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Ground Layer Response to Disturbance in the Pine-Dominated Eastern Foothill Region of West-Central Alberta, Canada

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GROUND LAYER RESPONSE TO DISTURBANCE IN THE PINE-DOMINATED
EASTERN FOOTHILL REGION OF WEST-CENTRAL ALBERTA, CANADA

by

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B.S., Austin Peay State University, 1995
M.N.S., Southeastern Missouri State University, 1999

A Dissertation
Submitted in Partial Fulfillment of the Requirements for the
Doctor of Philosophy

Department of Plant Biology
in the Graduate School
Southern Illinois University Carbondale
December 2011

DISSERTATION APPROVAL

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for the Degree of

Doctor of Philosophy

in the field of Plant Biology

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December 2011

AN ABSTRACT OF THE DISSERTATION OF

Rebecca Elizabeth Mooneyhan McClelland, for the Doctorate of Philosophy degree in Plant Biology, presented on October 24, 2011, at Southern Illinois University Carbondale.

TITLE: GROUND LAYER RESPONSE TO DISTURBANCE IN THE PINE-DOMINATED EASTERN FOOTHILL REGION OF WEST-CENTRAL ALBERTA, CANADA

MAJOR PROFESSOR: Dr. Dale H. Vitt

The canopy cover of the *Pinus contorta* forests of west-central Alberta, dictates colonization of the forest floor ground layer. This dynamic ground layer is a mosaic of feather mosses and reindeer lichens in a system driven by disturbance. In this project, anthropogenic was used to control canopy cover change and study its effects on the ground layer. Timber companies selectively mechanically thinned sections producing three experimental areas with uncut controls. Data were collected from 182, 6.5 m^2 plots located in the four thinning areas. Six general areas of inquiry were posed around determining ground layer responses to canopy opening: 1) vegetation, 2) plant species richness, 3) plant abundance, 4) diaspore availability, 5) environmental limiting factors, 6) moss and lichen establishment.

In 1997, three timber companies were involved in selective tree removal at three different stand percentages (20/40/60%), however, these were not consistent when measured in 2005. This variation in operational logging along with changes over the seven year time period, resulted in strong disparity for each of the thinning regimes. Percent canopy cover change for all thinned plots was ranked and three new groups created; least, moderate, most canopy change. These new groups formed the basis for the data presented in Chapter 3.

The three thinning groups had little to no effect on species richness, but overall showed a small decrease from measurements taken pre-harvest. Numbers of locally rare species were similar to pre-harvest levels, but there were some gains and losses of species between pre-harvest and seven years post-harvest. In contrast to the lack of change in diversity, the abundance of dominant species and

major vegetation components underwent dramatic changes. Dominant species of both vascular plants and bryophytes decreased with increasing canopy openness, with vascular plants being gradually affected while mosses were more affected at less intense canopy opening. Abundances of lichens showed no change.

When measuring limiting factors (biotic and abiotic) for ground layer mosses and lichens, diaspores (spores and fragments) were plentiful in all stands, but differed in abundance at the micro-scale. The position of feather mosses and reindeer lichen in the forest floor mosaic appears to be due to an intermingling of environmental influences (at both the meso- and micro-scale). With less environmental constraints on lichens and the widespread availability of lichen fragments, lichens are more tolerant to the conditions evoked by thinning than are mosses. Mosses are more restricted by environmental conditions and have more constrained diaspore dispersal than lichens. Thus, mosses are more limited both by diaspore dispersal and by harsh environmental conditions in open canopy habitats. Whereas relative humidity (RH) did not differ at the stand level, moss dominated areas had higher RH no matter where they occurred, lichen-dominated areas did not—suggesting the moss occurrence is at least partially controlled by micro-scale level factors.

Moss establishment is effected by the "ghosts" of past events and substrates. Mosses are widespread in formerly moss-dominated areas that contain organic substrates and high canopy cover. Lichen establishment is limited in previously moss-dominated areas. Species interactions weighed more heavily on moss establishment than on that of lichens.

