alpha = 0.05$. I calculated eta-squared ($\eta^2$) values when ANOVA's were significant to indicate the goodness of fit for a linear model. Analyses were conducted in SAS (v.9.1) using PROC GLM (SAS Institute Inc. 2010).

**Table 1.** List of measured environmental variables recorded at each functional group quadrat.

| Variable | Full variable name and description | Measurement method | Units |
|---|---|---|---|
| Mesotopo. | Mesotopographic position, using classes from Delong (2004) | Visual estimation | Six-class ranking system |
| Concavity | Topographic position of quadrat relative to adjacent space | Visual estimation | Five-class ranking system |
| Slope | Slope inclination (from horizontal) | Clinometer (Suunto PM-5/360) | Degrees |
| N-aspect | Cosine-transformed aspect (facing away from hill), index of northness | Compass | Radians (from degrees) |
| CoarFrag | Proportion of soil sample with grain size >75 mm in diameter | Electronic balance (± 0.5 g) | g |
| Gravel | Proportion of soil sample with grain size 2-75 mm in diameter | Electronic balance (± 0.5 g) | g |
| Fines | Proportion of soil sample with grain size <2.0 mm in diameter | Electronic balance (± 0.5 g) | g |
| Sand | Proportion of soil sample with grain size 0.05-2.0 mm in diameter | Electronic balance (± 0.5 g) | g |
| Silt+Clay | Proportion of soil sample with grain size <0.05 mm in diameter | Electronic balance (± 0.5 g) | g |
| LAI | Leaf area index, 2-D foliage area divided by 2-D ground area | Estimated from hemispherical canopy photos by GLA | N/A |
| WInDZ | Wind-influenced drip-zone | See Appendix C | N/A |
| CRDZ | Crown radius drip-zone | See section 2.3.3 | N/A |
| SWCC | Southwest canopy closure | Convex spherical densiometer | Percent |
| Total irrad. | Total irradiance / amount of above-canopy irradiance that reaches ground | Estimated from hemispherical canopy photos by GLA | Percent of above-canopy irradiance * |
| Direct | Direct-beam irradiance that reaches ground | Estimated from hemispherical canopy photos by GLA | Mols • $m^{-2}$ • $day^{-1}$ * |
| Diffuse | Diffuse irradiance that reaches ground | Estimated from hemispherical canopy photos by GLA | Mols • $m^{-2}$ • $day^{-1}$ * |
| localBA | Basal area of three closest trees / area of smallest circle including them | DBH tape | $m^2$ • $ha^{-1}$ |
| LFH | Sum of litter, fermentation, and humus layer thickness | Ruler, scaled to 0.1 cm | cm |
| Total N | Total inorganic nitrogen availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| $NO_3$ | Nitrate availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| $NH_4$ | Ammonium availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| Ca | Calcium availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| Mg | Magnesium availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| K | Potassium availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| P | Phosphorus availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| Fe | Iron availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| Mn | Manganese availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| Zn | Zinc availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| B | Boron availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| S | Sulphur availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| Al | Aluminum availability | PRS™ probes | μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$ |
| pH | Acidity / alkalinity of soil sample | pH meter and combination electrode | $-\log(H^+)$ |

* Note: GLA estimates of irradiance do not account for cloudiness, and are therefore more representative of potential (not actual) maximum direct irradiance, and potential minimum diffuse irradiance.

#### 2.3.4.2. Functional group abundance and environment

In order to better understand the habitat associations of each functional group, I used multiple linear regression, with environmental variables as predictors and functional group abundance as responding variables. The functional group regressions were run with all possible combinations (all-subsets) of seven or fewer variables, and ranked using Schwartz's Bayesian Criterion (SBC) scores (Schwartz 1978, Beal 2007). For each functional group I chose the model with the lowest SBC score as the 'best' (most parsimonious), provided that variance inflation factors (VIFs) were <8.0 for all predictor variables; VIF thresholds of 10.0 are more commonly used as indicators of significant collinearity among variables, but were considered too relaxed in this case (O'Brien 2007). Because the study goals are descriptive, and an all-subsets technique is computationally intensive, no model averaging was used to create a "true" model. Rather, I examined the top ten models from each combination of dependent and independent variables, then used criteria such as standardized beta coefficients, model adjusted-$R^2$ values, and residual normality to assess the relative strength of association between understory composition and the abiotic, biotic, and soil chemical environment. Nevertheless, the interpretation of results was focused on the best models for each group. With the exception of aspect, which was cosine-transformed to give a linear index of 'northness', environmental variables were transformed using log or power transformations where appropriate.

Because many of the environmental variables recorded are either highly correlated with each other, or logically related, multiple regressions are limited in how comprehensively they can examine the environmental associations of each functional group. In order to gain a more complete understanding of these associations, a second approach was used that both reduces multi-collinearity and allows the researcher to examine more complex, data-driven environmental gradients; namely, principal components regression (Graham 2003). Principal components analysis is an eigenvector ordination method that creates linear combinations of variables, or "principal components" (PCs) (Kenkel 2006). These principal components are useful both because they are orthogonal proxies of variables in the original data set, and because they may represent a latent variable, that is, one that is related to those measured but immeasurable itself. Each unit of measurement in the original data (i.e., plot, quadrat, etc.) is given a score on each principal component, based on the linear combinations of variables that were recorded in that unit, thereby generating a whole new dataset of orthogonal variables, each with a measurement (score) for every sample unit. Those component scores for individual sample units can then be included as truly independent variables in a multiple regression, and are interpreted in terms of the component loadings, or the strengths of associations between individual components and raw variables (McCune and Grace 2002, Graham 2003).

Principal components are produced in succession, and always represent the strongest gradient that exists in the data for that particular iteration; it is common to interpret only the first three or four components of a PCA (McCune and Grace 2002, Kenkel 2006). This is based on the understanding that they represent the strongest underlying gradients, and that PCs representing less variance may simply be random noise (McCune and Grace 2002). However, in the context of PC regression, particularly for species-environment relationships, it is often recommended to include as many components as one can, given that even weak or limited gradients may have biological importance and may therefore be relevant parameters to the regression model (Jolliffe 1982, Graham 2003, Hwang and Nettleton 2003).

Principal components analysis was performed on three subsets of environmental variables: 1) biotic or canopy variables, including direct, diffuse, and total light, local basal area, LAI, LFH depth, SWCC, and the two dripzone indices, WInDZ, and CRDZ; 2) abiotic variables, including aspect, slope inclination, slope position, and the relative abundance of soil texture classes; and 3) chemical variables, including soil pH nutrient availability. This produced a total of 9 PCAs, using three variable subsets for each functional group; results are presented using joint-plot diagrams to aid in interpretation (McCune and Grace 2002).

Since even principal components that explain only a small percentage of the variance may still be important predictors in the regression model, and collinearity was low even between components from different PCAs, all components were included in the initial model selection procedure (Jolliffe 1982, Graham 2003, Hwang and Nettleton 2003). Using an 'all subsets' regression technique, regression models using every combination of environmental principal components were produced for each functional group. Final model selection was based on Schwarz's Bayesian Criterion (SBC) scores, which have been shown to more consistently select the best model when the predictor variable to sample size ratio is relatively low (i.e., less than 1:10) and the resulting coefficient of determination ($R^2$) is in the range of 0.4 to 0.7 (Schwarz 1978, Gagné and Dayton 2002, Beal 2007). The responses of individual functional groups to abiotic, biotic, and chemical variables were interpreted based on the loadings (eigenvectors multiplied by the square root of the eigenvalue) for those variables on the principal components, and by the sign and strength of the standardized beta coefficients in the final models (Beals 2006).

The principal components analysis was conducted in SAS using PROC PRINCOMP, with a correlation matrix, and the all subsets regression analysis was performed in SAS using PROC REG (SAS Institute 2010). The correlation matrix method was chosen to ensure that disparities among measurement scales did not unfairly bias the analysis towards those attributes with naturally wide ranges or larger abundance.

# 2.4. Results

## 2.4.1. Functional group dominance and environment

### 2.4.1.1. Functional group distributions and composition

Not surprisingly, the total abundance of each functional group was greatest in the quadrat that represented that group (Figure 7). In addition, the abundance of each functional group was normally distributed within its namesake quadrat type, with skewness between -0.78 and 0.46, and kurtosis between -0.6 and 0.9 for all groups, thereby adhering to McCune and Grace's (2002) rule of thumb for distributional normality.

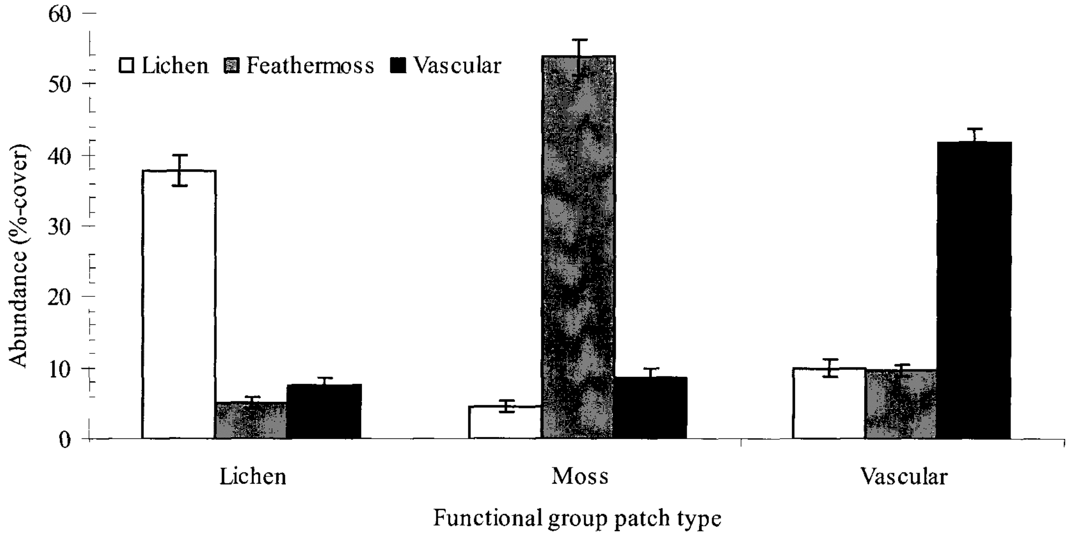

**Figure 7.** Mean abundance (± SE) of lichen, feathermoss, and vascular plants in each FG quadrat type.

Three *Vaccinium* species (*V. caespitosum*, *V. membranaceum*, and *V. vitis-idaea*), along with *Arcostaphylos uva-ursi*, *Cornus canadensis*, and *Linnaea borealis*, were by far the most commonly detected vascular species in both random and FG quadrats (Table 2). *Cladonia arbuscula*, *C. rangiferina*, cup-forming *Cladonia* spp., *Cetraria ericetorum*, and *Stereocaulon paschale* were the most common lichens, while *Pleurozium schreberi* was the most commonly detected feathermoss (Table 2). Other common taxa were *Peltigera malaceae*, *P. aphthosa*, *Dicranum* spp., *Polytrichum* spp., and liverworts (Table 2).

**Table 2.** Frequency of detection (%) for vascular species in random (n=216) and functional group (n=216) quadrats. Functional group quadrats are additionally broken down by FG type (indicated by L, M or V). Species that could not be identified in the field but were later found in laboratory samples were usually included in larger groups for field identification (indicated by indentation), and are marked with 'p' to indicate 'present'.

| Group | Species | Random | FG | (L) | (M) | (V) |
|---|---|---|---|---|---|---|
| Vascular plants | *Alnus tenuifolia* Nutt. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Aralia nudicaulus* L. | 0.0 | 0.5 | 0.0 | 1.4 | 0.0 |
| | *Arctostaphylos uva-ursi* Spreng. | 19.0 | 17.1 | 11.0 | 12.7 | 27.8 |
| | *Arnica cordifolia* Hook. | 5.6 | 2.8 | 1.4 | 1.4 | 5.6 |
| | *Aster conspicuus* Lindl. | 1.4 | 0.5 | 0.0 | 0.0 | 1.4 |
| | *Calamagrostis purpurascens* R.Br. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Chamerion* (syn. *Epilobium*) *angustifolium* (L.) Holub | 8.3 | 2.8 | 1.4 | 4.2 | 2.8 |
| | *Chimaphila umbellata* (L.) W.P.C. Barton | 1.9 | 0.9 | 0.0 | 0.0 | 2.8 |
| | *Cornus canadensis* L. | 41.2 | 39.8 | 38.4 | 43.7 | 37.5 |
| | *Empetrum nigrum* (syn. *hermaphroditum*) L. | 2.8 | 5.6 | 0.0 | 4.2 | 12.5 |
| | *Equisetum scirpoides* Michx. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Festuca occidentalis* Hook. | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Fragaria virginiana* Mill. | 0.0 | 1.9 | 1.4 | 2.8 | 1.4 |
| | *Galium boreale* L. | 2.3 | 1.4 | 1.4 | 1.4 | 1.4 |
| | *Gaultheria hispudula* (L.) Muhl. ex Bigelow | 0.9 | 0.5 | 0.0 | 0.0 | 1.4 |
| | *Geocaulon lividum* Fernald | 3.7 | 4.2 | 2.7 | 1.4 | 8.3 |
| | *Ledum groenlandicum* Oeder | 6.5 | 4.2 | 2.7 | 2.8 | 6.9 |
| | *Linnaea borealis* L. | 34.7 | 34.7 | 27.4 | 33.8 | 43.1 |
| | *Lupinus arcticum* S. Watson | 1.4 | 1.9 | 2.7 | 1.4 | 1.4 |
| | *Lycopodium annotinum* L. | 2.3 | 1.9 | 1.4 | 2.8 | 1.4 |
| | *Lycopodium complanatum* L. | 1.9 | 0.9 | 0.0 | 0.0 | 2.8 |
| | *Maianthemum canadense* Desf. | 0.5 | 0.5 | 0.0 | 0.0 | 1.4 |
| | *Mertensia paniculata* (Aiton) G. Don | 0.9 | 1.9 | 1.4 | 2.8 | 1.4 |
| | *Platanthera orbiculata* (Pursh) Lindl. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Oryzopsis asperifolia* Michx. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Oryzopsis pungens* (Torr. ex Spreng.) Hitchc. | 6.0 | 2.3 | 2.7 | 1.4 | 2.8 |
| | *Orthilia secunda* (L.) House | 6.9 | 3.7 | 1.4 | 5.6 | 4.2 |
| | *Pedicularis labridorica* Wirsing | 0.0 | 0.5 | 0.0 | 1.4 | 0.0 |
| | *Petasites frigidus* Macoun | 5.1 | 4.6 | 2.7 | 4.2 | 6.9 |
| | *Pyrola virens* Schweig. and Koerte | 3.7 | 3.7 | 2.7 | 4.2 | 4.2 |
| | *Rhododendron albiflorum* Hook. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Rosa acicularis* Lindl. | 6.0 | 4.2 | 4.1 | 0.0 | 8.3 |
| | *Rubus arcticus* L. | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Rubus pubescens* Raf. | 0.5 | 0.5 | 0.0 | 0.0 | 1.4 |
| | *Salix* sp. L. | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Shepherdia canadensis* Nutt. | 11.1 | 4.6 | 1.4 | 8.5 | 4.2 |
| | *Smilacina racemosa* Desf. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Solidago spathulata* DC. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Vaccinium cespitosum* Michx. | 19.0 | 19.9 | 15.1 | 16.9 | 27.8 |
| | *Vaccinium membranaceum* Douglas ex Torr. | 31.5 | 32.9 | 21.9 | 31.0 | 45.8 |
| | *Vaccinium vitis-idaea* L. | 35.6 | 30.1 | 32.9 | 25.4 | 31.9 |
| | *Viburnum edule* (syn. *opulus*) (Michx.) Raf. | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Viola renifolia* A. Gray | 3.2 | 2.3 | 2.7 | 1.4 | 2.8 |

**Table 2.** ...continued

| Group | Species | Random | FG | (L) | (M) | (V) |
|---|---|---|---|---|---|---|
| Mat-forming lichens | *Cetraria ericetorum* ssp *rangiferina* | 37.0 | 7.9 | 15.1 | 4.2 | 4.2 |
| | *Cladonia arbuscula* (incl. *mitis*) (Wallr.) Flotow | 66.2 | 63.4 | 95.9 | 45.1 | 48.6 |
| | *Cladonia mitis* Sandst. | | p | p | p | p |
| | *Cladonia rangiferina* (L.) Weber ex F.H. Wigg. | 44.0 | 50.0 | 78.1 | 32.4 | 38.9 |
| | *Cladonia stellaris* (Opiz.) Pouzar and Vězda | 0.5 | 1.4 | 4.1 | 0.0 | 0.0 |
| | *Cladonia uncialis* (L.) Weber ex F.H.Wigg. | 22.7 | 21.3 | 42.5 | 5.6 | 15.3 |
| | *Cladonia* spp. (cup-forming) Hill ex P. Browne | 81.0 | 55.1 | 80.8 | 35.2 | 48.6 |
| | *Cladonia bellidiflora* (Ach.) Schaer. | | p | p | | |
| | *Cladonia botrytes* (K.G. Hagen) Willd. | | p | | p | |
| | *Cladonia carneola* Fr. | | p | p | | |
| | *Cladonia cenotea* (Ach.) Schaer. | | p | p | | |
| | *Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng. | | p | p | p | |
| | *Cladonia coniocraea* (Flörke) Spreng | | p | p | p | p |
| | *Cladonia cornuta* (L.) Hoffm. | | p | p | p | p |
| | *Cladonia crispata* (Delise) Vain. | | p | p | | p |
| | *Cladonia ecmocyna* (Robbins) Ahti | | p | p | p | p |
| | *Cladonia fimbriata* (L.) Fr. | | p | p | | p |
| | *Cladonia gracilis* ssp. *turbinata* (Ach.) Ahti | | p | p | | p |
| | *Cladonia phyllophora* Ehrh. ex Hoffm. | | p | p | | p |
| | *Cladonia pyxidata* (L.) Hoffm. | | p | p | | |
| | *Cladonia scabriuscula* (Delise) Leight. | | p | | | p |
| | *Cladonia sulphurina* (Michx.) Fr. | | p | p | p | p |
| | *Stereocaulon* spp. Hoffm. | 26.4 | 17.0 | 31.5 | 11.3 | 8.3 |
| | *Stereocaulon paschale* (L.) Hoffm. | | p | p | | |
| | *Stereocaulon tomentosum* Fr. | | p | p | | p |
| Leaf lichens | *Nephroma arcticum* (L.) Torss. | 1.4 | 0.9 | 0.0 | 2.8 | 0.0 |
| | *Peltigera aphthosa* (L.) Willd. | 21.8 | 24.5 | 24.7 | 25.4 | 23.6 |
| | *Peltigera conspersa* ined. Goward | 1.4 | 0.5 | 0.0 | 0.0 | 1.4 |
| | *Peltigera* spp. (mostly *malaceae*) Willd. | 28.7 | 17.6 | 31.5 | 7.0 | 13.9 |
| | *Umbilicaria* sp. Hoffm. | 6.9 | 3.7 | 4.1 | 2.8 | 4.2 |
| Crust lichens | *Anzina carneonivea* (Anzi) Scheid. (Goward et al. 1996) | | p | p | | |
| | *Icmadophila ericetorum* (L.) Zahlbr. | 1.4 | 0.5 | 1.4 | 0.0 | 0.0 |
| | *Micarea denigrata* (Fr.) Hedl. | | p | p | | |
| | *Xylographa soralifera* Holien and Tønsberg | | p | p | | |
| Feather-moss | *Hylocomium splendens* (Hedw.) Schimp. | 13.4 | 11.6 | 4.1 | 19.7 | 11.1 |
| | *Pleurozium schreberi* (Brid.) Mitt. | 61.6 | 66.7 | 45.2 | 98.6 | 56.9 |
| | *Ptilium crista-castrensis* (Hedw.) De Not. | 15.7 | 14.8 | 2.7 | 28.2 | 13.9 |
| Other mosses | *Brachethecium* spp. Schimp. | 3.7 | 1.4 | 0.0 | 1.4 | 2.8 |
| | *Bryum* spp. Hedw. | 6.5 | 2.3 | 4.1 | 1.4 | 1.4 |
| | *Bryum pseudotriquetrum* (Hedw.) Gaertn. et al. | | p | | | p |
| | *Bucklandiella heterosticha* (Hedw.) Bednarek-Ochyra and Ochyra | | p | p | | |
| | *Buxbaumia aphylla* Hedw. | | p | p | | |
| | *Ceratodon purpureus* (Hedw.) Brid. | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Dicranum* spp. Hedw. | 57.9 | 37.5 | 46.6 | 32.4 | 33.3 |
| | *Dicranum fuscescens* Turn. | | p | p | p | p |

**Table 2.** …continued

| Group | Species | Random | FG | (L) | (M) | (V) |
|---|---|---|---|---|---|---|
| | *Dicranum scoparium* Hedw. | | p | | p | |
| | *Drepanocladus* sp. (C. Müll.) G. Roth | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Eurynchium praelongum* (Hedw.) Schimp. | | p | p | | |
| | *Pohlia nutans* (Hedw.) Lindb. | 8.8 | 1.9 | 2.7 | 0.0 | 2.8 |
| | *Polytrichum* spp. Hedw. | 27.3 | 12.5 | 15.1 | 14.1 | 8.3 |
| | *Polytrichum commune var. Commune* Hedw. | | p | | | p |
| | *Polytrichum juniperinum* Hedw. | | p | p | p | |
| | *Pseudoleskeella tectorum* (Funck ex Brid.) Kindb. | | p | p | | |
| | *Sanionia uncinata* (Hedw.) Loeske | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Sphagnum* sp. L. | 0.0 | 0.5 | 1.4 | 0.0 | 0.0 |
| Liverworts | All liverworts | 62.0 | 32.9 | 34.2 | 28.2 | 36.1 |
| | *Barbilophozia barbata* (Schmid. ex Schreb.) Loeske | | p | | p | |
| | *Barbilophozia hatcheri* (Evans) Loeske | | p | p | p | p |
| | *Barbilophozia lycopodioides* (Wallr.) Loeske | | p | | | p |
| | *Cephalozia bicuspidata* (L.) Dum. | | p | p | | p |
| | *Cephaloziella divaricata* (Sm.) Schiffn. | | p | p | | p |
| | *Lophozia longidens* (Lindb.) Macoun | | p | p | p | |
| | *Lophozia ventricosa* (Dicks.) Dum. | | p | | | p |
| | *Ptilidium pulcherrimum* (G. Web.) Hampe | | p | p | | |

The total frequency of species detection was similar between random and FG quadrats, even for many species that were not abundant (Table 2). As expected, vascular FG quadrats showed higher detection frequencies of vascular species than feathermoss quadrats, and feathermoss quadrats had higher frequency of detection of vascular species than lichen quadrats. Similarly, feathermosses were most frequently detected in feathermoss FG quadrats, followed by vascular FG quadrats and lichen FG quadrats. Mat-forming lichens were most frequently detected in lichen FG quadrats, followed by vascular and feathermoss quadrats. Three species that did not follow the trend of similarity between random and FG quadrats were *Cladonia stellaris*, which was three times more abundant in FG quadrats, *Chamerion angustifolium*, which was three times more abundant in random quadrats, and *Shepherdia canadensis*, which was just over twice as abundant in random quadrats (Table 2).

#### 2.4.1.2. Environmental variability among functional groups

Copper, lead and cadmium were present at insufficient quantities ($<0.2$ μg • 10 $cm^{-2}$ • 6 $weeks^{-1}$) for reliable detection in over 90% of samples, and were therefore omitted from the analysis. Several nutrients had non-normal distributions despite transformation, making it necessary to remove outlying records. My field notes indicated that these PRS™ probes may have been tampered with, and were therefore not accurate representations of the sites. For virtually all environmental variables measured, the inter-site variability was greater than that among functional groups. Abiotic variables (soil texture and topography) differed among sites but not among functional groups. In contrast, many soil chemistry and most biotic (canopy) variables showed significant variation among both sites and functional groups.

All soil texture classes differed significantly among sites ($F_{(23, 190)} = 2.92$-$9.80$, $p < 0.0001$, $\eta^2 = 0.26$-$0.54$), but not among functional groups (Figure 8). On average, coarse fragments made up 37% of a soil sample, gravel was 24%, and finer texture classes (sand, silt+clay) were 38% (Figure 8). Sand was the dominant contributor to the 'fines' texture class, making up a mean 88% of fines (33% of the whole sample), while silt and clay combined only made up 12% of fines (4% of the whole sample). The mean ratio of particles greater than 2 mm to particles less than 2 mm in diameter was approximately 5:3, and the ratio of sand to silt+clay was approximately 8:1. Duff layer (LFH) thickness significantly differed among sites ($F_{(23, 190)} = 9.77$, $p < 0.0001$, $\eta^2 = 0.53$) and among functional groups ($F_{(2, 190)} = 4.77$, $p = 0.0095$, $\eta^2 = 0.02$), with lichen quadrats showing the thinnest LFH (7.5 ± 1.3 cm), and vascular quadrats showing the thickest (9.1 ± 1.5 cm); however, LFH thickness in vascular quadrats was statistically indistinguishable from that in feathermoss quadrats.

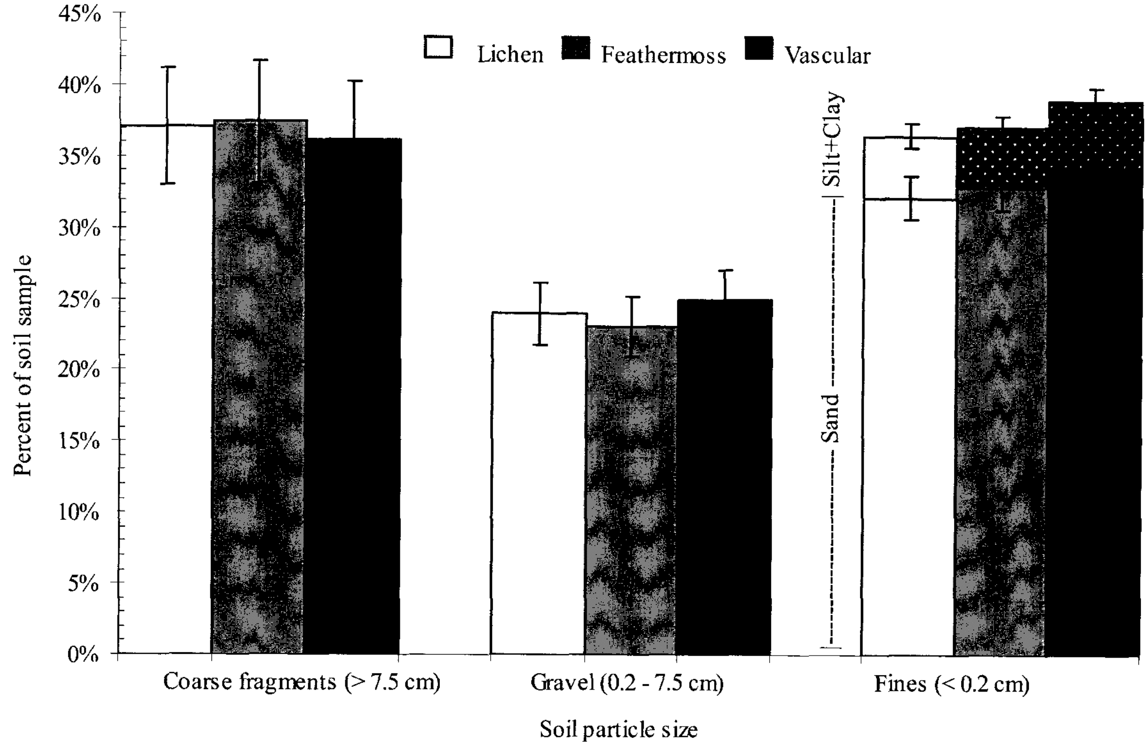

**Figure 8.** Mean (± SE) percent of soil sample in each of three particle size-classes from functional group quadrats. Note the finer subdivision of the 'Fines' class into Sand and Silt+Clay.

Drip-zone and canopy cover indices showed two main patterns of functional group association: WInDZ and LAI were both greatest in feathermoss patches and lowest in lichen patches, while CRDZ and SWCC were greatest in vascular patches and lowest in lichen patches (Figure 9). All indices showed significant differences among functional groups except for LAI (for WInDZ, $F_{(2,190)} = 3.06, p = 0.0493, \eta^2 = 0.21$; for CRDZ, $F_{(2,190)} = 4.85$, $p = 0.0089, \eta^2 = 0.23$; for SWCC, $F_{(2,190)} = 4.07, p = 0.0186, \eta^2 = 0.34$). All measures of irradiance were lowest in feathermoss-dominated patches, but these differences were only significant for direct irradiance ($F_{(2,190)} = 3.46, p = 0.0333, \eta^2 = 0.48$). Diffuse and total irradiance did not differ significantly among functional groups (Figure 10).

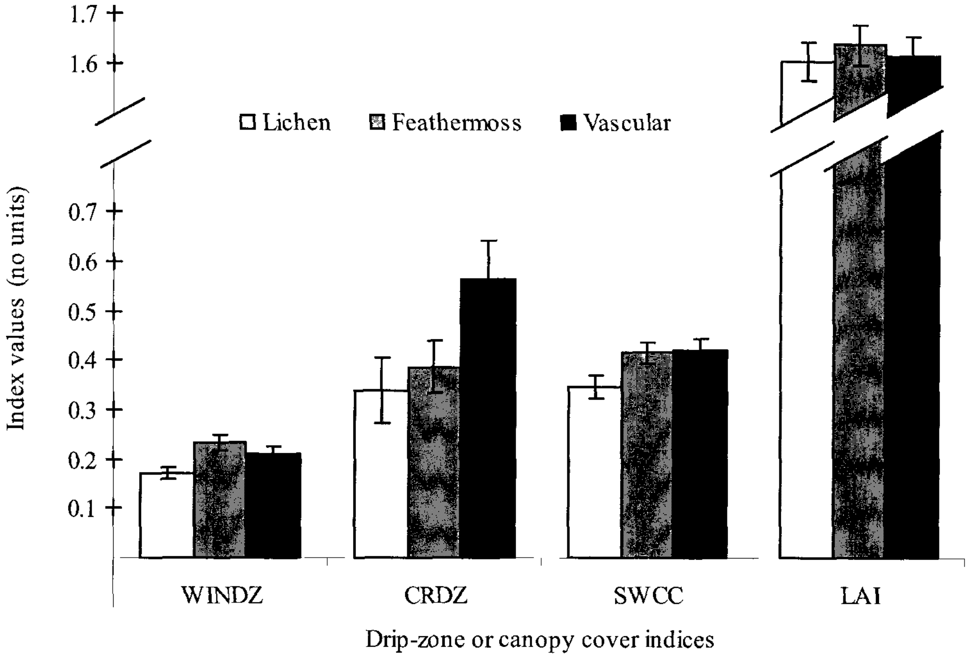

**Figure 9.** Mean (± SE) drip-zone and canopy cover index values, by functional group quadrat type.

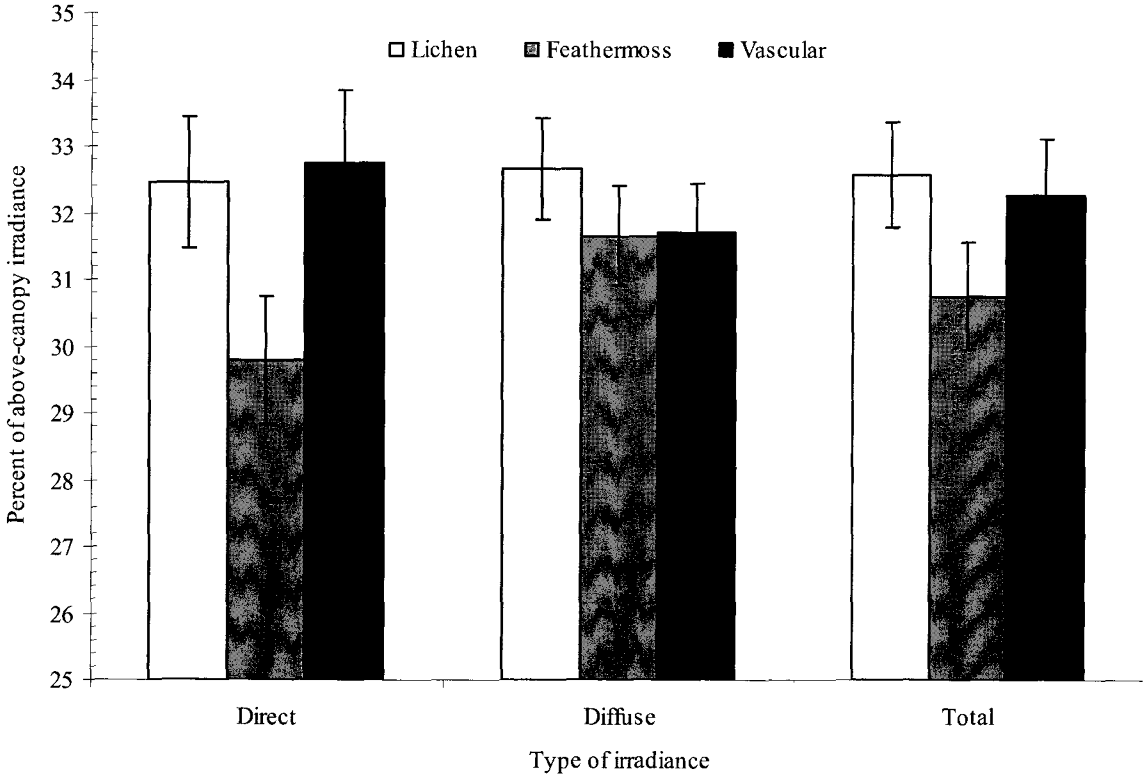

**Figure 10.** Mean (± SE) transmitted irradiance, expressed as a percentage of the above-canopy direct, diffuse, and total irradiance, by functional group.

Soil pH was significantly lower in feathermoss than in lichen patches, with vascular plant patches intermediate ($F_{(2, 181)} = 3.73, p = 0.0259, \eta^2 = 0.02$). Yet, the difference between the highest and lowest functional group means was less than 0.2 pH units, and all samples were mildly acidic (Figure 11). Zinc, iron, and aluminum availability tended to be lowest under feathermoss and highest under vascular plants, with lichens occupying intermediate positions; however, none of these differences was significant (Figure 12).

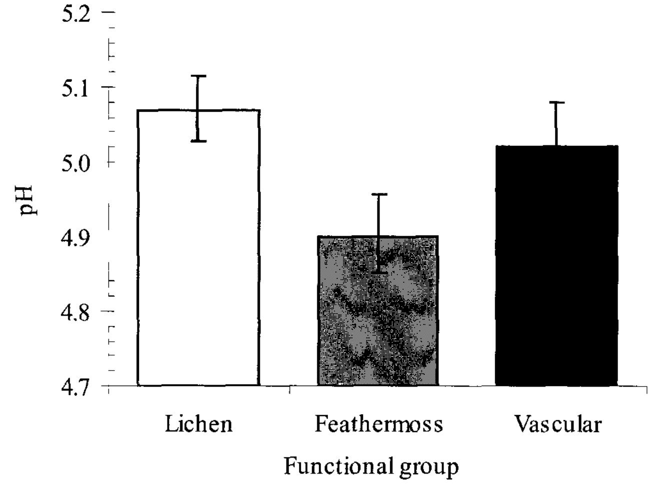

**Figure 11.** Mean (± SE) pH of soil samples from different FG quadrat types.

Calcium, magnesium, potassium, phosphorus, and manganese availability were highest in vascular plant quadrats, intermediate in feathermoss quadrats, and lowest in lichen quadrats ($F_{(2, 181)} > 5.64, p < 0.0042, \eta^2 = 0.04 - 0.21$). With the exception of phosphorus, these were also the most available nutrients throughout the study area (Figure 12).

Nitrate availability was similar among functional groups, while ammonium and total nitrogen availability were highest under feathermoss and lowest under vascular plant quadrats ($F_{(2, 181)} = 6.83, p = 0.0014, \eta^2 = 0.05$; $F_{(2, 181)} = 7.45, p = 0.0008, \eta^2 = 0.05$; Figure 12). Boron was the least available nutrient, and did not differ among either sites or functional group quadrats. Further ANOVA results are presented in tabular form in Appendix D.

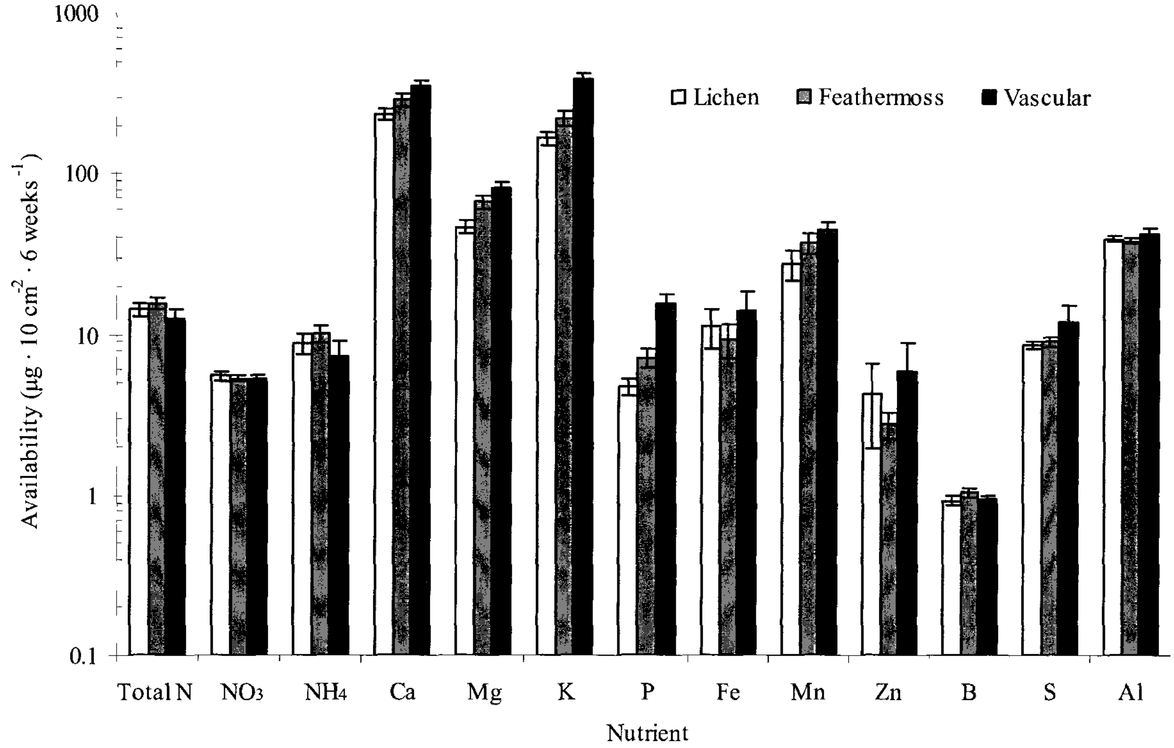

**Figure 12.** Mean (± SE) availability of soil nutrients by functional group quadrat type. Units of measurement are micrograms of nutrient per 10 $cm^2$ of resin-membrane surface, over the entire six week burial period; these units cannot be broken into a daily rate, because the rate of nutrient absorption changes after the initial labile nutrient pool is depleted.

## 2.4.2. Functional group abundance and environment

### 2.4.2.1. Multiple regression

The abundance of each functional group was normally distributed within its namesake quadrat type, so the raw values (%-cover) were used in each model. Many good models (i.e., models ranked by SBC scores to be the ten best) for each functional group were significant overall ($p$ <0.0001), but only the best models (i.e., the model for each functional group with the lowest SBC score) had parameter estimates that were all significantly different from zero at $\alpha = 0.05$. In addition, the best model was clearly differentiated from other good models in each case, with the difference in SBC scores being at least four times greater between the first and second best models than the difference between the second and third best for all functional groups. The best models showed varying levels of predictive accuracy, but most had a slight tendency towards overestimating functional group abundance at low values and underestimating abundance at high values. Nevertheless, residuals were approximately normally distributed about the mean in all cases. Model fit decreased from the lichen (adj. $R^2 = 0.68$) to the vascular plant model (adj. $R^2 = 0.38$), with the feathermoss model intermediate (adj. $R^2 = 0.50$; Table 3). In general, soil chemistry variables were more influential in the models than other types of variables, as indicated by the greater number of significant contributing variables and by their relatively large standardized parameter ($\beta_s$) estimates.

**Table 3.** Best multiple regression models (models with lowest SBC score), with functional group abundance as a product of environmental variables; standardized parameter estimates ($\beta$s) are parameter ($\beta$) estimates divided by the ratio of the dependent variable's standard deviation to the independent variable's standard deviation. Although an equal number of quadrats were surveyed for each vegetation type, outlier removal resulted in sample sizes varying slightly from one to the next.

| Model | DF model | DF error | *p*-value | *Adjusted $R^2$ | Variable | $\beta$ | $\beta_s$ | *p*-value |
|---|---|---|---|---|---|---|---|---|
| Lichen | 4 | 65 | <0.0001 | 0.68 | Ca | -28.92 | -0.44 | <0.0001 |
| | | | | | Al | 55.89 | 0.40 | <0.0001 |
| | | | | | LAI | -19.08 | -0.34 | <0.0001 |
| | | | | | P | -14.01 | -0.27 | 0.0005 |
| Moss | 4 | 66 | <0.0001 | 0.50 | Mg | 56.46 | 0.88 | 0.0001 |
| | | | | | Ca | -53.38 | -0.73 | 0.0007 |
| | | | | | Total_irrad | -1.85 | -0.57 | <0.0001 |
| | | | | | Zn | -18.59 | -0.27 | 0.0058 |
| Vascular | 3 | 61 | <0.0001 | 0.37 | Mn | -9.55 | -0.33 | 0.0048 |
| | | | | | Mg | 14.40 | 0.33 | 0.0045 |
| | | | | | LFH | 6.37 | 0.33 | 0.0060 |

*Adjusted $R^2 = 1-(1-R^2)\cdot[(N-1)/(N-k-1)]$, where 'N' is the sample size, and 'k' is the number of predictor variables used in the model (SAS Institute 2010).

The best lichen model was significantly influenced by four environmental variables: phosphorus and calcium availability, and LAI were negatively associated with lichen abundance, while aluminum availability was positively associated with it (Table 3). Among other good lichen models, the same three soil chemistry variables from the best model were always retained, and most included LAI. Several good models had another biotic variable instead of or in addition to LAI (SWCC or Diffuse irradiance), although the sign of association remained the same. Two other good models included negative associations with northern aspects, one included a positive association with pH, one included a negative association with silt+clay content, and one included a positive association with total nitrogen availability.

The best feathermoss model was significantly influenced by four environmental variables: magnesium and calcium availability had positive and negative associations with feathermoss abundance, respectively, and were also the most influential variables in the model (Table 3). Total irradiance and zinc availability both had a negative association with feathermoss abundance in the best model, and appeared to be less influential than other variables (Table 3). All of the top ten best feathermoss models included the same nutrient availability variables, and all but one included total irradiance; several others also included positive associations with ammonium or total nitrogen, and negative associations with silt+clay content. Less commonly, top models indicated that feathermoss abundance was positively associated with SWCC and fines or sand content, and negatively associated with diffuse irradiance.

Vascular-plant abundance was positively influenced by magnesium availability as well as LFH thickness, and negatively influenced by manganese availability (Table 3). Although all of the top vascular plant models indicated positive associations with LFH thickness, only four included magnesium or manganese availability as predictor variables. Other top models commonly included negative associations with diffuse irradiance, sand content, and (in one case) northern aspects, as well as positive associations with direct irradiance, fines content, and slope inclination.