Therefore, the effects of canopy change on the ground layer are variable corresponding to moss decreases, but not lichens. Seven years post-harvest species diversity is unchanged, but vegetation, as a whole, has been affected.

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CHAPTER 1

GENERAL INTRODUCTION TO THE PINE-DOMINATED EASTERN

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1.1 Introduction

The study of ground layer dynamics in relation to disturbance provides information integral to understanding boreal montane plant communities. Information on these relationships is valuable for this system, in particular, as locally threatened woodland caribou (*Rangifer tarandus* L.) use the area for winter lichen forage of terrestrial lichens. This thesis contains a number of studies that address various facets of ground layer dynamics with particular emphasis on the dominant bryophytes and lichens. Ecology of the ground layer is closely tied to biotic and abiotic factors of the forest floor and tree canopy. The diversity and yet dominance of just a few species in the ground layer led to my initial question concerning location of bryophytes and lichens on the forest floor, "Why is it here and not there?". This question opened the door to what may be some of the underlying factors in this system, those that are limiting and also those that are critical to understanding disturbance and establishment. Furthermore, do these factors differ between bryophyte and lichen dominated areas found in the ground layer of the coniferous forest of western central Alberta? This first chapter gives a summary of the region, its ground layer, disturbance regimes, and study area.

1.2 Biogeography of the region

1.2.1 *Geology and soils*

According to Heusser (1956) this region is chiefly underlain with sedimentary rock whose origin dates to a Pre-Cambrian sea. The most common age of the sedimentary limestone bedrock outcrops are Mesozoic (with some Paleozoic and Tertiary) (Heusser 1956). Marine shales and non-marine

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sandstones can be found on the eastern edge of the Upper Foothills (Mellon and Kramers 1972). The folds and faults of these sedimentary strata form north-west ridges that increase in elevation westward, and as they are not resistant to erosion the outline is generally rounded. This region was glaciated during the previous glacial maximum (18,000 – 12,000 yr BP) (MacDonald and Cwynar 1991) and so these bedrock outcrops, throughout much of the area, are commonly covered by morainal deposits. In areas with steeper terrain, colluvium (material transported by gravity) and residuum (weathered bedrock) can be found. Interactions between underlying geology and climate influence edaphic features.

This overall region is overtopped by glaciofluvial deposits that consist of coarse-textured and well-drained sediments with till-covered ridges (Bennett *et al.* 1983). Regional upland soils are luvisolic and brunisolic (Corns and Annas 1986) with a mesic moisture regime (Beckingham *et al.* 1996). These soils are characterized as being rapidly drained, poor in nutrients, and acidic (Beckingham *et al.* 1996). Study area soil texture was either loamy sand or sandy loam (based on field soil texture tests, Kalra and Maynard 1991) with an average pH of 4.88 (Pharo and Vitt 2000). Humus form is mor, having a distinct boundary between the organic and mineral layer with little to no intermixing (Beckingham *et al.* 1996).

1.2.2 *Forest type*

Boreal forests have been classified in a number of ways by different researchers over the past several decades. Boreal forests (including the boreal-montane forests studied in this study area) are broad, transcontinental forests that cover over 14.7 million km^2 (~11 % of the Earth's land area) (Bonan and Shugart 1989). Holdridge *et al.* (1971) and Hare and Ritchie (1972) believed the boreal coniferous forest biome was best defined using climatic factors, e.g. latitude and altitude. Walter (1979), who classified the geo-biosphere into nine zonobiomes, named the eighth as "cold –temperate (boreal)".

North American boreal forests are generally considered to be conifer-dominated with closed-canopies (Johnson *et al.* 2001).

Within the large North American forest system, the majority of boreal forests are located in Canada. Both Halliday (1937) and Rowe (1959, 1972) described the Canadian forests. Rowe's descriptions are more commonly used as he (1972) named eight forest regions, the first and largest being the Boreal Forest Region. Rowe's boreal region is primarily coniferous with a few broadleaf trees. Within the Canadian boreal region, a montane ecoregion exists containing the Upper Foothills Forest Section, in west-central Alberta, this ecoregion was further delimited by Rowe (1959, 1972), who divided it into 45 different Forest Sections based on distinctive vegetational patterns and physiography. He describes the Upper Foothills Forest Section (B. 19c), which encompasses my research area, as a long narrow strip of coniferous forest that runs along the east slope parallel to the Rocky Mountains. These foothills are located between the Lower Foothills to the east and comprise the transition from Boreal Forest Region to Subalpine Forest Region to the west. While commonly used, these descriptors have undergone changes due to availability of modern data capturing techniques such as GIS (geographic information system), which has become closely integrated with cartography.

Using the Physical Land Classification hierarchy nested within the Ecological Land Classification mapping techniques (Archibald *et al.* 1984) the Natural Regions Committee (2006) of Alberta reclassified subregion divisions based on physiographic subregions in order to present the landscape in discrete units (from 1: 1,000,000 to 1: 250,000 scale). These subregions are more distinct and give a more accurate description of the area in general (Alberta Research Council 1992). The region encompassing my research area underwent minor changes. Current descriptions are as follows: the broad Boreal-Cordilleran transition Ecoclimatic Province contains the Foothills Natural Region, which can be divided into the Upper and Lower Foothills Natural Subregion. My study area lies within the

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Upper Foothills Natural Subregion (Fig. 1.1). This subregion forms a slim belt, sandwiched between the

Rocky Mountain Natural Region to the west (containing Alpine, Subalpine, and Montane Natural

Subregions), and the Grassland Natural Region to the east (containing Dry Mixedgrass, Mixedgrass,

Northern Fescue, and Foothills Fescue Natural Subregions).

The Upper Foothills encompass 21,537 km^2 in total area. Elevations of the Upper Foothills

range from approximately 900 to 1500 m (Beckingham *et al.* 1996) and are forested to their summits.

The dominant tree species is *Pinus contorta* Loud. (lodgepole pine) which forms mixed stands with

Picea glauca (Moench) Voss (white spruce) (Smithers 1961, Rowe 1972, Beckingham *et al.* 1996). The

term Upper Foothills Natural Subregion or Upper Foothills will be used when describing the research

area, but comparisons and discussion are developed within the context of the boreal forest.
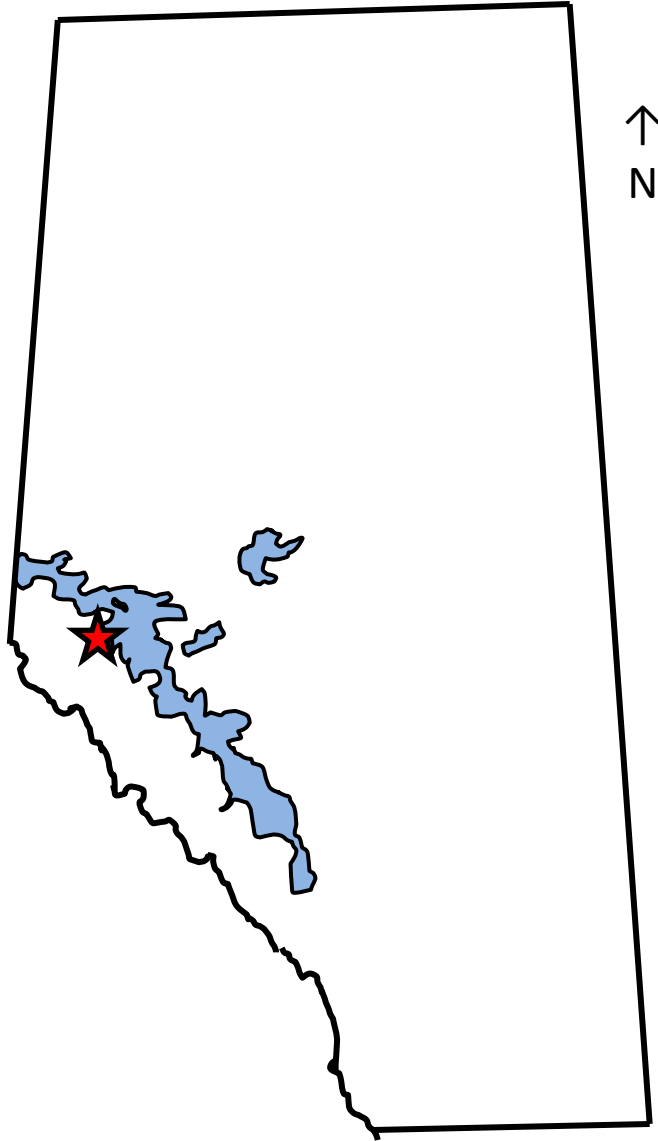
Figure 1.1. Map of the Upper Foothills Natural Subregion (in blue) of Alberta. The research area is marked with a star.