### 2.4.2.2. Principal components analyses

For brevity, only those PCA results that are relevant to subsequent multiple regressions are presented here. Specifically, for each combination of functional group and environmental variable subset, the first principal component is discussed along with any components that were included in subsequent regression models. If an even number of components from a certain PCA were selected for the subsequent models, another component from that PCA is also presented for joint-plot diagrams, since the diagrams require two components (axes) and thus an even number overall. Principal components often showed strikingly similar loadings among functional groups, presumably due to the strong influence of a few environmental gradients that were not unique to a particular patch type (e.g., the first biotic component was positively associated with indices of canopy cover and negatively associated with measures of irradiance for all functional groups; Table 4). I will hereafter refer to principal components by a code indicating their component number (1-14), and their variable subset (a = abiotic, b = biotic, c = soil chemistry) and functional group (subscript: lichen, moss, vascular) of origin.

#### 2.4.2.2.1. Lichen PCA

The first lichen abiotic component ($a1_{lichen}$) primarily represents a gradient of soil stoniness, such that quadrats with high coarse-fragment content load negatively while quadrats with more particles <2 mm in size tended to load positively (Figure 13a). The second abiotic component ($a2_{lichen}$) represented a gradient from south-facing, approximately level sites to north-facing steeper slopes (Figure 13a). These components represented approximately 44% and 19% of the variance in abiotic environmental variables, respectively, from lichen patches. In addition, $a1_{lichen}$ and $a2_{lichen}$ appeared to interact, indicating a possible sampling bias; quadrats with more northerly aspects and greater slope inclinations tended to have moderate abundance of both coarse fragments and fines (Figure 13a).

**Table 4.** Loadings of environmental variables on principal components. Only values >0.24 reported for most components; when components had few loadings >0.24, loadings as small as 0.14 are reported but marked with an asterisk to indicate that they would be considered marginally nonsignificant correlations at alpha = 0.05.

| PC | Negative loadings | Positive loadings | Gradient interpretation |
|---|---|---|---|
| $b1_{lichen}$ | Total_irrad (-0.95), Diffuse (-0.91), Direct (-0.78) | LAI (0.89), SWCC (0.63), CRDZ (0.60), localBA (0.52), LFH (0.47), WInDZ (0.23) | Generalized canopy closure |
| $c3_{lichen}$ | Ca (-0.62), Mg (-0.58), K (-0.21)* | S (0.69), Fe (0.53), Al (0.45), P (0.37) | Base-cation deficiency |
| $c4_{lichen}$ | Mn (-0.23)*, Fe (-0.20)* | B (0.77), S (0.40), P (0.33), K (0.25) | Boron and macronutrient availability |
| $c7_{lichen}$ | P (-0.40), Zn (-0.37) | pH (0.52), Al (0.28), Total N (0.24) | Alkalinity or biological weathering |
| $b1_{moss}$ | Total_irrad (-0.95), Diffuse (-0.93), Direct (-0.82) | LAI (0.89), LFH (0.63), SWCC (0.63), local BA (0.45), CRDZ (0.44), WInDZ (0.35) | Generalized canopy closure |
| $c10_{moss}$ | $NH_4$ (-0.17)*, Fe (-0.16)* | Zn (0.37), $NO_3$ (0.16)*, S (0.15)* | Zn availability or N form |
| $c12_{moss}$ | Al (-0.15)* | Ca (0.14)* | Ca to Al ratio |
| $b1_{vascular}$ | Total_irrad (-0.93), Diffuse (-0.94), Direct (-0.80) | LAI (0.90), SWCC (0.62), LFH (0.53), localBA (0.50), CRDZ (0.44) | Generalized canopy closure |
| $b4_{vascular}$ | SWCC (-0.37) | LFH (0.70), WInDZ (0.25), Direct (0.24) | Low to high LFH thickness and dryness |
| $b5_{vascular}$ | CRDZ (-0.30) | SWCC (0.56), WInDZ (0.25) | Overhead to westward-dominated canopy cover |
| $b6_{vascular}$ | CRDZ (-0.37) | local BA (0.42) | Overhead to peripheral canopy cover |
| $a6_{vascular}$ | Sand (-0.20)* | Silt+Clay (0.44) | Ratio of sand to silt+clay |

The first lichen biotic component ($b1_{lichen}$) was positively loaded with drip-zone and canopy closure indices (LAI, SWCC, CRDZ) as well as LFH thickness and local BA, and was negatively loaded with all measures of irradiance (Table 4, Figure 13b). This component appears to represent a generalized gradient of canopy closure, with little directional or spatial signal incorporated (Figure 13b); $b1_{lichen}$ represented approximately 49% of the variance from biotic environmental variables. The second biotic component ($b2_{lichen}$) represented approximately 15% of the variance from biotic environmental variables, and was positively loaded with WInDZ, local basal area, and SWCC, but negatively loaded with LFH thickness (Figure 13b). Component $b2_{lichen}$ appears to be a gradient from high canopy but low stem density, to high stem but low canopy density (Figure 13b).

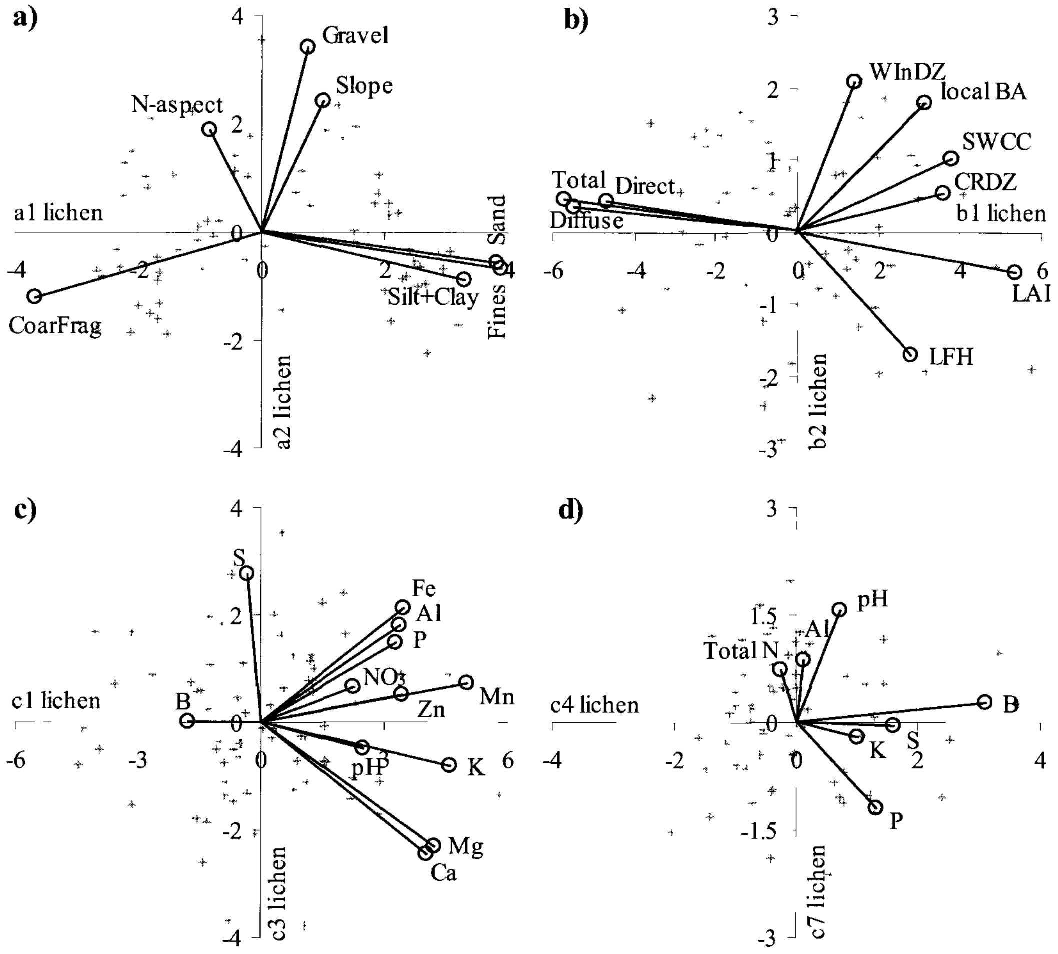

**Figure 13.** PCA ordination joint-plots of (a) abiotic, (b) biotic, and (c-d) soil chemistry variables from lichen-dominated quadrats, showing variable loadings (red circles) overlaying quadrats (gray +'s).*

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* Joint-plot diagrams consist one diagram overlaid on top of another, and are often used in ordination to display multiple patterns at once. The main diagram is a scatter-plot showing the relationship between any two principal components, with points representing the scores (x and y coordinates) of individual samples on each principal component (x and y axes). The second diagram consists of principal component loadings, which are calculated as the product of the eigenvector and the square-root of the eigenvalue for a given variable-component combination. Loadings are equivalent to the correlation coefficients between original variables and principal components, with values between negative one and one. Points are plotted using principal component loadings as the x and y coordinates, and vectors (the hypotenuse of the x and y coordinates) are drawn from each point to the origin, indicating the strength of the loading. This second diagram is then scaled to the same dimensions as the first, such that the maximum value on the first diagram corresponds to a perfect loading.

The first chemical component ($c1_{lichen}$) from lichen patches represented approximately 28% of the variance in soil chemistry variables. This component had positive loadings of the availability of all nutrients except ammonium and sulphur, which had insignificant correlations, and boron, which was negatively correlated, indicating that $c1_{lichen}$ represents an overall gradient of nutrient availability (Figure 13c). The third chemical component ($c3_{lichen}$) explained 14% of the variance in soil chemistry variables, and represented a gradient of base-cation deficiency or biological weathering; sulphur, iron, phosphorus, and aluminum were positively correlated with $c3_{lichen}$, while calcium, magnesium, and potassium were negatively correlated with it (Table 4, Figure 13c).

Boron, sulphur, phosphorus, and potassium availability loaded positively, while iron and manganese availability loaded negatively on component four ($c4_{lichen}$) from lichen patches, which explained approximately 9% of the variance from soil chemistry variables. Component $c4_{lichen}$ may represent a gradient of boron and macronutrient availability, though more emphasis is on boron because of its relatively strong loading. Soil chemistry component seven explained approximately 6% of the variance from soil chemistry variables; $c7_{lichen}$ probably represents a gradient of alkalinity and nitrogen availability. It is difficult to explain the negative association between $c7_{lichen}$ and phosphorus availability, and the positive association with aluminum availability, given their known relationships with pH. These apparently contradictory associations may be a statistical artefact; the small range of pH observed along $c7_{lichen}$ may not be enough for a chemically meaningful alkalinity gradient.

#### 2.4.2.2.2. Feathermoss PCA

The first two abiotic components from the feathermoss PCA showed similar patterns to those from lichen patches; $a1_{moss}$ was positively loaded with the proportion of soil particles less than 2 mm in size and negatively loaded with coarse fragments, while $a2_{moss}$ was positively loaded with north-facing aspects and steeper slope inclinations (Figure 14a). Components $a1_{moss}$ and $a2_{moss}$ therefore represented gradients of soil stoniness (or the lack thereof), and northness or steepness, respectively (Figure 14a). Component $a1_{moss}$ represented 45% of the variance in abiotic variables, and $a2_{moss}$ represented 15% of the variance in abiotic variables.

Biotic component one from the feathermoss patch data ($b1_{moss}$) was also very similar to the same component from the lichen patch data. Approximately 51% of the variance in biotic variables was explained by this component, whereas the second biotic component ($b2_{moss}$) explained 18% of the variance in biotic variables. As in the lichen biotic components, b1 moss represented an overall gradient of canopy closure (Table 4); all drip-zone and canopy cover indices, as well as local basal area and LFH thickness loaded positively on $b1_{moss}$, while all measures of light loaded negatively on it (Figure 14b). Also similar to the lichen biotic PCA was the second moss biotic component: drip-zone indices, direct light, and local basal area loaded positively on $b2_{moss}$, while LFH thickness and LAI loaded negatively (Figure 14b). This component likely represents a complimentary gradient of canopy density vs. tree density (Table 4).

The first soil chemistry component from moss patches ($c1_{moss}$) was also similar to that produced by the lichen patch PCA, with the exception that boron loaded positively and total nitrogen loaded negatively (the opposite of $c1_{lichen}$). Ammonium and sulphur also showed strong negative loadings on $c1_{moss}$, whereas in $c1_{lichen}$ these loadings were weak at best (Figure 14c). With the exception of nitrate, which was not significantly correlated, all other nutrient availability measurements showed positive and significant correlations to $c1_{moss}$. The ninth soil chemistry component ($c9_{moss}$) showed a strong positive loading by sulphur, weak positive loadings of magnesium and calcium, and weak negative loadings by zinc and pH (Figure 14c). Feathermoss soil chemistry components one and nine explained respectively 28% and 2% of the variance in soil chemistry variables, and represented gradients of nutrient availability / nitrogen deficiency, and of sulphur availability (Table 4).

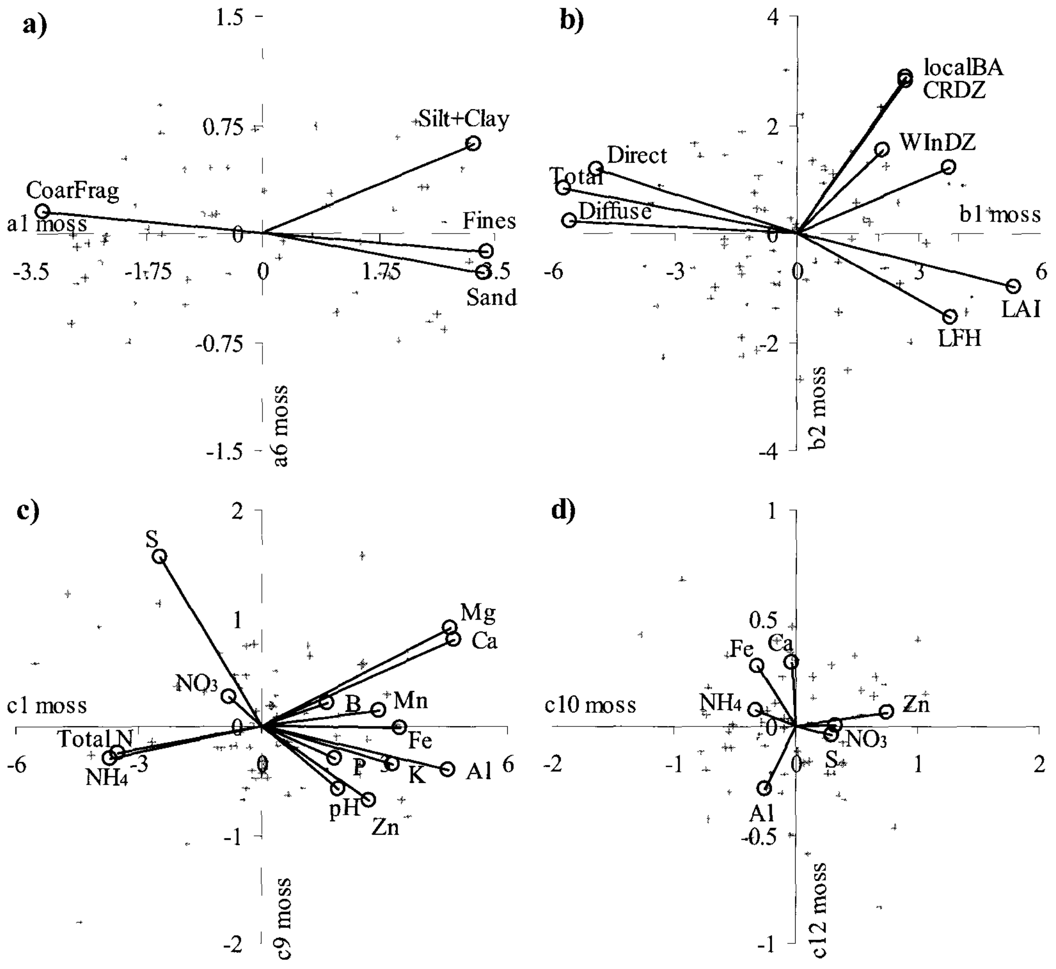

**Figure 14:** PCA ordination joint-plots of (a) abiotic, (b) biotic, and (c-d) soil chemistry variables from feathermoss-dominated quadrats, showing variable loadings (red circles) overlaying quadrats (gray +'s). Note that $a6_{moss}$ and $c9_{moss}$ are presented even though they were not in the best model, because joint plots require two components, and because these two may be somewhat relevant since they were in other top models. The y-axes of (c) and (d) are scaled ×2 for loadings to increase visual clarity, because loadings were small.

Similarly to $c9_{moss}$, $c10_{moss}$ and $c12_{moss}$ explained approximately 2% and 1% (respectively) of the variance in soil chemistry from feathermoss patches, and had only a small number of weak loadings. Component $c12_{moss}$ was positively loaded with iron and calcium, but negatively loaded with aluminum, while $c10_{moss}$ was positively loaded with zinc, nitrate, and sulphur, but negatively loaded with ammonium, iron, and aluminum (Table 4, Figure 14d). Because the loadings are mostly weak, it is difficult to say with confidence what gradients these components represent, but since the strongest influence on $c10_{moss}$ was zinc, it is likely that $c10_{moss}$ is primarily a zinc availability gradient, and to a lesser extent one of inorganic nitrogen form, while component $c12_{moss}$ may represent the ratio of available calcium to aluminum (Table 4, Figure 14d).

#### 2.4.2.2.3. Vascular plant PCA

The first vascular plant abiotic component showed similar patterns to those of the feathermoss and lichen patches; $a1_{vascular}$ primarily represented a gradient of soil stoniness, with coarse fragments loading negatively and particles <2 mm loading positively on it (Figure 15a), and it represented approximately 48% of the variance in abiotic variables for this functional group. Abiotic component six from the vascular plant patches ($a6_{vascular}$) represented a soil texture gradient, which was most strongly correlated with the proportion of silt and clay (particles <0.05 mm) in the soil (Table 4, Figure 15a).

Chemical component one from the vascular patches ($c1_{vascular}$) was similar to $c1_{moss}$, in that it was positively correlated with everything but sulphur, but it was also negatively correlated with nitrate availability and likely represents a gradient of overall nutrient availability (Figure 15b). Similarly, $c2_{vascular}$ showed comparable patterns to $c2_{moss}$ and $c2_{lichen}$, in that it had strong positive loadings from metallic micronutrients, sulphur, and nitrogen, but negative loadings from basic cations, boron, and pH (Figure 15b). Component $c2_{vascular}$ therefore represented a gradient of base-cation scarcity and metal availability. Components $c1_{vascular}$ and $c2_{vascular}$ explained 27% and 20% of the variance in soil chemistry from vascular plant patches.

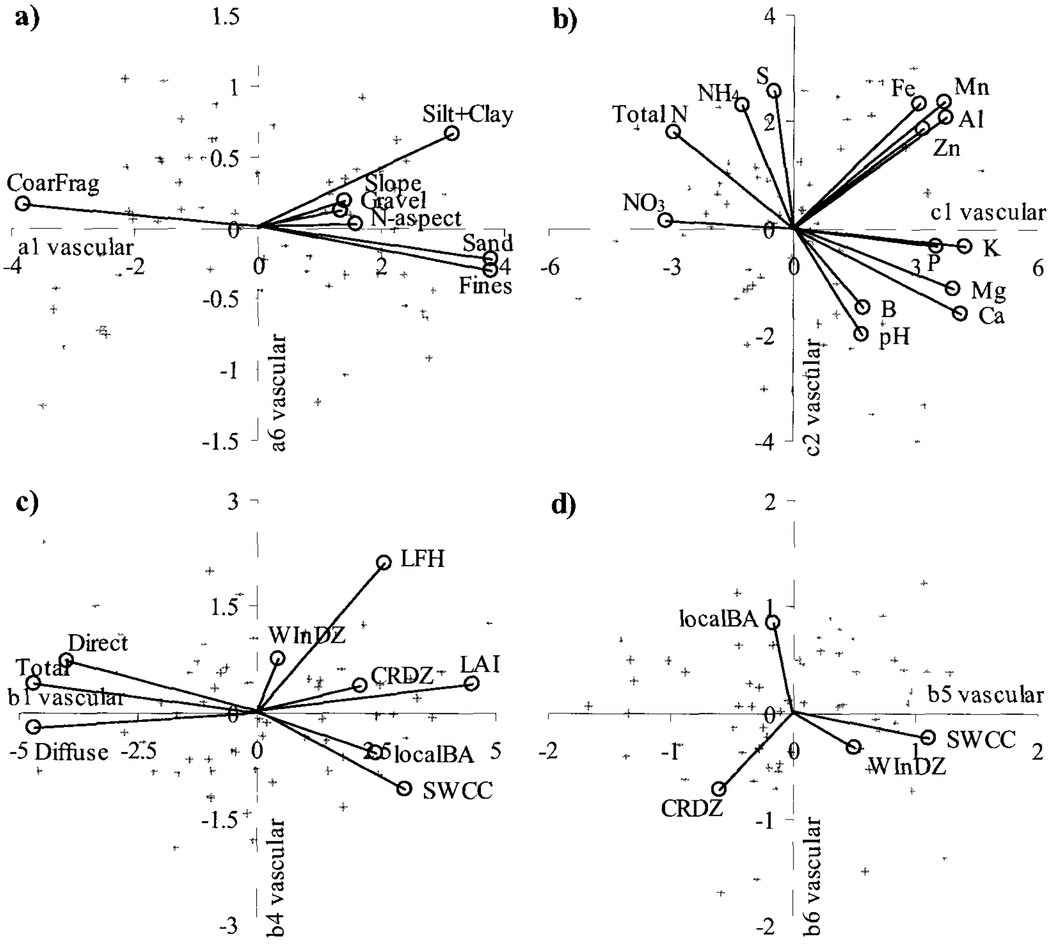

**Figure 15:** PCA ordination joint-plots of (a) abiotic, (b) soil chemistry, and (c-d) biotic variables from vascular plant-dominated quadrats, showing variable loadings (red circles) overlaying quadrats (gray +'s).

Once again, the fist biotic component (b1$_{\text{vascular}}$) was a gradient of generalized canopy closure, negatively loaded by measures of irradiance, and positively loaded by drip-zone indices, canopy cover indices, LFH thickness and local basal area (Table 4; Figure 15c); b1$_{\text{vascular}}$ explained 48% of the variance in biotic variables from vascular plant patches. Biotic component four (b4$_{\text{vascular}}$) represented only 9% of the variance in biotic variables, but in contrast to b1$_{\text{vascular}}$, was highly spatially structured. Biotic component four was positively loaded with LFH thickness, WInDZ, and direct irradiance, but negatively loaded with SWCC (Table 4, Figure 15c). The strength of the LFH thickness correlation was nearly twice that of the next strongest variable on b4$_{\text{vascular}}$, indicating that this gradient is primarily one of LFH thickness (Table 4). However, $b4_{vascular}$ may also represent a gradient of soil dryness, which would increase with proximity to the tree trunk on southern exposures (WInDZ and direct irradiance), and decrease with increasing afternoon shade (SWCC; Table 4).

Six percent of the variance in biotic variables is explained by $b5_{vascular}$, which represents a gradient from windward to leeward sides of trees in the dripzone of their canopies, or from locations directly under trees to those on the northwest sides of trees (Table 4). Accordingly, both WInDZ and SWCC loaded positively, whereas CRDZ loaded negatively on $b5_{vascular}$ (Figure 15d). The sixth biotic component ($b6_{vascular}$) explains four percent of the variance in biotic variables, and is influenced less by the direction of the canopy tree in its gradient representation than $b5_{vascular}$ or $b4_{vascular}$. Specifically, $b6_{vascular}$ represents a gradient from locations within the crown projection of one or more (probably large) canopy trees in areas with low stem density, to locations with several (probably small) canopy trees nearby that are sufficiently distant to have little of the crown radius directly overhead. This gradient is apparent through the relatively strong influence of two variables: CRDZ loads negatively on it, while local basal area loads positively (Table 4, Figure 15d).

#### 2.4.2.3. Multiple regression on principal components

The regression model with lowest SBC scores was chosen as superior to all others for each functional group, and is described in detail below. Yet, for the regression on principal components (PC regression), the difference between the best model and other top models (from the same functional group) was far less prominent than it was when using ordinary multiple regression. For example, the second and third best lichen models using principal components were both less than 0.5 SBC points away from the very best model; this was less than one-fourth of the difference between the best and next best ordinary multiple regression models. This suggests that several other good principal component regression models may include relevant information. In order to include as much of this relevant information as possible, I will briefly mention aspects of these models that deviate from -or reinforce - aspects of the best model for each functional group.

The best lichen model was significant overall (adj. $R^2 = 0.60$, $p < 0.0001$), and it contained a single biotic component and three chemical components; lichen abundance was negatively associated with generalized canopy closure ($b1_{lichen}$) and boron / macronutrient availability ($c4_{lichen}$), but positively associated with base-cation deficiency / biological weathering ($c3_{lichen}$), and alkalinity / biological weathering ($c7_{lichen}$). Several individual nutrients were also consistently associated with lichen abundance through these chemical components. Specifically, aluminum availability showed a consistent positive association with lichen abundance, while phosphorus and potassium showed consistent negative associations with lichen abundance in 2 out of 3 soil chemical components. Based on standardized parameter estimates ($\beta_s$), generalized canopy closure had the strongest association with lichen abundance, followed by base-cation deficiency, alkalinity / biological activity, and boron / macronutrient availability (Table 5). Several other top models (i.e., those ranked by SBC scores to be among the top ten most parsimonious) included components $a2_{lichen}$, $b2_{lichen}$, $b9_{lichen}$, or $c2_{lichen}$, and many also included $c1_{lichen}$ (as a negative influence), either in addition to or instead of $c4_{lichen}$.

The best feathermoss model was significant overall (adj. $R^2 = 0.48$, $p < 0.0001$), and was influenced by one biotic and two chemical components, representing generalized canopy closure ($b1_{moss}$), soil zinc availability / nitrogen form ($c10_{moss}$), and the ratio of available soil calcium to aluminum ($c12_{moss}$). Standardized beta coefficients indicated that generalized canopy closure ($b1_{moss}$) was almost three times as strongly associated with feathermoss abundance as other variables, and that $c12_{moss}$ was more influential than $c10_{moss}$ (Table 5). Other good models (i.e., the top ten) covered an SBC difference of up to 1.6 from the best model; $a6_{moss}$ (ratio of sand to silt+clay) and $c10_{moss}$ were negatively associated with feathermoss abundance in six of these models, while $c9_{moss}$ (mostly sulphur availability) positively associated with feathermoss abundance in the same number. All top models included generalized canopy closure and the ratio of available calcium to aluminum.

**Table 5.** Principal component regression model results, with functional group abundance as a product of principal components; sample size varies slightly for each model based on the number of outliers in the data set; standardized estimates ($\beta_s$) are z-score transformed parameter estimates ($\beta$).

| Model | $DF_{model}$ | $DF_{error}$ | *p* | Adjusted $R^2$ | Variable | $\beta$ | $\beta_s$ | *p* |
|---|---|---|---|---|---|---|---|---|
| Lichen | 4 | 65 | <0.0001 | 0.60 | b1 | -4.00 | -0.46 | <0.0001 |
| | | | | | c3 | 4.42 | 0.34 | <0.0001 |
| | | | | | c7 | 5.60 | 0.27 | 0.0370 |
| | | | | | c4 | -2.87 | -0.17 | 0.0009 |
| Feathermoss | 3 | 67 | <0.0001 | 0.48 | b1 | 6.65 | 0.65 | <0.0001 |
| | | | | | c12 | -19.60 | -0.25 | 0.0046 |
| | | | | | c10 | -7.00 | -0.18 | 0.0453 |
| Vascular plant | 5 | 59 | <0.0001 | 0.40 | b1 | 2.50 | 0.34 | 0.0008 |
| | | | | | b4 | 5.57 | 0.34 | 0.0009 |
| | | | | | a6 | 8.28 | 0.30 | 0.0042 |
| | | | | | b5 | 6.10 | 0.30 | 0.0033 |
| | | | | | b6 | 5.85 | 0.24 | 0.0177 |

The best vascular plant model was influenced by four biotic components and one abiotic component, with the biotic having greater influence than the abiotic both in terms of the number of contributors to the model and their individual strength of influence (Table 5). Specifically, the vascular model used $a6_{vascular}$, $b1_{vascular}$, $b4_{vascular}$, $b5_{vascular}$, and $b6_{vascular}$, had an adjusted R-squared of 0.48 and was significant overall (*p* <0.0001). In other words, the proportion of silt and clay in soil (soil texture) is positively related to vascular plant abundance, as are gradients of generalized canopy closure, LFH thickness / dryness, westward canopy cover, and diffuse peripheral canopy cover, while direct overhead canopy cover seems to be negatively related to vascular plant abundance. Although the 'best' model according to SBC scores contained only biotic and abiotic components, several other 'good' models (comparably parsimonious) included other abiotic or chemical components, which were added in addition to the components present in the best model. The seventh abiotic component ($a7_{vascular}$) was negatively associated with vascular plant abundance in four good models, while $b3_{vascular}$, $c2_{vascular}$, and $c6_{vascular}$ were negatively associated with it in two models each.

## 2.5. Discussion

### 2.5.1. Vegetation-environment relationships

#### 2.5.1.1. Abiotic influence

Soils with a higher proportion of fine particles can generally hold more water than soils with a higher proportion of coarse particles, due to their greater surface area to volume ratio of particles in finer-grained soils (Barber 1995, Hillel 1998). Despite concerns that the relative coarseness of soils from all sites would obscure any effect of soil texture on abundance of one functional group over another, the selection of a soil texture gradient ($a6_{vascular}$) in the best vascular PC model suggests that even small variations in fine fraction content of the soil may be associated with understory composition; specifically, vascular plants were positively related to the proportion of silt+clay. Curiously, a similar gradient of sand to silt+clay was often present in sub-optimal but still 'good' feathermoss PC regression models, with the opposite sign of association, indicating a positive relationship between feathermoss abundance and soil coarseness. It appears that coarse-textured soils disfavour vascular plants, and may therefore favour feathermosses and lichens, while finer soils favour vascular plants. These results agree with other studies that have documented more prolific lichens on coarse-textured soils and more vascular plants on finer-textured soils (Lechowicz and Adams 1974, Pharo and Beattie 1997, Piercey-Normore 2005), but have gone a step further by testing the association on a continuous, rather than a categorical scale.

It is possible that the soil-texture associations are due to something other than the moisture regime, such as the availability of exchange sites for dissolved ions, or some process of biological weathering. Certainly the influence of shading, litter deposition, and accumulation of necromass can all increase moisture retention in coarse textured soils (Bonan 1990, Gilliam and Roberts 2003), and there was no obvious threshold of soil coarseness beyond which vascular plants were always absent. However, LFH thickness and soil chemistry were accounted for separately by the biotic and soil chemistry principal components. Furthermore, it is the texture of mineral soil that abiotic principal components represent, and the mineral soil is unlikely to have undergone much physical change during several decades of understory development. It is not unreasonable to suggest that finer-textured soils, and therefore, more mesic moisture regimes, may promote establishment and growth of vascular plants over other groups. Hence, soil texture could potentially be used to differentiate among the niche spaces of lichens or feathermosses and vascular plants.

If soil texture differentiates among functional group niches, why were soil texture variables excluded from ordinary multiple regression models? The ratio of sand to silt + clay ($a6_{vascular}$) was the only significant abiotic component included in the vascular PC regression models, but more importantly, it explained only 4% of the variance in abiotic variables from the PCA in which it was derived; this gradient is obscured by something else at larger scales, and likely represented only a small subset of the vascular plant patch data.

Sites that loaded quite high on the positive end of $a6_{vascular}$ tended towards having sandier soils, but were also somewhat geographically restricted: many of them were located in the Upper Osilinka River valley (sites 44-51, west of Usilika Lake). Most of these sites also had frequent exposed boulders (high soil stoniness) and rolling topography on the scale of several metres. Yet, within many of these sites, some quadrats also had relatively fine soil texture, and loaded on the negative end of $a6_{\text{vascular}}$. One explanation for this is that sites within the Upper Osilinka River valley have unique parent materials and therefore greater variation in soil texture than other locations. Nevertheless, a 'site' influence is not entirely satisfactory from a biological perspective, because it is not informative as to why the difference occurs, and closer inspection of the data shows that the Upper Osilinka Valley to have similar ranges in soil texture to other sites.

Another interpretation of the strong soil-texture gradient being realized only for sites in the Upper Osilinka Valley is the lack of a homogenizing influence from litter deposition on soil moisture regime. Soil moisture retention is usually greater with greater amounts of organic matter and litter accumulation in other pine dominated forests (Berendse 1998). Thick LFH layers would likely reduce the importance of soil texture in regulating moisture content, since organic soils can both hold more moisture and provide better insulation from evaporative pressures than coarse mineral soils. Most sites examined in the Upper Osilinka River valley had exceptionally thin LFH layers throughout ($\bar{x} = 3.3 \pm 0.3$ cm for lichen, $\bar{x} = 4.9 \pm 0.6$ cm for vascular, and $\bar{x} = 6.1 \pm 0.9$ cm for feathermoss quadrats). It was these same vascular quadrats that loaded at the extreme ends of component $a6_{\text{vascular}}$; those with more abundant vascular plants loaded on the positive end, while those with more abundant lichens or feathermosses loaded on the negative end.

These results are in agreement with those of Brown et al. (2000), who found that lichen abundance declined substantially when duff depth increased to more than 5 cm. The presence of frequent fire-scars on trees in these sites highlights the potential importance of low-intensity wildfire in maintaining such thin LFH layers, and therefore in maintaining habitat suitability for lichens (Brown et al. 2000, Jasinski and Payette 2005, Girard et al. 2009).

However, if the soil texture is relatively fine during stand initiation, it may also be more likely to accumulate organic material on top (due to greater rates of plant growth) than less favourable soil types. The favourability of sites for vascular plants would be expected to benefit the most from increases in LFH thickness, but sites with coarse-textured soils are probably less likely to accumulate organic material. Indeed, out of the ten most coarse-textured vascular quadrats, an LFH thickness of less than 5.5 cm was found in three, while seven were greater than 8.0 cm, indicating that a coarse-textured patch is less likely to be dominated by vascular plants if the LFH layer is thin. A closer examination of one vascular quadrat with an LFH thickness of less than 5.5 cm revealed that it supported only 18% cover of vascular plants, compared to 28% cover of lichens; the entire plot had low abundance of vascular plants throughout, and 18% cover was the most dominance for vascular plants that surveyors could find. When soils are coarse textured (i.e., silt+clay content <10%), high vascular plant abundance is unlikely unless a minimum LFH thickness of between 5 and 8 cm is present. When LFH layers are thinner, vascular plant abundance is limited by the proportion of silt and clay (and presumably, of moisture) in the mineral soil.

Other researchers have found slope aspect to significantly influence plant community composition on scales ranging from hundreds of meters (Warren 2008) to several centimetres (Kershaw and Larson 1974, Økland et al. 2008). Given the commonality of such findings, and the close relationships between slope aspect, inclination, or position and the temperature and moisture status of the soil (Jones 1983, McCune and Keon 2002, Warren 2008), I had expected topographic variables to show significant influences on all functional groups. It was therefore surprising that, of all the topographic variables (and principal components), none had a strong enough association with functional group abundance to be included in any of the regression models. One explanation for this apparent lack of association is that the slope inclination was simply too small on most sites to result in biologically significant alteration of ground-level temperature and moisture regimes.

To explore this further, I examined the relationship between a more directly biologically meaningful parameter, the potential direct incident radiation, and slope inclination. Using values of slope, aspect, and latitude from FG quadrats, and the equations formulated by McCune and Keon (2002), I calculated the potential direct incident radiation (PDIR) for each quadrat. Next, I plotted the PDIR against slope inclination, and compared it with a histogram showing the number of quadrats in each five-degree class of slope inclination. This revealed a clear separation of quadrats into north and south-facing aspects, but only above a threshold slope of about five degrees (Figure 16b). This threshold coincides perfectly with the mode of quadrat frequency shown in the histogram, indicating that almost half of the quadrats sampled had inclinations of less than five degrees (Figure 16a).

These patterns are exactly what one would expect if the prevalence of slopes with small slope inclinations predisposed analyses towards failing to detect an association between aspect and vegetation abundance. Accordingly, I may conclude that aspect exerts little influence on the ground-layer thermal operating environment for understory species when slope inclination is less than five degrees, and therefore exerts little influence in my sampling quadrats; future investigations into the role of slope inclination (at least in north-central B.C.) should bias their sampling designs towards slopes of more than five degrees.

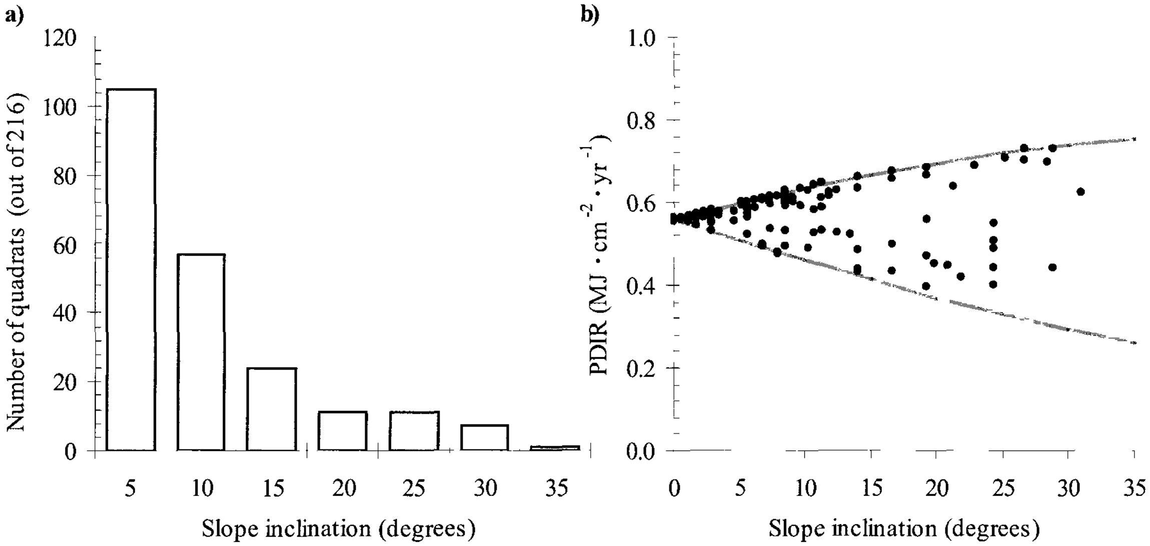

**Figure 16.** (a) Histogram showing the number of quadrats for increasing five-degree classes of slope-inclination, and (b) scatter-plot showing the influence of slope inclination on potential direct incident radiation with maxima (SW-facing aspects) and minima (N-facing aspects) depicted respectively by upper and lower gray lines.

#### 2.5.1.2. Biotic (canopy) influence

Biotic component one (b1) from all three functional group PCAs was positively correlated with leaf area index, duff (LFH) thickness, drip-zone indices, and local basal area, but negatively correlated with measures of light, indicating that it represents a gradient of generalized canopy closure similar to that examined in many previous studies of lichen-rich forest succession (Carroll and Bliss 1982, Brown et al. 2000, Coxson and Marsh 2001, Bainbridge and Strong 2005, Uotila et al. 2005). Further agreement with these studies is demonstrated by the signs of association between generalized canopy closure and functional group abundance, the negative association with lichen abundance, and the positive associations with feathermoss and vascular plant abundance. The presence of this generalized canopy closure gradient in all PC regression models, despite inclusion of other components, supports the idea that the forest canopy itself may be an important environmental determinant of understory composition.

Generalized canopy closure influenced the feathermoss model most strongly, where it was more than twice as influential in the model as any other variable. The feathermoss-canopy closure association was further supported by the ANOVA results, in which feathermoss patches had conspicuously less light and more shade than other groups. The greater strength and consistency of association between feathermosses and canopy variables was somewhat surprising, since the lichen functional group was hypothesized to be most closely aligned with the amount of light that penetrated the forest canopy. Although lichens did associate with canopy cover in the opposite way from feathermosses, the lack of an overridingly strong association with estimates of irradiance suggests that light itself is not a strong limiting factor in these communities. Rather, the measures of canopy closure examined here may be more indicative of moisture stress than of light limitation, a conclusion that supports initial hypotheses regarding the predominance of moisture gradients in determining feathermoss niche space.

Many mat-forming lichens are relatively desiccation tolerant, a trait that may be advantageous by allowing them to occupy locations that are stressful to other groups. Nevertheless, their photosynthetically active period (and resulting growth rate) may be prolonged by altering their morphology and patch structure to conserve moisture (Kershaw 1985), or by preferentially occupying locations with afternoon shade caused by variable topography (Kidron 2005). This is because most mat-forming lichens associate with chlorophytes (green algae) as their photobiont, thereby allowing them to photosynthesize with relatively low levels of thallus hydration (Kershaw 1985, Nash 1996). Although a slope-aspect influence was not detected, lichen patches had consistently lower dripzone or canopy cover index scores than other patch types. Hence, the local orientation or spatial distribution of canopy trees may have a similar influence to that of slope-aspect.

More specifically, lichen patches tended to score significantly lower than other patch types on the SWCC and CRDZ indices. The lower scores on SWCC indicate that lichens are less likely to dominate leeward patches with afternoon shade than other functional groups, and the lower scores from CRDZ indicate that lichens are unlikley to dominate locations directly under the crown-radius projection of canopy trees. Since vascular plants and feathermosses had higher SWCC scores, it is possible that these groups are more sensitive to the thermal stress of locations with greater solar exposure in the afternoon, whereas lichens are more tolerant. The negative association shown by both lichens and feathermosses with CRDZ is both intuitive and supported by previous observations; the combination of high litter-fall rates and precipitation interception in patches close to the tree-bole inhibit feathermoss and lichen growth because of their slow growth rates, whereas vascular plants can grow faster and therefore become dominant (Bonan and Shugart 1989).

Component $b5_{\text{vascular}}$ reinforced these associations in the vascular PC regression; plant abundance was positively associated with patches outside of the dry / high-LFH thickness zone with greater afternoon shade (Figure 17). The positive association between vascular plant abundance and $b6_{\text{vascular}}$ similarly indicated that high SWCC and WInDZ scores were positively associated with vascular plant abundance, but also that high CRDZ could be a negative influence. The negative influence of CRDZ is probably specific to plots with exceptionally high litter deposition, or species-specific negative responses to the dry conditions (as implicated by their additional preference for locations with greater afternoon shade). Certain species of vascular plants in particular (e.g., *Cornus canadensis*) were infrequently seen within the heavy litterfall zone around tree bases.

On the other hand, it seems unlikely that all or even most vascular-plant relationships with local gradients of canopy influence were mediated through water relations, because most of the vascular species examined are mycorrhizal (see Appendix A) and should be able to obtain moisture from adjacent soils if direct deposition is limited under a crown radius projection. Rather, the higher vascular patch scores for CRDZ and SWCC, combined with their positive association with direct irradiance and LFH thickness, indicates that vascular plants are most dominant or abundant in locations where exposure to direct irradiance is high but afternoon heat stress is low due to afternoon shade (high SWCC or CRDZ) or thermal buffering (high LFH). Another mechanism of association for vascular plants and canopy cover may be increased nutrient availability of patches that are in close proximity to canopy trees (Moore 1980), though this should have been accounted for by chemical PCs.

**Figure 17.** North-facing photograph (by author) from Site 27, showing a strong inhibition of lichen growth near canopy trees. Note the vascular plant growth in these areas where lichens appear to be inhibited, and the non-symmetric (right-skewed) distribution of litter around the base of trees.

#### 2.5.1.3. Soil chemistry

Results agreed with hypotheses regarding associations among FG types and nutrient availability, as vascular plant patches had consistently greater availability of most soil macro- and micronutrients than other quadrats. In many instances, these associations were further supported by multiple regression and PCA regression results, where lichen abundance negatively associated with many of the same nutrients that vascular plants positively associated with, particularly for more abundant macronutrients.

That calcium, magnesium, and potassium are the most available cationic nutrients in the soils of the study area agrees well with other studies of high-altitude or high-latitude environments (Darmody et al. 2004, Hamel et al. 2004, Lemarche et al. 2004). One or more of these three nutrients (Ca, K, or Mg) had the strongest influences on each multiple regression model, and they were often strongly associated with the principal components used in PC regression models, and often increased opposite to metals such as aluminum and iron. For the most part, these associations were consistent for each functional group using both regression model types; calcium availability was negatively associated with lichen and feathermoss abundance, and magnesium availability was positively associated with both feathermoss and vascular plant abundance. All three basic cations were positively associated with vascular plant dominance.

It was interesting that vascular plants were positively associated with magnesium availability in the multiple regression model, while the PC regression model did not use any chemical components. Yet, as mentioned in the results section, chemical components were present in other ‘good’ models for vascular plant abundance, and these models indicated a positive relationship between plant abundance and basic cation availability. Both the positive abundance-availability relationships and the association between high base cation availability and vascular plant dominance indicate that vascular plants are either creating or selecting for patches with more available base cations.

The low abundance of basic cations under lichen and feathermoss mats may be the result of slower nutrient cycling and decomposition (Moore 1984, Sedia and Ehrenfeld 2006). Nutrient cycling and decomposition tend to be slower under these functional groups, because of the high carbon to nitrogen ratio in moss and lichen litter, and their tendency to produce recalcitrant organic acids (Cole 1995, Sedia and Ehrenfeld 2006). In addition, microbial mineralization rates may be slowed due to the maintenance of cool or anaerobic soil under these mats (Bonan and Shugart 1989), and basic cations may be more easily lost because exchange sites are dominated by aluminum. Whether lichens or feathermosses actually cause increased aluminum availability is unknown, but the association has been documented in other studies (Darmody et al. 2004, Hamel et al. 2004). In contrast, most vascular plants tend to promote increased rates of nutrient cycling and decomposition (Kelly et al. 1998, Sedia and Ehrenfeld 2006). Nevertheless, the availability of many basic cations can also be highly dependent on the type of parent materials, in which case patterns of vascular plant abundance or dominance may be the result of pre-existing variation in soil chemistry (Cole 1995, Lemarche et al. 2004).

Phosphorus is known to be one of the most highly conserved nutrients in natural systems, and can be limiting to vascular plant growth both directly and through the limitation of soil mycorrhizae (Barber 1995, Smithwick et al. 2005, Vitousek et al. 2010). Phosphorus limitation may result from relatively greater abundance of other nutrients, such as nitrogen, which creates a greater biological demand for phosphorus (Wardle et al. 2004), and metallic micronutrients, which increase the amount of phosphorus that is unavailable (Giesler et al. 2002). Similarly, sulphur is often found to be a limiting factor for tree growth in northern

British Columbia, since it is primarily derived from organic sources, and because acidic soils cause inorganic sulphur to become strongly adsorbed, making it unavailable to plants (Sanborn et al. 2005).

Given that the ratio of mean nitrogen to phosphorus or sulphur availability ranged from 5.0 in lichen quadrats to 0.5 in vascular quadrats, nitrogen is probably more limiting than phosphorus or sulphur in the study area (Wardle et al. 2004). This would explain the lack of an influence from phosphorus or sulphur availability on vascular plant models, since they are less likely to be linearly associated with vegetation that they are not limiting for. Nevertheless, both phosphorus and sulphur tended to be more available in vascular-dominated patches than in feathermoss or lichen patches, indicating that some association exists. This greater abundance may result from the accumulation of organic sulphur and phosphorus from decomposing litter. Alternatively, lichen and feathermoss dominance may actually inhibit sulphur and phosphorus cycling in lichen and feathermoss patches, resulting in relatively higher availability in vascular plant patches.

Previous investigations have found that lichen mats tend to reduce rates of soil microbial decomposition and respiration, and generally increase carbon to nitrogen ratios due to their high N-use efficiency and temperature or moisture regulating properties (Bonan and Shugart 1989, Kershaw 1985, Sedia and Ehrenfeld 2005, Sedia and Ehrenfeld 2006). Other authors have suggested that mat-forming lichens can have an allelopathic influence on soil microbes or on other vegetation through the leaching of secondary metabolites into the soil or directly onto the other organisms (Cornelissen et al. 2007, Lawrey 1994, Nash 1996). Feathermosses produce several strongly chelating compounds, which can increase the availability of metallic compounds by displacing them from adsorption sites in mineral soil (Darmody et al. 2004, Nilsson and Wardle 2005, Turetsky 2003). Lichens are also known to produce a myriad of organic acid compounds, albeit mostly hydrophobic ones (Huneck 1999), which may have a similar effect. Although recent studies have shown that there is little evidence to support allelopathy as a mechanism as being functionally important in the field (Stark et al. 2002, Stark et al. 2007, Kytöviita and Stark 2009), chemical modification of the absorption complex may serve as another explanation for the low sulphur and phosphorus under lichen quadrats.

The negative associations between soil ammonium, iron, or magnesium availability and feathermoss abundance was surprising, since feathermosses were predicted to favour chemical conditions that would be unfavourable to vascular plants. There are three possible explanations for this phenomenon: 1) feathermosses are contributing to or causing the increased nutrient availability; 2) feathermosses are actually preferentially occupying these sites because they are actively taking up some soil nutrients; or 3) feathermosses are associating with vascular plants (which select for sites with greater nutrient availability) due to the microclimatic regulation the vascular plants provide.

It is has often been stated that feathermosses are more likely to reduce soil nutrient availability than increase it; potential mechanisms for this include mosses acting as a barrier to nutrient deposition (in crown leachate or rainfall), maintaining efficient internal recycling (Turetsky 2003), being able to quickly reabsorb nutrients lost to solution (Startsev and Leiffers 2006), having relatively slow decomposition of dead tissues (Sedia and Ehrenfeld 2005, Turetsky 2003), or by maintaining lower soil temperatures which inhibit microbial activity (Bonan 1990, Turetsky 2003). Yet, more recent research has shown that mosses, and feathermosses in particular, may actually increase nitrogen availability in ecosystems due to their association with nitrogen fixing cyanobacteria and their apparent utilization of nutrient enriched crown leachate solution (Turetsky 2003, Nilsson and Wardle 2005, Hart and Chen

2006, Houle et al. 2006). This is additionally supported by the observations that $NH_4^+$ and total N availability were significantly higher under feathermosses than under other functional groups. Under conditions where the soil is relatively well-drained, feathermoss mats may also provide resistance to evaporative stress of microbial communities, thereby increasing rates of decomposition and mineralization (Turetsky 2003, Sedia and Ehrenfeld 2005). It is also possible that feathermosses are leaching nutrients into the soil, since leaching of organic carbon and nitrogen (which can then benefit microbial communities) has already been observed for some species (Wilson and Coxson 1999, Turetsky 2003).

Some moss species can effectively take up nitrogen from the soil under laboratory conditions, but this was demonstrated using acrocarpous mosses that had direct contact between living tissue and the soil (Ayres et al. 2006). But this is an unlikely mechanism for feathermosses, which are pleurocarpous and tend to accumulate necromass faster than it is decomposed, resulting in a separation between living tissue and the soil surface. Indeed, even acrocarpous mosses use relatively more solution-dissolved nitrogen than soil nitrogen, indicating that leachate deposition may be a far more important source of nutrients (Ayres et al. 2006). It is unlikely that feathermosses are more abundant in some quadrats directly because of increased soil ammonium availability.

An indirect association with vascular plants via microclimatic regulation, and perhaps increased availability of nutrient-rich litter (Berendse 1998), seems most likely. Although this is not necessarily true for all vascular plants, some common species are known to associate with feathermosses at the patch scale, such as *Cornus canadensis*, *Shepherdia canadensis*, *Ledum groenlandicum*, and some *Vaccinium* species (Figure 18). In addition, *Vaccinium* species exhibit relatively fast decomposition and nutrient release rates (Wardle et al. 2003), which may further benefit feathermoss mats when the litter is deposited on top of them. Larger and early colonizing (shrubby) vascular species in particular, such as *Shepherdia canadensis*, may provide long-term microclimatic regulation for bryophytes at a patch scale, thereby allowing them to establish and proliferate.

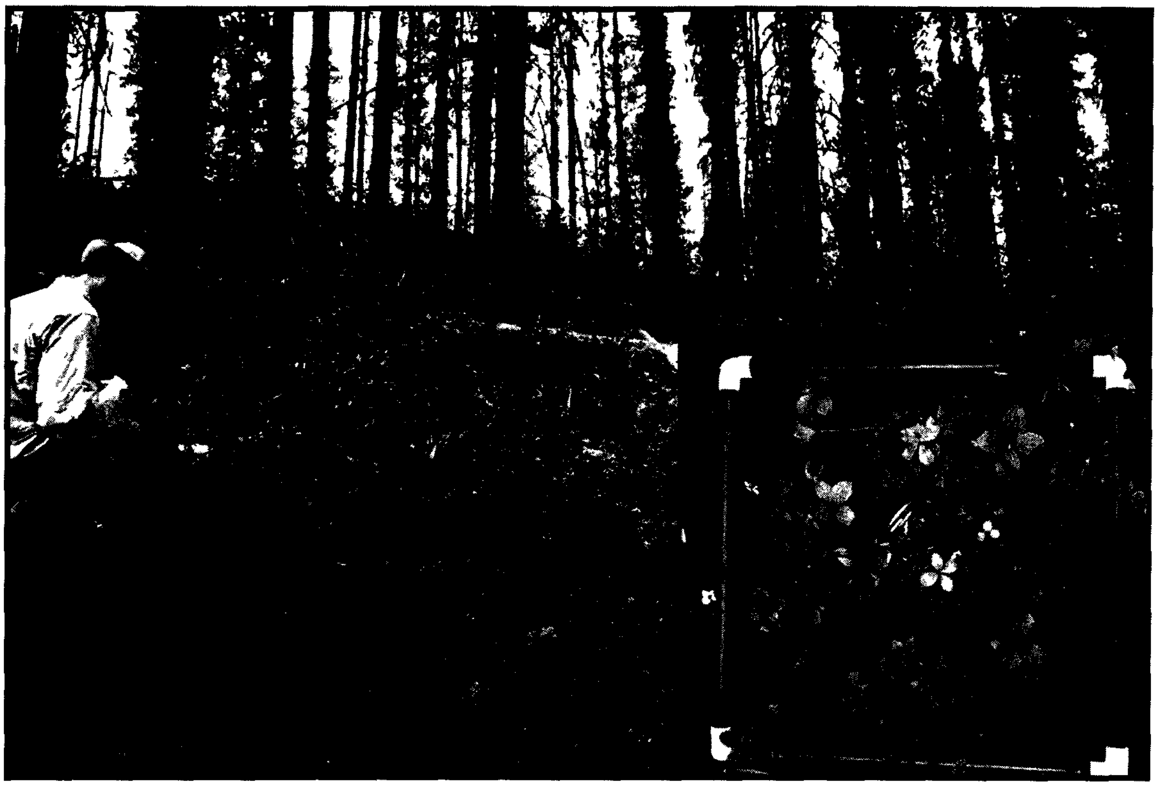

**Figure 18.** Plot and quadrat (inset) level photos demonstrating positive associations between feathermosses and vascular plants. In the plot photo, the observer is sitting in a thicket of *Shepherdia canadensis* while examining a feathermoss plot; the feathermoss quadrat photo shows *Cornus canadensis*, *Vaccinium membranaceum*, and *Ledum groenlandicum* growing with *Pleurozium schreberi.*

One must then ask, why did vascular plants not also associate with greater nitrogen availability? Indeed, both vascular plant abundance and dominance were negatively associated with total nitrogen and ammonium availability, while the abundance of lichens and feathermosses were both positively associated with it. This is probably an artefact of the time of year in which samples were taken: since the majority of plant growth occurs during spring and early summer, it is likely that patches occupied by vascular plants would be depleted of nitrogen to a greater extent than other functional groups. Patches dominated more completely by lichens or feathermosses tend to have fewer vascular plants, and are therefore less depleted of nitrogen in mid to late summer. These patterns also indicate that vascular plants are more limited by nitrogen than other nutrients.

### 2.5.2. Methodological limitations

Interestingly, the biotic variable subset was the only one for which the first principal component contributed significantly to functional group abundance models. None of the chemical components for any functional group type represented more than 14% of the total variance from their respective PCAs, yet chemical components were present in two of the three models. Even more impressive was the significant influence from $a6_{\text{vascular}}$, which only represented approximately 4% of the variance in abiotic variables for that patch type. These observations agree with those of Joliffe (1982) and Graham (2003), who found that even low-eigenvalue components could be relevant. Indeed, if not for the inclusion of low-eigenvalue components, the interaction between LFH thickness and soil texture would not have been detected.

Although some may argue that a linear species response to environmental variables (as is implicit in PCA and multiple regression) is ecologically unrealistic, there is also an emerging realization that traditional parabolic models of niche space can be even more unrealistic, at least as far as their relevance for the range of environmental variability examined in most ecological field studies (Kenkel 2006, Yee 2006). Most field studies fail to incorporate enough environmental variability to adequately represent the entire distribution of all species or functional groups detected; a study that seeks to do so for more than two functional groups of species would have to be impossibly extensive. To emphasize this point, consider the response of lichen and feathermoss abundance to stand age in Figure 3. Lichen abundance shows a unimodal relationship to stand age, while feathermoss abundance seems to exhibit a sigmoidal response. If we examined only a narrow portion of the stand age gradient, say, those sites between 100 and 200 years old, the responses would appear to be linear, making techniques that assume linear relationships preferable. Furthermore, the purpose of this study was to highlight the within-stand ecological niches of each functional group, rather than documenting the rise and fall of successional stages, making analytical methods based on measures of linear association more appropriate.

Although the traditional approach to variable-reduction by PCA is to perform a single PCA on all variables at the same time, Beals (2006) has demonstrated that this multiple subset reduction technique is appropriate for examining the relative contributions of different types of variables, as well as the overall contributions of individual variables in multiple regression analysis. Beals (2006) used non-metric multidimensional scaling (NMS) for her analysis, but ended up with low $R^2$ values for the models (mostly $<0.20$), and attributed this to problems with the data. However, after brief experimentation with Beals' (2006) method, I found that automated NMS tended to select a very small number of axes (usually just 1-2 axes from many variables) resulting in abstract latent variables that were difficult to interpret. In addition, NMS axes tended to represent too many of the original variables at once, so that the strong positive influence of one was often diluted by the negative influence of another. Principal components analysis has been commonly used with multiple regression in the past (e.g., Graham 2003), and may be better suited to use with multiple regression than NMS because it results in as many axes as there are original variables, and recombines only variables that are linearly related and relatively easy to interpret.

### 2.5.3. Summary and Conclusions

Of all functional groups in the understory, the abundance and dominance of feathermosses seemed to be most strongly and exclusively associated with canopy influence.

Overall, feathermoss dominance and abundance are strongly associated with locations just outside of the dry, high litter-fall zone directly under tree crowns, especially those on the north sides of trees that have greater shade throughout the day. Similarly, lichens are positively associated with locations outside of the high litter-fall zones directly around trees. Lichens differ from feathermosses, however, in that they also associated positively with patches that had greater southern exposure. These observations supported initial hypotheses that lichens would associate with patches under high light conditions, while feathermosses associated with patches that had lower light and, therefore, higher conservation of moisture.

In contrast, vascular plants positively associated with zones of high litter input, especially those that were most exposed to high light conditions. Both this association, and the more direct associations with measures of nutrient availability, indicate that nutrient availability is closely linked to dominance and abundance of vascular plants. Indeed, greater quantities of most macronutrients were detected in the soils of vascular plant quadrats. Of particular interest was the significantly greater availability of calcium (and indeed, most basic cations) in vascular plant quadrats, because it showed significant negative associations with both feathermoss and lichen abundance.

That many of the nutrients shown to positively associate with vascular plant dominance had negative associations with feathermosses or lichens seems to support the hypothesis that non-vascular functional groups may be prevented from dominating a location with high nutrient availability due to competition from vascular plants, although it is also likely that vascular plants enhance the nutrient availability of plots they occupy through litter deposition. Suppression of soil nutrient cycling by mosses and lichens is also a possible explanation for these results.

The patch-level focus of this study conferred several advantages over more traditional stand-level studies. First of all, doing so allowed for the examination of local canopy influences, which are ordinarily obscured by the large-scale measurement of a net influence. This showed that the canopy can have both a positive and a negative influence on understory vegetation, and that this influence is both guild-specific and spatially explicit. Secondly, while it fell short of conclusively demonstrating the mechanism of association, it was more conducive to theoretical discussion of potential mechanisms of understory interaction than stand-level analyses, which tend to focus on succession of the entire ecosystem. Last, it allowed for the assessment of the relative importance of biological, soil chemical, and abiotic or physical properties in the patch-dynamics of these systems, because using such a small sampling quadrat allowed for more precise measurement of the variation that is associated with different functional groups at the scale of the individual, variation that is normally obscured by focus on the forest stand.

# 3. Plot-level compositional and environmental associations among understory species and functional groups in north-central British Columbia

## 3.1. Abstract

Much of the past research on lichen-rich forests has focused on analyzing stand-level patterns of dominance and abundance in the understory, but has often limited the breadth to a small number of stand types, rather than examining the variation within a large selection of stands. In addition, the concepts of competition or environmental regulation of species composition in the understory are often invoked without explicitly testing for the mechanisms by which understory composition is influenced. Here I present a description of the associations between understory composition and environmental variation at the stand scale, coupled with descriptions of associations among understory functional groups themselves, from pine-lichen forests of north-central British Columbia. Using a combination of multiple linear regression, ordination, and principal component regression techniques, I detected two primary compositional gradients: one that was dominated by lichens at one end and feathermosses at the other, and a second that represented variation in vascular plant species. These gradients were primarily related to patterns of forest canopy structure, base-cation or metal availability in the soil, and soil acidity, with less of the variation attributed to soil texture and topography. Vascular plants, mat-forming lichens, and feathermosses occupy approximately equal proportions of the understory in these forests, suggesting similar contributions to ecosystem function, but patterns of group association suggest that competition among mat-forming lichens, feathermosses, and vascular plants may be relatively unimportant. Future studies of lichen-rich forests should give greater consideration to understory vascular plant function and soil properties.

## 3.2. Introduction

Edaphic factors can influence whether an understory-species assemblage qualifies as 'lichen-rich', and in many cases, researchers have examined and described soil properties that coincide with a particular type of lichen-rich community (Lechowicz and Adams 1974, Johnson 1981, Carroll and Bliss 1982, Morneau and Payette 1989, Ahti and Oksanen 1990, Sulyma and Coxson 2001, Girard 2009). Yet few have considered it useful to examine whether edaphic properties vary continuously with understory composition (but see Pharo and Vitt 2000). Broad categorical approaches in ecology are not uncommon, due to the widespread perception that ecosystems are too complex to be accurately represented as a sum of their parts. This belief is certainly true when sample sizes, measurement accuracy, and the breadth of measured variables are limited, in which case a generalized ecosystem comparison may indeed be more appropriate, but it does not countermand the potentially valuable insights about specific mechanisms of interaction, nor does it the help to focus future investigations on those aspects that are most relevant (Mikkelson 2001). Rather, a phenomenological approach, without mind to the potential mechanisms that underlay the system, becomes a self-perpetuating argument *ad-infinitum*, and though truthful, cannot be extrapolated to phenomena that occur outside of the system (Levin 1992).

The widely observed decline in the abundance of terrestrial lichens during boreal-forest succession is often attributed to competition with faster-growing species, such as feathermosses or vascular plants, as the canopy closes and the understory becomes more shaded (Oksanen 1986, Ahti and Oksanen 1990, Crittenden 2000, Sulyma and Coxson 2001). Strong support for this theory has primarily been either through documenting compositional associations observed in chronosequences (Ahti and Hepburn 1967, Kershaw 1977, Morneau and Payette 1989, Coxson and Marsh 2001), or through short-term observations of dramatic compositional changes that are initiated following disturbance or experimental manipulation (Vagts and Kinder 1999, Skrindo and Økland 2002, Sedia and Ehrenfeld 2003, Williston et al. 2006). These two methods have implicitly different scales of observation; the former is focused on the stand or plot scale (but see Sulyma and Coxson 2001), while the latter is on the microsite or lichen patch scale. The latter approach is best supported by plant-strategy theory; the neighbourhood-patch, centred on individual organisms, is most appropriate for examination of competition (Silander and Pacala 1985, Tilman 1988), and even studies of population dynamics should be based on these smaller scales (Burton 1993).

A less common approach to studying competition in lichen-rich systems is the association-based approach for study of potential interactions (Pharo and Vitt 2000, Williston et al. 2006). In this method, one examines the negative or positive association (by correlation or linear regression) between two species or groups that are measured in a series of quadrats, and thereby infer a potential interaction type. Strong negative correlations or regression slopes may indicate competition, while positive ones may indicate facilitation. Note that the qualifier 'potential' is important in describing the application of this technique, as the abundance of two species or groups from the same set of plots is never statistically independent. The method can nevertheless be useful in highlighting potential interactions, because, among others, a 'potential' explanation for one species occupying or not occupying a proportion of that plot is that another observed species out-competed it, and the current distribution is simply a snapshot of results of that competitive process in a single time slice. Of course, there is nothing to necessarily indicate that either species formerly occupied more than its currently occupied space, so the application of such methods should be limited to situations in which there exists previous empirical support for such interactions occurring, and for which a logical argument can be made, considering the biology of each species or species group being considered. Ideally, one would follow this type of analysis with reciprocal-transplant or greenhouse-competition experiments, to observe and evaluate competitive processes over time.

Nevertheless, much of the available literature on lichen-rich forests indicates that important ecological interactions do indeed occur at the stand scale (Ahti and Hepburn 1967, Kershaw 1977, Morneau and Payette 1989, Coxson and Marsh 2001). These stand-to-stand differences are commonly described in terms of stand age or disturbance history, tree-layer composition, stem basal area or volume, canopy closure, stem density and the size structure of trees. Furthermore, the stand scale is socially relevant because data are most commonly collected at the stand scale during study of vegetation in managed (timber-producing) forests, and biologically relevant because many stands develop as a single ecological unit (initiated by large-scale disturbances), or because stand-level units are managed for wildlife (Pegau 1968, Kumpula et al. 2004, Bainbridge and Strong 2005).

In order to address the potential importance of large-scale variation, to make this study more comparable to others, and to more accurately depict the compositional variation within the forest understory of the study area, it was necessary to conduct a plot-scale analysis of vegetation-environment associations using randomly located quadrats. Because examination of compositional variation required the use of random sampling, this also provided an opportunity to examine the potential interactions among functional groups, via measures of association. Using randomly selected quadrats from the plots described in Chapter 2, this chapter will address the following questions: 1) what is the composition of an 'average' plot understory for the study area; 2) Are compositional patterns more strongly related to edaphic factors than to biotic factors such as canopy closure at the plot level; and

3) are there patterns of association / dissociation that may indicate interactions among the functional groups themselves?

Given the emphasis on lichens and mosses (and the lack of emphasis on vascular plants) in the ecological literature from lichen-rich forests (Ahti and Oksanen 1990), I expected that the average plot understory would be dominated by lichens or feathermosses, with a smaller component of vascular plants. In the terminology of Grime (1998), lichens and feathermosses are expected to be the 'subordinates' of these forest communities, while vascular plants are 'transients'. Similarly, the emphasis by other researchers on describing soil characteristics (despite the lack of quantitative analyses on them), and the recognition that only edaphically "poor" sites will become lichen-rich forests, suggests that edaphic factors will likely be significantly related to understory composition at the stand level (Lechowicz and Adams 1974, Johnson 1981, Carroll and Bliss 1982, Ahti and Oksanen 1990, Coxson and Marsh 2001). Although the *a-priori* selection of sites that are dominated by lodgepole pine would reduce the breadth of variation in edaphic properties, the sites are sufficiently variable biologically that they are likely to also have sufficient environmental variation for such an analysis. Based on the results from Chapter 2, I put forward the same hypotheses to be tested at a larger (plot) scale: 1) that coarser, and more nutrient-poor or acidic soils should favour lichens; 2) soils with greater nutrient availability will favour vascular plants; and 3) soils with greater moisture retention will favour feathermosses.

I also expected that, at the quadrat scale, each of the three functional groups will show negative and important associations with the other two. Given the historic emphasis on successional trajectories moving from lichen to feathermoss dominance in these systems (Kershaw 1977, Sulyma and Coxson 2001), the negative association should be strongest between lichens and feathermosses, followed by lichens and vascular plants. The association between vascular plants and feathermosses will be weaker, since several vascular species may facilitate or be facilitated by feathermosses.

## 3.3. Methods

See Chapter two for a complete review of the study area and data collection protocols. For brevity, this section will only outline additional analytical methods used for the plot-level analysis of associations among species groups and their environment, but brief clarification of the two scales of investigation used for analysis of random quadrats in this chapter is necessary. Specifically, the data used for observational analysis of potential inter-functional group competition are from individual 0.25-m$^2$ random quadrats, of which there were three per 100-m$^2$ plot, for a total of 216 quadrats in 72 plots. The analysis of vegetation-environment relationships was conducted using plot-scale averages of species abundance in random quadrats, as well as canopy-tree and topographical environmental variables that were recorded at the plot scale, for a total of 72 plots.

I also used the mean values of several variables from the non-random functional group quadrats in these analyses (Chapter 2), but only if those variables showed considerably more variation among sites than within plots, and only if they showed evidence of spatial autocorrelation within plots. Ideally, the same variables would have been recorded for both quadrat types, but this would have been prohibitively expensive. By ensuring that variables used in plot-level analyses were autocorrelated at within-plot scales, the potential bias from non-random sampling was limited, and variables could be assumed to consistently represent their plot. Table 6 provides descriptions of all variables used in this analysis.

Variables recorded at the plot level included slope, aspect, basal area, and crown depth (Table 6), as well as the density of seedlings and saplings. Canopy-tree species richness and the proportion of trees in different decay classes or size classes were also recorded at the plot level, but were not included in the following summaries due to being relatively invariant across plots. Tree height was not included in subsequent analyses due to highly non-normal distributions making it unamenable to transformation.

**Table 6.** Variables used in plot-level regression models of species composition.

| Variable | Description | Source |
|---|---|---|
| Total N | sum of available inorganic nitrogen forms ($NO_3 + NH_4$) | PRS$^{TM}$ probes |
| $NO_3$ | nitrate availability | PRS$^{TM}$ probes |
| $NH_4$ | ammonium availability | PRS$^{TM}$ probes |
| Ca | calcium availability | PRS$^{TM}$ probes |
| Mg | magnesium availability | PRS$^{TM}$ probes |
| K | potassium availability | PRS$^{TM}$ probes |
| P | phosphorus availability | PRS$^{TM}$ probes |
| Fe | iron availability | PRS$^{TM}$ probes |
| Mn | manganese availability | PRS$^{TM}$ probes |
| Zn | zinc availability | PRS$^{TM}$ probes |
| B | boron availability | PRS$^{TM}$ probes |
| S | sulphur availability | PRS$^{TM}$ probes |
| Al | aluminum availability | PRS$^{TM}$ probes |
| pH | acidity / alkalinity | Soil sample |
| CoarFrag | % soil sample with particles >75 mm | Soil sample |
| Gravel | % soil sample with particles 2 - 75 mm | Soil sample |
| Fines | % soil sample with particles <2 mm | Soil sample |
| Sand | % soil sample with particles 0.05 - 2 mm | Soil sample |
| Silt+Clay | % soil sample with particles <0.05 mm | Soil sample |
| Slope | slope inclination, in degrees | On site measurement |
| N-aspect | cosine transformed aspect, or Northness | On site measurement |
| Mesotopo | index of topographic position, from depression to hill crest | On site measurement |
| LAI* | effective leaf area index | Modeled |
| Total irrad. | total transmitted light (irradiance) under the forest canopy | Modeled |
| Diffuse | potential transmitted diffuse light (under forest canopy) | Modeled |
| Direct | potential transmitted direct light (under forest canopy) | Modeled |
| LFH | combined depth of litter, fermentation, and humus layers | On site measurement |
| CD | average crown depth of canopy trees in plot | On site measurement |
| BA | canopy tree basal area ($m^2$ per ha), from DBH measurements of all trees in plot | On site measurement |
| Age | stand age, mean of three increment cores of dominant canopy trees per plot | On site measurement |
| Seedlings | number of individual seedlings in 3.99 m plot | On site measurement |
| Saplings | number of individual saplings in 3.99 m plot | On site measurement |

* Note: Gap Light Analyzer estimates of leaf area index include vegetation stems, and are therefore more equivalent to effective leaf area index (Frazer et al. 2000); GLA estimates of irradiance do not account for levels of cloudiness, and are therefore more representative of potential maximum transmitted direct irradiance, and minimum transmitted diffuse irradiance. See Frazer et al. (1999) for details on GLA software.

### 3.3.1. Ordinating and modelling stand-level functional group abundance

Ordination with non-metric multidimensional scaling (NMS) is considered one of the best methods for analysis of ecological community data, especially when dealing with large numbers of species and abundance measures, and is an excellent tool for highlighting species compositional gradients (McCune and Grace 2002, Avella and Covington 2006, Beals 2006, Salemaa et al. 2008). I averaged the abundance of species within each plot and analyzed species composition using NMS, then plotted the results on an ordination diagram to display compositional patterns. The species scores (calculated by weighted averaging) and correlation coefficients between NMS axes and principal components or environmental variables were overlaid on the ordination diagrams, to highlight the species and habitat associations of each compositional gradient. In addition, NMS axis scores were treated as dependent variables in subsequent principal component regression models with the same suite of environmental variable principal components as independent variables. Non-metric multidimensional scaling was performed using the Sorenson (Bray-Curtis) distance measure, random starting coordinates, 40 runs with real data, a Monte-Carlo test based on 400 runs to assess the probability of obtaining a similar level of stress (an inverse measure of goodness of fit) in the result by chance, and an instability criterion of 0.00001 (the standard deviation of stress from preceding iterations).

I examined environmental data for the random quadrats for linearity and normality, and transformed or standardized where necessary, using logarithmic or exponential transformations (Kenkel 2006). Variables were grouped into the same three subsets used in chapter two: abiotic, biotic, and soil chemical variables. I performed a correlation matrix-based principal components analysis (PCA) for each variable subset, and components were named sequentially based on the variable category to which they belonged. For example, components chem 1, chem 2, chem 3, etc. were the first, second, and third principal components from the PCA of soil chemical variables (nutrient availability and pH).

Topographic and soil texture variables were labelled as abiotic, and variables relating to canopy properties or litter deposition were labelled as biotic.

A common approach with PCA is to interpret only those components that have eigenvalues lower than a specific threshold (the value 1.0 is commonly used, as it indicates that the PC explains more variance than a single input variable would); however, as Joliffe (1982) pointed out, small eigenvalue components may contain biologically significant information. I therefore treated all components as potentially valuable in subsequent regression models.

I used linear multiple regression to examine the associations between species compositional gradients (NMS axes) and either the original environmental variables or the principal components, using the approach described by McCune and Grace (2002). The two methods were used because they are complimentary; regression using the original environmental variables is easier to interpret, though it may have lower explanatory power because of limitations relating to the necessity of removing highly correlated variables (despite their potential relevance to the responding variable), and because gradient interpretation is constrained to what was measured, with all the same limitations as the measurement tools used therein. Regression with principal components can be more difficult to interpret ecologically, but will be less likely to suffer from multicollinearity and may highlight environmental associations that were not explicitly measured, or that represent multiple environmental variables, which together form an important environmental gradient.

Model selection was made using Schwarz's Bayesian Criterion scores (SBC; Schwarz 1978, SAS Institute 2010), which were calculated for all possible models with less than seven variables, and used to rank the models from most to least parsimonious. Because the study goals are descriptive, and an all-subsets technique is computationally intensive, no model averaging was used to create a “true” model. Rather, I focused analyses on the best model (lowest SBC score), and subsequently examined other top 10 models from each combination of dependent (NMS axes) and independent (principal components or measured) variables. I used criteria such as standardized parameter estimates (a.k.a. standardized beta-coefficients, or $\beta_s$), adjusted-$R^2$ values, and residual normality to assess the relative strength of association between understory composition and abiotic, biotic, and chemical attributes.

Non-metric multidimensional scaling was conducted using PC-ORD (McCune and Mefford 1999), while multiple regression and principal components analyses were conducted using SAS v. 9.2 (SAS Institute 2010).

### 3.3.2. Functional group associations

The random quadrats were also used to examine the nature of potential interactions among the three functional group types. By examining how the abundance of each group changes in relation to the others, I was able to gain insight into the possible importance and intensity of associations among them. I modelled the abundance of each group as a function of the two others, and interpreted the resulting fit statistics in a similar fashion to the ‘size distance-regression’ technique used by Weldon and Slauson (1986), where the slope of the line indicates the intensity of competition, while the $R^2$ value indicates the importance. Random quadrats that contained fewer than two functional groups were omitted from the analysis, and analyses were performed with graphical functions in Microsoft Excel 2003.

## 3.4. Results

### 3.4.1. Characterization of vegetation in the study area

Stand ages ranged from 45 years to 191 years old, with a mean age of 130 ± 4 (mean ± SE) years. Canopy tree height averaged 14.4 ± 0.4 m, and basal area averaged 33.1 ± 1.7

$m^2 \cdot ha^{-1}$. The understory was characterized by approximately equal proportions of vascular plants, mat-forming lichens, and feathermosses (12 - 14%), and almost half (49%) of the ground area was occupied by litter (Figure 19).

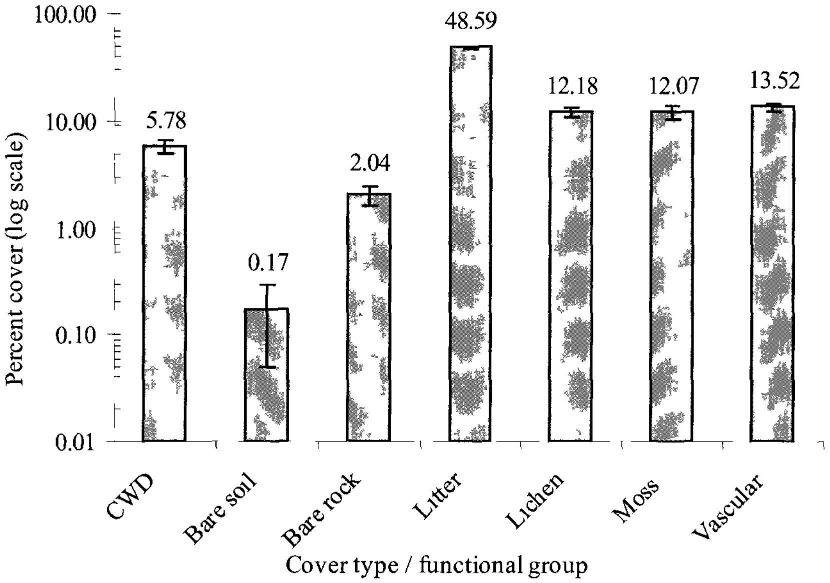

**Figure 19.** Study-wide mean (± SE) plot-level abundance (% - cover) of abiotic cover types and functional groups, as estimated from the average of each cover type in each plot (n = 72). A log-scale was used to increase the comparability among cover types, which varied widely in ground coverage.

### 3.4.2. Species composition and environment

#### *3.4.2.1.* Species composition with NMS

The NMS analysis of species composition resulted in a final configuration with two axes; after 122 iterations, the final stress was 16.74 and the final instability was 0.00001. The first axis explained 12.3 % of the variance in species composition, while the second explained 69.3 %, for a combined total of 81.6 % of the variance explained*. The axes were 99.3 % orthogonal, indicating that they represent two very different gradients of species composition. Mat-forming lichens showed distinct clustering, had a strong positive

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* Unlike PCA, NMS axes are constructed simultaneously, and the numbering is arbitrary; axis number does not relate to the percent of variance explained, axis importance, etc. (McCune and Grace 2002).

association with axis two, and had a weakly negative association with axis one (Figure 20a). Feathermosses showed slightly more diffuse clustering and the opposite relationship with axis two, but greater variation along axis one (Figure 20a). Vascular plants occupied much of the space between feathermosses and lichens along axis two, but showed substantial overlap with feathermosses and none with mat-forming lichens, and had considerably more variation along axis one than either of the other functional groups (Figure 20a).

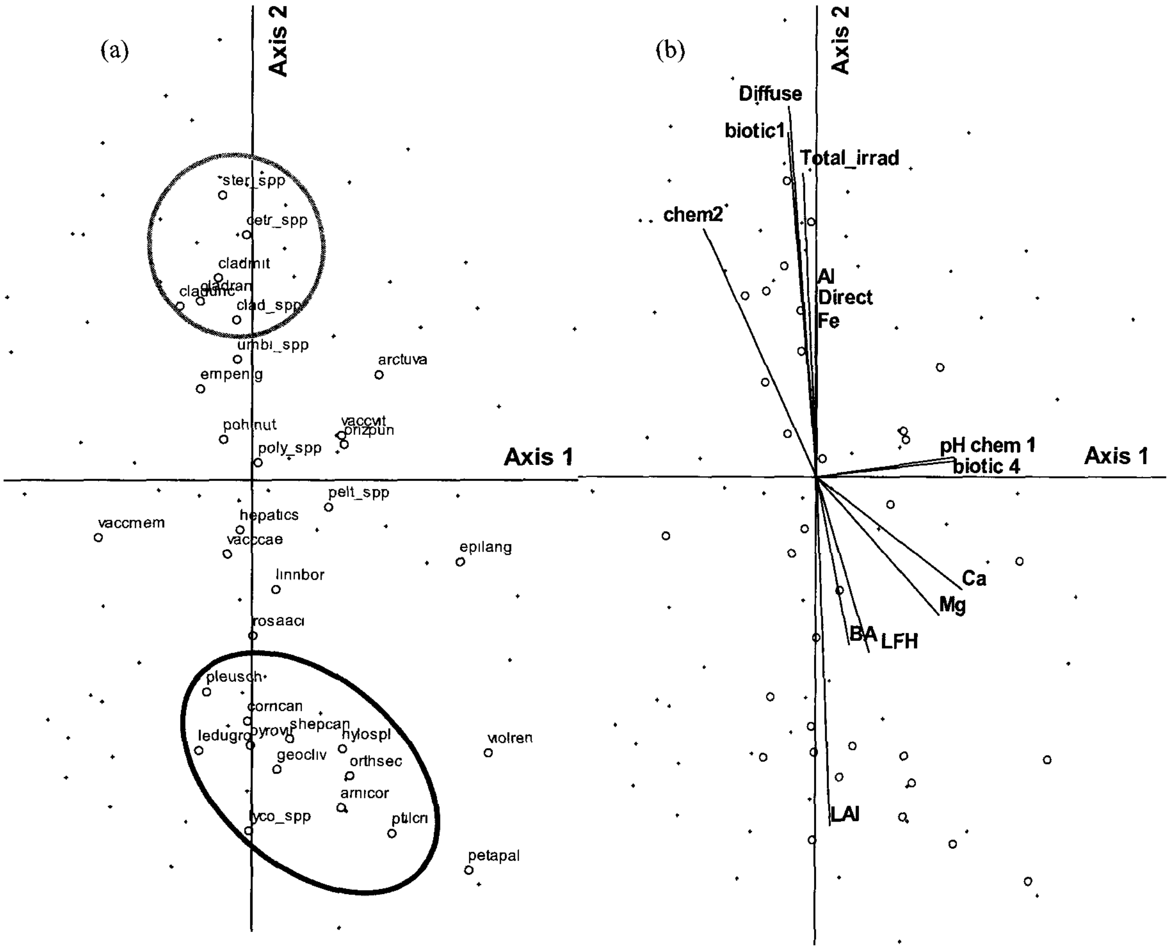

**Figure 20.** NMS ordination diagrams based on plot-level species abundance from random quadrats, overlaid by: (a) species scores, depicted as open circles with four-letter species codes (e.g., vaccmem is *Vaccinium membranaceum*), with feathermosses (as well as several vascular plants) circled in green, and mat-forming lichens circled in lavender; or (b) vectors representing correlations with environmental variables and the principal components derived from environmental variables. Only those environmental variables and PCs with squared Pearson's r of >0.20 are presented. Vectors (in red) are scaled to 150% to reduce clutter in the diagram.

Overlays of environmental variables and principal components (PCs) revealed the most obvious environment-composition association to be one of canopy openness (light) and axis two, as shown by the strength of the axis correlations with biotic component 1, as well as with the biotic environmental variables themselves (Figure 20b). This gradient ran parallel to the compositional gradient from feathermosses to lichens, such that lichens were positively associated with high light levels, while feathermosses were positively associated with canopy closure.

The second strongest environment-composition association was between base-cation deficiency (chem 2) and both NMS axes; base-cation deficiency was negatively related to axis one and positively related to axis two. Axis two also showed strong positive associations with the original environmental variables that loaded most negatively on chem 2, namely magnesium and calcium availability, and pH. Compared to other functional groups, lichens had a strong positive association with base cation deficiency, while vascular plants ranged from a weak positive to a strong negative association, and feathermosses showed a moderate to strong negative association (Figure 20b).

Complete listings of species scores and correlations among NMS axes and environmental variables or principal components can be found in Appendix F. Within the lichen group, *Stereocaulon* and *Cetraria* species appeared to prefer the most well-lit and nutrient-poor conditions, while *Cladonia* spp. were slightly weaker in this regard. Among the vascular plants, both *Empetrum nigrum* and *Arctostaphylos uva-ursi*, and to a lesser extent all dwarf shrubs, associated most positively with habitat that is almost as open as the lichen group does. Dwarf shrubs were separated primarily by their associations with pH: *A. uva-ursi* associated positively with less acidic conditions and *Vaccinium membranaceum* associated positively with more acidic conditions, while other species were intermediate.

Not surprisingly, the vascular plant species that showed similar associations to feathermosses included *Shepherdia canadensis*, *Cornus canadensis*, and *Ledum groenlandicum*, all species that are known to be more abundant on mesic sites in boreal conifer forests (Delong 2004). Although feathermoss species were all relatively strongly associated with high canopy closure, they differentiated somewhat on a line parallel to that of the base-cation deficiency gradient, such that *Pleurozium schreberi* occupied the most and *Ptilium crista-castrensis* the least base-cation deficient soils.

Out of all individual nutrients examined in this study, aluminum availability showed the strongest association with any of the compositional gradients represented by the NMS axes. Specifically, it showed a strong positive association with axis 2, the compositional axis representing a feathermoss or vascular plant to lichen gradient.

#### 3.4.2.2. Multiple regression with environmental variables

Independent-variable coefficients in the best regression models were all significantly different from zero and had acceptably small variance inflation factors ($p$ <0.03, VIF <1.7). The best regression model for the first NMS axis, using environmental variables directly as predictors, was significant overall ($p$ <0.0001), contained five variables, and had an adjusted $R^2$ of 0.48 (Table 7). The number of saplings was the most influential variable in the model ($\beta_s = -0.33$), followed closely by phosphorus availability ($\beta_s = 0.31$), then by pH and sulphur availability ($\beta_s = 0.26$ and -0.25, respectively). Mean crown depth was the least influential variable ($\beta_s = 0.18$). The second-best model lacked only crown depth but had a very close SBC score, while other top models showed at least five times the relative difference in SBC between the best and second-best models. Several other top models (i.e., within the ten most parsimonious, as ranked by SBC scores) demonstrated positive relationships between NMS axis 1 and magnesium availability, LFH thickness, and slope inclination, as well as negative relationships with ammonium availability, manganese availability, and sand content.