1.2.3 *Climate*

Bonan and Shugart (1989) and the Natural Regions Committee (2006) define the climate of the boreal forest as having short, cool, moist summers and long, cold, and snowy winters. At the northern limit of this zone, the cold season extends beyond eight months with the growing season limited to June through August. An average daily temperature greater than 10 ^{o}C lasts for only 30 days. Lieth *et al.* (1999) reported daily mean minimum temperature for January (coldest month) at -11.6 ^{o}C and the daily mean minimum temperature for July (warmest month) at 13.4 ^{o}C. The yearly mean temperature in central western Alberta is 1.3 ^{o}C (Natural Regions Committee 2006). The growing season length is around 165 to 170 days, and the frost-free period is around 79 days (Natural Regions Committee 2006). At the southern boundary, the cold season extends beyond six months and the average daily temperature is greater than 10 ^{o}C for 120 days. Holdridge *et al.* (1971) used climatic information, as well, and defined the boreal region as having a mean annual biotemperature that ranges from 3 ^{o}C to 6 ^{o}C. Due to weather trends, the Rocky Mountains and front ranges receive more rain than other Natural Regions in Alberta. Elevation and aspect have effects on annual precipitation rates, typically the precipitation levels for the entire Ecoclimatic Province ranges from 500 to 800 mm, with an average yearly precipitation of 632 mm (Natural Regions Committee 2006). Maximum monthly precipitation is 29 mm in January, typically the driest month, and 54 mm in July, which has the wettest average.

1.2.4 *Vegetation*

Climate plays an important role in local vegetation and vegetation is used to define regions. For boreal systems, Moss (1955), Walter (1979), and Shelford (1963) reported that the dominant overstory coniferous species shift as one moves northwest across the area, with approximately four genera found in the coniferous belt of the mountain regions (Hare and Ritchie 1972). The conifer-dominated forests (*Pinus* and *Picea*) are usually associated with mean annual precipitation amounts greater than 500 mm

and mean yearly temperatures between -2.0 and +1.0 $^{\circ}$C (Natural Regions Committee 2006). *Pinus contorta* is the most widely distributed pine in western North America (La Roi and Hnatiuk 1980) and is typically the "subclimax dominant of burned areas" in mountainous boreal forests (Walter 1979). Due to the natural pyrogenic disturbance regime, *P. contorta* often forms even-aged monospecific stands on the Rocky Mountain eastern slopes (Fahey and Knight 1986). *Picea glauca* (dominant shade-tolerant tree) is the successional climax tree species of these forests before fire (Day 1972). Post-fire *P. glauca* are replaced by *P. contorta* as the major tree species. Without the reinitiation of succession by periodic fire *P. contorta* would be replaced over time by the current understory tree, *P. glauca* (Day 1972). *Pinus'* serotinous cones are dependent upon pyriscence (fire triggers cone release), and the seedling trees are shade-intolerant, prefer high light, have a fast rate of initial growth (three to four times the height of *Picea* (Day 1972)) and thus out-compete *Picea* seedlings (Moss 1955). The denseness of *Pinus'* mature canopy limits much understory tree growth, however *Picea* saplings are often abundant. Many authors (Clarke and Cowan 1945, La Roi and Hnatiuk 1980) agree that *P. contorta* communities are temporary as fire usually re-occurs at long intervals (around 80-100 years). This perpetuates re-setting of the pine community before succession of vegetation can reach the mature spruce (*Picea*) community stage (Smithers 1961, Walter 1979). Current dominance of *P. contorta* in the Upper Foothills is a combination of factors; regular intervals of disturbance, preference for light after disturbance, rapid growth rate, long lifespan, (290 years for *P. contorta* (Horton 1956)), and evergreen cold-tolerant needles that maximize photosynthesis before deciduous leaf-out (Walter 1979).

1.3 Geography and dominant species

This Upper Foothills Natural Subregion of the Canadian Rocky Mountains has experienced much climatic change within the last epoch. The glaciation events removed almost all previous vegetation. Ritchie (1987) noted that 95% of Canada was glaciated at 18,000 yr BP by the Wisconsinan

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(Cordilleran and Laurentide) ice sheets. Glaciers of the Cordilleran complex covered present day British Columbia, advanced into the western part of Alberta and reached south of Calgary (Heusser 1956). The Laurentide ice sheet covered the balance and extended into the United States for up to 600 km (Ritchie 1987). The glacial events removed all previous vegetation, but with the melting of the Cordilleran ice sheet, plant recolonization became possible. *Picea glauca* forests first dominated the region around 10,000 yr BP (MacDonald 1987). *Pinus contorta* began extending its range from southern refugia in the United States into western Canada over the course of the warmer, drier early Holocene to become the region's dominant conifer species (La Roi and Hnatiuk 1980, MacDonald and Cwynar 1985, 1991; MacDonald 1991). Heusser (1956) postulated that increased disturbance (fire) on the landscape was a possible cause for advances in *Pinus* populations. Based on pollen analysis MacDonald and Cwynar (1991) found that *P. contorta* var. *latifolia* S. Wats. (the current regional dominant tree species) was the final tree species to become established after glaciation in the North American boreal region.

1.4 Community stratification

The overall structure of the Upper Foothills consists of vegetation at several levels. Much of the literature divides and subdivides the plant strata based on height (Achuff and La Roi 1977, La Roi and Hnatiuk 1980, McCune and Antos 1981). The present study is mostly concerned with the effects of overstory on the ground layer so, here too, the plant community has been separated into four groupings based on vertical location: overstory (trees = or >5 m), understory (trees < 5 m), shrub layer (> 1 m and including the herb and field layers), and ground layer. Forest overstory is dominated by *Pinus contorta* with a sparse secondary canopy of *Picea glauca*, constituting the understory. The shrub layer (the layer of vegetation below the understory and above the ground layer) ranges from dense to sparse, depending on location, and contains small woody vascular plants, shrubs, grasses, and non-woody flowering plants. *Ledum groenlandicum* Oeder (Labrador tea), *Vaccinium membranaceum* Hook. (tall bilberry), *V. vitis-*

idaea L. (bog cranberry), *Cornus canadensis* L. (bunchberry), *Rosa acicularis* Lindl. (prickly rose),

Arctostaphylos uva-ursi (L.) Spreng. (bearberry), and *Linnaea borealis* L. (twin-flower) (Moss 1955) are

the most common species in the shrub layer. The ground layer (the lowest layer of living material on the

forest floor) is largely composed of a mosaic of bryophytes and lichens that vary with denseness of the

P. contorta canopy. The most abundant species in the ground layer are: *Pleurozium schreberi* (Brid.)

Mitt., *Ptillium crista-castrensis* (Hedw.) De Not., *Hylocomium splendens* (Hedw.) Schimp (feather

mosses), and *Cladina mitis* (Sandst.) Hustich (a fruticose lichen) (Moss 1955).