**Table 7.** Multiple regression model results, with species composition (represented by NMS axes) as a product of environmental variables; n = 72 for each model, standardized estimates ($\beta_s$) are parameter estimates ($\beta$) divided by the ratio of the dependent variable standard deviation to the regressor standard deviation.

| Dependant variable | $DF_{model}$ | $DF_{error}$ | *p*-value | *adj. $R^2$ | Independent variables | $\beta$ | $\beta_s$ | *p*-value |
|---|---|---|---|---|---|---|---|---|
| NMS axis 1 | 5 | 66 | <0.0001 | 0.48 | Saplings | -0.09 | -0.33 | 0.0005 |
| | | | | | P | 0.58 | 0.31 | 0.0008 |
| | | | | | pH | 0.40 | 0.26 | 0.0067 |
| | | | | | S | -1.00 | -0.25 | 0.0103 |
| | | | | | CD | 0.67 | 0.18 | 0.0451 |
| NMS axis 2 | 5 | 66 | <0.0001 | 0.70 | Mg | -1.41 | -0.43 | <0.0001 |
| | | | | | Diffuse | 0.30 | 0.41 | <0.0001 |
| | | | | | Mn | 0.81 | 0.37 | <0.0001 |
| | | | | | pH | 0.81 | 0.31 | 0.0001 |
| | | | | | Saplings | -0.08 | -0.17 | 0.0110 |

*Adjusted $R^2 = 1 - (1-R^2)\cdot[(N-1)/(N-k-1)]$, where 'N' is the sample size, and 'k' is the number of predictor variables used in the model (SAS Institute 2010).

The best regression model for axis two was significant overall (*p* <0.0001), used five variables, and had an adjusted $R^2$ of 0.70 (Table 7). The most influential variable in the model was magnesium availability ($\beta_s = -0.43$), followed by diffuse irradiance ($\beta_s = 0.41$). Manganese availability and pH were positively associated with NMS axis 2 ($\beta_s = 0.37$ and 0.31), while the number of saplings was negatively associated with it ($\beta_s = -0.17$). Among other top models, few were similarly parsimonious (<1.0 SBC difference). Calcium and magnesium availability appeared to have interchangeable roles in other models; any that didn't show a negative relationship between NMS axis 2 and magnesium did so with calcium, but the two nutrients were never present together in the same model. Nitrate availability and basal area had negative model influences in several models, while boron availability had a positive influence in two models.

### 3.4.2.3. PCA of environmental variables

The strongest abiotic gradient (abiotic 1) is one of substrate water-holding ability; it represents soil texture, from the coarsest to finest-textured soils, and explains 32% of the abiotic variance (Table 8, Figure 21a). Other abiotic principal components are loaded with soil texture and topography variables such that they represent gradients of water shedding potential, but are distinguished from each other by emphasizing above-ground or below-ground drainage processes (Table 8). Abiotic component 4 may represent a tendency towards mostly surficial drainage, with negative loadings from gravel content (-0.30), and positive loadings from slope inclination (0.63), sand content (0.47), and mesotopographic position (0.46); the gradient is from coarse-textured benches and lower slopes to fine-textured slopes and crests, and explains 13% of the abiotic variance (Table 8, Figure 21b). Abiotic component 5 is negatively loaded by slope position (-0.25) and positively loaded by gravel (0.55) and sand content (0.47), representing a gradient from upper slopes and crests to benches or lower slopes dominated by soil particles <75 mm. Abiotic component 5 explains 9% of the abiotic variance, and may be an indicator of water infiltration rate (Table 8, Figure 21b).

Most of the biotic principal components represent some aspect of canopy structure, including general canopy openness (biotic 1), stand age (biotic 2), canopy heterogeneity (biotic 4), and sub-canopy cover, which included suspended (dead) stems and sub-canopy trees (biotic 8; Table 8, Figure 22). Biotic component one explains 49% of the variance in biotic variables, and represents generalized canopy openness; leaf area index (-0.94), basal area (-0.70), and LFH thickness (-0.64) all load negatively on biotic 1, while total (0.97), diffuse (0.95), and direct (0.85) irradiance load positively (Table 8, Figure 22a). Biotic component two explains 16% of the biotic variance, and represents a reverse gradient of stand age (from old to young sites), with negative loadings from stand age (-0.73) and basal area (-0.41), and positive loadings from the number of saplings (0.72), LFH thickness (0.34), and crown depth (0.30; Table 8, Figure 22a).

**Table 8.** Principal component (PC) correlations with environmental variables, as represented by either negative or positive coefficients, with a description of the gradient represented by each component and a simplified gradient interpretation. Only variables with loadings greater than 0.24 (corresponds with minimum significant value of Pearson's r at $\alpha = 0.05$) are presented for most principal components; if none were greater than ± 0.24, variables with loadings of 0.14 to 0.24 (corresponding with Pearson's r for significance when $\alpha$ is between 0.05 and 0.1) were given with an asterisk to indicate lower strength. Variable names are defined in Chapter 2.

| PC | Negative loadings | Positive loadings | Gradient interpretation |
|---|---|---|---|
| abiotic 1 | CoarFrag (-0.94) | Fines (0.96), Silt+Clay (0.85) | Soil stoniness |
| abiotic 4 | Gravel (-0.30) | Slope (0.63), Sand (0.47), Mesotopo (0.46) | Surficial drainage |
| abiotic 5 | Slope (-0.25) | Gravel (0.55), Sand (0.47) | Infiltration rate |
| biotic 1 | LAI (-0.94), BA (-0.70), LFH (-0.64) | Total-irrad (0.97), Diffuse (0.95), Direct (0.85) | Canopy openness |
| biotic 2 | Age (-0.73), BA (-0.41) | Saplings (0.72), LFH (0.34), CD (0.30) | Stand age |
| biotic 4 | Saplings (-0.62), Age (-0.27) | CD (0.42), LFH (0.36) | Canopy heterogeneity |
| biotic 8 | | LAI (0.16)* | Sub-canopy cover |
| chem 1 | Total N (-0.68), $NH_4$ (-0.64), S (-0.43), $NO_3$ (-0.26) | K (0.70), Ca (0.63), Mg (0.59), Al (0.59), pH (0.56), Fe (0.52), Mn (0.48), P (0.41), Zn (0.30), B (0.27) | Nitrogen deficiency and base cation availability |
| chem2 | Ca (-0.56), Mg (-0.52), pH (-0.37), $NO_3$ (-0.24) | Fe (0.69), Mn (0.67), Al (0.67), Zn (0.60), S (0.48) | Base-cation deficiency and metal availability |
| chem 9 | Mg (-0.23)*, Ca (-0.22)* | pH (0.31), K (0.27) | Base cation form, alkalinity |

Biotic component 4 explains 9% of the variance in biotic variables, and is a gradient of canopy heterogeneity; biotic 4 negatively associates with both the number of saplings (-0.62) and the stand age (-0.27), while it positively associates with crown depth (0.42) and LFH thickness (0.36; Table 8, Figure 22b). On the negative end of biotic 4, highly heterogeneous plots were apparently the result of localized disturbance (e.g., small windthrow events or low-intensity fire) causing incomplete canopy removal in old forests and increasing the number of saplings, while on the positive end of biotic 4 plots had mature trees of uniform size and distribution. Biotic component 8 represents a gradient of sub-canopy cover, such that sites at the negative end have relatively little between the forest canopy and the understory, whereas sites on the positive end have suspended fallen trees, subcanopy fir and spruce, or other components that increase the amount of overhead cover. Biotic component 8 was positively associated with LAI, but only weakly so (0.16), and explained <1% of the variance in biotic variables (Table 8, Figure 22b).

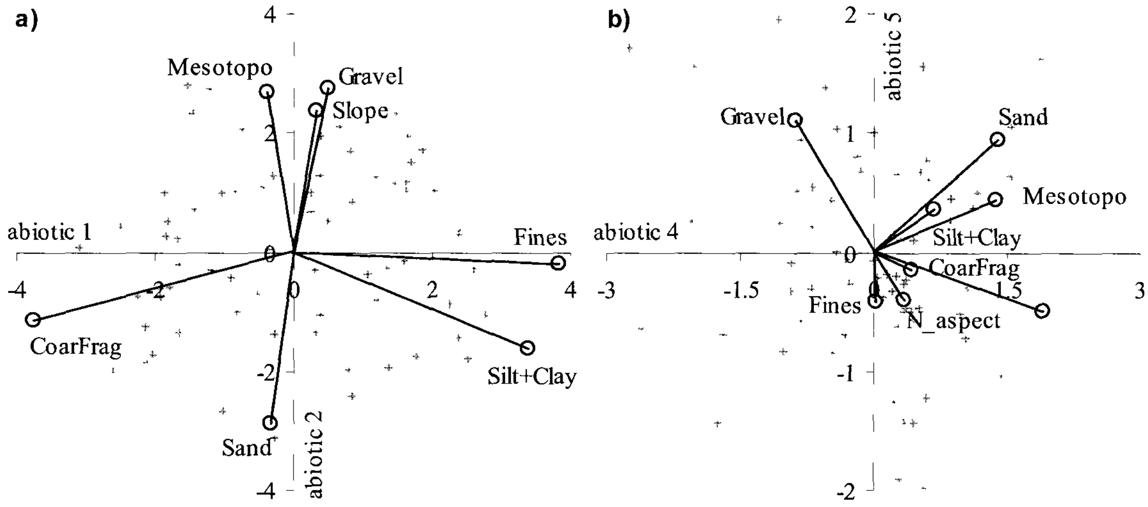

**Figure 21.** Joint-plots of abiotic principal components and variables from plot-level averages or measurements, showing variable loadings (red circles and lines) overlaying quadrats (gray +'s).*

Soil-chemistry variables form three distinct groups among the first two chemical components: nitrogen and sulphur availability all negatively load on chem 1, the availability of phosphorus and basic cations all positively load on chem 1 and negatively load on chem 2, and all metallic micronutrients positively load on both chem 1 and chem 2. The first chemical component explains 27% of the variance in soil chemistry; total nitrogen (-0.68) and sulphur availability (-0.43) load negatively on chem 1, but all other soil chemistry

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* Joint-plot diagrams consist of one diagram overlaid on top of another, and are often used in ordination to display multiple patterns at once. The main diagram is a scatter-plot showing the relationship between any two principal components (axes), with points representing the scores (x and y coordinates) of individual samples on each principal component. The second diagram consists of principal component loadings, which are calculated as the product of the eigenvector and the square-root of the eigenvalue for a given variable-component combination. Loadings are equivalent to the correlation coefficients between original variables and principal components, with values between -1.0 and 1.0. Points are plotted using principal component loadings as the x and y coordinates, and vectors (the hypotenuse of the x and y coordinates) are drawn from each point to the origin, indicating the strength of the loading. This second diagram is then scaled to the same dimensions as the first, such that the maximum value on the first diagram corresponds to a perfect loading (1.0 or -1.0).

variables load positively (Table 8, Figure 23a). This indicates that sites that are nitrogen-poor have more available basic cations and metals, while sites that are nitrogen rich have relatively low levels of basic cations and metals.

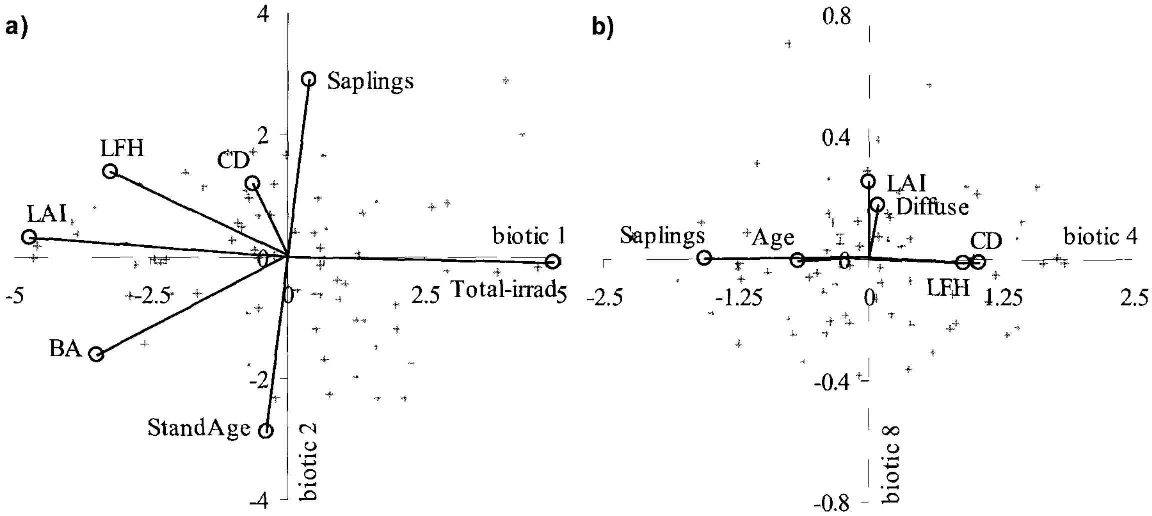

**Figure 22.** Joint-plots of biotic principal components and variables from plot-level averages or measurements, showing variable loadings (red circles and lines) overlaying quadrats (gray +'s).

Chemical component two (chem 2) explains 20% of the variance in soil chemistry variables, with basic cation availability and pH being greater at the negative end, and metal availability being greater at the positive end, suggesting that chem 2 primarily represents a gradient of base-cation deficiency and metal availability, which is at least partly related to soil pH (Table 8, Figure 23a). Similarly, chem 9 was negatively related to magnesium (-0.23) and calcium availability (-0.22) but unlike chem 2, was positively related to pH (0.31) and potassium availability (0.27; Table 8, Figure 23b). Since chem 9 represents only about 3% of the variance in soil chemistry data, and the pH range is small (roughly 4.8 - 5.5 from low to high scores on chem 9), it is unlikely that variation in pH is responsible for the differential patterns of nutrient availability. Rather, chem 9 probably represents a gradient of base cation form, or the ratio of available magnesium and calcium to available potassium, from plots with approximately equal availability of all three to plots with more available potassium.

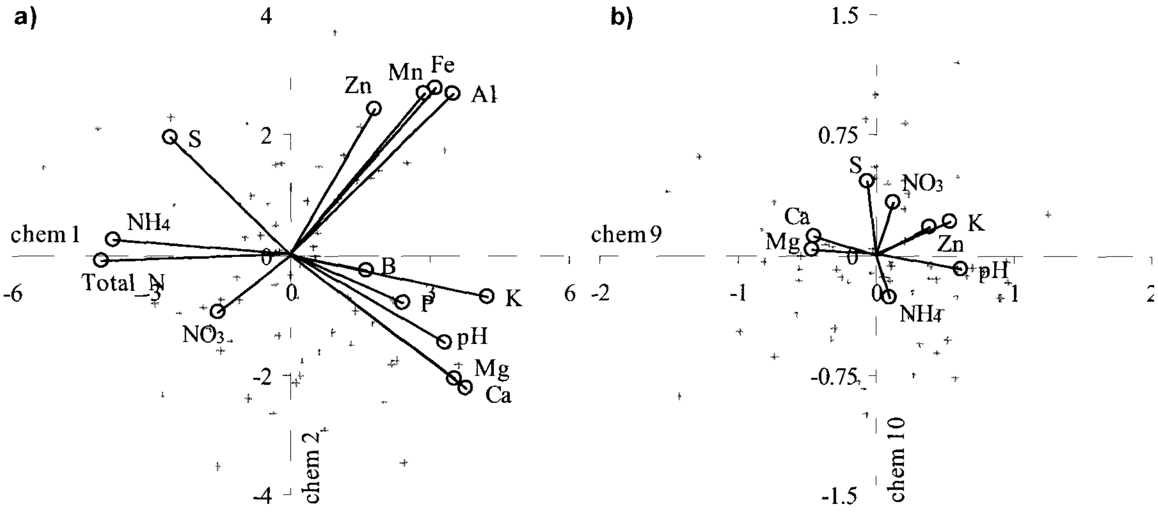

**Figure 23.** Joint-plots of soil chemistry principal components and variables from plot-level averages or measurements, showing variable loadings (red circles and lines) overlaying quadrats (gray +'s). Loadings for chem 10 are scaled ×2 (maximum y-axis score of ± 0.5) for increased visual clarity.

### 3.4.2.4. Multiple regression with principal components

The best regression model for NMS axis one is significant overall (*p* <0.0001), used five components, and had an adjusted $R^2$ of 0.54 (Table 9). Chemical components one and two are the second-most and most influential components in the model ($\beta_s$ = 0.32 and -0.42, respectively), indicating that the first plant compositional gradient (NMS axis 1) is strongly and positively related to pH, base-cation availability, and nitrogen depletion, and negatively related to metal availability (Table 9). After chem 1, biotic components 2, 4, and 8, representing stand age, canopy heterogeneity, and the amount of secondary structure respectively, have the strongest influence on plant composition ($\beta_s$ = 0.29, -0.25, and -0.17, respectively). The coefficients for these components indicate that, along NMS axis 1, plant composition positively associates with younger trees, stands with patchy canopies, and those with less secondary structure. Lastly, abiotic component five, or soil infiltration rate, is negatively associated with NMS axis one ($\beta_s = -0.17$), indicating that soils on the positive end are less permeable than those on the negative end (Table 9).

All of the top ten most parsimonious models for NMS axis 1 include components chem 1, chem 2, biotic 2, and biotic 4 (with the same sign of association), and several include chem 4, biotic 8 (negatively associated), and biotic 7 (positively associated). Furthermore, all of the top ten models were within a single SBC point of the best, indicating little difference in parsimony among them.

**Table 9.** Principal component regression model results, with species composition (represented by NMS axes) as a product of linear combinations of environmental variables (from PCA); n=72 for each model, standardized estimates (βs) are parameter (β) estimates divided by the ratio of the standard deviations of the dependant variable to that of the regressor variables.

| Dependant variable | $DF_{model}$ | $DF_{error}$ | *p*-value | adj. $R^2$ | Independent variable | β | $\beta_s$ | *p*-value |
|---|---|---|---|---|---|---|---|---|
| NMS axis 1 | 6 | 65 | <0.0001 | 0.54 | chem 2 | -0.13 | -0.42 | <0.0001 |
| | | | | | chem 1 | 0.08 | 0.32 | 0.0004 |
| | | | | | biotic 4 | 0.17 | 0.29 | 0.0013 |
| | | | | | biotic 2 | -0.10 | -0.25 | 0.0067 |
| | | | | | biotic 8 | -0.42 | -0.17 | 0.0384 |
| | | | | | abiotic 5 | -0.10 | -0.17 | 0.0483 |
| NMS axis 2 | 5 | 66 | <0.0001 | 0.66 | biotic 1 | 0.19 | 0.46 | <0.0001 |
| | | | | | chem 2 | 0.17 | 0.33 | 0.0001 |
| | | | | | chem 9 | 0.35 | 0.25 | 0.0007 |
| | | | | | abiotic 4 | -0.16 | -0.18 | 0.0137 |
| | | | | | chem 1 | 0.06 | 0.14 | 0.0433 |

The second understory compositional gradient, NMS axis 2, is most parsimoniously modeled as a function of five components ($p < 0.0001$, adj. $R^2 = 0.66$; Table 9). Canopy openness (biotic 1) has a positive influence on the model ($\beta_s = 0.46$), and is the most influential component. Base-cation deficiency and metal availability (chem 2) are positively associated with NMS axis 2 ($\beta_s = 0.33$), as are alkalinity (chem 9; $\beta_s = 0.25$) and nitrogen depletion (chem 1; $\beta_s = 0.14$). Surface drainage potential (abiotic 4) is negatively related to NMS axis 2, indicating plots with higher scores on the compositional gradient are more likely to have level topography and gravelly soils, while those with lower scores are more likely on steeper slopes with greater surface runoff.

Among the top ten most parsimonious models for NMS axis 2, all include biotic 1, chem 2, and chem 9, all with the same signs of association. Six top models show a negative influence from abiotic 4, four have a negative influence from chem 10, and four show a positive influence from chem 1. Chemical components 6 and 7, and biotic 4 all have a positive influence in two top models. The best model for NMS axis 2 was more different, in terms of relative SBC scores, from other top models than was the case for NMS axis 1. Specifically, the relative difference between the best and second best models was 0.21, and for subsequent models the relative difference rose considerably to 0.80 or greater.

### 3.4.3. Functional group associations

Lichen abundance was negatively related to both feathermoss and vascular plant abundance, with slopes of -0.38 and -0.55, respectively (Table 10). This moderately strong negative association suggests that competition may be taking place. Yet, the $R^2$ values are only 0.24 and 0.22, respectively, indicating that whatever association or aversion occurs is of relatively low importance, in terms of exlpaining the overall varaition in abundance.

Feathermoss abundance was negatively related to lichen abundance but positively related to vascular plant abundance (-0.63 and 0.52, respectively). The $R^2$ values were 0.24 for feathermoss interaction with lichen, and 0.12 for interaction with vascular plants (Table 10). This suggests that feathermoss may be a strong competitor with lichen, and it may be facilitated by vascular plants, but that these interactions are relatively unimportant. Similarly, vascular plant abundance was only weakly positively related to feathermoss abundance (0.23), indicating possible weak facilitation for some species, and negatively related to lichen abundance (-0.40), indicating possible competition. But once again, these interactions were relatively unimportant, as indicated by the low $R^2$ values of 0.22 and 0.12 (Table 10).

**Table 10.** Potential net association (interaction) parameters for all functional groups, as estimated by a modification of the size-distance regression technique.

| Independent FG | Dependent FG | Intensity (slope) | Importance ($R^2$) | Potential interaction type |
|---|---|---|---|---|
| Lichen | Feathermoss | -0.38 | 0.24 | competition |
| | Vascular plant | -0.55 | 0.22 | competition |
| Feathermoss | Lichen | -0.63 | 0.24 | competition |
| | Vascular plant | 0.52 | 0.12 | facilitation |
| Vascular plant | Lichen | -0.40 | 0.22 | competition |
| | Feathermoss | 0.23 | 0.12 | tolerance |

Unfortunately, being from randomly selected quadrats meant functional group abundances were highly kurtotic and positively skewed, even after removing quadrats with only a single functional group present. Therefore, although the observations of positive and negative associations are still useful in highlighting the potential type of interaction among functional groups, the $R^2$ values, and therefore the potential interaction importance, were probably underestimated.

## 3.5. Discussion

Overall, this plot-level examination agrees very well with published literature on lichen woodlands, in that the strongest vegetative gradient is dominated by feathermosses at one end and by mat-forming lichens at the other (NMS axis two), and in that characteristics of the forest canopy that may influence light transmittance and moisture are strongly associated with this compositional gradient (Kershaw 1978, Johnson 1981, Carroll and Bliss 1982, Morneau and Payette 1989, Coxson and Marsh 2001, Bainbridge and Strong 2005, Hunt et al. 2005). Nevertheless, this study also illustrated that there is a large amount of ecological space between the lichen and feathermoss functional groups, and that this space tends to be dominated by various vascular plants. Lichen-rich systems are much more than a dichotomous successional trajectory of lichens to feathermosses: lichens and feathermosses merely represent endpoints on one ecological gradient of many that exist.

### 3.5.1. Environmental associations of species composition

The dominant biotic gradient I detected was, predictably, that of generalized canopy closure. Other biotic gradients were in some sense echoes of this canopy closure gradient, indicative of variations in the height of the trees, the patchiness of the canopy, and the recent or historical influence of disturbance. And, true to form, these biotic gradients showed significant relationships to the feathermoss-lichen gradient in all analyses, often supporting previously demonstrated associations such as stand age and leaf area index (both positively associated with feathermoss abundance; Coxson and Marsh 2001). Yet, they were not the only variables that did so, nor were they always the strongest influences present in models.

Although abiotic associations with understory composition were not detected using multiple regression on measured variables, significant influences were apparent with both compositional gradients in the PC-regression models. This reinforces the idea that, although soil texture and topography show some association with understory species composition, the strongly linear associations with canopy characteristics and soil chemical properties obscure this abiotic influence. The abiotic components in this chapter differ from those in Chapter 2, in that they represent both topography and soil texture, suggesting gradients of water drainage.

The feathermoss-lichen gradient (NMS axis 2) was negatively associated with surficial drainage (i.e., water shedding), as indicated by the combination of soil texture and topography associations with abiotic component 4. This agrees with initial hypotheses, in that lichen-dominated sites tend to shed water, while feathermoss-dominated ones tend to receive it. The vascular plant compositional gradient (NMS axis 1) was negatively associated with the soil infiltration rate (abiotic 5), which is a combination of reduced soil stoniness and relatively water-receiving positions. This suggests that mesophytic plants, such as *Chamerion angustifolium* and *Viola* spp., occupy locations that tend to be water-receiving and water-holding, while *Vaccinium membranaceum* occupies locations that are water shedding, both through above and below-ground processes.

Base-cation availability tends to increase with soil alkalinity, and is often negatively correlated with both aluminum availability and lichen cover in northern or alpine soils (Moore 1980, Darmody et al. 2004, Hamel et al. 2004). Results presented here support this association: base-cation deficiency, metal availability, and acidity positively relate to the 'lichen' end of the main understory compositional gradient (NMS axis 2). However, it was the first NMS axis that most strongly associated with gradients of soil chemistry, and this compositional gradient was dominated primarily by species of vascular plants. Particularly notable was the separation of *Vaccinium membranaceum* from other dwarf shrubs and vascular plants along an environmental gradient dominated by pH; this agrees with McKechnie (2009) who suggested that *V. membranaceum* may be more acidophilic than other *Vaccinium* species, perhaps because of unique mycorrhizal associations.

See and Bliss (1980) found that alpine lichen-rich forest understory composition related significantly to changes in pH, and Kershaw (1977) acknowledged that pH may be a significant factor in determining site suitability for lichen propagules. Although the range of variation examined by See and Bliss (1980) was twice what it was in my analysis, and Kershaw (1977) was referring specifically to post-fire soil conditions, my results suggest that even smaller pH ranges (4.0 - 6.5) and later-stage associations may be biologically relevant.

Nitrogen deficiency was also greater at the 'lichen' (positive) end of the main compositional gradient (NMS axis 2), and at the positive end of the secondary compositional gradient (NMS axis 1). The former was not surprising, because feathermosses are known to associate with nitrogen fixing bacteria (Houle et al. 2006), mat-forming lichens have extremely efficient internal N-cycling (Kytoviita and Crittenden 2007), and vascular plants are predicted to outcompete lichens on more fertile soils (Crittenden 2001). The latter result was unexpected; a gradient bounded on the positive end by mesophytic species such as *Viola* spp. and *Chamerion angustifolium*, and at the negative end by xerophytic species such as *Vaccinium membranaceum*, should have been positively associated with nitrogen (Klinka et al. 1989, Haeussler et al. 1990). However, given that measurements were taken in the latter part of summer, this association probably represents seasonal nitrogen depletion caused by the greater nitrogen demand in plots with greater abundance of the mesophytic species.

Generally, the strongest principal components and variables in the multiple regression models supported associations seem in the NMS diagrams, but it was interesting that the relative strength of influence of environmental variables or principal components on the models were different than would be expected based on the NMS diagrams and correlation overlays alone. For example, despite appearing to have a much stronger association with NMS axis two, biotic component one and the canopy variables contributed only slightly more than other variables to the best direct and principal component regression models for NMS axis two. In fact, the only predictor variables that had notably greater model influence, for either the PC regression models or the multiple regression models, were the chemical components or chemical variables with models for NMS one. These observations suggest that, although canopy closure certainly seems to be an important environmental gradient, it is not exclusively so. Rather, canopy closure appears to exert a disproportionately large influence when examined in isolation from soil properties, perhaps because some of these soil properties vary in concert with some of the canopy layer gradients. By using the principal components analysis to ensure that soil chemical and canopy properties remained mathematically orthogonal, I have demonstrated that much of the variance in vegetative composition can be related to soil chemical and physical properties, rather than to canopy attributes alone.

My use of principal components regression, as compared to the direct variable regression, was also largely responsible for the detection of associations between compositional gradients and soil properties. In comparing the direct and PC regression model for NMS axis one, I showed that only the latter included soil physical properties and topography, and attributed comparable influence to them as to biotic components. If I had simply used multiple linear regression with measured variables, these potentially significant environmental associations would have been overlooked. Given that these variables were observed to have associations of ecological significance *a priori*, as inferred by their widespread use in describing generalized habitat types or successional stages in previous studies (Johnson 1981, Carroll and Bliss 1982, Coxson and Marsh 2001), this detection suggests that principal components regression is achieving a higher level of ecological resolution than multiple regression itself. Comparing the relative influences of measured abiotic variables and biotic variables (the canopy) on other biotic variables (the understory) directly may very well result in greater biological abstraction than the use of a multivariate technique such as principal component regression.

### 3.5.2. Species composition and functional group importance

Because understory vascular plants in these forests are overdispersed, compared with the more continuous cover of lichens or mosses (personal observation), they appear to be less abundant, and may therefore be regarded as transient species (*sensu lato* Grime 1998). From the emphasis on feathermosses and lichens in relevant literature (Ahti and Oksanen 1990), this seemed to be a common view, and was the basis for my initial hypotheses. In contrast, I found that vascular plants occupy approximately the same amount of ground space in the study area as lichens or feathermosses do (12-13%); this is more consistent with vascular plants being 'subordinates' (i.e., subordinate to the trees) than transients (Grime 1998). According to the 'mass-ratio' hypothesis, species (or groups) should have an influence on their environment that is proportionate to their contribution to the ecosystem primary productivity, of which biomass or abundance may be an indicator (Grime 1998, McLaren and Turkington 2010). Vascular plants should be considered at least as important in these forests as lichens and feathermosses.

It is also clear that vascular plants are more functionally heterogeneous as a group than either feathermosses or lichens. The relatively low variability among species of the lichen group may have contributed to their apparently more unified response to multiple environmental controls in Chapter 2, as well as their tendency towards larger $R^2$ values. While all lichen species tended to respond in a similar way to the environment, vascular plants seemed to have many more species-specific traits, thereby having opposite influences on models and decreasing the overall amount of variance explained. This hypothesis is supported by results of the NMS used to examine the actual associations of species in random quadrats; all lichen species examined formed a cohesive group that was clearly separated from non-lichen species, whereas vascular plants showed relatively little cohesion as a group (Figure 20).

### 3.5.3. Functional group associations

In the absence of a temporal trajectory upon which to measure species or functional group interactions, I elected to examine 'potential competition', based on a combination of association-based inference and competition theory (Weldon and Slauson 1986, Burton 1993). If patches that are currently occupied by more than one functional group represent habitat that is suitable for both, the three functional groups I examined here exhibit a wide variety of interaction types. Specifically, lichens may compete with each of the other groups, but seem to be more negatively influenced by the presence of vascular plants. Feathermosses may be negatively influenced by lichen presence, and positively influenced by vascular plant presence, and vascular plants are negatively influenced by lichens and weakly but positively influenced by feathermosses. Given that the $R^2$ values from all of these associations are less than 0.25, we may say that these interactions are relatively unimportant for the community as a whole.

This lack of interaction importance may be reflective of a general trend in low-productivity systems. When the resource supplying power of a system is such that it limits the growth of individuals independently of other processes, negative interactions will be weak, at best (Tilman 1988, Goldberg and Novoplansky 1997, Keddy et al. 1997). The competition-productivity gradient hypothesis additionally suggests that facilitation will be more common in low-productivity or early seral systems, but the present analysis does not support high levels of facilitation among lichens, feathermosses, and vascular plants either. This interaction weakness may be partly because of the random sampling strategy I used; the high proportion of unoccupied space in the understory may be due to high litter inputs that apparently limit growth of many species (Bonan 1990). Indeed, while each functional group occupied approximately 12-13% of the sampled areas, litter accounted for over 48%, indicating a high amount of unsuitable habitat, presumably as the result of canopy influence. Overall, these data seem to indicate that, although some weak species interactions may be taking place, direct environmental regulation (i.e., niche partitioning), or founder effects are dominating community organization in these systems.

### 3.5.4. Summary and Conclusions

My results support the existence of a compositional gradient bounded by lichen and feathermoss at the stand level, as well as the general strength of associations between overstory and understory properties. However, the dominance of this compositional gradient does not operate in exclusion or override the importance of other environmental controls, such as soil texture and topography, base cation deficiency, and nitrogen availability. All of these components contribute to understory composition in lichen-rich systems, and generally concur with the hypotheses that vascular plants associate with aspects of soil nutrient availability, while lichens and feathermosses associate with gradients of light and moisture availability or retention.

The predominance of a lichen-to-feathermoss compositional gradient does not suggest that vascular plants are unimportant in these systems. Rather, lichens and feathermosses merely represent endpoints on this compositional gradient. Another important compositional gradient appears to be that of acidophitic to mesophitic vascular and bryophyte species, and many vascular species are distributed along the lichen to feathermoss gradient itself. Competition among functional groups may be relatively unimportant, but this requires further investigation along a temporal gradient as well as an environmental one.

# 4. Spatial autocorrelation in nutrient availability, soil texture, and overstory properties in some boreal lodgepole pine forests in British Columbia

## 4.1. Abstract

*In-situ* sampling of soil nutrient availability using ion-resin technology has allowed ecologists to reduce the problems associated with temporal variability, but many of these technologies have been developed in relatively homogenous agricultural systems, and their applicability to relatively low-productivity forest soils is uncertain. Spatial autocorrelation can be problematic in examinations of vegetation-environment relationships, particularly when non-independent units are treated as independent, because the artificially increased degrees of freedom increase the chance of type I error. Using measurements of forest-canopy properties, soil texture, and soil-nutrient availability (using PRS$^{TM}$ probes) taken at small quadrats within a hierarchical sampling design (three spatial scales), I tested for an association between dissimilarity in environmental variables and geographic distance, using Mantel's correlograms. Soil-texture and forest-canopy variables tended to show significant autocorrelation within and among plots and among nearby sites (0-10 km). Soil-nutrient availability exhibited highly variable responses, typically with no autocorrelation at within-plot distances (0 to 12 m), but with significant autocorrelation among-plots (15-76 m) and nearby sites (0.1-10 km). An exception to this was total nitrogen availability, which showed similar patterns of autocorrelation to the forest canopy. Owing to the small number of quadrats within each plot, statistical power was low and some variables were not adequately replicated at smaller distance classes, suggesting that a different sampling strategy would be beneficial for future research.

## 4.2. Introduction

Choosing the correct scale at which to measure natural phenomena is of great importance in ecology. If the number, size or dispersion of sample units is too small or too large, or if the tools we use to measure patterns do not accurately represent those patterns at the same scale as the sample unit, the perceived variance in measured parameters may be artificially inflated or reduced (Kenkel et al. 1989, McCune and Lesica 1992, Cressie 1993, Jalonen et al. 1998). This can obscure our ability to accurately describe the patterns of interest, to measure the processes that cause these patterns, and to obtain meaningful results from statistical tests used on resulting data (Ver Hoef and Cressie 2001).

In lichen-rich forests, using stand-scale investigations to study the environmental relationships of understory vegetation has been historically prevalent due to convention in forest science or wildlife management (Carroll and Bliss 1982, Harris 1996, den Herder et al. 2003), despite evidence that the microsite-scale is both theoretically justified and biologically important (Beard and de Priest 1996, Sulyma and Coxson 2001). Although it is generally accepted that the realized size and distribution of sample units may be less than optimal, due to financial or logistical constraints, it is common for researchers to simply maximize sample size without regard to sample independence or the biologically relevant scale of measurement (Legendre and Fortin 1989). Yet, if statistical tests are to be performed on such data, clustered or stratified-random sampling designs must still meet the requisite distributional or sampling assumptions, such as independence among sample units (Kenkel 1989, Diekmann et al. 2007, Lajer 2007, Økland 2007). In the absence of sufficient pilot study resources, researchers may use additional analyses to confirm sample independence after sampling is conducted, and make adjustments where necessary.

A common source of non-independence among sample units in soil ecology is the daily or seasonal variation in weather conditions; both short and long-term changes in soil moisture and temperature can decrease the labile nutrient pool that is available for measurement by *in-situ* methods, and can even change the rates of biological activity, which will further alter nutrient cycling and decomposition (Gibson 1986, Wild 1988, Foth and Ellis 1996, Wardle 1998, Grayston et al. 2001, Bell et al. 2008, Björk et al. 2008). Ecologists often compensate for this temporal variability by removing all soil samples within a discrete time interval (Gross et al. 1995, Brosofske et al. 2001), by repeated sampling within a growing season (Moore 1980, Farley and Fitter 1999), or by ensuring comparable pre-sampling weather patterns (Hooper and Vitousek 1998). Unfortunately these approaches also limit studies to using smaller numbers of sample locations or fewer samples that could be assessed in a short amount of time and within available budgets. Recent advances in ion-resin technology have substantially decreased the temporal variability associated with measurement of soil nutrient availability, because ion-resin bags or membranes are typically left in the ground over several weeks, and will therefore integrate the effects of weather and seasonality over time (Hangs et al. 2004). Ion-resin membranes may be more biologically relevant measures of nutrient availability than traditional soil core sampling, because their ability to absorb nutrients is limited by the same factors that limit nutrient uptake by plants, and they are largely uninvasive in deployment (Hangs et al. 2005).

Because of their ability to integrate temporal variability, and because of their non-invasive deployment, Plant-Root Simulator probes (PRS™ probes; WAII 2007) were chosen for assessing nutrient availability in the present study. These probes are simply ion-resin membranes encased in plastic spikes. The manufacturer's recommendation for deployment is to use four pairs of probes (a pair is one anion probe and one cation probe) to represent a

100 $m^2$ area (WAII 2007). By extension, each probe pair may adequately represent an area of approximately 25 $m^2$. Assuming each probe pair is placed in the center of a 25-$m^2$ plot, they could be given a 'representation-radius' of approximately 2.82 m. However, considering that deployment guidelines were developed in temperate or agricultural systems, it is unknown whether WAII's (2007) recommendations could be applied to a northern lodgepole pine forest.

Studies in natural terrestrial ecosystems have shown soil chemistry and nutrient availability to vary on different spatial scales both within and among sample locales (Jackson and Caldwell 1993, Farley and Fitter 1999, Garten et al. 2007), indicating that the relevant sampling scale can be both location- and property-specific. Estimation of some soil properties can be sensitive to the survey methods used; for example, Farley and Fitter (1999) found ammonium and nitrate to differ significantly at minimum scales of 2 m using soil core sampling, but at minimum scales of 0.2 m when using a soil solution sampler. In addition to the effects of underlying differences in parent materials and topographic slope position, soil property heterogeneity may be associated with the influence of individual plants (their influence is directly related to their size, and may vary among species), with microbial community composition, or with localized disturbances such as gap-formation (Moore 1980, Rossi 1996, Økland et al. 1999, Prescott 2002, Bengston et al. 2007, Barbier et al. 2008, McLaren and Turkington 2010).

The combination of using single (rather than bulked) sample analysis, with an irregular distribution of PRS$^{TM}$ probes within each plot, presented a unique opportunity to test for the presence of spatial associations in nutrient availability. Using both the spatial information as well as the environmental measurements described in Chapter 2, I addressed three questions by means of spatial analysis: 1) Are the manufacturers recommendations for

PRS$^{TM}$ probe deployment applicable in low-productivity pine forest as they are in other ecosystems? 2) Is there evidence of spatial autocorrelation in the measured environmental variables from functional group quadrats? and 3) Are the chosen scales and sampling strategies appropriate for investigation of understory-environment relationships?

## 4.3. Methods

For brevity, this section will emphasize only methods used in the analysis of data relevant to this section. The reader may refer to Chapter 2 for a complete review of the study area and data collection protocols.

Mantel tests are akin to simple correlation analyses, but test for associations between two dissimilarity matrices. Most commonly, one of the matrices is the Euclidean distance calculated between pairs of geographic (x, y) coordinates, while the other may be a dissimilarity matrix of anything from environmental data to species abundance, infection rates, or sociological classifications (Mantel 1967, Rossi 1996, McCune and Grace 2002, Fortin and Dale 2005, Goslee and Urban 2007). A positive association between the two matrices indicates that the measured variable(s) from any two sample units become more different with increasing geographic distance. I used Mantel tests here to examine the relationship between geographic distance and the environmental variables recorded at functional group quadrats. Specifically, matrices of Euclidean distances were computed, using every possible pair of quadrats separated by geographic distances ranging from 0.7 m to 105 km. One matrix was calculated for every environmental variable, based on transformed (where necessary) variable dissimilarities, and one was calculated from the geographic coordinates of each sample quadrat (UTMs). For each environmental variable, these two measures of quadrat dissimilarity were then tested for linear association in several distance classes, using Mantel's r statistic, with a permutation procedure (100,000 permutations) for evaluating the probability of obtaining each r-value by chance.

Minimum sample sizes of 100 to 225 are recommended for spatial analyses of this type, but fewer samples are permissible if the spatial signal is expected to be strong (Webster and Oliver 2001, Fortin and Dale 2005). Of course, the spatial dispersion of sample data is equally important, because the tests are carried out individually on each distance class, and irregular sampling (i.e., more samples at certain distances than others) may cause an uneven distribution of statistical power among distance classes (Dutilleul et al. 2000, Fortin and Dale 2005). The total number of samples I used met recommended criteria (n = 216), which allowed emphasis to be placed on ensuring appropriate binning of data, such that adequate numbers of pairwise comparisons were present, and the calculated statistics could be considered reliable. Because the quadrats were clustered within plots, which were clustered within sites, and sites tended to be somewhat clustered over the study area, it was necessary to define irregular distance classes (bins) that had adequate numbers of pairwise comparisons in order to accurately represent multiple scales. I grouped samples into 12 distance classes, based on this combination of adequate numbers of comparisons in each class and the relevancy of the scale.

At the within-plot level, only 216 comparisons were available to divide among distance classes, so the possible number of intervals was limited. Four distance classes were chosen, 0 - 3 m, 3 - 5 m, 5 - 8 m, and 8 - 15 m, with respective numbers of pairwise comparisons being 39, 69, 74, and 35. Rather than choose the theoretical maximum within-plot distance of 11.28 m (plot diameter) as the upper bound, 15 m was used in order to accommodate the possibility that quadrats were located slightly outside of the normal sampling area due to obtaining adequate functional group representation (see Appendix B).

During exploration of the data, it was apparent that using a single-within plot distance class allowed for detection of autocorrelation at that scale for variables that did not have strong enough signals to be broken up into separate classes. Therefore, with nutrient availability measurements I present additional results for these analyses that are not represented in the figures.

I used a single among-plot (within site) scale, because within a site all plots were systematically arranged to be 50 m apart. Nevertheless, to allow for error in plot layout, and for the possibility that the two quadrats used in a given pair may be at the closest or farthest ends of their adjacent plots, the plot-level distance interval was set at 15 - 76 m; 76 m is the maximum theoretical distance, assuming maximum separation of quadrats in nearby plots and maximum GPS or observer error in plot layout, while 15 m is the upper bound of the last distance category. The number of pairwise comparisons in this distance class was 626.

Large-scale among-site comparisons were far more numerous than within-site comparisons, and tended to show consistent responses within specific large-range distance intervals during exploratory analysis, so I emphasized equal binning in these classes. The first four distance intervals were approximately 10 km each (from 0 - 40 km). The fifth large-scale interval was 40 - 55 km, the sixth was 55 - 75 km, and the seventh was 75 - 105 km. All but the largest of these distance intervals had between 2700 and 4300 pairwise comparisons; the largest distance interval had 1134. Because these large distances were determined by site selection protocols, the Mantel tests using larger distance classes served the role of statistical controls; significant autocorrelation among more than the closest sites would have indicated that the significance level was too low for the data being used.

Tests were deemed significant if the calculated r-value was greater than 99 % of randomized values ($\alpha = 0.01$); this restrictive significance criterion was employed to compensate for the inflated type 1 error rate that results from performing multiple Mantel tests with each variable, albeit using different pariwise comparisons. Mantel's r values were then plotted for each distance interval to create correlograms for ease of interpretation. All analyses were conducted using the 'ecodist' package in R, v. 2.8.1 (Goslee and Urban 2007, R Foundation for Statistical Computing 2008).

Because the many of the within-plot distance intervals tended to have relatively small numbers of pairwise comparisons, the data generated in my exploratory analyses were ideal for examining the potential influence of small effective sample sizes on detection of statistical significance. I examined the frequency with which significant Mantel's coefficients were produced using a given number of pairwise comparisons and variable subset, then plotted the results graphically. The recommended minimum sample size was estimated to correspond with the asymptote for proportion of significant tests.

## 4.4. Results

### 4.4.1. Mantel tests / correlograms

#### 4.4.1.1. Soil texture and canopy variables

Dissimilarity in soil texture showed a positive association with geographic distance within plots, as well as among plots from the same sites (Figure 24). At distances of 10 km, this association turned negative for the sand and silt + clay texture classes, indicating inter-site similarity in soils with particle sizes <2 mm is unlikely even at small inter-site distances. In contrast, dissimilarity in the gravel content continued to show a significant positive association with geographic distance up to the first inter-site distance class (0.1 - 10 km), followed by negative or non-significant associations thereafter. Above the first inter-site distance class, significance detection was sporadic and unlikely to be the result of true autocorrelation for any texture classes. Both LFH thickness and variables that were derived from hemispherical photos (i.e., canopy variables) tended to show similar patterns of peak and decline in autocorrelation (Figure 25). This pattern incorporated positive and significant ($p$ <0.01) Mantel coefficients for all within-plot distances, all among-plot distances and the two lowest inter-site distances. At larger distance classes, the associations were largely nonsignificant.

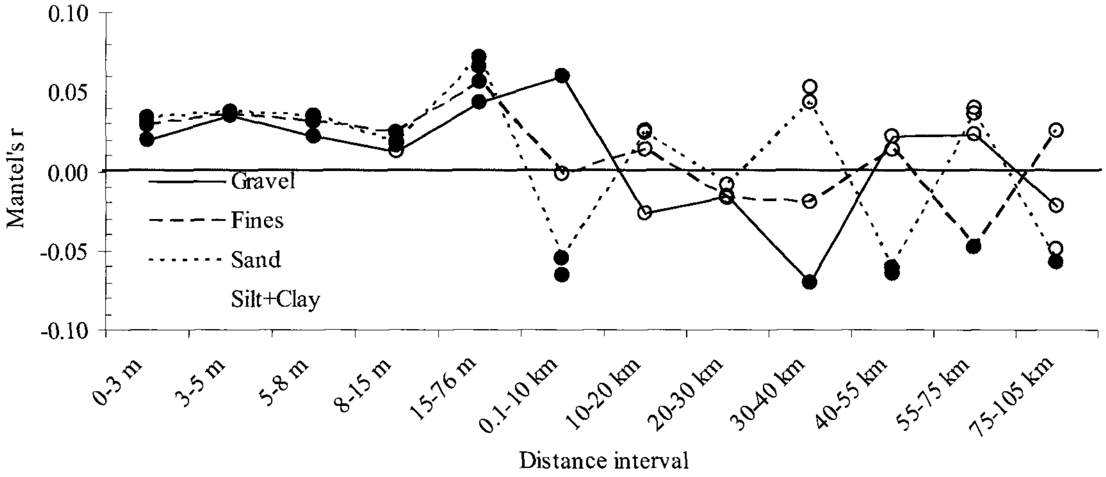

**Figure 24.** Dissimilarity in soil texture as related to distance; filled circles represent significant ($p$ <0.01) relationships for their respective distance classes.

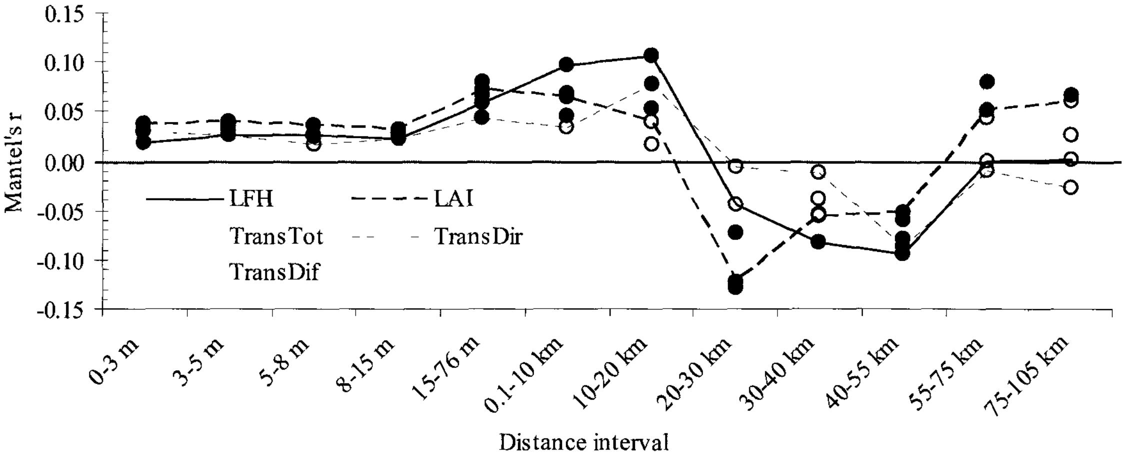

**Figure 25.** Dissimilarity in canopy variables as related to distance; filled circles represent significant ($p$ <0.01) relationships for their respective distance classes.

### 4.4.1.2. Macronutrients

Of all the macronutrients examined, only availability of nitrogen showed significant autocorrelation within plots, though this was inconsistent at best (Figure 26). The scale at which nitrate showed autocorrelation was slightly lower than that of ammonium; nitrate was positively autocorrelated at a maximum of 15 -76 m, whereas total nitrogen and ammonium showed significant positive autocorrelation up to the 0.1 - 10 km. Total nitrogen availability exhibited stronger autocorrelation than nitrate or ammonium (Figure 26).

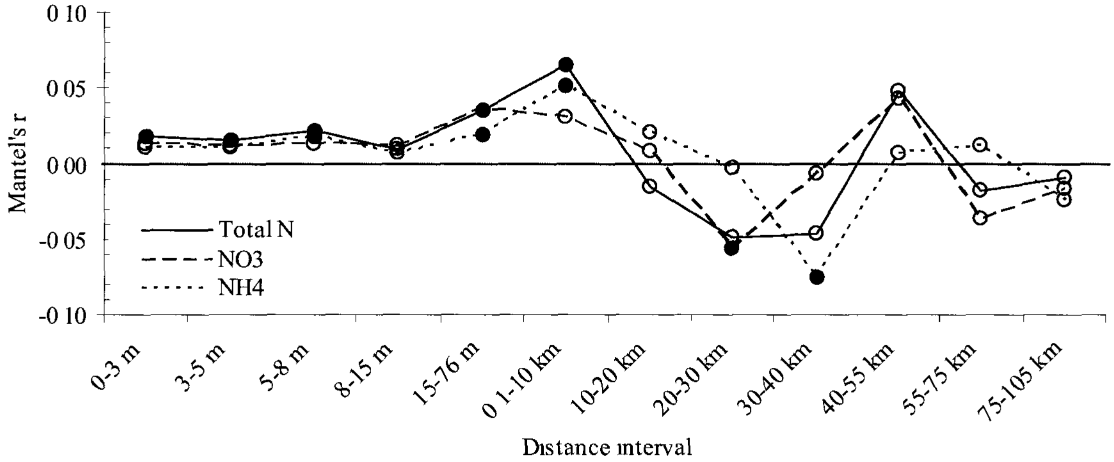

**Figure 26.** Dissimilarity in nitrogen availability as related to distance, filled circles represent significant ($p$ <0.01) relationships for their respective distance classes

Availability of base cations showed comparable patterns of autocorrelation across distance intervals (Figure 27). None were significantly autocorrelated within plots, though all Mantel coefficients were positive. All basic cations showed significant positive autocorrelation among plots (15 - 76 m), and both calcium and magnesium continued to do so at the first among-site distance interval (0.1 - 10 km). Calcium and magnesium both showed significant negative autocorrelation at the 30 - 40 km distance interval. Potassium was not autocorrelated at any of the among-site distances (Figure 27).

Sulphur availability showed patterns of autocorrelation similar to those of magnesium and calcium; significant positive autocorrelation was detected among plots, and among sites up to distances of 10 km, but significant negative autocorrelation was detected between 30 and 40 km (Figure 28). Phosphorus was more similar to potassium in its spatial structure, showing positive autocorrelation among plots and nearby sites, but none at other distance intervals (Figure 28).

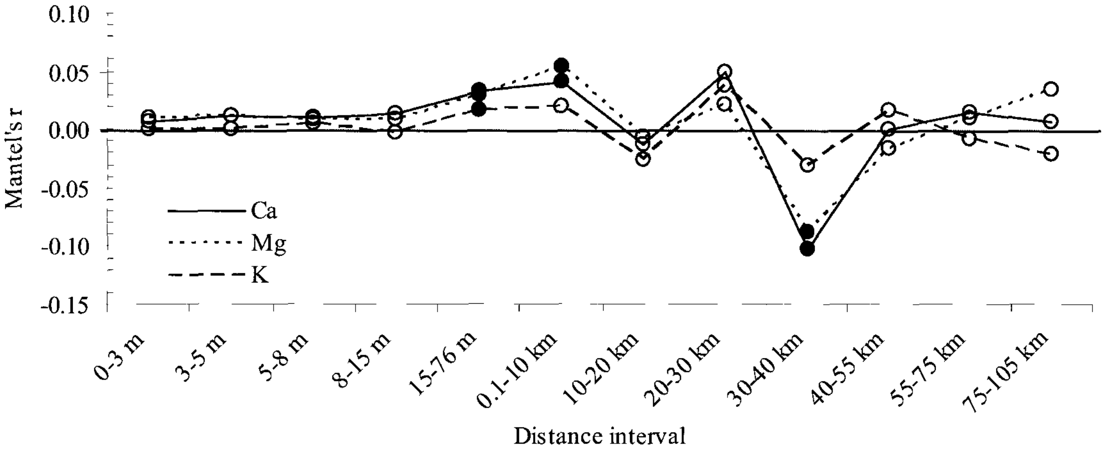

**Figure 27.** Dissimilarity in base-cation availability as related to distance; filled circles represent significant ($p$ <0.01) relationships for their respective distance classes.

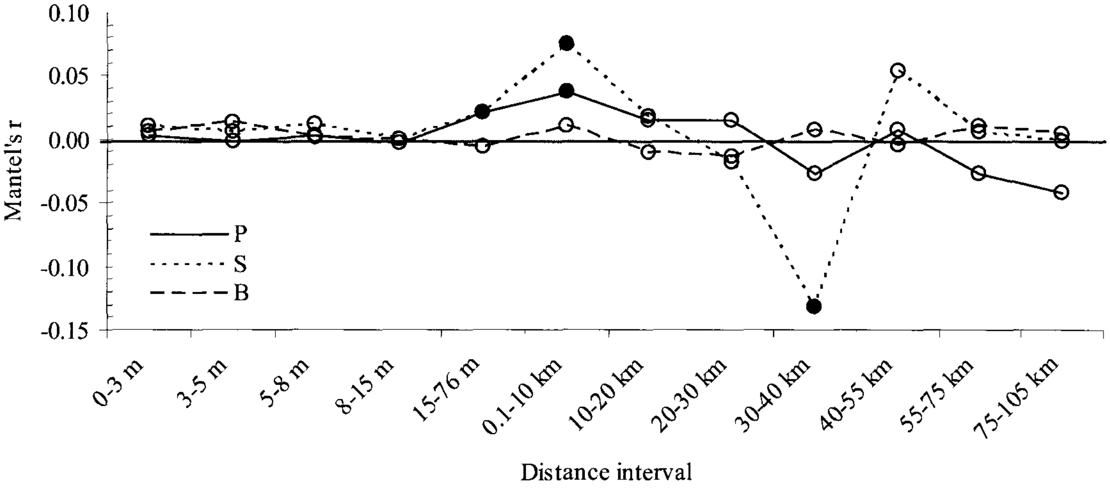

**Figure 28.** Dissimilarity in P, S, and B availability as related to distance; filled circles represent significant ($p$ <0.01) relationships for their respective distance classes.

#### 4.4.1.3. Micronutrients

Boron availability was not autocorrelated at any of the distance intervals (Figure 28). All metals showed positive autocorrelation in at least one distance interval at the within-plot level (Figure 29). Specifically, iron was significantly autocorrelated at the 0-3 m and 5-8 m distance intervals (and marginally nonsignificant at the 3-5 m distance interval), manganese was significantly autocorrelated at the 0-3 m distance interval, zinc was positively autocorrelated at the 3-5 m distance interval, and aluminum was autocorrelated at the 5-8 m distance interval (Figure 29). All metals showed significant positive autocorrelation among plots, while only manganese and iron also did so among nearby (0.1 - 10 km) sites.

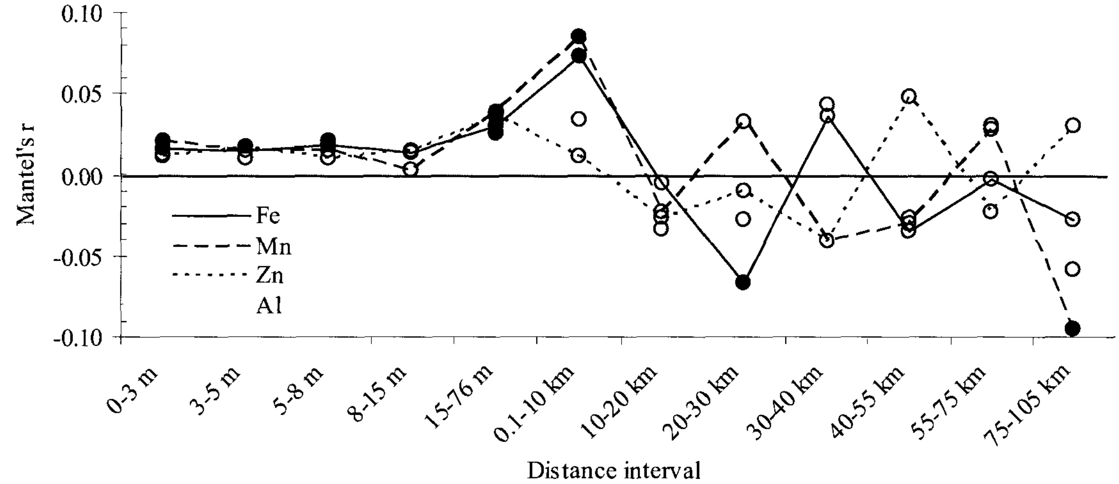

**Figure 29.** Dissimilarity in micronutrient availability as related to distance; filled circles represent significant relationships for their respective distance classes.

Despite the lack of significance at several within-plot distances for many of the soil nutrients, there was evidence that most soil nutrients were indeed autocorrelated within plots. Soil nutrient availability was re-tested using a single distance class for all 216 within-plot pairwise comparisons with striking results: only potassium, phosphorus, and boron were not autocorrelated at within-plot distances, and the probability that this result was due to chance (*p*-value) was exceptionally low in each positive case (Table 11).

**Table 11.** Revised Mantel tests for nutrient availability using a single within-plot distance class; r is the Mantel statistic, while *p* is the estimated probability of obtaining that positive test by chance.

| | Total N | $NO_3$ | $NH_4$ | Ca | Mg | K | P | S | B | Fe | Mn | Zn | Al |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| r | 0.0336 | 0.0248 | 0.0245 | 0.0213 | 0.0194 | 0.0017 | 0.0005 | 0.0142 | 0.0101 | 0.0316 | 0.0268 | 0.0269 | 0.0292 |
| *p* | <0.0001 | <0.0001 | <0.0001 | <0.0001 | 0.0001 | 0.7389 | 0.9176 | <0.0001 | 0.0397 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |

### 4.4.2. Sensitivity to sample size

Several themes were consistent throughout exploratory analyses of all variables: a distance interval size of 1.0 m (and often up to 2.5 m) resulted in too few pairwise comparisons for the lowest and highest within-plot distance classes, such that significant Mantel statistics were unlikely for all but the strongest spatial signals at those distance classes. In addition, canopy and soil texture variables appeared to have stronger spatial signals than nutrient availability overall, as indicated by their greater frequency of significance detection for intervals with low numbers of pairwise comparisons. A near-maximum likelihood (asymptote) of significance-detection for canopy-influenced variables and soil texture variables was attained with sample sizes as small as 20-40, while significance-detection for soil nutrient availability may have been constrained by sample size for upwards of 70 pairwise comparisons or more (Figure 30).

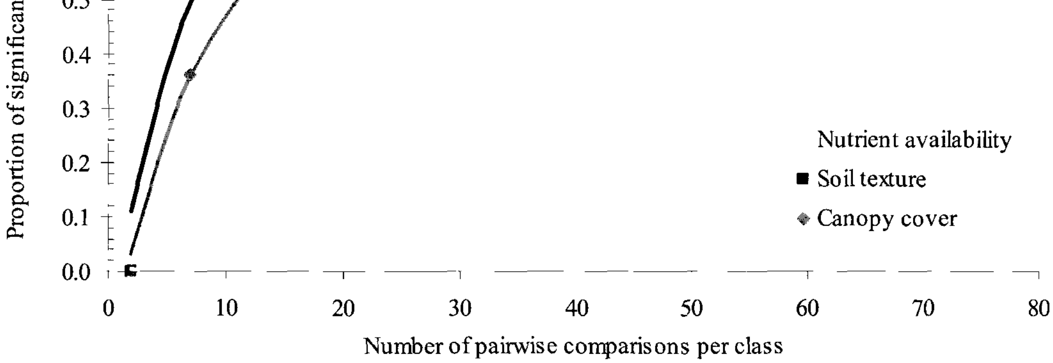

**Figure 30.** Likelihood of detecting significant spatial relationships (with a Mantel test) as a function of the sample size (number of pairwise comparisons) per test, for different variable types. Curves were fit using the line-smoothing function in MS Excel 2003.

## 4.5. Discussion

The maximum distance at which soil texture was autocorrelated was approximately 0.1-10 km, or the smallest inter-site distance class. This range corresponds with the approximate size of surficial geological units in the southern part of the study area (Plouffe 1997a, 1997b). The abrupt change from positive to negative, or nonsignificant spatial autocorrelation observed for many of the variables at greater distances may therefore indicate a change in the geological parent materials from which soils are derived; positive or negative autocorrelation detected at greater scales was too inconsistent to be interpreted as true autocorrelation, and is most likely to be an artefact of the site selection protocols. Although information on the surficial geology of the study area was only available for 7 out of 24 sites, all of which were located either on ice-contact deposits (often with eskers present) or glacial-fluvial terrace sediments (Plouffe 1997a, 1997b), similar landforms were observed in much of the study area.

The autocorrelation range for properties of the forest canopy was larger than that observed for soil texture. This is somewhat surprising, considering that surficial geology is likely an important determinant of forest composition, but may be explained as the result of stand-replacing disturbance having a homogenizing influence on the surrounding forests. The primary disturbance in the study area is wildfire (Delong 2004), and although the disturbance severity may change slightly due to differences in growth characteristics that can be traced to surficial geology, wildfires are unlikely to abruptly halt at the boundaries of different geological units. Indeed, though not presented above, it was common for nearby sites to have similar stand ages, indicating a possible shared origin, and a similar homogenizing influence.

Soil nutrient availability did indeed show positive autocorrelation, but detection of this was impeded by low numbers of pairwise comparisons at small spatial scales, and thus required coarser resolution to detect. Bengston et al. (2007) examined the spatial dependency of soil nutrient availability using PRS$^{TM}$ probes in forests dominated by *Tsuga heterophylla* (Raf.) Sarg. and *Pseudotsuga menziesii* (Mirbel) Franco, and found several similar results: ammonium was autocorrelated at 30-60 m, while iron and aluminum showed autocorrelation at 60 - 110 m. Their analyses were also limited by small sample sizes, particularly in smaller distance classes, but similarly indicate that soil nutrient availability is autocorrelated at the stand scale (Bengston et al. 2007).

Small-scale variability in soil chemistry is often attributed to differences in the horizontal and vertical distribution of plants, microbes, and moisture, in addition to the relatively static parent material composition. Yet, these influences can also change on a temporal scale. Some plants can grow root tissues in modules, responding to the changing availability of soil nutrients by maximizing growth and activity of one area over another between local periods of 'feast and famine' (Farley and Fitter 1999). Microbial activity rates and community composition can change rapidly in response to changes in soil properties, vegetation composition, and disturbance (Lunquist et al. 1999, Ohtonen and Väre 1998), and both nutrient and moisture availability may undergo daily and seasonal fluctuation. Although there is both good theoretical and biological support for small-scale spatial variation that is related to the influence of individual plants, studies that examine small-scale spatial differences in soil chemical properties have almost always used samples that are both spatially and temporally discrete (Moore 1980, Farley and Fitter 1999, Gill et al. 2006), such that there is a danger of spatial relationships being a mis-interpreted form of temporal ones. Bengston et al. (2007) found that the range of autocorrelation in mineral soil ammonium availability was only 18.7 m when measured with one-time samples from soil cores, but was over 60 m when measured with PRS$^{TM}$ probes (which integrated ion availability over several weeks), despite using the same number and dispersion of sub-samples. Researchers who use long-term measurements should be aware of the potential for increased temporal scale to homogenize what would otherwise be spatially discrete patterns.

Because the Omineca Mountain's soils are relatively young, it is possible that many nutrients are derived from inorganic sources (weathered parent materials) rather than from organic sources (Davies and Jones 1988, Gallardo and Paramá 2007). Gallardo and Paramá (2007) found that Ca, Mg, K, and Fe tended to be less patchily distributed in early successional communities than they were in older communities, and suggested that this was due to the nutrient source being predominantly inorganic parent materials in the former and organic soils in the latter. In the Omineca Mountains, the range of autocorrelation was more alike between nutrients and soil texture than between nutrients and forest canopy properties. Furthermore, the organic horizons from the study area were of the mor humus form and often thin (Delong et al. 2004), indicating that nutrient cycling was slow and that spatial signals resulting from the influence of vegetation may require more time to develop.

The understory functional groups that were used to stratify sample quadrats were patchily distributed, and if the distribution of plants is related to the environmental variables examined, it is possible that results showing a lack of spatial structure could simply be a by-product of spatially structured vegetation. Yet, if the sampling strategy used did bias the spatial signal, it would have biased the tests towards not finding spatial autocorrelation between nearby plots, and may therefore be seen as a more conservative (decreased chance of type I error) assessment of those spatial relationships. In fact, spatial relationships were detected in many soil texture and forest canopy variables, indicating that the sampling bias did not make detection of spatial signals so unlikely as to render results inadmissible. Furthermore, significant autocorrelation was detected when a larger distance class was used for within-plot scales, suggesting that, while nutrients were perhaps more different among functional groups than would have occurred if random or systematic sampling was employed, they still became more different at increasing distances within plots.

For the within-plot distance intervals in particular the effective sample sizes were quite small, ranging from 35 to 74 pairwise comparisons. When the number of pairwise comparisons was low, which was more common for the smallest and largest intra-plot distance intervals, the likelihood of detecting significant spatial autocorrelation was reduced. Smaller distance intervals used in this analysis may therefore have suffered from inflated type II error (failing to reject a false $H_0$), but the larger distance intervals should be considered reliable for detection of autocorrelation. The sensitivity analysis also showed that the likelihood of detecting autocorrelation varies substantially from one type of variable to another. An effective sample size (within each distance class) of 30 should be adequate for detection of a spatial signal in canopy and soil texture variables, but for nutrient availability measurements, much larger effective sample sizes are required.

### 4.5.1. Summary and Conclusions

Canopy-based variables, soil texture, and most soil nutrients are autocorrelated within sites in the study area, and are often autocorrelated among nearby sites as well. The likelihood of detection for significant autocorrelation may have been hampered by low numbers of pairwise comparisons in the smallest distance classes, but was also likely reduced by the non-random quadrat selection procedures that were used; quadrats were selected to be more different than would have occurred by chance. Using 30-40 pairwise comparisons for such spatial analyses appears to be appropriate for canopy and soil texture variables, but much larger effective sample sizes, between 70 and 200 pairwise comparisons, and a different sampling strategy are recommended to do the same with most measures of soil nutrient availability.

Western Ag Innovation's recommendations are to regularly distribute probes at densities of four per 100 $m^2$, with the intention of using all four as a single bulked sample to give accurate estimates of nutrient availability at the 100 $m^2$ (or nominally 10 m x 10 m or 5.64 m radius) scale. The results presented here support this recommendation, and further suggest that as few as three pairs of PRS™ probes may be suitable for representing an area of this size, provided they are randomly or systematically distributed. If the objectives of a researcher are to characterize an even larger ecological unit, three groups of three probe pairs distributed across a site (0.125 ha) may do so effectively. Indeed, three pairs may even represent much larger (0.1-10 km diameter stands) areas of forest that coincide with uniform geological parent materials and disturbance history, but sampling with finer spatial resolution in the 100 m to 10 km range is required before a firm upper-limit can be recommended. Further analysis of associations between geological formations and ecological properties could be useful in predicting the occurrence or successional trajectories of lichen-rich forests, and should be attempted once geological information becomes available for the entire study area.

# 5. Microclimate above the ground-layer vegetation in lichen-rich forests of north-central British Columbia

## 5.1. Abstract

The influence of atmospheric moisture on the distribution, dominance, and abundance of vegetation is well studied from a physiological perspective, but generally neglected in habitats that are not considered climatically exceptional. To investigate the potential associations between microclimate and patterns of abundance or dominance of understory vegetation, I recorded temperature and relative humidity above the ground-cover vegetation during 25 summer days in three vegetative patch types: mat-forming lichen, feathermoss, and vascular plants. Data were summarized for raw microclimate attributes and daily water potential of the air, as well as in terms of modelled equilibrium water content of moss or lichen thalli. Analysis of variance revealed significant differences in the water potential of air above the three patch types under sunny conditions, but not under cloudy conditions. The total time above selected water content thresholds was positively correlated with climatic temperature variables and a wind-influenced dripzone (forest canopy) index, and negatively associated with lichen cover and the ratio of sand to silt + clay in the soil. The strongest environmental associations with microclimate were between macroclimatic variables, and to a lesser extent, soil texture or topography. Vegetative variables (both ground-cover and canopy) were only associated with atmospheric moisture during sunny periods. These data suggest that, although both the forest canopy and understory vegetation may predict microclimate to some extent during sunny periods, macroclimate is still the strongest associate of microclimatic conditions.

## 5.2. Introduction

Given that the greatest diversity of lichens and mosses occurs in locations with exceptionally high rainfall, the relative importance of precipitation over other types of atmospheric water is clear (Goward and Spribille 2005, Hauck and Spribille 2005, Turner et al. 2006, Radies et al. 2009). This is most apparent for epiphytic cyanolichens (those with cyanobacterial photobionts), which require liquid water to become photosynthetically active (Nash 1996, Radies et al. 2009). Yet, in many terrestrial habitats, precipitation is more limited; non-precipitative atmospheric moisture (NPAM), such as dew or fog, may be the only source of water for lichens and mosses in such places, which nevertheless contain rich cryptogamic communities (Lange et al. 1991, Kidron et al. 2002).

Many studies have described the influence of humidity, water potential, and other measures of atmospheric moisture on physiological activity in bryophytes, lichens, and vascular plants under controlled conditions (Longton 1988, Proctor 2000). It is less common to find studies of association between atmospheric moisture and the distribution, abundance, or dominance of terrestrial vegetation in the field outside of extreme habitats such as deserts or tundra (e.g., Kershaw and Larson 1974, Lange et al. 1991, Kidron et al. 2002). The first objective of this chapter is to examine whether measurements of atmospheric moisture are related to the dominance or abundance of lichens, feathermosses, or vascular plants in the understory of a boreal pine forest.

The frequency or duration of NPAM can, like precipitation, be described at macro-climatic scales, but may also be affected by small-scale variation in vegetation cover or topography, particularly when this variation affects whether or not a given patch receives direct irradiance from the sun (Jones 1983, Kidron 2005). This leads to an interesting ecological question: for the evaluation of vegetation-NPAM relationships, which scale is the most important, and when? The second objective of this chapter is to examine the relative strength of association (importance) of macroclimatic variables and other abiotic factors with measurements of atmospheric moisture (microclimate) in ground-cover functional group quadrats, and compare them with the associations between vegetative cover (at both ground and forest canopy levels) and microclimate.

## 5.3. Methods

### 5.3.1. Data logger deployment

See Chapter 2 for detailed methods for vegetation characterization including the study area description and site selection protocols. Temperature and relative humidity (RH) data loggers (Hobo® U23-001, Onset Computer Corporation) were placed at one functional group quadrat (chosen randomly in the first site, and systematically thereafter) in the centre plot of each site, amidst the ground-layer vegetation. Although having a data-logger at every quadrat of each site would have been ideal, such intensive data collection would have been prohibitively expensive. This alternative strategy was thought to be an optimal trade-off between regional and microsite representation, which yielded sufficient data to examine the associations of environmental variables and vegetative cover directly with atmospheric moisture. The records from these quadrats appeared to be representative of the trends observed for the study; for example, the mean canopy closure at feathermoss and vascular plant quadrats was approximately 50%, and it was 48% for lichen quadrats.

Among sites, logger placement alternated from lichen to feathermoss to vascular-plant dominated quadrats of the center plot, so that each functional group (FG) received approximately equal representation (Table 12). Data loggers were secured to the north-facing side of a wooden stake, at a height of approximately 2 cm above the ground. To minimize the difference between temperatures at the top and bottom of the unit, loggers were oriented horizontally, and shielded from the sun by a 10 × 12 cm aluminum foil pan, approximately 5 cm above the top of the logger. Relative humidity and temperature were recorded once every 5 min. for 6 weeks. During the second stage of data collection, data were downloaded and loggers were removed from the site.

**Table 12.** Distribution of temperature and RH data loggers throughout study area. Latitude, longitude, and elevation were obtained from GPS data, whereas canopy closure was measured via hemispherical-lens photography and digital image analysis.

| Site | Dominant vegetation | Date and time of deployment | Time (days) | Latitude (Dec. °) | Longitude (Dec. °) | Elevation (m) | Canopy closure (%) |
|---|---|---|---|---|---|---|---|
| 7 | lichen | 08/04/2008 08:00 | 49 | 56.034 | -125.238 | 935 | 39 |
| 13 | lichen | 07/19/2008 12:10 | 46 | 55.832 | -125.216 | 985 | 56 |
| 18 | lichen | 07/31/2008 15:05 | 46 | 56.377 | -125.469 | 932 | 49 |
| 28 | lichen | 07/28/2008 14:30 | 46 | 55.653 | -124.682 | 1091 | 49 |
| 43 | lichen | 07/30/2008 09:40 | 46 | 56.411 | -125.671 | 951 | 59 |
| 48 | lichen | 07/16/2008 12:15 | 46 | 56.037 | -125.428 | 983 | 50 |
| 51 | lichen | 07/17/2008 16:15 | 46 | 56.081 | -125.573 | 1043 | 45 |
| 100 | lichen | 08/03/2008 09:45 | 44 | 56.311 | -125.320 | 965 | 41 |
| 1 | moss | 07/29/2008 09:00 | 33 | 55.806 | -125.305 | 1005 | 53 |
| 6 | moss | 08/04/2008 13:35 | 44 | 56.020 | -125.275 | 993 | 46 |
| 9 | moss | 08/03/2008 15:45 | 44 | 56.146 | -125.152 | 868 | 55 |
| 12 | moss | 07/18/2008 15:35 | 46 | 55.831 | -125.207 | 978 | 53 |
| 17 | moss | 08/01/2008 09:15 | 45 | 56.370 | -125.440 | 911 | 49 |
| 29 | moss | 07/26/2008 13:55 | 57 | 55.658 | -124.682 | 1108 | 48 |
| 41 | moss | 07/30/2008 15:30 | 46 | 56.404 | -125.623 | 977 | 49 |
| 46 | moss | 07/15/2008 17:15 | 46 | 56.041 | -125.390 | 1009 | 54 |
| 49 | moss | 07/17/2008 10:00 | 46 | 56.078 | -125.598 | 1013 | 42 |
| 19 | vascular | 08/01/2008 15:20 | 45 | 56.373 | -125.423 | 983 | 51 |
| 27 | vascular | 07/20/2008 09:45 | 45 | 56.016 | -125.229 | 969 | 52 |
| 33 | vascular | 08/05/2008 09:10 | 39 | 55.927 | -125.189 | 993 | 46 |
| 34 | vascular | 07/18/2008 10:00 | 46 | 55.952 | -125.197 | 1017 | 47 |
| 42 | vascular | 07/31/2008 09:00 | 53 | 56.407 | -125.601 | 1027 | 55 |
| 44 | vascular | 07/15/2008 10:45 | 46 | 56.037 | -125.396 | 946 | 49 |
| 45 | vascular | 07/16/2008 16:35 | 46 | 56.036 | -125.411 | 958 | 50 |

Temperature and RH data were collected for approximately six weeks at each quadrat, but the recording periods of these quadrats were not synchronous. To reduce the potentially inflated variability associated with having non-synchronous time periods over which data were collected (with the added influence from time of year, or seasonality), the recording window to be used in analyses was narrowed to a 25-day period from the 5th to the 30th of August, 2008. These dates corresponded with the last deployment and first retrieval of the data loggers, ensuring that they experienced the same overall weather patterns during the same time period.

### 5.3.2. Water potential

I calculated the water potential of air ($\Psi_{air}$) from temperature and RH measurements for each five-minute recording period (n = 7201). The water potential of air is a more direct indicator of the dehydrating power of the air than either temperature or RH is alone (Jones 1983, Nobel 2005). Because mosses and lichens are poikilohydric and can absorb water in either liquid or vapour form, water potential additionally represents the water-supplying power of air, and can be used to calculate the equilibrial water content of plants and lichens (Heatwole 1966, Bayfield 1973, Proctor 2000, Jonsson et al. 2008).

For each site, I took the average of daily minimum, mean, and maximum water potentials under either 'sunny' or 'cloudy' conditions, yielding six summaries of $\Psi_{air}$ for each site. Next, I tested these $\Psi_{air}$ summary statistics to see if any differences occurred among functional groups (lichen, feathermoss, or vascular plant), using factorial ANOVA followed by Tukey-Kramer multiple comparison tests. The significance level was increased (from $\alpha = 0.05$ to $\alpha = 0.10$) for this chapter over previous ones, because of the much smaller sample sizes and increased chance of type II error. Tests were conducted using SAS v. 9.2.1 (SAS Institute 2010), with the GLM procedure.

### 5.3.3. Water content thresholds

Jonsson et al. (2008) used a similar derivation of water potential to determine its relationship with the equilibrium water content ($WC_{eq}$) of *Cladonia rangiferina* (L.) Weber ex F.H. Wigg. They determined that the two measures showed an exponential relationship, which can be represented by the equation:

$$WC_{eq} = WC_{sat} \bullet e^{(W_{eq} \bullet \Psi_{air})},$$

where $WC_{sat}$ is the water content at full saturation (cell turgidity) in the lichen thallus, and $W_{eq}$ is a species-specific constant, related to the tissue structure of the species and how readily it absorbs and holds water (Jonsson et al. 2008). Since the authors expressed water content as the observed weight of water divided by the weight of water at saturation, $WC_{eq}$ is expressed as a percentage between zero and 100, while $WC_{sat}$ is constant at 100 (Jonsson et al. 2008). This measure of water content is commonly described as the relative water content (RWC), or percent saturation, and is useful when comparing across multiple taxa. Indeed, the minimum RWC of mosses at turgidity seems to be remarkably similar among species (approximately 70%), and because full turgidity coincides with maximum photosynthetic rate ($P_{max}$), RWC is an appropriate indicator of potential physiological status (Proctor 2000).

Using Jonsson et al.'s (2008) formula, water content at equilibrium for *C. rangiferina* was calculated for each five-minute measurement interval in all quadrats. These data were then summarized for each site as the frequency (proportion of total measurements) for which one of four $WC_{eq}$ thresholds was exceeded. The thresholds used were 10%, 20%, 40%, and 70% saturation, corresponding to $\Psi_{air}$ values of -19.19, -13.41, -7.64 and -2.97 MPa, respectively. These critical values are subsequently referred to as low, medium, high, and highest $WC_{eq}$ thresholds, and coincide with published data on physiologically important thresholds for several species of lichen or moss. For example, $P_{min}$ often corresponds with 10% relative water content (RWC), the water compensation point corresponds with 20% relative water content, and $P_{max}$ ranges from 40-70% RWC depending on the species

(Heatwole 1966, Kershaw 1972, Bayfield 1973, Jones 1983, Alpert and Oechel 1985, Longton 1988, Williams et al. 1996, Csintalan et al. 2000, Proctor 2000, Uchida et al. 2002, Coxson and Wilson 2004). The RWC threshold exceedence frequencies were tested for linear relationships with understory functional group abundance and several environmental variables (Table 13) using Pearson's correlation tests; it was expected that feathermoss quadrats would show greater durations of time above all water content thresholds, while lichen quadrats would show the least. Analyses were conducted using SAS v. 9.2.1 (SAS Institute 2010), with the CORR procedure.

**Table 13.** Names, descriptions, and sources of variables used in correlation analysis. ClimateBC is a linear climate interpolation model (Wang et al. 2006), TRIM is the terrain resources inventory management digital GIS layer, and DEM is the digital elevation model used in TRIM (Geo B.C. 2008), GLA is a program that analyzes hemispherical photos (Frazer et al. 1999).

| Variable name | Description | Source |
|---|---|---|
| Vascular | Vascular plant abundance (% cover) in quadrat | Measured |
| Lichen | Mat-forming lichen abundance (% cover) in quadrat | Measured |
| Moss | Feathermoss abundance (% cover) in quadrat | Measured |
| MAT | Mean annual temperature | ClimateBC |
| TD | Difference between highest and lowest monthly temperatures | ClimateBC |
| MAP | Mean annual precipitation | ClimateBC |
| DDltz | Degree days less than zero | ClimateBC |
| NFFD | Number of frost free days | ClimateBC |
| WInDZ | Wind-influenced drip-zone (see chapter two) | Modelled |
| CRDZ | Crown radius drip-zone (see chapter two) | Modelled |
| SWDZ | South-west facing densiometer measurement (see chapter two) | Measured |
| LFH | Thickness of litter, fermentation, and humus layers | Measured |
| LAI | Estimated effective leaf area index | GLA |
| Total_irrad | Total transmitted irradiance (direct + diffuse) | GLA |
| Trans Dir | Transmitted direct irradiance | GLA |
| Coarses | Percent content of coarse fragments and gravel (>2 mm) | Measured |
| Gravel | Percent content of gravel in soil (0.2-7.5 cm) | Measured |
| Sand : Silt+Clay | Ratio of sand (0.05 - 2 mm) to silt and clay (<0.05 mm) | Measured |
| Mesotopo | Topographic position on a scale of 10-50 m | Measured |
| N-aspect | Cosine-transformed mesotopographic aspect (northness index) | Measured |
| Slope | Slope inclination (degrees) on a scale of 10-50 m | Measured |
| SNaspect | Cosine-transformed macro-slope aspect from digital elevation model | TRIM DEMs |
| EWaspect | Sine-transformed macro-slope aspect from digital elevation model | TRIM DEMs |
| Elevation | Estimated elevation from digital elevation model | TRIM DEMs |

### 5.3.4. Ambient weather conditions

Because no weather stations were located in the study area itself, and observers were not present to document weather conditions between August 5th and August 30th, it was necessary to use the data from the Hobo® data loggers themselves to determine local weather conditions. This was done by examining the daily variation in temperature over the sampling period, and based on whether the variation was large or small, determining whether the day was sunny or cloudy. Of course, using those classifications to explain differences in the relationships between water potential and environmental variables in the subsequent analyses is a somewhat circular argument. Consequently, it was necessary to examine how these daily variations in the study area related to the actual weather conditions. Two data sources were compared to records from the first six data loggers (all installed by July 18th), and were used to provide support for this approach: (1) observations of ambient conditions during the plot-establishment period, and (2) observations of temperature and precipitation at the nearest weather stations of the area, from July 18th to August 5th. I expected that data logger records would show a greater range in temperature than measurements of ambient conditions since the former were measuring ground layer temperature, but that the changes in variability (i.e., daily temperature range) would be synchronous. Data were obtained from the National Climate Data and Information Archive (Environment Canada 2010).

Using 56 ° N latitude and 125.5 ° W longitude as the starting point, and the online search tool for Environment Canada's 'National Climate Data and Information Archive' (http://www.climate.weatheroffice.gc.ca), only a single climate station was located within 100 km (Germansen Landing), and no data were available for that station after 1979. The search was then extended to a 200 km radius of the study area, and yielded six stations, of which four had daily records during the summer of 2008. I downloaded temperature and precipitation data (RH was not available) that were recorded at each station from July 18th until August 30th to use in subsequent analyses.

## 5.4. Results

### 5.4.1. Water potential

The average daily maximum water potential was not significantly different among patch types, regardless of weather conditions. Yet only above feathermoss patches did the mean $\Psi_{air}$ reach maximum values of -3.0 MPa or more on a regular basis; vascular quadrats did so for only a few minutes of a few days, while lichen quadrats did not exceed this threshold at all (Figure 31). The average daily minimum $\Psi_{air}$ differed significantly among functional groups under all weather conditions ($F_{(2,21)} = 6.19, p = 0.008, \eta^2 = 0.37$ for sunny and $F_{(2,21)} = 3.07, p = 0.068, \eta^2 = 0.23$ cloudy conditions), though differences were minimal under cloudy conditions (Figure 31). The average daily mean $\Psi_{air}$ differed significantly among functional groups under sunny conditions ($F_{(2,21)} = 3.58, p = 0.046, \eta^2 = 0.25$), but not under cloudy conditions.

Multiple comparison testing confirmed that the air above feathermoss patches tended to have more moisture than that above other functional groups; numbers in brackets indicate the mean and standard error of $\Psi_{air}$, in MPa. The average daily minimum $\Psi_{air}$ above feathermoss (-135.81 ± 7.77) was significantly greater than that above lichens (-180.75 ± 9.22) or vascular plants (-169.76 ± 12.78) under sunny conditions (Figure 32). Under cloudy conditions, the average daily minimum $\Psi_{air}$ was also significantly greater above feathermoss (-32.72 ± 3.99) than above lichens (-48.24 ± 4.45), while vascular plant patches were intermediate and not significantly different from either group (Figure 32). Similar trends were observed for daily mean $\Psi_{air}$ during sunny conditions. On average, daily mean $\Psi_{air}$ was significantly greater over feathermosses (-50.32 ± 1.45) than lichens (-66.31 ± 1.97), with vascular plants being intermediate and not significantly different from the other patch types (Figure 32).