1.5 Canopy cover

As the coniferous forest ages, the canopy becomes more dense and the level of light reaching the

forest floor is reduced. Understory and ground layer vegetation can be affected by intense shade which

can have negative effects on abundance of some species (Anderson *et al.* 1969, Halpern *et al.* 1999,

Coxson and Marsh 2001). The transition from open to closed canopy slowly diminishes lichen

abundance and promotes increased numbers of bryophytes. Eventually (often late in succession) the

ground layer is dominated by bryophytes (De Grandpré *et al.* 1993). Amplified canopy cover is

associated with increased moisture levels Robinson *et al.* (1989) reported that pleurocarpous species

(feather mosses) abundance increased with rising moisture. This indicated heightened vulnerability to

moisture stress by pleurocarpous species over acrocarpous species. Species composition can be affected

by competition with more canopy cover. Increased shade from canopy closure and higher moisture

levels can enhance bryophyte growth. This increasing moss mat growth can outcompete and suppress

other forest layers, including seedling stage trees (Jonsson and Esseen 1990).

1.6 Forest management

Management of the forests in this ecozone is a recent issue, since the success of wildfire

suppression (Niemelä *et al.* 1993, Johnson *et al.* 2001) has resulted in more mature forests that

are managed for timber harvest. Harvesting of lumber has replaced fire (Burton *et al.* 2003) as the major natural disturbance that initiates new stand development in the Boreal-Cordilleran transition Ecoclimatic Province. Current tree harvesting techniques mimic fire on the landscape and suspend forest succession at the pre-climax stage. It is suggested that the secondary succession occurring within clear-cut areas results in understory vegetation compositionally similar to stands of mature fire-origin (Bainbridge and Strong 2005). In west-central Alberta regulations for timber removal to preserve caribou habitat are being put into place by forest managers (Hervieux *et al.* 1996). Coxson *et al.* (2003) studied some of these partial cutting practices and their impact on arboreal lichen species and found that clear cutting resulted in loss of tree dwelling lichen species. In Finland, Kuusinen and Siitonen (1998) found that old growth stands contained a more diverse lichen flora than did managed stands; they suggest increasing time (>120 years) between silvicultural practices to supply specialist habitat and for founding of late successional species. Newmaster *et al.* (2005) found that the species richness of the bryophyte community was more diverse in old forests (>250 yr) than in young forests (80 yr). Supervision of timber and non-timber harvest areas is necessary for sustainable forest management practices, which is a contemporary application in Canadian forests. These management practices attempt to maintain a balance between tree harvest and conservation.

1.7 Succession

There are community assemblage changes that are more or less predictable throughout time. These changes constitute succession, which is a gradual replacement of one plant community by another over the course of time (McEvoy 2004). Two types of succession have been described: primary and secondary. Primary succession is initiated on newly formed soils or previously unexposed non vegetated substrates (e.g., shifting sand dunes, glacial retreat, etc.). Secondary succession is a process of

re-establishing vegetative communities on preexisting soil in an area affected by disturbance. Forested

ecosystems experience only secondary succession following a disturbance event (e.g., wind, fire, etc.).

The theories behind plant succession began to develop in the nineteenth century. In an address titled

"The Succession of Forest Trees", Henry David Thoreau (1860) illustrated plant succession by animals

and wind in a logged Oak-Pine forest in New England. But, it was H. C. Cowles (1899), following his

studies of sand dunes along the shores of Lake Michigan, who developed a more formal concept of plant

succession. Cowles reported that dune age could be equated with initial vegetational establishment to

produce a trend of floristic change; this used to propose a particular sequence or sere derived from

distance from the lakeshore including abiotic and biotic alterations. Resulting from the initial work of

Cowles, Frederick Clements (1916) developed a very logical and long dominating theory of succession

that stated sequences of communities (or associations) were extremely predictable and culminated in a

stable climax community. He considered the community that developed through time as an integrated

whole or 'superorganism' with clear boundaries. In direct contrast with the Clementsian (or organismal)

view of succession, Henry Gleason (1917, 1926) perceived the community as being composed of

individual species that independently respond to environmental gradients. Gleason's view, known as the

individualistic continuum concept, ultimately stated that coexisting species are a consequence of species

having similar tolerance limits and requirements, leading to blurred boundaries between communities.