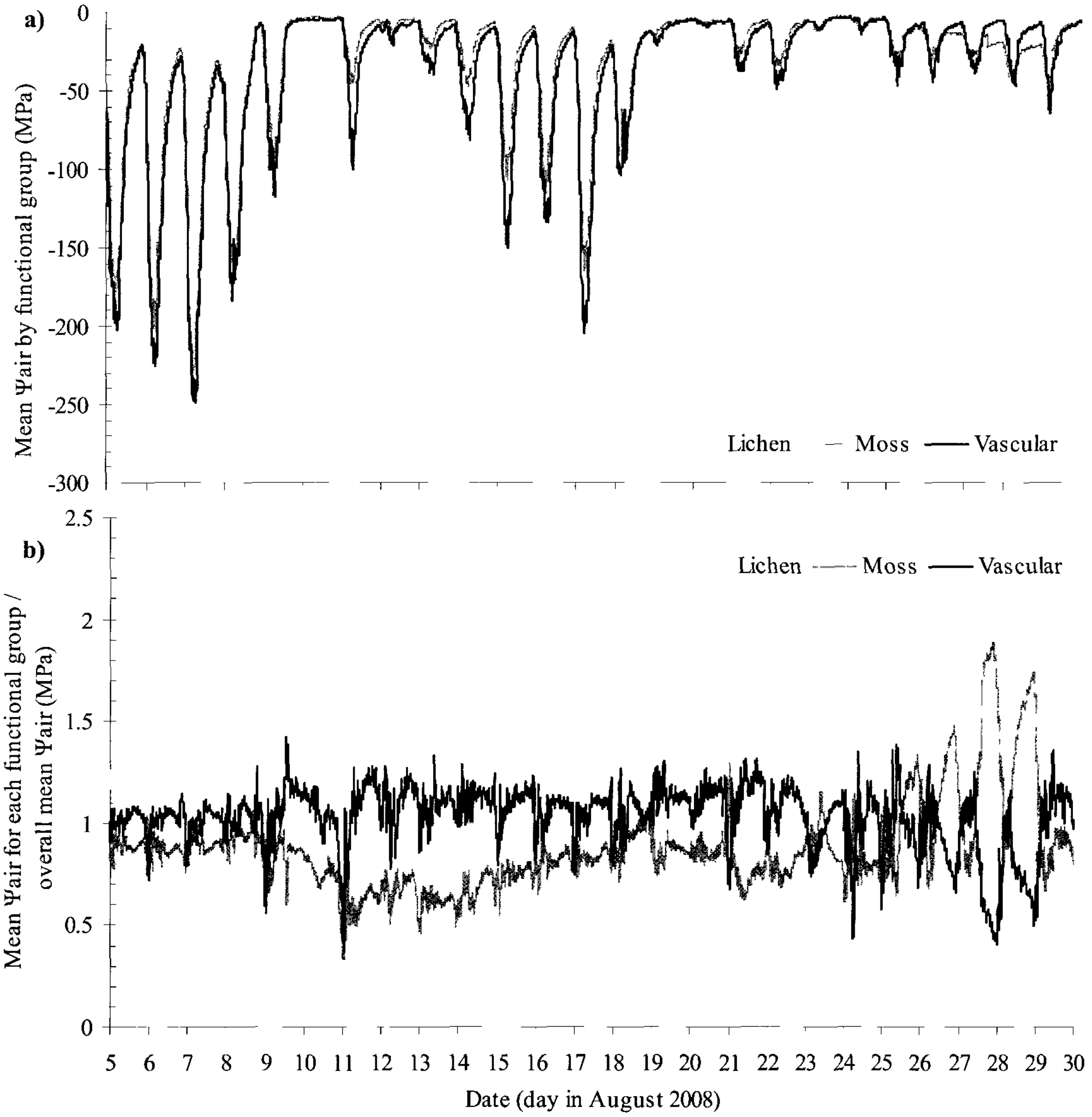

**Figure 31.** (a) Raw mean water potential of air, and (b) standardized (functional group mean / overall mean) mean water potential of air over three types of understory vegetation, measured 2 cm above the vegetation in three functional groups of understory vegetation over 25 days in August, 2008.

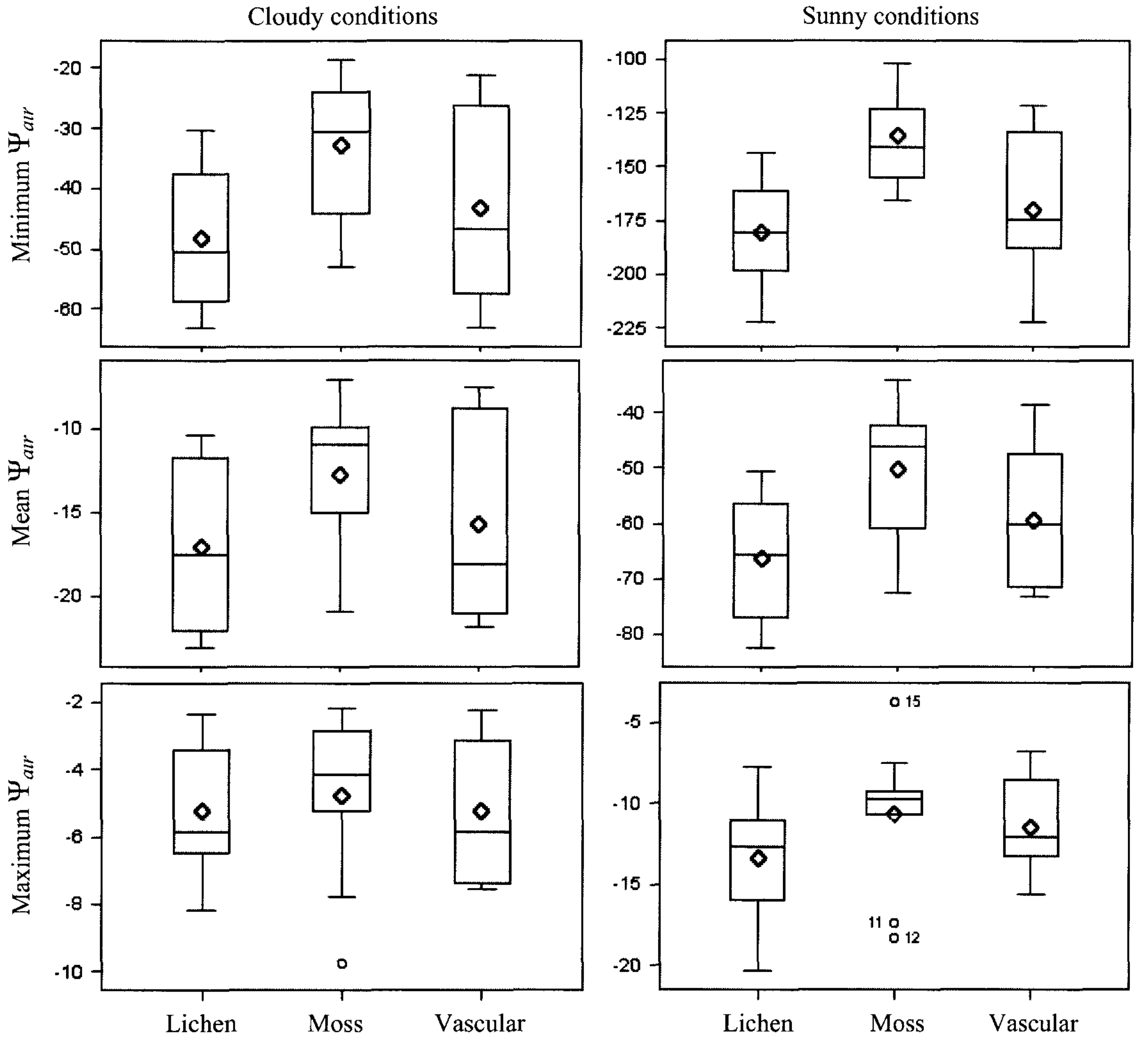

**Figure 32.** Daily minimum, mean, and maximum water potential of air ($\Psi_{air}$, in MPa), calculated from measurements of temperature and relative humidity taken 2 cm above ground-cover vegetation in lichen (L), feathermoss (M), and vascular plant (V) patches. Diamonds represent the mean, boxes show the median and 25-75 interquartile range, whiskers represent the bounded maximum and minimum values, and labelled circles represent outliers.

### 5.4.2. Water content thresholds

Throughout this section, whenever multiple r and *p*-values are presented, they are in order from the lowest (10%) to the highest (40%) $WC_{eq}$ thresholds; due to a high number of zero values (i.e., 29% of quadrats did not attain a water potential of more than -2.97 MPa), the highest (70%) $WC_{eq}$ threshold (as originally defined) was excluded from the analysis. Correlation analyses revealed a small number of significant associations between the frequency at which $WC_{eq}$ thresholds were exceeded in given quadrats and the environmental or vegetative variables. That few correlations were significant, and that few significant correlations were strong was consistent with the influence of small sample sizes (n = 24), and indicates that more measurements per functional group are required to provide substantial support for the observed relationships.

Vegetative ground cover and canopy cover show associations with time above $WC_{eq}$ thresholds primarily when conditions were sunny, while abiotic variables (climate, soil texture) showed significant correlations under both sunny and cloudy conditions, but with stronger correlations during cloudy conditions (Table 14). Lichens were the only functional group that showed significant abundance-microclimate correlations, and only with the low and medium $WC_{eq}$ thresholds under sunny conditions, yet these correlations were weak at best ($r = -0.40$ and $-0.36$; $p = 0.054$ and $0.087$, with the low and medium $WC_{eq}$ thresholds, respectively). Similarly, wind-influenced drip-zone was the only canopy variable that had a significant positive relationship with $WC_{eq}$ threshold exceedence, and it only did so under sunny conditions ($r = -0.36$ and $-0.36$; $p = 0.081$ and $0.083$, with the low and medium $WC_{eq}$ thresholds respectively; Table 14). Curiously, transmitted direct irradiance, despite being the product of canopy light interception, was negatively correlated with low and medium $WC_{eq}$ threshold exceedence during cloudy conditions ($r = -0.35$ and $-0.36$; $p = 0.0975$ and $0.0879$).

Mean annual temperature was negatively correlated with time above all $WC_{eq}$ thresholds during cloudy conditions ($r = -0.41$, $-0.38$, and $-0.40$; $p = 0.049$, $0.071$, and $0.054$), while this relationship was weaker under sunny conditions where it was only significant for time above the highest $WC_{eq}$ threshold ($r = -0.48$, $p = 0.018$; Table 14). The number of frost-free days was the strongest single predictor of $WC_{eq}$ threshold exceedence frequency; it was consistently negatively correlated with time above all $WC_{eq}$ thresholds under both sunny (r =

-0.36, -0.39, and -0.54; $p = 0.076$, 0.059, and 0.006) and cloudy conditions (r = -0.49, -0.46, and -0.49; $p = 0.016$, 0.023, and 0.015). The number of degree-days less than zero was positively correlated with time above the highest $WC_{eq}$ threshold under sunny conditions (r = 0.40, $p = 0.054$), and with time above the lowest $WC_{eq}$ threshold under cloudy conditions (r = 0.42, $p = 0.043$).

The ratio of sand to silt and clay was negatively correlated with time above the lowest sunny-condition $WC_{eq}$ threshold (r = -0.35, $p = 0.099$), as well as with time above all three cloudy-condition $WC_{eq}$ thresholds (from low to high $WC_{eq}$: r = -0.39, -0.36, and -0.37; $p =$ 0.059, 0.086, and 0.074). Slope inclination was the only other abiotic variable to show a significant correlation, and it was negatively related to time above the highest sunny-condition $WC_{eq}$ threshold (r = -0.37, $p = 0.073$).

**Table 14.** Correlation coefficients (Pearson's r) and *p*-values for variables that showed a significant relationship with time above at least one of the water content thresholds. Coefficients are in bold for the data subset in which they were significantly associated.

| | | Sunny conditions | | | Cloudy conditions | | |
|---|---|---|---|---|---|---|---|
| Variable | Statistic | Low (10%) | Medium (20%) | High (40%) | Low (10%) | Medium (20%) | High (40%) |
| Lichen abundance | r | **-0.40** | **-0.36** | -0.31 | -0.34 | -0.33 | -0.32 |
| | *p* | 0.0542 | 0.0871 | 0.1434 | 0.1032 | 0.1208 | 0.1323 |
| MAT | r | -0.28 | -0.31 | **-0.48** | **-0.41** | **-0.38** | **-0.40** |
| | *p* | 0.1872 | 0.1450 | 0.0177 | 0.0488 | 0.0705 | 0.0544 |
| Degree days <0 | r | 0.24 | 0.26 | **0.40** | **0.42** | 0.34 | 0.32 |
| | *p* | 0.2669 | 0.2195 | 0.0540 | 0.0434 | 0.1071 | 0.1257 |
| NFFD | r | **-0.37** | **-0.39** | **-0.54** | **-0.49** | **-0.46** | **-0.49** |
| | *p* | 0.0757 | 0.0593 | 0.0063 | 0.0155 | 0.0225 | 0.0153 |
| WInDZ | r | **0.36** | **0.36** | 0.33 | 0.12 | 0.11 | 0.15 |
| | *p* | 0.0809 | 0.0832 | 0.1123 | 0.5889 | 0.5937 | 0.4725 |
| Direct irradiance | r | -0.14 | -0.15 | -0.09 | **-0.35** | **-0.36** | -0.32 |
| | *p* | 0.4991 | 0.4820 | 0.6825 | 0.0975 | 0.0879 | 0.1321 |
| Sand : Silt + Clay | r | **-0.35** | -0.34 | -0.29 | **-0.39** | **-0.36** | **-0.37** |
| | *p* | 0.0987 | 0.1075 | 0.1716 | 0.0592 | 0.0857 | 0.0742 |
| Slope inclination | r | -0.29 | -0.31 | **-0.37** | -0.24 | -0.18 | -0.16 |
| | *p* | 0.1675 | 0.1384 | 0.0733 | 0.2584 | 0.4029 | 0.4550 |

### 5.4.3. Ambient weather conditions

Although the time spent in the field was not constant from July 18th until August 5th, both sunny and cloudy conditions were recorded for at least several days in succession. The single sunny stretch of four days coincided well with a period of increasing daily temperature range for both regional weather stations and study area data loggers, as well as with decreasing daily minimum RH from data loggers and zero precipitation for weather stations (Figure 33). Both of the cloudy periods showed the opposite pattern: decreasing or low daily temperature ranges, high relative humidity, and measurable precipitation (Figure 33). These observations agree with the prediction that patterns in the average daily temperature range and minimum RH of data loggers could be used to classify days as sunny or cloudy in the absence of observers. Specifically, the sunny days were August 5-9, 11, 14 - 17, and 28 - 29, while days estimated to be cloudy were August 10, 12 - 13, and 18 - 27.

## 5.5. Discussion

Although few significant correlations were observed between ground cover vegetation and time spent above equilibrial water content thresholds, the feathermoss quadrats clearly showed greater minimum and mean daily water potential than the other two functional groups (Figure 32). It is somewhat surprising that maximum water potential was not more strongly associated with feathermoss dominance, especially considering the relative infrequency of water potentials that correspond with photosynthetic optima observed in the literature (Proctor 2000). One explanation for this lack of association may be that the maximum water potentials observed were simply not long enough in duration to be of biological relevance. True equilibrium between plant or lichen water content and atmospheric water potential is rarely achieved under natural settings (Jonsson 2008). More often, changes in tissue water content will lag behind changes in atmospheric water potential, though this lag time tends to be greater for lichens than for mosses (Heatwole 1966, Kershaw 1985, Hernández-García et al. 1999, Jonsson 2008).

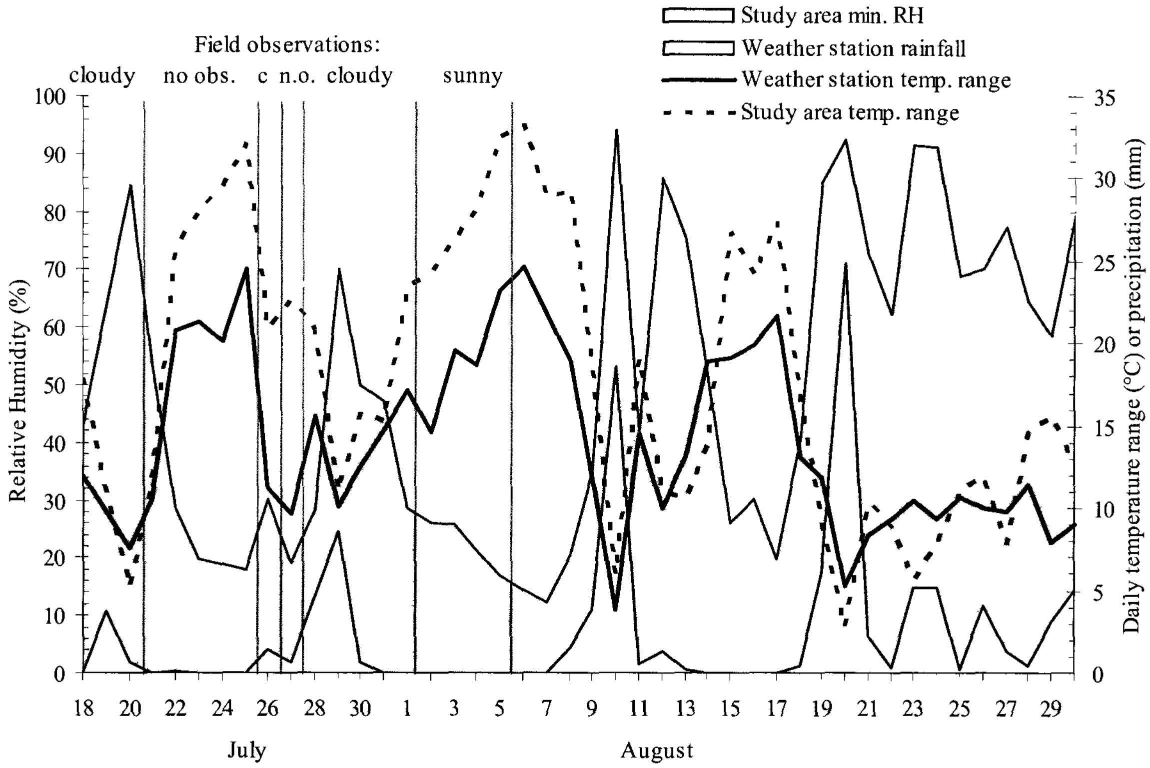

**Figure 33.** Daily temperature range, relative humidity, and precipitation as recorded at ground level in study area and as ambient conditions at regional weather station. Overlaid vertical bars and text at the top-left indicate observations of general weather conditions for periods when observers were in the study area (no obs. and n.o. indicate that the observers were not present to observe or record ambient conditions at these times).

Daily maximum water potentials (and the 40 or 70% $WC_{eq}$ thresholds) were generally reached in the early morning hours, before sunrise; this agrees well with observations of diurnal fluctuation in photosynthesis and moisture levels (Moser and Nash 1978, Lechowicz and Adams 1973). This may suggest that maximum daily water potentials are of little biological importance, since having greater water content during early morning hours is unlikely to be of much benefit if there is no light for photosynthesis. Indeed, in the absence of light, dark respiration rates are also positively associated with hydration (Lechowicz and

Adams 1973). Yet, by maintaining greater moisture levels throughout the night, photosynthetic activity is surely prolonged once light becomes available again in the latter part of the morning. Therefore, daily maximum water potentials may be seen as a measure of resistance to moisture depletion for a given microclimate. Nevertheless, differences in $\Psi_{air}$ among patch types were only detected for daily minimum and mean values, indicating that differences in the severity of moisture depletion during the day are, in fact, the most relevant in differentiating among patch types, and may be more physiologically relevant.

Cloudy days differ from early morning hours in that diffuse light is still present. On these days, minimum water potentials and the frequency of water content threshold exceedence is a much more direct indicator of photosynthetic activity in the vegetation (Moser and Nash 1978). That assumes, of course, that the vegetation is obtaining its water only in the form of NPAM. The water potential of air is less ecologically relevant if rain is periodically allowing lichens and mosses to become fully saturated, because the vegetation will be operating at $P_{max}$ for some time even after the cessation of rainfall due to having an accretion of 'external capillary space water' (Moser and Nash 1978, Kershaw 1985, Proctor 2000, Jonsson 2008). If the nearest weather stations were an appropriate indication of days with precipitation (and it is likely that they were given their close correspondence with measured temperature and RH), it would indicate that a large proportion of the time over which these data loggers were active was not moisture limiting (i.e., NPAM was not the only available source of moisture). If this is correct, the relationships detected during these times are not as relevant for detecting differences in microclimate among functional groups.

Both understory and canopy vegetation may exert some control on the amount of atmospheric moisture present at ground level, given that minimum and mean daily $\Psi_{air}$ differed among functional groups, and that both WInDZ and lichen cover were associated with time above $WC_{eq}$ thresholds. It also seems likely that the physical environment of the quadrat has an effect on the microclimate, since macroclimatic variables were associated with time above $WC_{eq}$ thresholds during both sunny and cloudy periods, and soil texture was primarily associated with time above $WC_{eq}$ thresholds during cloudy periods. Soil texture and slope inclination only had weak associations with microclimate, but this was to be expected given the relative paucity of slopes with sufficient inclination to change the heat-loading at ground level (Chapter 2). Given the relatively weak association documented in other studies where vegetation had a prevailing influence (Balisky and Burton 1995), it is somewhat remarkable that a small-scale association with slope inclination was detected at all.

The positive association between WInDZ and the time above $WC_{eq}$ thresholds indicates that both the direction and the density of canopy cover are important in regulating microclimate. Specifically, patches with higher densities of trees on their windward (western) sides tend to have higher water potential. Whether this is due to the protection from prevailing winds afforded by close tree proximity, or due to the interception of direct irradiance during the more strongly desiccating afternoon time periods (McCune and Keon 2002) is unknown. Nevertheless, the combination of a generally low wind speed at ground level in all quadrats (personal observation), and the stronger association between WInDZ and time above $WC_{eq}$ during sunny periods, lend support to the latter explanation.

Macroclimate has a consistently stronger association with atmospheric moisture than vegetation, under both sunny and cloudy conditions; this suggests that macroclimate is the main influence under both conditions, and that the correlation seen between vegetation and microclimate may be a product of the influence that macroclimate has on vegetation itself. Yet, because the influence of canopy cover, vegetative cover, and abiotic factors were all found to correlate with atmospheric moisture, it is conceivable that the vegetation accentuates those aspects of microclimate that favour their own growth during periods that are otherwise moisture-limiting, thereby facilitating it's own persistence.

Unfortunately, there were no unoccupied (bare ground) control quadrats, and quadrat selection was biased towards well-vegetated patches, making it difficult to determine whether one vegetation type is capable of influencing or responding to microclimate more than another, and in what way. Although the drier conditions observed in lichen quadrats may suggest that lichen mats reflect the conditions of an unvegetated patch, lichen quadrats are naturally predisposed to occupy patches that are drier and more exposed (Chapter 2), and mat-lichen cover can actually increase moisture and decrease temperature near the ground (Rouse and Kershaw 1971, Kershaw and Field 1975, Kershaw 1985). It is more likely that exposed but unvegetated patches are even warmer and drier than lichen-dominated patches, and that similarly unvegetated patches in shady conditions would be somewhat moist and cool even without feathermoss cover.

### 5.5.1. Summary and Conclusions

The water potential of air above different vegetative functional groups differs with group identity; feathermosses patches tend to exhibit the highest (least negative) $\Psi_{air}$, while lichens have the lowest, and vascular plants are intermediate. This is most apparent when using minimum daily $\Psi_{air}$ as the metric (rather than maximum or mean), and during sunny conditions, when precipitation is unavailable and evaporative stresses are greater. The time spent above water content thresholds of 10, 20, and 40% was most consistently related to macroclimatic variables, but was also negatively related to soil coarseness and slope inclination, positively related to windward canopy cover during sunny periods, and negatively related to lichen cover during sunny periods.

Macroclimate and abiotic factors appear to be the most consistently important variables to influence microclimate. Vegetative cover (both understory and canopy) may also have an influence, but this is primarily during sunny conditions and it is difficult to determine whether this influence is truly one of vegetation on microclimate or a by-product of the influence that macroclimatic conditions have on the vegetation. Given this dominance of macroclimate in microclimatic associations, vegetation management may have limited benefit in terms of improving conditions for one functional group over another. If forest managers are seeking to promote one type of understory vegetation over another, and overstory or understory vegetation is thought to be contradicting that management objective, consideration should be given to whether macroclimatic conditions are such that they would render vegetation modification ineffective in achieving the desired management outcomes.

Further study of microclimatic conditions should include control (unvegetated) patches for comparison, and should more directly examine the role of vegetation in regulating microclimatic conditions by use of reciprocal transplants, vegetation removal, and direct measurement of water content or water stress. In addition, microclimatic measurements should include measures of local precipitation, to further elucidate the relative biological importance of NPAM and precipitation.

# 6. Synthesis: discussion, applications, and conclusions

## 6.1. Discussion

Ecologists have often examined both edaphic and canopy attributes of lichen-rich forests in a categorical fashion, rather than using continuous measures of understory-environment associations, thereby limiting the generalizability of their results (Johnson 1981, Carroll and Bliss 1982, Hunt et al. 2003, Bainbridge and Strong 2005, Uotila et al. 2005). Although canopy measurements are often stand-level averages of several systematic measurements, edaphic factors are usually assessed by using a single measurement or soil pit (Johnson 1981, Carroll and Bliss 1982, Hunt et al. 2003, Bainbridge and Strong 2005). It is rare for researchers to measure canopy influence at the microhabitat scale (e.g., Sulyma and Coxson 2001, Kembel and Dale 2006), and even rarer for the same to be done for edaphic properties (e.g., Kershaw and Larson 1974). Studying understory-environment relationships with stand-scale measurements may indeed be appropriate for certain applications, because both forest canopies and surficial geology tend to be autocorrelated at intermediate scales. Nevertheless, understory vegetation is not always uniformly distributed in lichen-rich forests, suggesting that the variation within forest stands is both ecologically interesting and relevant, particularly from a mechanistic point of view.

I measured canopy and edaphic attributes at both the microhabitat and stand scales, with an emphasis on the former, to examine 'within-stand' variation, and compare it to more traditional approaches. Using this approach allowed me to detect functional group associations with microclimate, small-scale edaphic gradients, such as soil texture and nutrient availability, and spatially explicit canopy gradients, such as the potential effects of morning vs. afternoon sun, high to low direct or diffuse irradiance, north vs. south shading, high to low litter deposition rates, and varying rates of throughfall precipitation or interception. When explicitly defined and measured (or modelled), these gradients associated as strongly with functional group abundance at the microhabitat scale as generalized canopy cover did with understory compositional gradients at the stand scale. In addition, these microhabitat-based gradients illuminate potential mechanisms of interaction, because they were spatially explicit. This effect was also partly attributable to my use of principal components analysis to create linear combinations of environmental variables. Because principal components represented sequential subsets of the data, I was able to highlight potentially important environmental gradients that would have otherwise been obscured by more prominent ones.

To further illustrate the directionality (and perhaps the mechanism) that was implicit in principal components, I illustrated several of the canopy (biotic) components that contributed significantly to the vascular plant principal component regression model (Chapter 2). Figure 34 depicts a forest stand with trees of varying size from an oblique angle, with several biotic (canopy) gradients overlaid as vectors. With the exception of the generalized canopy closure gradient that was common to all regression models (summarized by the black arrows), all biotic components are spatially or directionally explicit. For example, patches within the crown radius projection of canopy trees score high on the LFH thickness / dryness gradient, as indicated by the blue arrows, particularly when they are on the leeward (eastern) side of a tree (Figure 34); these patches tend to have greater abundance of vascular plants, but lower abundance of lichens and feathermosses.

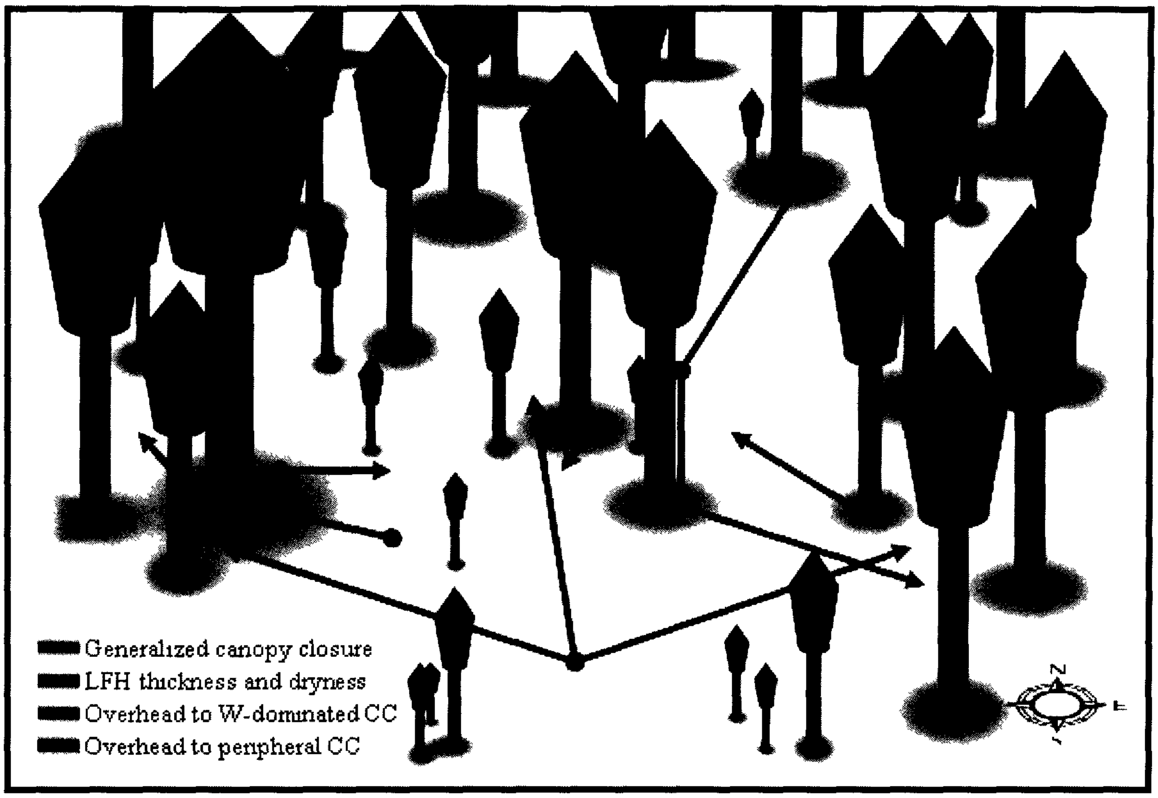

**Figure 34:** Diagrammatic representation (oblique view) of biotic gradients from Chapter 2; directionality is important because of the azimuth of the sun during the growing season, such that patches on the south sides of trees will be more directly lit than those on the north sides. Rust-coloured circles around tree bases represent areas of high LFH thickness within the crown-radius projection. The bulbous ends of arrows represent patches that score negatively on the gradient, while pointed ends represent patches that score positively. All these gradients were positively associated with vascular plant abundance.

The differences I observed between lichen, feathermoss, and vascular plant patches generally agreed with my initial hypotheses at both microhabitat and stand-scales. At the microhabitat scale, feathermoss dominance and abundance are most strongly associated with canopy cover, particularly towards the west, indicating an aversion to moisture-stressed environments; in contrast, lichen dominance and abundance are negatively associated with canopy cover, and seem to be positively related to moisture-stressed environments (Chapter 2). Stands dominated by lichens tend to be more open than those dominated by feathermosses but also have better surficial drainage, indicating that they can be drier even in the absence of high irradiance (Chapter 3). This observation is further supported by patch-scale microclimatic measurements: the air above feathermoss-dominated patches regularly has higher water-potential than that above lichen-dominated patches, but feathermoss and lichen abundance are only weakly associated with time above certain moisture thresholds. Microclimates of feathermoss patches tend to be wetter than those of lichens, and it seems unlikely that such differences are exclusively due to the influence of vegetation on its own environment (Chapter 5).

Vascular plants are important components of the understory in the study area (Chapter 3), and appear to have their own unique microhabitat and stand-scale associations. Most macronutrients (and some micronutrients) have greater availability under vascular plants than under other functional groups, and nitrogen appears to be much more depleted in vascular plant patches than others, at least in mid to late-summer (Chapters 2 and 3). Vascular plants also tend to be more abundant in patches (or stands) with fine-textured soils, and like feathermosses, show positive associations with afternoon shade (Chapters 2 and 3). Unlike the other functional groups, vascular plants are positively associated with direct irradiance in locations that have thick organic layers, such as those directly beneath the crown radius projection on the south-facing side of an individual tree (Chapter 2). The microclimate of vascular plant-dominated patches is intermediate to that of lichens and feathermosses (Chapter 5).

Although it is clear that abiotic factors, such as soil, climate, and topography, all influence community composition, stand-replacing fires may have more influence over stand development (and eventual canopy conditions) than the initial soil characteristics. Since forest canopies are more consistently autocorrelated at larger distances than soil texture, fire may be seen as a homogenizing agent (Chapter 4). Nevertheless, the surficial geology is apparently quite closely related to understory composition, and these relationships should be explored further once additional data become available.

Ultimately, many of these differences among patch types may be attributed as easily to vegetation influence on the environment as the converse, and therefore, one may infer that initial floristics determine vegetation dynamics as well as environmental properties. The limited temporal scale at which I explored these habitat relationships relegates interpretation almost exclusively to the domain of association, even when the fundamental questions of interest are of causation, and even though several aspects of it were intentionally designed to emphasize differences among functional groups that may alter the outcome of competitive interactions in lichen-rich forest understories. Yet, the strength of environmental associations shown here do indicate that environmental filtering of species is a more likely mechanism for determining understory patch dominance than biological interactions.

One way of further addressing the association vs. causation dichotomy is to compare the growth and reproductive strategies of the competitors (Bazzaz 1979); if we can determine that the growth and dispersal traits of functional groups are theoretically affiliated with specific life-history strategies, it will provide additional support for or against the inferred mechanism of occupancy. For example, if one group has greater dispersal ability than another because of greater propagule production or smaller propagule size, the inverse will likely be true for competitive ability. By extension, if two groups have similar dispersal ability, they are also likely to have similar competitive abilities, indicating that the eventual patch dominance is more likely the result of environmental filtering (growth or establishment limitation).

Mat-forming lichens have long been thought of as 'tolerator' species (Connell and Slatyer 1977), due to their slow growth rates, the relatively infrequent appearance of fruiting bodies, and the belief that they reproduce primarily by thallus fragmentation (Thompson 1967, Hammer 1997, Heinken 1999, but see Ahti 1961). Yet, their distribution within suitable habitat has a decidedly 'weedy' appearance; they appear as matrix species within several decades of disturbance, forming thick carpets and 'cushions' only when mature, and often form a thin but continuous cover in early stages of development (Yarranton 1975). In addition, recent genetic research has demonstrated both high incidence of polymorphism among mats and higher than expected frequencies of apothecia in mature mats, suggesting that sexual, spore-based dispersal may be an important mechanism in some areas (Beard and DePriest 1996, Jahns et al. 2004, Robertson and Piercey-Normore 2007, Kotelko et al. 2008). Because dispersal is probably not limiting, it seems likely that most available habitat patches in a mature forest have received lichen propagules during their development, and that patches without lichens are either unsuitable to them or more favourable to other functional groups.

Many of the understory vascular plants in lichen-rich forests colonize new habitats by increasing their production of both seeds and underground runners or rhizomes after disturbance; dwarf shrubs in particular can increase their abundance dramatically in short periods of time (Crane 1989, Morneau and Payette 1989, Howard 1993, Coxson and Marsh 2001, Cichowski and Williston 2008). Although growth from seed tends to be quite slow, the growth from rhizomes, which often survive wildfires, can be quite vigorous under suitable conditions (Williston et al. 2006, McKechnie 2009). The combination of relatively high growth rates and high potential dispersal suggests that vascular species also have abundant opportunities to colonize available habitat patches, and are therefore limited by competition or environmental properties when not present.

Dispersal processes are less well known in feathermosses; most species reproduce both vegetatively, through fragmentation and lateral growth, and by spore production, but whether one mode is more dominant under natural conditions, or responds to environmental parameters is uncertain (Frego and Carleton 1995b, Økland and Bakkestuen 2004, Kotelko et al. 2008). Observations that they have similar genetic diversity to vascular plants (Cronberg et al. 2006), and that they can rapidly increase in response to changes in environmental conditions (Nelson and Halpern 2005), indicate that they are unlikely to be dispersal limited, despite relatively low sporophyte frequency in some locations (Frego and Carleton 1995a). Rather, where not present they are probably limited by the environmental conditions, such as high light and low throughfall precipitation, or by competition with faster growing species.

The species composition of habitats that are "neutral" niche space (i.e., the combination of microhabitat variables do not necessarily favour establishment of one vegetative cover type over another) is more likely a result of initial floristic composition than of competition, as stochastic dispersal events are the dominant assembly mechanism (Egler 1954). Although zones of symmetric competition are rare in nature, this symmetry (neutral niche space) does indeed exist, and may be more common in low productivity systems (Shipley and Keddy 1994, Golberg and Novoplansky 1997, Keddy et al. 1997). However, the possibility that some of the habitat investigated here was a type of neutral niche space, whereby the eventual patch dominance was a product of one species simply being there first, was unlikely to bias results. Given the mean age of stands and the patch selection protocols, patches were more likely to be in equilibrium and dominated by a single group, thereby representing a type of optimum niche space for that group. In addition, the dominance of macroclimatic associations (Chapter 5) with microclimate suggests that many of the potential mechanisms of environmental filtering could result from abiotic influence, rather than from the vegetation, and abiotic attributes are unlikely to have changed since stand initiation.

Given that each functional group seems to have the potential for rapid recolonization of disturbed habitats, it is likely that they have similar life-history strategies, and therefore similar competitive abilities. Certainly most vascular plants have the capacity to grow more rapidly than feathermosses, which have the capacity to grow more rapidly than mat-forming lichens, but in environments that are heavily resource limited, such as the boreal lodgepole pine forests examined here, environmental filtering probably dominates as the determinant of understory composition. Indeed, although further research is warranted due to the limited temporal scale, measures of inter-functional group association indicated that competition, if present, is likely unimportant.

## 6.2. Applications

### 6.2.1. Managing lichen-rich systems

Forest-management strategies that seek to enhance lichen production should be informed by multiple environmental attributes, rather than emphasizing a single environmental gradient, such as canopy closure. Lichens and feathermosses do indeed show strong affinities to opposite ends of a light and moisture gradient commonly represented in ecological research on these systems; lichens associate with more light and less moisture, and feathermosses associate with less light and more moisture. But this gradient is not always the strongest or the most important, and it is certainly never the only gradient of importance. The understory functional groups examined here also associated strongly and consistently with characteristics such as coarse soil texture and base cation availability. Soil acidity appears to be an important associate of vascular plant composition, particularly in the case of *Vaccinium membranaceum*, and *Arctostaphylos uva-ursi*, which are most common on more acidic sites and more neutral sites, respectively.

Much effort has recently been put into examining the use of logging and prescribed burning as management tools to promote increased lichen abundance in lodgepole pine forests of British Columbia (Miége et al. 2001a, 2001b, Sulyma 2003, Marzoas et al. 2005, Williston et al. 2006, Sulyma and McNay 2009). Although the concept is not new (Ahti 1959, Ahti and Hepburn 1967), there has been particular emphasis on it in recent years due to declining woodland caribou populations, especially for forests that are undergoing rapid changes in response to the widespread infestation of mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Williston et al. 2006, Whittaker and Wiensczyk 2007, Sulyma and McNay 2009). This approach is supported by the frequent observation that many apparent climax lichen-rich stands are those that have undergone low-intensity burning, such that the majority of the forest canopy is maintained, if somewhat thinned (Ahti and Hepburn 1967, Girard et al. 2009).

The research presented in this thesis does not explicitly address the influence of fire, but does give some guidelines as to the goals that prescribed burning should seek to achieve. Generally, these include reduction of the duff layer thickness and thinning of the canopy; removal of potential understory competitors is probably less important if the environmental modification is successfully conducted. However, the financial and environmental cost of using prescribed burning could become considerable if it was applied indiscriminately to all forests, and the resulting benefits could be limited in duration. A better approach would be to target those communities with characteristics of overmature climax-stage lichen-dominated forests, or those that are less likely to undergo some sort of transition towards feathermoss or vascular plant dominance of the understory.

To this end, burning should be prescribed only for those forests that: 1) have overall coarse-textured, stony soils, but more specifically are less than 10% silt and clay, 2) have low ratios of available calcium to aluminum (<4:1), and low overall nutrient availability, 3) have canopy cover resulting in more than 70% reduction of direct irradiance at ground level, and LFH thickness >5 cm. The first two criteria relate specifically to whether the treatment will be lasting, the last relates to whether the treatment is warranted; if the LFH thickness is <5 cm and the canopy is quite open, prescribed burning is unlikley to improve lichen growth conditions.

### 6.2.2. Future research

Although long-term observational studies are excellent for understanding the net effects of biological, physical, and chemical variables interacting on a plant community, they are almost exclusively applicable to the stands examined in that particular study. A mechanistic approach is superior in that it allows the researcher to understand how one variable acts upon another, thereby allowing generalizations to be applied to other systems as well. To this end, further field studies should be conducted that measure single variables more precisely and in ways that avoid overlap with other variables (e.g., separating the influences of heat stress, light, and precipitation interception in the WInDZ index used in Chapter 2). Simple procedures such as examining edaphic factors after canopy removal, or examining light influence after replacing canopy trees with chemically inert shade-screens, could be helpful in this regard.

Great potential also lies in studying the population dynamics of dominant understory species (i.e., dispersal and establishment processes or genetic structure), and in measuring the interactions among species. This is especially true in lichen-rich systems, as little is known about how lichens interact with other vegetation, or whether they are truly dispersal limited, as many have suggested (e.g., Heinken 1999). Furthermore, exploration of how understory vegetation interacts with and influences the growth of soil microbial species would be useful, particularly for the mycorrhizae that associate with dominant tree species (Stark et al. 2007).

## 6.3. Conclusions

Linear associations, based on continuous environmental measurements at the microhabitat scale, are effective in showing environmental relationships of understory vegetation. Ecological oversimplification that may result from focusing exclusively on categorical associations and the stand scale; that is, representing the system as a dichotomy - either lichen or feathermoss dominated - and inferring that this dichotomy is a product canopy influence. Patterns of patch dominance by lichens, feathermosses, and vascular plants are indeed influenced by canopy conditions, but not exclusively so. Edaphic properties almost certainly contribute to habitat configuration for any species:

> *"The principal causes which enable a certain assemblage of plants thus to maintain their ground against all others depend, as is well known, on the relations between the physiological nature of each species, and the climate, exposure, soil, and other physical conditions of the locality... Where the soil of a district is of so peculiar a nature that it is extremely favourable to certain species, and agrees ill with every other, the former get exclusive possession of the ground..."* (Lyell 1853, p. 670)

When we cannot detect this influence it is because of our own methodological limitations, not an ecological truth.

The dominant gradients observed or measured in the abiotic, chemical, and canopy-layer biotic environments are not always the ones that have the most measurable associations with the forest understory. Despite their obvious potential importance to vegetation composition, variables such as soil texture, slope position, and aspect appear to interact with a multitude of other attributes to produce a myriad of different habitat combinations; it is not difficult to see why some of these associations can be obscured by others that are slightly stronger, more consistent, or more linear in their relationship. For abiotic variables in particular, direct associations are likely to be distorted by vegetative feedbacks and interactions that have taken place over the development of a forest stand, such that it can be surprising to witness any association between understory and abiotic factors at all. This is a problem that has been encountered in ecological study of lichen-rich forests in the past – the prevailing ecological gradient that associates with dominance of feathermosses or lichens is that of canopy closure, resulting in a tendency towards arboricentric experimental designs and interpretations.

Whether the composition of lichen-rich forest understories is primarily regulated by competition, initial floristics, or environmental filtering remains conjecture. Yet, I have demonstrated that both species and functional groups of species in lichen-rich forests have distinct and sometimes predictable associations with their environments. These environmental attributes can be effectively represented independently, as mathematically orthogonal abstractions, or directly, as the interactions of biotic and abiotic attributes that we can measure. But the environmental associations of species or functional groups are part of a continuum of variability that cannot be accurately summarized as simply lichen- or feathermoss-dominated, exposed or sheltered. Great taxonomic or morphological differences between groups, such as lichens and vascular plants, do not preclude biological interactions, especially when they are so well integrated throughout the understory. Rather, they suggest that, by using an ecologically relevant scale of investigation, differences in niche space should be apparent. Individual patch and forest stand scales are both ecologically relevant to understory vegetation, but only the individual patch scale can effectively portray environmental interactions in a mechanistic light, and should, therefore, be the scale of choice for generalizable understory ecology.

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# Appendix A. Nomenclature, morphology and phylogeny of dominant genera

This section gives a brief overview of the physical appearance, the current phylogenetic classification and nomenclature, and the life-history traits for the dominant genera observed in this study. For the sake of consistency, the same nomenclature is used throughout all chapters, and follows Goward et al. (1994) or Goward (1999) for lichens, Crum (1973) for mosses, and MacKinnon et al. (1992) for vascular plants.

## A.1. Lichens

### *Cladonia (Cladina)*

*Cladonia* Hill ex P. Browne species are fruticose (shrub-like) or squamulose-fruticose (having scaly bases with fruticose stalks) lichens of the family Cladoniaceae, within the Lecanorales (Ascomycota: Lecanoromycetes). Most species in this genus are lightly coloured, from white to light gray or green, and associate with the green-algal symbiont *Trebouxia*. In northern regions, *Cladonia* spp. are largely epigeic (grow on soil), but some species are epixylic (grow on wood), epilithic (grow on rock), or epiphytic (grow on living trees). The secondary thallus (fruticose stalk) is often irregularly branched, with (for most *Cladonia* spp.) or without (for the *Cladina* group) cup-shaped apothecia.

Until recently, the dominant theories of *Cladonia* dispersal held that mat-forming species colonize new sites almost exclusively by short-distance wind-blown dispersal of broken thalli, while cup-forming species rely on long-distance wind-blown dispersal of soredia and ascospores (Thompson 1967, Yarranton 1975, Johnson 1982, Kershaw 1985, Hammer 1997, Heinken 1999). Since then, researchers have found evidence that mat-forming *Cladonia* species may use sexual reproduction more frequently than previously thought. For example, examination of the genetic structure of epigeic lichen communities in

Manitoba led Robertson and Piercey-Normore (2007) to conclude that *Cladonia arbuscula* did indeed reproduce sexually, though several other reproduction methods, including fragmentation, were also supported. Beard and DePriest (1996) found that significant genetic variation occurred among *Cladina subtenuis* cushions, indicating these colonies had undergone sexual reproduction and spore dispersal, but that within cushions, individual thalli were of clonal origin (by fragmentation). Finally, Jahns et al. (2004) found that *Cladonia rangiferina* produced abundant apothecia, particularly in favourable sites, that these apothecia often had mature ascospores, and that the ascospores were quite viable in culture. They further suggested that previous researchers may have missed apothecia because they are often produced below the infertile branch tips on individual thalli (Jahns et al. 2004).

Once established, within 3 - 15 years after disturbance, thalli of mat-forming *Cladonia* spp. can grow at a rate of 5 - 10 mm per year under favourable conditions (Pegau 1968, Thompson 1967). Expressed on a percent-mass basis, they can increase by as much as of 17% per year under favourable conditions (den Herder et al. 2002). Favourable conditions would be those that prolong the amount of time for which a thallus is saturated or almost saturated with moisture while receiving insolation, thereby increasing the duration of photosynthetic activity (Cooper et al. 2001, Kershaw 1985, Palmqvist and Sundberg 2000). For this reason, one could expect mat-forming *Cladonia* spp. that grow in coastal areas, with abundant precipitation or fog, to grow faster, while lichens that grow in continental locations would grow more slowly.

For ease of classification, *Cladonia* species of northern regions have traditionally been subdivided into two genera: *Cladina* and *Cladonia.* Morphologically this is a helpful separation, as *Cladina* species do not form primary squamules or a cortex, but do form continuous mats over the ground, whereas *Cladonia* spp. form primary squamules and cortecies, and tend to exist in smaller patches. Although mat-forming *Cladonia* species are still commonly referred to by the generic name *Cladina* in much of the forest and wildlife ecology literature (Boudreau and Payette 2004, Herder et al. 2007, Jasinski and Payette 2005, Sulyma and Coxson 2001), morphological and molecular evidence has shown that *Cladina* lichens are too little differentiated from other *Cladonia* species to represent a true genus, or even a subgenus (Stenroos et al. 2002). For the sake of taxonomic accuracy, both *Cladina* and *Cladonia* species are referred to using the generic name *Cladonia* throughout this thesis; where finer subgeneric division is warranted, the term 'mat-forming lichens' is used to refer to those species that form continuous mats and lack both a primary squamulose thallus and a cortex, and the term 'cup-forming lichens' is used to refer to those species that have a primary squamulose thallus and form (usually) cup-like apothecia.

### *Stereocaulon*

In northern boreal regions, *Stereocaulon* Hoffm. species are fruticose mat-forming epigeic lichens. The primary thallus is often crust-like and closely appressed to the substrate, and it contains green-algal symbionts, usually of the genus *Trebouxia* (Brodo et al. 2001). The secondary thallus extends upwards from the primary thallus and is irregularly branched, with small fibrous cephalodia containing cyanobacterial symbionts such as *Nostoc* or *Stigonema* (Brodo et al. 2001). *Stereocaulon* species have comparable growth rates to mat-forming *Cladonia* spp. (Boudreau and Payette 2004b).

The genus *Stereocaulon* belongs in the family Stereocaulaceae, which has recently been shown to represent a subgroup of the Cladoniaceae (Myllys et al. 2005). Despite the apparent subordinacy of the former, the two families are both still considered valid taxonomic groups, due to Stereocaulaceae's monophyly and to the widely accepted conventions on naming associated with each group (Myllys et al. 2005).

### *Cetraria*

The genus *Cetraria* has historically been classified either as a member of the Parmeliaceae, or given its own family, the Cetrariaceae. Wedin et al. (1999) supported the inclusion of *Cetraria* in the Parmeliaceae, but still distinguished a monophyletic group to which *Cetraria* and *Vulpicida* belonged within the Parmeliaceae. More recently, Crespo et al. (2007) concluded that this phylogeny was correct, and included other morphologically similar genera such as *Tuckermanopsis* and *Flavocetraria* in a greater 'Cetraroid group', that was part of the monophyletic Parmeliaceae.

*Cetraria* is a grey-brown to olive green coloured foliose lichen that is epigeic or epilithic in habit; it associates with green-algal symbionts, most likely of the genus *Trebouxia* (Brodo et al. 2001). *Cetraria* species are frequently associated with mats of *Cladonia* spp. in dry boreal forests. Two species are commonly found in the study area, *Cetraria islandica* and *Cetraria ericetorum.*

## A.2. Feathermosses

In this study, feathermosses are a polyphyletic group of three species from the order Hypnales (Bryopsida), which form loosely-packed continuous mats covering the ground in circumpolar boreal and temperate coniferous forests. All three species are easily identified in the field, due to distinct branching patterns and leaf morphology. Feathermosses form a significant proportion of the biomass in boreal forest understories (Nilson and Wardle 2005), and are frequently associated with nitrogen fixing cyanobacteria (Houle et al. 2006), although their contribution to ecosystem nitrogen fixation has yet to be determined. Similarly to the lichens, all are poikilohydric, and depend primarily on precipitation for moisture, but can also utilize water vapour (Proctor 2000, Økland 2004); nutrients are largely supplied by precipitation (and by the associated cyanobacteria within mats), and are highly conserved within the mats (Startsev and Lieffers 2006).

### *Pleurozium*

Represented by a single species in the northern hemisphere (*Pleurozium schreberi* (Brid.) Mitt.), *Pleurozium* forms loosely packed mats on the forest floor of coniferous boreal and sub-boreal forests. It is the most abundant moss of northern forests, and can often form continuous ground-cover over large areas (Mackinnon et al. 1999). It is a robust moss, with a reddish coloured stem and irregular once-pinnate branches.

*Pleurozium* has been repeatedly shuffled from one family to another in the last several decades, classified at different times as part of Brachytheciaceae, Amblystegiaceae, and Hylocomiaceae (Crum 1976, Lawton 1971, ITIS 2009). Recent studies have suggested that *Pleurozium* either is an outgroup of or included in the Hylocomiaceae, but further molecular-phylogenetic study is needed before this can be confirmed (Chiang and Schaal 2000, Hedenas 2004).

Reproduction in *Pleurozium* is thought to be largely vegetative, by growth and expansion of individual stems, particularly via lateral expansion (Frego and Carleton 1995(a), MacKinnon et al. 1999), but genetic evidence suggests that sexual reproduction does occur (Kotelko et al. 2008).

### *Hylocomium*

Two species of this genus are known from western North America, but *Hylocomium splendens* (Hedw.) Schimp. is by far the most common, with a circumpolar boreal and sub-boreal distribution (Lawton 1971), and is also the only one found in Northern British Columbia. *Hylocomium* has a similar mat-forming structure to *Pleurozium*, and is a dominant species in many forests, but is often less abundant on less productive sites where it may form only small patches. *Hylocomium splendens* can also have a red stem, but it is less robust than the stem in *Pleurozium*; in addition, the stem is finely branched two or three times, and has smaller leaves than *Pleurozium*. *Hylocomium* is the type genus for the family Hylocomiaceae, and as a result it is not shuffled among different families as the other feathermoss genera are, but still requires further molecular phylogenetic study in order to determine it's similarity to other genera within the Hylocomiaceae.

Growth of *Hylocomium* is modular, and can display annual periodicity, though there is some variation as to the extent of annual growth among regions; reproduction is primarily vegetative, through lateral expansion, but may also occur via fragmentation and spore production (Cronberg et al. 1996, Økland and Bakkestuen 2004, Cronberg et al. 2006).

### *Ptilium*

*Ptilium* is quite distinct from other feathermosses in its usual growth form; abundant once-pinnate and opposite branchlets with falcate-secund leaves give it a feather-like appearance. Despite the small-scale morphological differences, *Ptilium* still forms loosely-packed mats in the forest understory, and likely performs a similar ecological role to the other feathermosses.

Like *Pleurozium*, *Ptilium* is a genus with only a single species, *Ptilium crista-castrensis* (Hedw.) De Not. *Ptilium* belongs to the family Hypnaceae, and like *Hylocomium*, the phylogenetic placement of *Ptilium* is relatively stable, having consistently been within a single family over recent decades. Reproduction in Ptilium is not well-studied, but probably shows similar patterns to other feathermosses.

## A.3. Vascular plants

### *Arctostaphylos*

*Arctostaphylos* is a genus of shrubs and dwarf shrubs, in the family Ericaceae (Magnoliopsida: Ericales). Although there are many known species of *Arctostaphylos* distributed throughout North America, only two occur in pine woodlands of British Columbia. The two are easily distinguishable, but *Arctostaphylos uva-ursi* (L.) Spreng. is the most common (MacKinnon et al. 1999). *Arctostaphylos uva-ursi* is an evergreen trailing shrub, and can be readily distinguished in the field by its alternate, spoon-shaped, leathery leaves, small drooping pink flowers, and bright red berries (MacKinnon et al. 1999).

*Arctostaphylos uva-ursi* widely reproduces vegetatively by underground rhizomes in the field, despite the seeds being well-dispersed by wildlife and often stored in the soil (Crane 1991). Naturally, *A. uva-ursi* is found in sandy or rocky soils, often in mountain ecosystems, and is a significant component of the understory vegetation in Rocky Mountain lodgepole pine forests (Rosatti 1987, La Roi and Hnatiuk 1980). In the BWBS of northern B.C., *Arctostaphylos uva-ursi* is most common on the poorest and driest sites, specifically those with soil nutrient regimes (SNRs) of A or B and soil moisture regimes (SMRs) of 1 or 2, and may be intolerant of shade (Beaudry et al. 1999). *Arctostaphylos uva-ursi* is known to associate with many of the same ectomycorrhizal species as *Pinus*, and may even be responsible for maintaining mycorrhizal communities during post-disturbance periods when trees are germinating and regenerating (Visser 1995). The habit of growing in close proximity to tree boles of *Pinus* spp. may be a result of these shared associations.

### *Cornus*

The genus *Cornus* is a member of the Cornaceae (Magnoliopsida: Cornales). Many members of this genus are shrubby, but the single species encountered in this study (*Cornus* *canadensis* L.) is herbaceous; specifically, Crane (1989) identified *Cornus canadensis* as a 'sub-shrub', due to its woody rhizomatous habit. *Cornus canadensis* is commonly found in well-drained, moist boreal and temperate forests of North America (Crane 1989). Although it can establish naturally from seed and may be dispersed widely by birds and mammals that consume the bright red berries, *Cornus canadensis* reproduces mostly by cloning from an underground rhizome (Crane 1989).

*Cornus canadensis* is easily identified by the terminal whorl of four (sometimes six) broadly obovate leaves with several strong longitudinal veins, the white tetrapartite flowers, and the bright red drupe that looks like a cluster of several berries when mature (MacKinnon et al. 1999). *Cornus candensis* is potentially evergreen, but in northern regions the leaves turn orange-brown in the fall and are replaced almost every year (Crane 1989, MacKinnon et al. 1999). *Cornus canadensis* is present under virtually all SNRs and SMRs of northern B.C.'s BWBS, but is less common on the driest and most nutrient-poor sites (Beaudry et al. 1999).

### *Linnaea*

Twinflower (*Linnaea borealis* L.) is a stoloniferous, evergreen dwarf shrub, and is the only species within the genus *Linnaea*. *Linnaea borealis* is a member of the Caprifoliaceae (Magnoliopsida: Dipscales). It has paired (opposite), stalked leaves that are regularly spaced along the horizontal stem, and upright stalks (5-10 cm) with two small drooping flowers at the tip; flowers bear small brown seed-capsules. Roots are fibrous and often at shallow depths, such that they may be entirely in the forest floor (Howard 1993).

Twinflower's distribution is circumpolar, and it occupies a wide range of both forested and open habitats throughout boreal, temperate, and arctic or alpine ecosystems. Studies of twinflower have shown it to be tolerant of a wide range of soil moisture and nutrient conditions, successional stages, and climates (Howard 1993). In the BWBS of northern BC, *Linnaea* is known to be common in all but the wettest or driest sites (Beaudry et al. 1999).

### *Vaccinium*

Similarly to *Arctostaphylos*, *Vaccinium* is a member of the family Ericaceae (Magnoliopsida: Ericales). Three species of *Vaccinium* are commonly found in the study area, including *Vaccinium membranaceum* Douglas ex Torr., *Vaccinium vitis-idaea* L., and *Vaccinium caespitosum* Michx. *Vaccinium* species are mostly rhizomatous dwarf shrubs (some species are larger but those are not found in the study area), ranging from a few centimetres to half a metre in height, and like other Ericaceae are mycorrhizal (Gorzelak 2009, McKechnie 2009). They produce small black or blue to reddish berries, enabling bird- or mammal-facilitated dispersal, but more often reproduce asexually through rhizome spread and layering (McKechnie 2009). *Vaccinium* species vary widely in leaf morphology and size, but those found in the study area have leaves that are elliptical to oblong or lance-shaped, alternate, and (with the exception of *V. vitis-idaea*), deciduous.

*Vaccinium* species are drought tolerant when mature, and are frequently found in well-drained soils or exposed sites. Those species mentioned above generally occupy low to mid-ranges in the soil nutrient and moisture regimes of the BWBS in northern BC (Beaudry et al. 1999). They also thrive in recently burned forests, provided the fire was not so severe as to destroy the underground rhizome (McKechnie 2009).

## Appendix B. Key for selection of functional group quadrats

A good starting point for determining the habitat associations of functional groups is to look for their optimum niche space, or the conditions in which those species grow that allow them to thrive the most. It follows that a sampling bias towards the most completely dominated patches is a reasonable approach to take when selecting quadrats. In addition, if the plots in which quadrats are located are essentially stratified or random in their distribution, bias is still minimal. Nevertheless, in field situations the choice of quadrat location may not always clear, and it may fall to the surveyor to choose between several similar patches.

The choice among several similarly dominated patches may appear random, but the reality is that all observers have the potential to introduce more bias than is experimentally desirable. Even when physical constraints limit quadrat selection to some extent (e.g., PRS$^{TM}$ probes cannot be inserted into solid rock), there can be multiple choices left to the surveyor. For example, in areas of high contiguous lichen cover, illustrated by the photographs below (Figure 35), an observer instructed to find the most completely dominated patch of lichen within the 5.64 m radius plot would have multiple choices, and may tend to select patches that are more open, or patches that are in sunlit areas rather than shady ones. Such selection processes could result in biased assessments of environmental associations with functional group dominance, if not performed correctly.

To ensure minimal observer bias was introduced, an assistant was instructed to follow a hierarchy of rules during plot selection. These rules are as follows:

1)
   a) One patch of each ground cover type is clearly more dominant than others (i.e., has highest cover of desired group, and lowest cover of others): *patch selection is clear.*
   b) One patch is not clearly dominant over others for every functional group → 2

2)
   a) More than one similar "best" patch of one or more functional groups exists: *choose patch closest to plot center.*
   b) Functional group not represented in plot → 3

3)
   a) Functional group is present within one or two metres of plot border outside plot: *extend potential selection area by one or two metres, select most dominant patch.*
   b) Functional group not present within one or two metres of plot border outside of large plot: *choose another replicate of a different functional group.*

**Figure 35.** Photographs (by author) from a lichen dominated stand (Site 7), showing the many potential 'lichen-dominated' quadrat locations, and how other factors such as light may make one location may appear to be more completely dominated than others

# Appendix C. Calculation of Wind-Influenced Drip-Zone (WInDZ) index

Trees exert a tremendous influence on understory vegetation composition and abundance. Their effect on the amount of light reaching the forest floor is probably the most easily quantifiable part of that influence, and it is therefore one of the best studied aspects of canopy-understory interactions (Gilliam and Roberts 2003). Unfortunately it can be difficult to separate the effects of light interception from the effects of precipitation interception, soil nutrient depletion, and more direct influences such as the deposition of litter or dissolved nutrients that have leached out of leaves and bark (Bazzaz 1979, Moore 1980, Økland et al. 1999, Barbier 2008, Salemaa et al. 2008). Bazzaz (1979) suggested that the primary method for determining which aspect(s) of canopy influence predominate(s) should be manipulative experimentation. Assuredly, this approach is scientifically ideal and has been effective in some situations, but is probably not as practical with groups such as lichens, feathermosses, and dwarf shrubs (the dominant component of the vascular group), because of their relatively slow growth rates and the low survival rates in greenhouse trials (Thompson 1967, Nash 1996). Others have suggested that comparison of different measurement methods or predictive models to field observations, or comparative analysis of spatial patterns in environmental variables associated with spatial patterns of vegetation can assist in determining how such influences interact as effectively as manipulative experimentation, and that such methods have the advantage of increased realism (Økland 2007, McIntyre and Fajardo 2009).

Similar to ecological field theory models, which are used to calculate zones of plant-plant interaction (Walker et al. 1989), dripzones have been quantified as linear functions of distance from a tree in previous studies (Neitlich and McCune 1997, Goward and Arsenault

2000), or as non-linear influences that can be symmetrically applied around a tree of influence (Økland et al. 1999). Although this may be quite effective in forests with relatively tall or dense canopies, where windspeed near the ground in is effectively zero and most of the throughfall precipitation lands directly below the tree crown, it is unlikely to give a realistic portrayal of the influence of crown leachate (present in throughfall precipitation) on ground vegetation in low-productivity lodgepole pine forests. This is because low-productivity lodgepole pine forests are characterized by relatively short stems, a large amount of space between trees, and relatively low crown biomass – all factors that allow wind to have a greater influence on the pathway of falling objects from the canopy.

To build an index of dripzone influence on ground vegetation while accounting for the influence of wind, one must estimate the average horizontal distance travelled by a water droplet from the tree in the direction of the spot in which one is interested. Patches of ground that fall beyond this average distance would experience relatively little dripzone influence, while those that lay between the tree stem and the average distance would experience greater influence. Ground immediately next to the tree would be the most influenced due to stemflow (Moore 1980, Økland et al. 1999). Given sufficient information on the horizontal and vertical forces applied to a water droplet, and knowledge of the canopy tree height, we should be able to estimate this average horizontal distance quite accurately, or at least in a way that is more functionally relevant than a linear distance from the tree. If the pathway of a water droplet from the top of each tree to the ground is assumed to be a product of a constant acceleration due to gravity (which it is), and a constant horizontal velocity due to the average windspeed (which is not quite true, but fairly close given the forest characteristics), and we know the total vertical distance travelled (tree height), we can approximate the average distance travelled by using simple falling object equations

(Equations 1a, 1b, Table 15). An obvious ommission in this assumption is that the 'average' drop of throughfall precipitation would not fall from the top of the tree, but from the branches of the canopy. However, by using the tree top as the starting point, we may avoid multiple unnecessarily tree-specific calculations.

Equation 1a ($k_t$ = horizontal distance travelled by falling object): $k_t = v_w \times t_t$, and

Equation 1b ($t_t$ = time from top to bottom of fall): $t_t = \sqrt{h_t / (a/2)}$

**Table 15.** Wind-influenced dripzone index variables and their formulaic representation.

| Categorical / constants | Continuous / Quantitative |
|---|---|
| Measured variables | |
| Tree species = Sp | Diameter at Breast Height = DBH |
| Wildlife Tree Classification = w | Distance from plot = x |
| Tree number = i (1 to 3) | Direction from plot = d |
| Derived or modelled variables | |
| WTC height scaler = $A_w$ | Height = h (Table 17) |
| Acceleration due to gravity (a) = 9.81 m/s$^2$ | Mean windspeed at plot = $v_w$ |
| WTC crown-loss estimator = $c_w$ | Mean windspeed frequency = $f_a$ |

According to Oke (1987), windspeed tends to decline in a reverse logistic fashion as it passes over an object (Figure 36b). Once multiple similarly sized objects are included before and after the object of interest, the logarithmic nature of the relationship between object height and windspeed is degraded, such that the 'plane of zero displacement' (where windspeed effectively equals zero) is well above the actual ground level (Figure 36a); this plane is thought to be approximately two-thirds of the height of the forest canopy in the average coniferous forest (Oke 1987). Nevertheless, given sufficient spacing between trees, this effect would become far less pronounced, and the windspeed profile curve will once again be approximately reverse logistic between trees (Figure 36b).

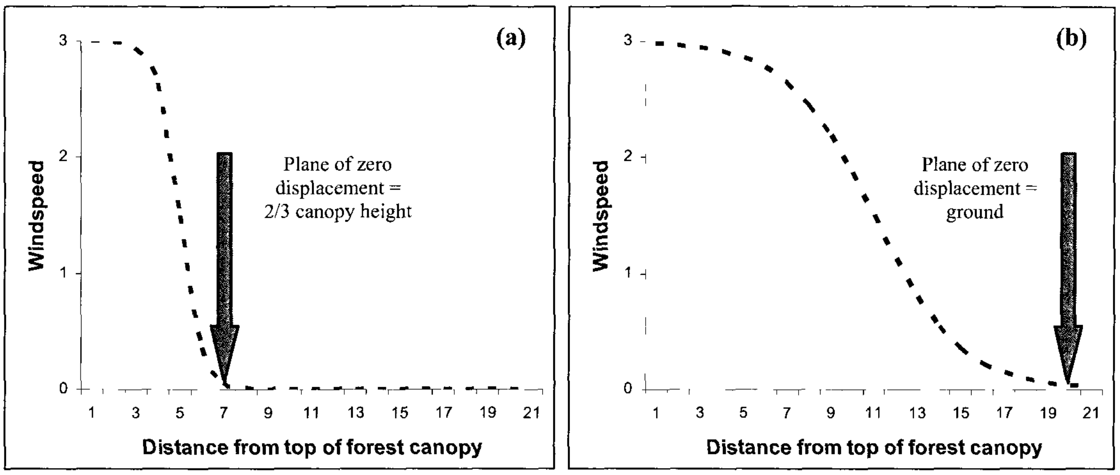

**Figure 36.** The theoretical change in windspeed with increasing distance from the top of the forest canopy (decreasing distance from ground), using tree height of 20 m and above-crown windspeed of 3 m/s: a) representing the abrupt change in windspeed that occurs in typical, densely spaced forests, where the plane of zero displacement is approximately 2/3 the canopy height b) representing the more gradual change in windspeed in passing over a single object.

The lodgepole pine stands in this study are considerably more open than many other forest types. In addition, the profile of trees in these forests, characterized by a small, sparse bulge of a crown near the top of the tree, and a long, unbranched bole, is such that the reduction of windspeed due to drag is likely minimal. Therefore, when we calculate the path of a falling water droplet from the top of the tree, the small reduction in the horizontal distance travelled that is missed (by failing to account for a decrease in windspeed with height) is likely offset by the assumption that a the droplet origin is the centre of the crown, rather than a starting point at the outer edge of a crown. This method of calculating the horizontal distance is likely preferable to estimating the decrease in windspeed and the average crown radius, since an empirically derived method of estimating crown radius, such as the model used by Bechtold (2004), or application of an uninformed version (no data on the wind resistance profile were collected) of a logarithmic model to estimate windspeed decline as a function of tree height, may both be subject to more measurement error than estimation of simple tree height and application of a constant windspeed. Indeed, the index developed here is likely a much more conservative estimate, while further estimation of other tree characteristics, such as crown radius, could lead to problems with model over-fitting.

Despite the advantages of keeping an index relatively simple, the influence of wind directionality cannot be ignored in the construction of a drip-zone index. If directionality was ignored, the index may as well be using mean crown radius rather than windspeed to determine where droplets will usually fall, because the influence will be exactly the same all around the tree. In reality, most regions are dominated by winds originating in one or two main directions. This would skew the zone of leachate influence such that it approaches an elongate or elliptical shape rather than a circular shape (which is assumed in a simple crown-radius based model), and such that the tree does not represent the centre of this zone. A simple way to scale a windspeed-based dripzone index would be to use either a different mean windspeed for each direction, or to introduce a frequency term to scale the influence of constant windspeed by direction. For the dripzone index built here, the latter was chosen (Equation 2).

Equation 2 ($y_i$ = single tree dripzone index): $y_i = \frac{1}{1+e^{(\mathrm{x}_i - \mathrm{k}_i)}}$

A scalar term (Table 16) was derived from the Wildlife Tree Classification (WTC) System outlined by British Columbia Ministry of Forests and Range (2007), which specifically gives the height proportions used in the scalar. The WTC crown loss estimator was a negative logistic function (equation 1) deemed to approximate the rate of loss in crown foliage and branches, and was applied to classes 1-5, which represented the decline of the tree crown. It was estimated that both foliage and small branches of the tree crown would decline slowly between classes 1 and 2, followed by a sharp decline until class 4, a levelling off at class 5, and have little or no crown left by class 6. The "-3" term allowed the logistic threshold to occur in class 3 trees, thereby approximating the estimated loss of crown foliage and branches outlined by British Columbia Ministry of Forests and Range (2007).

**Table 16.** Wildlife Tree Classification number and corresponding height scalers for classes greater than 5.

| WTC | $A_w$ |
|---|---|
| <5 | 1 |
| 6 | 2/3 |
| 7 | 1/2 |
| 8 | 1/3 |
| 9 | 1/10 |

Equation 3 ($c_w$ = WTC Crown-loss estimator): $c_w = \frac{1}{1+e^{(w-3)}}$

The WInDZ index is intended to be an estimation of crown influence intensity on ground-level biota, as modified by average windspeed and direction-based frequency, the individual tree height and condition, and the distance and direction in which the plot is located relative to the tree. However, this same spatial extent may also represent the intensity of precipitation interception, thereby making the separation of nutrient enrichment from moisture deprivation (and possibly of litter deposition) difficult. Given that these two mechanisms likely occur in tandem under most natural situations, the separation of their influences may be less useful than an index that includes both (Equation 4).

Equation 4: $WInDZ = \sum (y_i \times f_{ai})$

Although height was measured for each tree within the 5.64 m plot, these heights were not recorded with spatial or individual reference, so heights of the three nearest trees to each quadrat had to be estimated. This was done by constructing a linear regression model for each tree species, using the height and DBH data recorded in the study (Table 17).

**Table 17.** Results for regression of tree height as a function of DBH, by species.

| Species | Code | n | β | *p* | $R^2$ |
|---|---|---|---|---|---|
| *Populus tremuloides* | At | 35 | 1.10593 | <0.0001 | 0.945 |
| *Abies lasiocarpa* | Bl | 11 | 0.56959 | <0.0001 | 0.856 |
| *Pinus contorta* | Pl | 840 | 0.96523 | <0.0001 | 0.944 |
| *Salix* spp. | Salix | 9 | 0.88801 | <0.0001 | 0.938 |
| *Picea mariana* | Sb | 14 | 0.73360 | <0.0001 | 0.944 |
| *Picea engelmannii x glauca* | Sx | 32 | 0.94849 | <0.0001 | 0.976 |

# Appendix D. Tabular summaries of ANOVA results

**Table 18.** ANOVA results for all environmental variables using site and FG type as categorical variables. Type one sum of squares calculations were used to ensure that the hierarchical sampling design was reflected in analyses, and $\eta^2$ values were included to indicate the percent of variance explained by the linear model. Three quadrat types are lichen, feathermoss, or vascular plant. Variable definitions in Chapter 2.

**Table 18**... continued

| Var. type | Variable | Source | DF | SS | MS | F-Value | Pr >F | $\eta^2$ |
|---|---|---|---|---|---|---|---|---|
| Abiotic | Coarse Fragments | Site | 23 | 10.4021 | 0.4523 | 5.50 | <0.0001 | 0.3998 |
| | | FG type | 2 | 0.0062 | 0.0031 | 0.04 | 0.9630 | 0.0002 |
| | | Error | 190 | 15.6107 | 0.0822 | | | |
| | | Total | 215 | 26.0190 | | | | |
| | Gravel | Site | 23 | 1.8665 | 0.0812 | 2.92 | <0.0001 | 0.2608 |
| | | FG type | 2 | 0.0053 | 0.0026 | 0.10 | 0.9093 | 0.0007 |
| | | Error | 190 | 5.2845 | 0.0278 | | | |
| | | Total | 215 | 7.1563 | | | | |
| | Fines | Site | 23 | 9.8554 | 0.4285 | 8.78 | <0.0001 | 0.5151 |
| | | FG type | 2 | 0.0051 | 0.0026 | 0.05 | 0.9489 | 0.0003 |
| | | Error | 190 | 9.2735 | 0.0488 | | | |
| | | Total | 215 | 19.1341 | | | | |
| | Sand | Site | 23 | 8.1747 | 0.3554 | 9.80 | <0.0001 | 0.5427 |
| | | FG type | 2 | 0.0017 | 0.0009 | 0.02 | 0.9765 | 0.0001 |
| | | Error | 190 | 6.8874 | 0.0362 | | | |
| | | Total | 215 | 15.0638 | | | | |
| | Silt+Clay | Site | 23 | 19.1250 | 0.8315 | 4.54 | <0.0001 | 0.3542 |
| | | FG type | 2 | 0.0763 | 0.0381 | 0.21 | 0.8122 | 0.0014 |
| | | Error | 190 | 34.7968 | 0.1831 | | | |
| | | Total | 215 | 53.9981 | | | | |
| | Slope inclination | Site | 23 | 23.2971 | 1.0129 | 9.37 | <0.0001 | 0.5311 |
| | | FG type | 2 | 0.0264 | 0.0132 | 0.12 | 0.8853 | 0.0006 |
| | | Error | 190 | 20.5383 | 0.1081 | | | |
| | | Total | 215 | 43.8617 | | | | |
| | N-aspect | Site | 23 | 43.8052 | 1.9046 | 6.59 | <0.0001 | 0.4435 |
| | | FG type | 2 | 0.0288 | 0.0144 | 0.05 | 0.9514 | 0.0003 |
| | | Error | 190 | 54.9350 | 0.2891 | | | |
| | | Total | 215 | 98.7690 | | | | |
| | Concavity | Site | 23 | 9.2488 | 0.4021 | 2.55 | 0.0003 | 0.2330 |
| | | FG type | 2 | 0.4815 | 0.2407 | 1.53 | 0.2199 | 0.0121 |
| | | Error | 190 | 29.9630 | 0.1577 | | | |
| | | Total | 215 | 39.6933 | | | | |
| | Ae thickness | Site | 23 | 39.7026 | 1.7262 | 5.04 | <0.0001 | 0.3788 |
| | | FG type | 2 | 0.0212 | 0.0106 | 0.03 | 0.9696 | 0.0002 |
| | | Error | 190 | 65.0865 | 0.3426 | | | |
| | | Total | 215 | 104.8103 | | | | |

**Table 18**... continued

| Var. type | Variable | Source | DF | SS | MS | F-Value | Pr >F | $\eta^2$ |
|---|---|---|---|---|---|---|---|---|
| Biotic | LFH | Site | 23 | 71.7442 | 3.1193 | 9.77 | <0.0001 | 0.5296 |
| | | FG type | 2 | 3.0491 | 1.5245 | 4.77 | 0.0095 | 0.0225 |
| | | Error | 190 | 60.6867 | 0.3194 | | | |
| | | Total | 215 | 135.4800 | | | | |
| | WInDZ | Site | 23 | 3.3743 | 0.1467 | 1.88 | 0.0119 | 0.1804 |
| | | FG type | 2 | 0.4783 | 0.2391 | 3.06 | 0.0493 | 0.0256 |
| | | Error | 190 | 14.8569 | 0.0782 | | | |
| | | Total | 215 | 18.7095 | | | | |
| | CRDZ | Site | 23 | 32.1266 | 1.3968 | 2.00 | 0.0061 | 0.1874 |
| | | FG type | 2 | 6.7598 | 3.3799 | 4.85 | 0.0089 | 0.0394 |
| | | Error | 190 | 132.5257 | 0.6975 | | | |
| | | Total | 215 | 171.4120 | | | | |
| | SWCC | Site | 23 | 24421.5556 | 1061.8068 | 3.81 | <0.0001 | 0.3068 |
| | | FG type | 2 | 2266.3333 | 1133.1667 | 4.07 | 0.0186 | 0.0285 |
| | | Error | 190 | 52921.4444 | 278.5339 | | | |
| | | Total | 215 | 79609.3333 | | | | |
| | LAI | Site | 23 | 15.5559 | 0.6763 | 14.25 | <0.0001 | 0.6324 |
| | | FG type | 2 | 0.0232 | 0.0116 | 0.24 | 0.7831 | 0.0009 |
| | | Error | 190 | 9.0203 | 0.0475 | | | |
| | | Total | 215 | 24.5994 | | | | |
| | Total irradiance | Site | 23 | 6302.7099 | 274.0309 | 13.69 | <0.0001 | 0.6172 |
| | | FG type | 2 | 106.7009 | 53.3505 | 2.67 | 0.0722 | 0.0104 |
| | | Error | 190 | 3802.7205 | 20.0143 | | | |
| | | Total | 215 | 10212.1313 | | | | |
| | Direct irradiance | Site | 23 | 353.9663 | 15.3898 | 7.24 | <0.0001 | 0.4583 |
| | | FG type | 2 | 14.7207 | 7.3604 | 3.46 | 0.0333 | 0.0191 |
| | | Error | 190 | 403.6418 | 2.1244 | | | |
| | | Total | 215 | 772.3289 | | | | |
| | Diffuse irradiance | Site | 23 | 237.1877 | 10.3125 | 16.15 | <0.0001 | 0.6583 |
| | | FG type | 2 | 1.7906 | 0.8953 | 1.40 | 0.2486 | 0.0050 |
| | | Error | 190 | 121.3058 | 0.6385 | | | |
| | | Total | 215 | 360.2840 | | | | |
| | localBA | Site | 23 | 9.8079 | 0.4264 | 3.89 | <0.0001 | 0.3074 |
| | | FG type | 2 | 1.2429 | 0.6214 | 5.66 | 0.0041 | 0.0390 |
| | | Error | 190 | 20.8542 | 0.1098 | | | |
| | | Total | 215 | 31.9049 | | | | |

**Table 18**... continued

| Var. type | Variable | Source | DF | SS | MS | F-Value | Pr >F | $\eta^2$ |
|---|---|---|---|---|---|---|---|---|
| Chemical | Total N | Site | 23 | 7.0352 | 0.3059 | 4.97 | <0.0001 | 0.3683 |
| | | FG type | 2 | 0.9184 | 0.4592 | 7.45 | 0.0008 | 0.0481 |
| | | Error | 181 | 11.1499 | 0.0616 | | | |
| | | Total | 206 | 19.1035 | | | | |
| | $NO_3$ | Site | 23 | 31.5802 | 1.3731 | 5.57 | <0.0001 | 0.4140 |
| | | FG type | 2 | 0.0729 | 0.0364 | 0.15 | 0.8627 | 0.0010 |
| | | Error | 181 | 44.6212 | 0.2465 | | | |
| | | Total | 206 | 76.2743 | | | | |
| | $NH_4$ | Site | 23 | 24.0693 | 1.0465 | 3.06 | <0.0001 | 0.2658 |
| | | FG type | 2 | 4.6657 | 2.3328 | 6.83 | 0.0014 | 0.0515 |
| | | Error | 181 | 61.8151 | 0.3415 | | | |
| | | Total | 206 | 90.5501 | | | | |
| | Ca | Site | 23 | 6.5735 | 0.2858 | 4.44 | <0.0001 | 0.3487 |
| | | FG type | 2 | 0.6139 | 0.3070 | 4.76 | 0.0096 | 0.0326 |
| | | Error | 181 | 11.6642 | 0.0644 | | | |
| | | Total | 206 | 18.8516 | | | | |
| | Mg | Site | 23 | 8.3070 | 0.3612 | 4.32 | <0.0001 | 0.3254 |
| | | FG type | 2 | 2.0724 | 1.0362 | 12.38 | <0.0001 | 0.0812 |
| | | Error | 181 | 15.1456 | 0.0837 | | | |
| | | Total | 206 | 25.5251 | | | | |
| | K | Site | 23 | 6.4338 | 0.2797 | 3.08 | <0.0001 | 0.2369 |
| | | FG type | 2 | 4.3029 | 2.1514 | 23.71 | <0.0001 | 0.1584 |
| | | Error | 181 | 16.4212 | 0.0907 | | | |
| | | Total | 206 | 27.1579 | | | | |
| | P | Site | 23 | 8.2262 | 0.3577 | 2.90 | <0.0001 | 0.2152 |
| | | FG type | 2 | 7.7152 | 3.8576 | 31.33 | <0.0001 | 0.2018 |
| | | Error | 181 | 22.2869 | 0.1231 | | | |
| | | Total | 206 | 38.2283 | | | | |
| | Fe | Site | 23 | 10.5323 | 0.4579 | 5.32 | <0.0001 | 0.4005 |
| | | FG type | 2 | 0.1953 | 0.0977 | 1.14 | 0.3235 | 0.0074 |
| | | Error | 181 | 15.5680 | 0.0860 | | | |
| | | Total | 206 | 26.2956 | | | | |
| | Mn | Site | 23 | 23.5600 | 1.0243 | 6.48 | <0.0001 | 0.4339 |
| | | FG type | 2 | 2.1150 | 1.0575 | 6.69 | 0.0016 | 0.0390 |
| | | Error | 181 | 28.6190 | 0.1581 | | | |
| | | Total | 206 | 54.2940 | | | | |
| | Zn | Site | 23 | 10.2903 | 0.4474 | 8.03 | <.0001 | 0.5013 |
| | | FG type | 2 | 0.1571 | 0.0785 | 1.41 | 0.2468 | 0.0077 |
| | | Error | 181 | 10.0793 | 0.0557 | | | |
| | | Total | 206 | 20.5267 | | | | |

**Table 18**… continued

| Var. type | Variable | Source | DF | SS | MS | F-Value | Pr >F | $\eta^2$ |
|---|---|---|---|---|---|---|---|---|
| | B | Site | 23 | 1.1140 | 0.0484 | 1.08 | 0.3739 | 0.1190 |
| | | FG type | 2 | 0.1119 | 0.0559 | 1.24 | 0.2905 | 0.0120 |
| | | Error | 181 | 8.1347 | 0.0449 | | | |
| | | Total | 206 | 9.3606 | | | | |
| | S | Site | 23 | 0.4087 | 0.0178 | 2.97 | <0.0001 | 0.2735 |
| | | FG type | 2 | 0.0040 | 0.0020 | 0.34 | 0.7136 | 0.0027 |
| | | Error | 181 | 1.0813 | 0.0060 | | | |
| | | Total | 206 | 1.4940 | | | | |
| | Al | Site | 23 | 1.8588 | 0.0808 | 4.71 | <0.0001 | 0.3713 |
| | | FG type | 2 | 0.0422 | 0.0211 | 1.23 | 0.2946 | 0.0084 |
| | | Error | 181 | 3.1052 | 0.0172 | | | |
| | | Total | 206 | 5.0062 | | | | |
| | pH | Site | 23 | 14.4220 | 0.6270 | 6.92 | <0.0001 | 0.4578 |
| | | FG type | 2 | 0.6759 | 0.3379 | 3.73 | 0.0259 | 0.0215 |
| | | Error | 181 | 16.4028 | 0.0906 | | | |
| | | Total | 206 | 31.5007 | | | | |

# Appendix E. Functional group quadrat PCA results

**Table 19.** Eigenvalues and estimated % of variance explained in principal components analysis at the microhabitat scale (Chapter 2). PC = principal component, and prefixes indicate variables used: a = abiotic, b = biotic, c = soil chemistry.

| | Lichen | | | Feathermoss | | | Vascular plant | | |
|---|---|---|---|---|---|---|---|---|---|
| PC | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative |
| a1 | 3.5275 | 0.4409 | 0.4409 | 3.6394 | 0.4549 | 0.4549 | 3.7311 | 0.4664 | 0.4664 |
| a2 | 1.5060 | 0.1883 | 0.6292 | 1.1909 | 0.1489 | 0.6038 | 1.3552 | 0.1694 | 0.6358 |
| a3 | 1.1601 | 0.1450 | 0.7742 | 1.1870 | 0.1484 | 0.7522 | 1.0739 | 0.1342 | 0.7700 |
| a4 | 0.7689 | 0.0961 | 0.8703 | 1.0154 | 0.1269 | 0.8791 | 0.8696 | 0.1087 | 0.8787 |
| a5 | 0.7199 | 0.0900 | 0.9603 | 0.7417 | 0.0927 | 0.9718 | 0.6736 | 0.0842 | 0.9629 |
| a6 | 0.3129 | 0.0391 | 0.9994 | 0.2205 | 0.0276 | 0.9994 | 0.2939 | 0.0367 | 0.9997 |
| a7 | 0.0047 | 0.0006 | 1.0000 | 0.0050 | 0.0006 | 1.0000 | 0.0027 | 0.0003 | 1.0000 |
| a8 | 0.0000 | 0.0000 | 1.0000 | 0.0000 | 0.0000 | 1.0000 | 0.0000 | 0.0000 | 1.0000 |
| PC | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative |
| b1 | 4.4351 | 0.4928 | 0.4928 | 4.5499 | 0.5055 | 0.5055 | 4.3171 | 0.4797 | 0.4797 |
| b2 | 1.3860 | 0.1540 | 0.6468 | 1.5875 | 0.1764 | 0.6819 | 1.3451 | 0.1495 | 0.6291 |
| b3 | 0.7874 | 0.0875 | 0.7343 | 0.8791 | 0.0977 | 0.7796 | 1.1386 | 0.1265 | 0.7556 |
| b4 | 0.7122 | 0.0791 | 0.8134 | 0.6418 | 0.0713 | 0.8509 | 0.8414 | 0.0935 | 0.8491 |
| b5 | 0.6418 | 0.0713 | 0.8847 | 0.5798 | 0.0644 | 0.9153 | 0.5415 | 0.0602 | 0.9093 |
| b6 | 0.5292 | 0.0588 | 0.9435 | 0.3895 | 0.0433 | 0.9586 | 0.3901 | 0.0433 | 0.9526 |
| b7 | 0.4525 | 0.0503 | 0.9938 | 0.3098 | 0.0344 | 0.9930 | 0.3700 | 0.0411 | 0.9938 |
| b8 | 0.0490 | 0.0054 | 0.9992 | 0.0543 | 0.0060 | 0.9990 | 0.0511 | 0.0057 | 0.9994 |
| b9 | 0.0068 | 0.0008 | 1.0000 | 0.0086 | 0.0010 | 1.0000 | 0.0051 | 0.0006 | 1.0000 |
| PC | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative |
| c1 | 3.9159 | 0.2797 | 0.2797 | 3.9651 | 0.2832 | 0.2832 | 3.8020 | 0.2716 | 0.2716 |
| c2 | 2.5086 | 0.1792 | 0.4589 | 2.6822 | 0.1916 | 0.4748 | 2.7618 | 0.1973 | 0.4688 |
| c3 | 2.0066 | 0.1433 | 0.6022 | 1.9744 | 0.1410 | 0.6158 | 2.0453 | 0.1461 | 0.6149 |
| c4 | 1.1398 | 0.0814 | 0.6836 | 1.2346 | 0.0882 | 0.7040 | 1.3053 | 0.0932 | 0.7082 |
| c5 | 1.0147 | 0.0725 | 0.7561 | 0.9820 | 0.0701 | 0.7742 | 1.0128 | 0.0723 | 0.7805 |
| c6 | 0.8815 | 0.0630 | 0.8191 | 0.8424 | 0.0602 | 0.8343 | 0.7458 | 0.0533 | 0.8338 |
| c7 | 0.7981 | 0.0570 | 0.8761 | 0.7506 | 0.0536 | 0.8880 | 0.5869 | 0.0419 | 0.8757 |
| c8 | 0.6033 | 0.0431 | 0.9192 | 0.5617 | 0.0401 | 0.9281 | 0.5581 | 0.0399 | 0.9156 |
| c9 | 0.3889 | 0.0278 | 0.9470 | 0.3344 | 0.0239 | 0.9520 | 0.4107 | 0.0293 | 0.9449 |
| c10 | 0.3081 | 0.0220 | 0.9690 | 0.2969 | 0.0212 | 0.9732 | 0.2887 | 0.0206 | 0.9655 |
| c11 | 0.2113 | 0.0151 | 0.9841 | 0.2260 | 0.0161 | 0.9893 | 0.2072 | 0.0148 | 0.9803 |
| c12 | 0.1260 | 0.0090 | 0.9931 | 0.0784 | 0.0056 | 0.9949 | 0.1369 | 0.0098 | 0.9901 |
| c13 | 0.0739 | 0.0053 | 0.9983 | 0.0604 | 0.0043 | 0.9992 | 0.0956 | 0.0068 | 0.9969 |
| c14 | 0.0233 | 0.0017 | 1.0000 | 0.0109 | 0.0008 | 1.0000 | 0.0428 | 0.0031 | 1.0000 |