By the 1950's ecologists were beginning to veer away from the 'superorganism' view and were starting

to emphasize species as individuals. The work of John Curtis (1959) and Robert Whittaker (1956)

helped to bring about this shift towards a more Gleasonian view, as they regarded communities as being

a framework consisting of individual species independently responding to underlying environmental

gradients. As ideas of succession evolved, F. E. Egler (1954) revisited Clementsian theory and

introduced 'relay floristics', where groups of species pass dominance like runners in a relay race pass a

baton. For a given ecoregion, without disturbance, succession would be repeatable and predictable

leading to the same climax. Egler (1954) also put forward the 'initial floristic composition' theory

which stated that all community members are present at the beginning of the successional sequence,

with relative abundance of species changing throughout time.

Connell and Slatyer (1977) focused on life history strategies and proposed three theoretical

models: facilitation, inhibition, and tolerance. In the model of facilitation there are autogenic (controlled

by species) changes within the community, where early species modify the environment to aid the next

successional species *et cetera*. The facilitation model is similar to relay floristics or Clementsian theory.

In the model of inhibition species interactions are entirely competitive. This model is based on initial

establishment and ability to consume resources and amend the environment making it less favorable to

other species. In the model of tolerance there is an interaction between life history traits and

competition, which is akin to initial floristic composition. This model suggests that emphasis is on the

start of succession, dispersal, and tolerance to changes. A more Gleasonian successional framework was

described by Noble and Slatyer (1980) who proposed that life history characteristics such as species

recovery, tolerance to competition, and longevity are vital to predict successional sequences.

Life history traits, again, became front and center as emphasis was placed on individual

responses to events on the landscape. MacArthur and Wilson (1967) presented the theory of *r*-(short-

lived, high reproductive rate, and rapid development) and *K-selection* (long-lived, low reproductive rate,

and slower development). This concept assumed deterministic environments (one stable and one

unpredictable) and did not well suit real world species. J. Grime (1977, 1979), for plants, extended the

previous concept by proposing a three-equilibrium point system. This system consists of *C*-strategists

(competitive), *S*-strategists (stress-tolerant), and *R*-strategists (ruderal or weedy) and all intermediate

forms. In Grime's *C-S-R* triangle the *R*-strategists are equivalent to MacArthur and Wilson's (1967) *r*-

selected species, *S*-strategists are at the *K-selected* end, and *C*-strategists fill in the gap between the two. Grime was successful at relating plant adaptations across differing habitats as his theory views succession as a shift in the three plant strategies in response to environmental changes.

Succession can also be investigated by looking at chronosequences; areas at different stages of succession. Bazzaz (1975) and Tilman (1988) both found that species richness increased in the first years following a disturbance event, or time since abandonment. Disturbance launches recolonization of early successional species. Connell (1978), working in tropical systems, found if disturbance frequency is high then diversity remains low and if disturbance is lacking later successional species will replace the early species, again keeping diversity low. But if there is a frequency of intermediate disturbance then competitive displacement is kept to a minimum equating high diversity. This pattern is referred to as the intermediate disturbance hypothesis (Horn 1975, Connell 1978 and 1979).

Watt (1947) took a different approach and described community as a working mechanism, which is defined by relations between its components in space and time. Successional processes over time, then, manifest themselves in a spatial pattern-"the unit pattern". This cyclic succession, rather than a linear process, can be driven by small scale disturbances like treefall gaps or wind. On the landscape, patchiness is widespread because species create patches, time and space restrict establishment, and after establishment species are unable to invade surrounding areas. The patch mosaic may not be explained by climate and edaphic features. The concept of succession was changed by the idea of cyclic replacement with never-ending succession. Bormann and Likens (1979) expanded on Watt's unit pattern with the introduction of the shifting mosaic steady-state. This concept views the community as a patchwork of different phases of successional development. Steady-state refers, statistically, to the average state of the forest, though each patch is in a constant state of change, overall characteristics (biomass) remain constant. The shifting mosaic refers to the different patches in various states of

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successional progress that comprise the community. Recurrent disturbances result in greater diversity

on the landscape.

1.8 Bryophytes and lichens in the ground layer

In boreal regions, bryophytes and lichens are as vital as seed plants (Newmaster and Bell 2002)

as they comprise the majority of the ground layer. Fruticose lichens are found most often on

intermediate and late successional mesic sites with a more open canopy, with feather mosses on mesic

higher nutrient habitats with a more closed canopy (Johnson 1981).