**Table 20.** Variable loadings on principal components from lichen functional group quadrats (Chapter 2). Since loadings are equivalent to Pearson's correlation coefficients calculated between variables and principal components, it is useful to highlight those values that would be considered significant in a correlation analysis; loadings >0.24 and <-0.24 are equivalent to the minimum significance level at $\alpha = 0.05$, and are presented in bold print to aid interpretation.

| Lichen Quadrats | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Abiotic principal components ($a1_{lichen}$, etc.) | | | | | | | | | | | | | |
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | | | | | |
| CoarFrag | **-0.924** | **-0.304** | 0.073 | 0.157 | 0.135 | 0.071 | 0.024 | 0.000 | | | | | | |
| Gravel | 0.184 | **0.846** | -0.174 | -0.180 | **-0.427** | 0.077 | 0.012 | 0.000 | | | | | | |
| Fines | **0.965** | -0.178 | 0.024 | -0.070 | 0.112 | -0.132 | -0.036 | 0.000 | | | | | | |
| Sand | **0.954** | -0.149 | -0.011 | -0.090 | 0.120 | -0.206 | 0.051 | 0.000 | | | | | | |
| Silt+Clay | **0.824** | -0.226 | 0.200 | 0.058 | 0.012 | **0.476** | 0.007 | 0.000 | | | | | | |
| Slope | **0.247** | **0.604** | -0.231 | **0.582** | **0.427** | 0.014 | 0.000 | 0.000 | | | | | | |
| N-aspect | -0.213 | **0.465** | **0.561** | **-0.449** | **0.469** | 0.032 | 0.000 | 0.000 | | | | | | |
| Concavity | 0.116 | 0.113 | **0.846** | **0.393** | **-0.299** | -0.119 | 0.000 | 0.000 | | | | | | |
| | Biotic principal components ($b1_{lichen}$, etc.) | | | | | | | | | | | | | |
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| LFH | **0.469** | **-0.577** | 0.182 | **0.508** | **0.247** | 0.034 | **0.307** | -0.006 | 0.001 | | | | | |
| WInDZ | 0.234 | **0.685** | **-0.453** | **0.504** | -0.055 | 0.117 | 0.028 | 0.000 | 0.001 | | | | | |
| CRDZ | **0.598** | 0.175 | **0.546** | **0.282** | **-0.414** | -0.116 | -0.219 | 0.019 | 0.000 | | | | | |
| SWCC | **0.629** | **0.337** | 0.134 | -0.013 | **0.605** | -0.217 | **-0.241** | 0.030 | 0.000 | | | | | |
| LAI | **0.888** | -0.192 | -0.120 | -0.137 | -0.050 | **0.334** | -0.046 | 0.161 | 0.000 | | | | | |
| Direct | **-0.784** | 0.137 | **0.301** | 0.082 | 0.168 | **0.470** | -0.136 | -0.018 | 0.038 | | | | | |
| Diffuse | **-0.911** | 0.110 | 0.029 | 0.085 | -0.025 | **-0.320** | 0.168 | 0.132 | 0.035 | | | | | |
| Total_irrad | **-0.950** | 0.145 | 0.188 | 0.117 | 0.092 | 0.108 | 0.016 | 0.061 | -0.064 | | | | | |
| localBA | **0.523** | **0.592** | **0.302** | **-0.272** | 0.009 | 0.088 | **0.450** | -0.012 | 0.000 | | | | | |
| | Soil chemistry principal components ($c1_{lichen}$, etc.) | | | | | | | | | | | | | |
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| Total_N | 0.156 | **0.901** | 0.189 | -0.060 | 0.135 | 0.126 | **0.244** | 0.042 | -0.060 | 0.117 | 0.016 | 0.016 | -0.019 | -0.105 |
| NO3 | **0.373** | **0.314** | 0.164 | -0.186 | **0.800** | 0.093 | -0.022 | 0.167 | -0.057 | -0.123 | 0.053 | -0.020 | 0.013 | 0.053 |
| NH4 | 0.013 | **0.882** | 0.155 | 0.091 | **-0.289** | 0.068 | 0.232 | -0.080 | -0.037 | 0.166 | -0.043 | 0.032 | 0.006 | 0.096 |
| Ca | **0.672** | 0.108 | **-0.617** | 0.132 | 0.050 | 0.056 | 0.020 | 0.034 | **0.306** | -0.003 | 0.045 | 0.111 | -0.153 | 0.007 |
| Mg | **0.700** | 0.233 | **-0.583** | 0.134 | 0.015 | 0.023 | 0.014 | -0.116 | 0.198 | -0.005 | -0.028 | -0.100 | 0.184 | -0.010 |
| K | **0.764** | 0.125 | -0.205 | **0.252** | -0.146 | -0.164 | -0.071 | -0.198 | **-0.369** | -0.125 | 0.224 | -0.003 | -0.022 | -0.001 |
| P | **0.544** | 0.035 | **0.369** | **0.328** | 0.216 | **-0.398** | **-0.403** | -0.092 | 0.007 | **0.241** | -0.149 | -0.032 | -0.033 | -0.005 |
| Fe | **0.576** | **-0.452** | **0.529** | -0.205 | 0.035 | -0.024 | 0.136 | -0.172 | 0.104 | 0.120 | 0.135 | 0.203 | 0.084 | -0.001 |
| Mn | **0.834** | 0.065 | 0.179 | -0.230 | -0.202 | 0.047 | 0.003 | -0.003 | -0.092 | **-0.266** | **-0.295** | 0.080 | -0.004 | -0.007 |
| Zn | **0.573** | -0.084 | 0.125 | -0.010 | **-0.277** | **0.467** | **-0.371** | **0.435** | -0.055 | 0.134 | 0.067 | -0.018 | 0.020 | 0.002 |
| B | **-0.296** | -0.227 | 0.000 | **0.774** | 0.223 | **0.413** | 0.085 | -0.053 | -0.096 | -0.034 | -0.090 | 0.109 | 0.032 | -0.005 |
| S | -0.058 | **0.332** | **0.690** | **0.399** | -0.184 | -0.199 | -0.020 | 0.183 | **0.255** | **-0.257** | 0.107 | -0.024 | 0.014 | -0.005 |
| Al | **0.559** | **-0.417** | **0.449** | 0.034 | -0.004 | **0.342** | **0.283** | **-0.251** | 0.073 | 0.018 | 0.005 | -0.200 | -0.076 | 0.005 |
| pH | **0.414** | **-0.433** | -0.122 | 0.178 | -0.001 | **-0.340** | **0.522** | **0.432** | -0.099 | 0.086 | -0.041 | -0.025 | 0.008 | 0.005 |

**Table 21.** Variable loadings on principal components from feathermoss functional group quadrats (Chapter 2). Since loadings are equivalent to Pearson's correlation coefficients calculated between variables and principal components, it is useful to highlight those values that would be considered significant in a correlation analysis; loadings >0.24 and <-0.24 are equivalent to the minimum significance level at α = 0.05, and are presented in bold print to aid interpretation.

| Feathermoss Quadrats | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Abiotic principal components | | | | | | | | | | | | | |
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | | | | | |
| CoarFrag | **-0.945** | 0.142 | **-0.244** | 0.126 | 0.036 | 0.100 | 0.027 | 0.000 | | | | | | |
| Gravel | 0.135 | **-0.337** | **0.898** | -0.220 | -0.112 | -0.032 | 0.011 | 0.000 | | | | | | |
| Fines | **0.965** | 0.034 | -0.238 | -0.015 | 0.024 | -0.093 | -0.036 | 0.000 | | | | | | |
| Sand | **0.953** | 0.057 | -0.224 | -0.042 | 0.032 | -0.184 | 0.052 | 0.000 | | | | | | |
| Silt+Clay | **0.906** | -0.070 | -0.030 | 0.043 | -0.097 | **0.403** | 0.010 | 0.000 | | | | | | |
| Slope | 0.060 | **0.654** | 0.177 | **-0.582** | **0.442** | 0.061 | -0.001 | 0.000 | | | | | | |
| N-aspect | 0.097 | **0.767** | 0.229 | 0.208 | **-0.554** | -0.029 | -0.001 | 0.000 | | | | | | |
| Concavity | 0.237 | 0.180 | **0.361** | **0.752** | **0.464** | -0.006 | 0.000 | 0.000 | | | | | | |
| | Biotic principal components | | | | | | | | | | | | | |
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | | | | | |
| LFH | **0.634** | **-0.386** | 0.169 | **0.470** | **0.323** | **0.279** | -0.130 | -0.019 | -0.002 | | | | | |
| WInDZ | **0.354** | **0.383** | **-0.804** | **0.262** | 0.038 | 0.038 | 0.098 | 0.001 | 0.001 | | | | | |
| CRDZ | **0.442** | **0.700** | 0.216 | 0.123 | **0.325** | **-0.359** | -0.133 | 0.006 | 0.000 | | | | | |
| SWCC | **0.627** | **0.298** | **0.322** | **0.376** | **-0.495** | -0.001 | 0.162 | 0.023 | 0.002 | | | | | |
| LAI | **0.888** | **-0.249** | 0.025 | -0.180 | 0.196 | -0.021 | 0.224 | 0.165 | 0.007 | | | | | |
| Direct | **-0.820** | **0.296** | 0.186 | 0.080 | **0.254** | 0.111 | **0.346** | -0.024 | -0.042 | | | | | |
| Diffuse | **-0.932** | 0.057 | -0.057 | 0.201 | -0.096 | 0.020 | -0.222 | 0.155 | -0.033 | | | | | |
| Total_irrad | **-0.951** | 0.202 | 0.087 | 0.136 | 0.104 | 0.086 | 0.065 | 0.037 | 0.075 | | | | | |
| localBA | **0.447** | **0.720** | 0.088 | **-0.312** | -0.016 | **0.400** | -0.125 | 0.018 | -0.001 | | | | | |
| | Soil chemistry principal components | | | | | | | | | | | | | |
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| Total N | **-0.589** | **0.515** | **0.543** | 0.095 | 0.156 | 0.156 | 0.050 | 0.112 | -0.063 | -0.091 | -0.046 | 0.010 | 0.001 | -0.076 |
| NO3 | -0.134 | 0.111 | **0.564** | **0.303** | **0.572** | **-0.368** | 0.216 | -0.113 | 0.067 | 0.164 | 0.074 | 0.002 | -0.009 | 0.022 |
| NH4 | **-0.619** | **0.537** | **0.405** | -0.017 | -0.011 | **0.313** | -0.003 | 0.160 | -0.075 | -0.165 | -0.034 | 0.036 | 0.008 | 0.067 |
| Ca | **0.778** | **-0.274** | **0.438** | 0.030 | -0.053 | 0.074 | -0.096 | 0.181 | 0.198 | -0.019 | -0.038 | 0.145 | -0.123 | -0.002 |
| Mg | **0.768** | -0.066 | **0.531** | 0.027 | -0.046 | 0.058 | -0.106 | 0.133 | 0.226 | -0.045 | -0.069 | -0.115 | 0.135 | 0.002 |
| K | **0.534** | 0.129 | **0.422** | **-0.297** | 0.007 | 0.225 | -0.020 | **-0.606** | -0.091 | -0.052 | -0.040 | 0.004 | -0.016 | 0.000 |
| P | **0.293** | -0.090 | 0.122 | **-0.711** | 0.001 | -0.028 | **0.579** | 0.198 | -0.076 | 0.054 | 0.014 | 0.017 | 0.022 | -0.002 |
| Fe | **0.560** | **0.424** | **-0.512** | 0.002 | **0.404** | -0.129 | -0.034 | -0.016 | -0.005 | -0.160 | -0.099 | 0.139 | 0.098 | -0.003 |
| Mn | **0.479** | **0.760** | -0.008 | -0.064 | -0.147 | -0.054 | -0.085 | 0.030 | 0.034 | -0.052 | **0.390** | 0.002 | 0.000 | -0.005 |
| Zn | **0.439** | **0.724** | 0.073 | 0.094 | -0.239 | 0.000 | -0.129 | 0.083 | -0.173 | **0.375** | -0.130 | 0.029 | 0.017 | 0.003 |
| B | **0.268** | 0.032 | -0.153 | **0.661** | **-0.293** | **0.264** | **0.543** | -0.109 | 0.051 | -0.023 | 0.013 | 0.030 | 0.025 | -0.001 |
| S | **-0.417** | **0.537** | **-0.400** | **-0.258** | 0.166 | **0.310** | 0.055 | -0.082 | **0.388** | 0.150 | -0.044 | -0.021 | -0.029 | -0.001 |
| Al | **0.757** | **0.431** | **-0.260** | 0.115 | **0.249** | -0.004 | 0.106 | 0.119 | -0.100 | -0.128 | -0.100 | -0.145 | -0.119 | 0.005 |
| pH | **0.312** | **-0.505** | -0.108 | 0.083 | **0.456** | **0.582** | -0.106 | 0.113 | -0.146 | 0.136 | 0.136 | -0.001 | 0.024 | -0.002 |

**Table 22.** Variable loadings on principal components from vascular plant functional group quadrats (Chapter 2). Since loadings are equivalent to Pearson's correlation coefficients calculated between variables and principal components, it is useful to highlight those values that would be considered significant in a correlation analysis; loadings >0.24 and <-0.24 are equivalent to the minimum significance level at α = 0.05, and are presented in bold print to aid interpretation.

Vascular Plant Quadrats

| | Abiotic principal components | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| CoarFrag | **-0.955** | -0.211 | -0.001 | 0.123 | 0.126 | 0.107 | 0.018 | 0.000 |
| Gravel | **0.395** | **0.729** | 0.199 | **-0.371** | **-0.368** | 0.017 | 0.008 | 0.000 |
| Fines | **0.949** | -0.215 | -0.130 | 0.088 | 0.083 | -0.146 | -0.028 | 0.000 |
| Sand | **0.946** | -0.185 | -0.096 | 0.113 | 0.081 | -0.201 | 0.039 | 0.000 |
| Silt+Clay | **0.785** | **-0.277** | **-0.310** | -0.094 | -0.082 | **0.441** | 0.004 | 0.000 |
| Slope | **0.354** | **0.244** | **0.496** | **0.739** | -0.090 | 0.126 | -0.001 | 0.000 |
| N-aspect | **0.337** | -0.173 | **0.725** | **-0.366** | **0.437** | 0.077 | 0.000 | 0.000 |
| Concavity | 0.109 | **0.730** | **-0.374** | 0.091 | **0.551** | 0.063 | 0.000 | 0.000 |

| | Biotic principal components | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| LFH | **0.534** | 0.054 | **-0.341** | **0.705** | 0.178 | 0.106 | -0.237 | 0.000 | 0.001 |
| WInDZ | 0.087 | 0.024 | **0.916** | **0.249** | **0.249** | -0.164 | -0.026 | 0.003 | -0.001 |
| CRDZ | **0.436** | **0.750** | -0.093 | 0.122 | **-0.297** | **-0.368** | 0.025 | 0.004 | 0.000 |
| SWCC | **0.623** | **0.277** | **-0.271** | **-0.367** | **0.557** | -0.123 | 0.017 | 0.028 | -0.002 |
| LAI | **0.901** | -0.206 | 0.042 | 0.130 | -0.092 | 0.078 | **0.296** | 0.158 | -0.001 |
| Direct | **-0.796** | **0.368** | -0.073 | 0.240 | 0.166 | 0.105 | **0.358** | -0.026 | 0.035 |
| Diffuse | **-0.938** | 0.111 | -0.009 | -0.073 | 0.003 | -0.053 | **-0.277** | 0.150 | 0.025 |
| Total_irrad | **-0.933** | **0.294** | -0.061 | 0.129 | 0.082 | 0.056 | 0.082 | 0.047 | -0.056 |
| localBA | **0.500** | **0.653** | **0.300** | -0.191 | -0.079 | **0.422** | -0.113 | 0.002 | 0.001 |

| | Soil chemistry principal components | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| Total N | **-0.495** | **0.445** | **0.684** | 0.039 | 0.215 | -0.018 | -0.053 | 0.090 | -0.022 | -0.048 | 0.049 | -0.032 | -0.003 | -0.152 |
| NO3 | **-0.522** | 0.032 | **0.453** | **0.500** | **0.392** | 0.108 | 0.101 | -0.139 | -0.192 | 0.093 | 0.145 | 0.026 | 0.033 | 0.087 |
| NH4 | -0.212 | **0.571** | **0.587** | **-0.306** | 0.141 | -0.165 | 0.048 | **0.269** | 0.150 | -0.069 | -0.179 | 0.034 | -0.004 | 0.094 |
| Ca | **0.690** | **-0.401** | **0.396** | 0.011 | -0.041 | 0.088 | **-0.355** | 0.142 | -0.054 | 0.000 | -0.004 | 0.094 | 0.197 | -0.001 |
| Mg | **0.657** | **-0.285** | **0.567** | 0.008 | -0.140 | 0.144 | **-0.243** | 0.089 | -0.065 | 0.022 | 0.074 | -0.057 | -0.209 | 0.028 |
| K | **0.703** | -0.085 | **0.429** | 0.049 | 0.077 | -0.148 | 0.177 | **-0.323** | 0.216 | **0.298** | -0.112 | -0.012 | 0.010 | -0.026 |
| P | **0.587** | -0.086 | **0.254** | **0.424** | **-0.290** | 0.106 | **0.473** | 0.144 | -0.151 | -0.178 | -0.099 | -0.006 | 0.017 | -0.017 |
| Fe | **0.517** | **0.584** | **-0.312** | **0.360** | 0.237 | -0.062 | -0.149 | -0.075 | -0.051 | -0.056 | -0.084 | 0.237 | -0.087 | -0.021 |
| Mn | **0.616** | **0.593** | 0.116 | -0.216 | -0.124 | -0.012 | 0.137 | -0.130 | 0.201 | -0.147 | **0.305** | 0.042 | 0.034 | 0.018 |
| Zn | **0.529** | **0.462** | -0.160 | **-0.438** | 0.084 | -0.177 | 0.124 | 0.160 | **-0.406** | 0.208 | 0.051 | -0.020 | 0.013 | -0.006 |
| B | **0.292** | **-0.380** | -0.189 | **-0.277** | **0.562** | **0.487** | 0.206 | 0.201 | 0.134 | 0.024 | 0.015 | 0.044 | -0.021 | -0.019 |
| S | -0.081 | **0.638** | -0.221 | **0.431** | **-0.287** | 0.233 | -0.049 | **0.333** | 0.179 | **0.258** | 0.043 | -0.029 | 0.018 | 0.002 |
| Al | **0.629** | **0.520** | -0.213 | 0.188 | **0.343** | 0.103 | -0.171 | -0.109 | -0.010 | -0.129 | -0.082 | **-0.242** | 0.045 | 0.017 |
| pH | **0.283** | **-0.504** | -0.180 | **0.336** | **0.295** | **-0.554** | 0.033 | **0.306** | 0.128 | -0.018 | 0.113 | -0.042 | -0.012 | -0.004 |

# Appendix F. Detailed plot-level PCA and NMS results

**Table 23.** Principal component eigenvalues and estimated variance explained at the plot scale (Chapter 3), expressed as a proportion and as a cumulative proportion of total variance in the correlation matrix (the sum of all eigenvalues).

| | Abiotic | | | Biotic | | | Soil Chemistry | | |
|---|---|---|---|---|---|---|---|---|---|
| PC | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative | Eigenvalue | Proportion | Cumulative |
| 1 | 2.5617 | 0.3202 | 0.3202 | 4.3723 | 0.4858 | 0.4858 | 3.8423 | 0.2744 | 0.2744 |
| 2 | 2.0398 | 0.2550 | 0.5752 | 1.4281 | 0.1587 | 0.6445 | 2.8225 | 0.2016 | 0.4761 |
| 3 | 1.0513 | 0.1314 | 0.7066 | 1.0758 | 0.1195 | 0.7640 | 2.1802 | 0.1557 | 0.6318 |
| 4 | 1.0008 | 0.1251 | 0.8317 | 0.8000 | 0.0889 | 0.8529 | 1.3719 | 0.0980 | 0.7298 |
| 5 | 0.7582 | 0.0948 | 0.9265 | 0.5466 | 0.0607 | 0.9136 | 1.0575 | 0.0755 | 0.8053 |
| 6 | 0.5339 | 0.0667 | 0.9932 | 0.4347 | 0.0483 | 0.9619 | 0.6899 | 0.0493 | 0.8546 |
| 7 | 0.0542 | 0.0068 | 1.0000 | 0.2884 | 0.0320 | 0.9940 | 0.6468 | 0.0462 | 0.9008 |
| 8 | 0.0000 | 0.0000 | 1.0000 | 0.0438 | 0.0049 | 0.9988 | 0.4057 | 0.0290 | 0.9298 |
| 9 | | | | 0.0104 | 0.0012 | 1.0000 | 0.3737 | 0.0267 | 0.9565 |
| 10 | | | | | | | 0.2440 | 0.0174 | 0.9739 |
| 11 | | | | | | | 0.1864 | 0.0133 | 0.9872 |
| 12 | | | | | | | 0.0926 | 0.0066 | 0.9938 |
| 13 | | | | | | | 0.0817 | 0.0058 | 0.9996 |
| 14 | | | | | | | 0.0049 | 0.0004 | 1.0000 |

**Table 24.** Variable loadings on principal components at the plot scale (Chapter 3), calculated as the eigenvector multiplied by the square root of the eigenvalue. Loadings considered 'significant' (i.e., loadings equivalent to the correlation coefficients that are statistically significant at α = 0.05 between given variable and principal component) are highlighted with bold formatting.

| | | | | | | Principal components | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Subset | Variable | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| Abiotic | CoarFrag | **-0.94** | **-0.29** | -0.03 | 0.14 | -0.08 | 0.01 | 0.08 | | | | | | | |
| | Gravel | 0.12 | **0.68** | **0.29** | **-0.30** | **0.55** | -0.20 | 0.01 | | | | | | | |
| | Fines | **0.96** | -0.05 | -0.12 | 0.00 | -0.21 | 0.10 | -0.09 | | | | | | | |
| | Sand | -0.08 | **-0.72** | 0.11 | **0.47** | **0.47** | -0.10 | -0.11 | | | | | | | |
| | Silt+Clay | **0.85** | **-0.41** | 0.00 | 0.23 | 0.18 | 0.01 | 0.17 | | | | | | | |
| | Slope | 0.08 | **0.59** | 0.03 | **0.63** | **-0.25** | **-0.43** | 0.01 | | | | | | | |
| | N-aspect | 0.03 | -0.03 | **0.95** | 0.11 | -0.20 | 0.19 | 0.00 | | | | | | | |
| | Mesotopo | -0.10 | **0.67** | -0.18 | **0.46** | 0.21 | **0.50** | 0.00 | | | | | | | |
| Biotic | LFH | **-0.64** | **0.34** | **-0.28** | **0.36** | **0.41** | 0.19 | 0.24 | -0.01 | 0.00 | | | | | |
| | LAI | **-0.94** | 0.07 | 0.13 | 0.00 | 0.08 | 0.10 | -0.23 | 0.16 | 0.01 | | | | | |
| | Total-irrad | **0.97** | -0.03 | 0.04 | 0.11 | 0.02 | 0.17 | 0.04 | 0.08 | -0.08 | | | | | |
| | Direct | **0.85** | -0.03 | 0.10 | 0.17 | 0.03 | **0.45** | -0.18 | -0.04 | 0.04 | | | | | |
| | Diffuse | **0.95** | -0.02 | -0.09 | 0.04 | -0.01 | -0.14 | **0.25** | 0.11 | 0.05 | | | | | |
| | CD | -0.13 | **0.30** | **0.83** | **0.42** | -0.13 | -0.08 | 0.08 | -0.01 | 0.00 | | | | | |
| | BA | **-0.70** | **-0.41** | -0.05 | -0.03 | **-0.44** | **0.31** | 0.23 | 0.01 | 0.00 | | | | | |
| | Stand Age | -0.08 | **-0.73** | **0.47** | **-0.27** | **0.40** | 0.04 | 0.10 | -0.01 | 0.00 | | | | | |
| | Saplings | 0.07 | **0.72** | 0.23 | **-0.62** | 0.01 | 0.17 | 0.11 | 0.00 | 0.00 | | | | | |
| Chemical | Total_N | **-0.68** | -0.03 | **0.66** | 0.00 | 0.22 | 0.17 | 0.07 | -0.01 | 0.05 | -0.08 | -0.04 | 0.00 | 0.02 | -0.05 |
| | NO3 | **-0.26** | **-0.24** | **0.30** | **-0.66** | **0.47** | -0.09 | **0.24** | 0.01 | 0.06 | 0.21 | 0.08 | -0.01 | 0.00 | 0.02 |
| | NH4 | **-0.64** | 0.06 | **0.67** | 0.22 | 0.09 | 0.20 | -0.01 | 0.00 | 0.05 | -0.18 | -0.08 | 0.01 | 0.02 | 0.04 |
| | Ca | **0.63** | **-0.56** | **0.34** | 0.18 | 0.08 | 0.14 | -0.10 | 0.09 | -0.22 | 0.07 | -0.02 | -0.18 | 0.10 | 0.00 |
| | Mg | **0.59** | **-0.52** | **0.48** | 0.15 | 0.11 | 0.04 | -0.09 | 0.06 | -0.23 | 0.02 | 0.09 | 0.18 | -0.10 | 0.00 |
| | K | **0.70** | -0.18 | **0.44** | 0.12 | -0.08 | -0.11 | -0.07 | **-0.35** | **0.27** | 0.13 | -0.17 | 0.01 | -0.02 | 0.00 |
| | P | **0.41** | -0.20 | **0.47** | -0.12 | **-0.48** | **-0.29** | **0.39** | **0.27** | 0.10 | -0.11 | -0.01 | -0.01 | 0.01 | 0.00 |
| | Fe | **0.52** | **0.69** | 0.06 | **-0.38** | -0.03 | 0.14 | 0.05 | -0.03 | -0.16 | 0.01 | -0.11 | 0.12 | 0.16 | 0.00 |
| | Mn | **0.48** | **0.67** | **0.39** | 0.08 | 0.06 | -0.10 | -0.06 | -0.18 | 0.07 | -0.10 | **0.31** | -0.04 | 0.04 | 0.00 |
| | Zn | **0.30** | **0.60** | 0.08 | **0.37** | **0.39** | -0.12 | -0.17 | **0.38** | 0.19 | 0.11 | -0.05 | 0.02 | 0.01 | 0.00 |
| | B | **0.27** | -0.07 | **-0.36** | **0.58** | **0.29** | 0.14 | **0.58** | -0.10 | 0.01 | 0.01 | 0.02 | 0.03 | 0.03 | 0.00 |
| | S | **-0.43** | **0.48** | **0.30** | 0.21 | **-0.50** | **0.30** | 0.10 | 0.03 | -0.04 | **0.30** | 0.07 | 0.00 | -0.03 | 0.00 |
| | Al | **0.59** | **0.67** | 0.10 | **-0.25** | 0.13 | 0.17 | 0.14 | 0.00 | -0.13 | -0.09 | -0.11 | -0.10 | -0.18 | 0.00 |
| | pH | **0.56** | **-0.37** | -0.21 | **-0.27** | -0.07 | **0.56** | -0.06 | 0.12 | **0.31** | -0.06 | 0.08 | 0.02 | 0.00 | 0.00 |

**Table 25.** Pearson's and Kendall's correlations between NMS axes (NMS conducted on species data at the plot scale, Chapter 3) and environmental variables or principal components.

| Variable | NMS Axis 1 | | | NMS Axis 2 | | | PC | NMS Axis 1 | | | NMS Axis 2 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | r | $r^2$ | τ | r | $r^2$ | τ | | r | $r^2$ | τ | r | $r^2$ | τ |
| Total_N | -0.317 | 0.101 | -0.203 | -0.241 | 0.058 | -0.183 | abiotic1 | 0.193 | 0.037 | 0.156 | -0.17 | 0.029 | -0.12 |
| $NO_3$ | 0.098 | 0.01 | 0.069 | -0.268 | 0.072 | -0.208 | abiotic2 | 0.278 | 0.077 | 0.178 | -0.004 | 0 | 0 |
| $NH_4$ | -0.379 | 0.144 | -0.238 | -0.177 | 0.031 | -0.126 | abiotic3 | -0.23 | 0.053 | -0.177 | -0.176 | 0.031 | -0.112 |
| Ca | 0.471 | 0.222 | 0.302 | -0.403 | 0.162 | -0.298 | abiotic4 | -0.029 | 0.001 | -0.022 | -0.299 | 0.089 | -0.198 |
| Mg | 0.432 | 0.187 | 0.315 | -0.45 | 0.202 | -0.31 | abiotic5 | -0.1 | 0.01 | -0.085 | -0.196 | 0.038 | -0.124 |
| K | 0.352 | 0.124 | 0.25 | -0.082 | 0.007 | -0.068 | abiotic6 | -0.204 | 0.042 | -0.124 | 0.222 | 0.049 | 0.113 |
| P | 0.413 | 0.17 | 0.306 | -0.134 | 0.018 | -0.083 | abiotic7 | 0.088 | 0.008 | 0.027 | 0.098 | 0.01 | 0.064 |
| Fe | 0.004 | 0 | -0.001 | 0.46 | 0.212 | 0.341 | abiotic8 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mn | -0.115 | 0.013 | -0.035 | 0.394 | 0.155 | 0.258 | biotic1 | -0.212 | 0.045 | -0.122 | 0.707 | 0.5 | 0.505 |
| Zn | -0.09 | 0.008 | -0.075 | 0.317 | 0.1 | 0.18 | biotic2 | -0.246 | 0.061 | -0.143 | -0.221 | 0.049 | -0.16 |
| B | 0.124 | 0.015 | 0.058 | 0.113 | 0.013 | 0.083 | biotic3 | 0.04 | 0.002 | 0.072 | 0.007 | 0 | 0.01 |
| S | -0.396 | 0.157 | -0.219 | 0.164 | 0.027 | 0.135 | biotic4 | 0.453 | 0.206 | 0.322 | 0.034 | 0.001 | -0.026 |
| Al | -0.01 | 0 | 0.011 | 0.524 | 0.275 | 0.376 | biotic5 | 0.108 | 0.012 | 0.095 | 0.094 | 0.009 | 0.11 |
| pH | 0.456 | 0.208 | 0.302 | 0.169 | 0.029 | 0.108 | biotic6 | 0.075 | 0.006 | -0.013 | -0.223 | 0.05 | -0.113 |
| CoarFrag | -0.246 | 0.061 | -0.177 | 0.149 | 0.022 | 0.087 | biotic7 | 0.077 | 0.006 | 0.049 | 0.088 | 0.008 | 0.034 |
| Gravel | 0.143 | 0.02 | 0.08 | -0.137 | 0.019 | -0.092 | biotic8 | -0.276 | 0.076 | -0.178 | 0.04 | 0.002 | 0.061 |
| Fines | 0.192 | 0.037 | 0.178 | -0.088 | 0.008 | -0.055 | biotic9 | -0.007 | 0 | -0.026 | 0.053 | 0.003 | 0.117 |
| Sand | -0.291 | 0.085 | -0.168 | -0.266 | 0.071 | -0.21 | chem1 | 0.461 | 0.212 | 0.311 | 0.157 | 0.025 | 0.112 |
| Silt+Clay | 0.037 | 0.001 | 0.06 | -0.227 | 0.051 | -0.153 | chem2 | -0.416 | 0.173 | -0.246 | 0.599 | 0.359 | 0.428 |
| Slope | 0.267 | 0.071 | 0.209 | -0.254 | 0.065 | -0.155 | chem3 | -0.014 | 0 | 0.031 | -0.267 | 0.071 | -0.16 |
| N_aspect | -0.242 | 0.059 | -0.169 | -0.123 | 0.015 | -0.075 | chem4 | -0.128 | 0.016 | -0.13 | -0.072 | 0.005 | -0.013 |
| Mesotopo | 0.072 | 0.005 | 0.042 | -0.021 | 0 | -0.025 | chem5 | -0.037 | 0.001 | -0.017 | -0.061 | 0.004 | -0.046 |
| LFH | 0.284 | 0.081 | 0.217 | -0.505 | 0.255 | -0.371 | chem6 | -0.057 | 0.003 | -0.026 | 0.219 | 0.048 | 0.121 |
| LAI | 0.142 | 0.02 | 0.107 | -0.71 | 0.504 | -0.52 | chem7 | 0.122 | 0.015 | 0.068 | 0.078 | 0.006 | 0.059 |
| Direct | -0.057 | 0.003 | -0.081 | 0.498 | 0.248 | 0.354 | chem8 | 0.184 | 0.034 | 0.082 | -0.039 | 0.002 | 0.047 |
| Diffuse | -0.206 | 0.042 | -0.135 | 0.733 | 0.537 | 0.54 | chem9 | 0.095 | 0.009 | 0.077 | 0.319 | 0.102 | 0.246 |
| Total_irrad | -0.149 | 0.022 | -0.097 | 0.664 | 0.441 | 0.472 | chem10 | 0.073 | 0.005 | 0.074 | -0.197 | 0.039 | -0.137 |
| CD | 0.167 | 0.028 | 0.147 | -0.123 | 0.015 | -0.117 | chem11 | -0.023 | 0.001 | -0.011 | 0.029 | 0.001 | 0.038 |
| BA | 0.223 | 0.05 | 0.113 | -0.493 | 0.243 | -0.339 | chem12 | 0.055 | 0.003 | 0.049 | -0.108 | 0.012 | -0.072 |
| Age | 0.15 | 0.022 | 0.115 | 0.134 | 0.018 | 0.181 | chem13 | 0.09 | 0.008 | 0.027 | -0.096 | 0.009 | -0.02 |
| Saplings | -0.441 | 0.194 | -0.288 | -0.154 | 0.024 | -0.125 | chem14 | -0.056 | 0.003 | -0.077 | -0.021 | 0 | 0.018 |

**Table 26.** Species scores on nonmetric multidimentional scaling (NMS) axes 1 and 2 at the plot scale, from Chapter 3.

| | Scores | |
|---|---|---|
| Species | NMS Axis 1 | NMS Axis 2 |
| *Ledum groenlandicum* | -0.19 | -0.96 |
| *Rosa acicularis* | 0.00 | -0.55 |
| *Shepherdia canadensis* | 0.13 | -0.92 |
| *Arctostaphylos uva-ursi* | 0.44 | 0.38 |
| *Empetrum nigrum* | -0.18 | 0.32 |
| *Vaccinium caespitosum* | -0.09 | -0.26 |
| *Vaccinium membranaceum* | -0.54 | -0.20 |
| *Vaccinium vitis-idaea* | 0.31 | 0.16 |
| *Arnica cordifolia* | 0.31 | -1.16 |
| *Cornus canadensis* | -0.02 | -0.85 |
| *Epilobium angustifolium* | 0.73 | -0.29 |
| *Geocaulon lividum* | 0.09 | -1.03 |
| *Linnaea borealis* | 0.08 | -0.39 |
| *Lycopodium spp.* | -0.01 | -1.24 |
| *Orthelia secunda* | 0.34 | -1.05 |
| *Pyrola virens* | -0.01 | -0.94 |
| *Petasites palmatus* | 0.77 | -1.38 |
| *Viola renifolia* | 0.83 | -0.96 |
| *Orizopsis pungens* | 0.32 | 0.13 |
| *Pelitgera spp.* | 0.27 | -0.09 |
| *Cladonia mitis* | -0.12 | 0.72 |
| *Cladonia rangiferina* | -0.18 | 0.64 |
| *Cetraria spp.* | -0.02 | 0.87 |
| *Cladonia spp.* | -0.06 | 0.57 |
| *Cladonia uncialis* | -0.26 | 0.62 |
| *Stereocaulon spp.* | -0.11 | 1.01 |
| *Umbilicaria spp.* | -0.06 | 0.43 |
| *Pleurozium schreberi* | -0.16 | -0.75 |
| *Ptilium crista-castrensis* | 0.49 | -1.25 |
| *Hylocomium splendens* | 0.31 | -0.95 |
| *Pohlia nutans* | -0.10 | 0.15 |
| *Polytrichum spp.* | 0.02 | 0.06 |
| *Hepatics* | -0.04 | -0.18 |

# Appendix G. Full Pearson's correlation analysis results

**Table 27.** Pearson's correlation coefficients (r) and respective *p*-values showing relationships between time above estimated water content thresholds and environmental variables (Chapter 5). Significant values ($\alpha = 0.10$) are in bold type.

| Variable | | Sunny days | | | Cloudy days | | |
|---|---|---|---|---|---|---|---|
| | | Low | Medium | High | Low | Medium | High |
| Vascular plant abundance | *r* | 0.230 | 0.187 | 0.131 | 0.231 | 0.163 | 0.118 |
| | *p* | 0.280 | 0.381 | 0.542 | 0.277 | 0.448 | 0.582 |
| Lichen abundance | *r* | **-0.398** | **-0.357** | -0.308 | -0.341 | -0.325 | -0.316 |
| | *p* | 0.054 | 0.087 | 0.143 | 0.103 | 0.121 | 0.132 |
| Feathermoss abundance | *r* | 0.319 | 0.301 | 0.308 | 0.255 | 0.266 | 0.291 |
| | *p* | 0.129 | 0.153 | 0.143 | 0.229 | 0.209 | 0.167 |
| Mean annual temperature | *r* | -0.279 | -0.307 | **-0.480** | **-0.406** | **-0.376** | **-0.398** |
| | *p* | 0.1872 | 0.1450 | 0.0177 | 0.0488 | 0.0705 | 0.0544 |
| Continentality | *r* | -0.069 | -0.062 | -0.066 | 0.093 | 0.001 | -0.063 |
| | *p* | 0.7492 | 0.7747 | 0.7587 | 0.6647 | 0.9981 | 0.7717 |
| Mean annual precipitation | *r* | 0.175 | 0.161 | 0.111 | -0.049 | 0.035 | 0.089 |
| | *p* | 0.4128 | 0.4518 | 0.6056 | 0.8214 | 0.8696 | 0.6801 |
| Degree days less than zero | *r* | 0.236 | 0.260 | **0.398** | **0.416** | 0.337 | 0.321 |
| | *p* | 0.2669 | 0.2195 | 0.0540 | 0.0434 | 0.1071 | 0.1257 |
| Number of frost free days | *r* | **-0.369** | **-0.390** | **-0.542** | **-0.488** | **-0.463** | **-0.489** |
| | *p* | 0.0757 | 0.0593 | 0.0063 | 0.0155 | 0.0225 | 0.0153 |
| Wind-influenced drip-zone | *r* | **0.363** | **0.361** | 0.333 | 0.116 | 0.115 | 0.154 |
| | *p* | 0.0809 | 0.0832 | 0.1123 | 0.5889 | 0.5937 | 0.4725 |
| Crown radius projection | *r* | -0.072 | -0.158 | -0.271 | -0.133 | -0.256 | -0.312 |
| | *p* | 0.7373 | 0.4595 | 0.2000 | 0.5368 | 0.2276 | 0.1381 |
| South-west canopy cover | *r* | 0.260 | 0.217 | 0.195 | 0.241 | 0.212 | 0.201 |
| | *p* | 0.2199 | 0.3086 | 0.3621 | 0.2567 | 0.3202 | 0.3454 |
| Duff thickness | *r* | 0.034 | 0.000 | -0.102 | 0.068 | -0.006 | -0.046 |
| | *p* | 0.8732 | 1.0000 | 0.6347 | 0.7510 | 0.9790 | 0.8299 |
| Effective leaf area index | *r* | 0.113 | 0.096 | -0.028 | 0.287 | 0.279 | 0.263 |
| | *p* | 0.5981 | 0.6542 | 0.8969 | 0.1743 | 0.1875 | 0.2141 |
| Total irradiance | *r* | -0.099 | -0.094 | -0.013 | -0.293 | -0.302 | -0.277 |
| | *p* | 0.6459 | 0.6627 | 0.9503 | 0.1643 | 0.1509 | 0.1908 |
| Direct irradiance | *r* | -0.145 | -0.151 | -0.088 | **-0.346** | **-0.356** | -0.316 |
| | *p* | 0.4991 | 0.4820 | 0.6825 | 0.0975 | 0.0879 | 0.1321 |
| Coarses | *r* | 0.090 | 0.106 | 0.082 | -0.012 | -0.101 | -0.124 |
| | *p* | 0.6768 | 0.6214 | 0.7046 | 0.9546 | 0.6392 | 0.5639 |
| Gravel | *r* | 0.077 | 0.057 | 0.090 | 0.125 | 0.027 | -0.041 |
| | *p* | 0.7193 | 0.7923 | 0.6766 | 0.5616 | 0.9002 | 0.8480 |
| Sand : Silt+Clay | *r* | **-0.345** | -0.337 | -0.288 | **-0.391** | **-0.358** | **-0.371** |
| | *p* | 0.0987 | 0.1075 | 0.1716 | 0.0592 | 0.0857 | 0.0742 |
| Mesotopographic position | *r* | -0.262 | -0.177 | -0.050 | -0.234 | -0.146 | -0.064 |
| | *p* | 0.2157 | 0.4093 | 0.8167 | 0.2712 | 0.4970 | 0.7671 |
| Meso-scale slope aspect (COS-transform) | *r* | 0.031 | 0.026 | 0.028 | 0.040 | 0.084 | 0.127 |
| | *p* | 0.8857 | 0.9036 | 0.8952 | 0.8544 | 0.6971 | 0.5542 |
| Slope inclination | *r* | -0.291 | -0.312 | **-0.372** | -0.240 | -0.179 | -0.160 |
| | *p* | 0.1675 | 0.1384 | 0.0733 | 0.2584 | 0.4029 | 0.4550 |