1.8.1 *Bryophytes*

Bryophytes are prominent elements of the ground vegetation in the boreal regions of North

America, Europe and Asia. Feather mosses, so called because of their pinnate branching pattern, are the

dominant mosses in boreal forests and due to their high abundances may cause a reduction in overall

bryophyte diversity within the forest (Jonsson and Esseen 1990, 1998). These authors demonstrated that

ground layer disturbance increased bryophyte species richness but reduced abundance of *Hylocomium*

splendens and *Pleurozium schreberi* from 35.1% (undisturbed) to 16.5% (disturbed) in a Fennoscandian

boreal forest. Jonsson and Esseen (1990) also reported that the feather mosses were still the dominant

species in both habitat types. Foster (1985) and Deluca *et al.* (2002) found that feather moss ground

cover increases with successional age of the forest, ultimately forming a continuous carpet that can

account for 60 to over 80% of the ground cover in boreal forests. According to Moss (1955) the feather

mosses (*H. splendens*, *P. schreberi* and *Ptilium crista-castrensis*) form a continuous circumpolar ground

cover at northern latitudes of the boreal region (Crum 1973, Shaw 2001). Gimingham and Birse (1957)

classify these feather mosses as having the growth-form type of weft, "loose inter-twining of straggling

shoots and branches, often ascending and luxuriant". All of the feather mosses are pleurocarpous,

producing the sporophytes laterally from a perichaetial bud. According to Vitt (1989), the evolution of

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pleurocarpy advanced mosses with this growth form to be comparable to a long-lived perennial. The advancement of pleurocarpy leads to improved competitive ability (Vitt 1984). According to Harper (1977), this important competitive ability may be due in part to longevity of zygote-produced genets of these forest floor species.

Although these mosses are circumboreal and restricted by a temperature range of 20 to 25° C (Furness and Grime 1982), they have different distributions. *Hylocomium splendens* is dioicous and has a wide geographical distribution; alpine, subalpine, boreal and arctic, and occurs in a variety of habitats and vegetation types (Tamm 1953, Busby *et al.* 1978, Potter *et al.* 1995). *Hylocomium splendens* produces an annual growth increment that has been used to examine seasonal growth related to light, nutrients, and nitrogen retention (Tamm 1953, Busby *et al.* 1978, Callaghan *et al.* 1978, Økland 1995, Eckstein 2000). *Hylocomium splendens* distribution is determined by levels of shade, moisture availability, and high nutrient levels (Tamm 1953). *Pleurozium schreberi* is a common moss (Busby *et al.* 1978) that occurs on the North American continent, Greenland, Africa, Europe and Asia, from around 5000 m elevation down to just above sea level (Deluca *et al.* 2002). *Pleurozium schreberi* is dioicous and can be found in both sub-arctic and temperate regions (Longton and Greene 1969). This ubiquitous moss is the most frequent feather moss in the boreal forest (Foster 1985). Ross-Davis and Frego (2004) reported that patches of *P. schreberi*, even under catastrophic conditions, outcompete pioneer species and become dominant over time. All of the three dominant feather mosses have a key relationship with a cyanobacterium (e.g. *Nostoc*) for nitrogen fixation in pristine mid- to late-successional northern European boreal forests (Deluca *et al.* 2002, Zackrisson *et al.* 2009). Of the three feather mosses, *Ptilium crista-castrensis* has the most restricted range globally and is rarely prominent in boreal systems (Busby *et al.* 1978). The Upper Foothills contain these mosses in abundances equal to those described for other boreal systems.

1.8.2 *Lichens*

Lichens are symbiotic organisms that have two partners, a mycobiont (fungal) component and a photobiont (photosynthetic) component, which are usually a cyanobacterium and/or green alga. In boreal/montane forests, *Trebouxia* (Ahmadjian, 1993) is the algal genus associated with terricolous mat-forming lichens. These lichens can exist with great frequency in the forest ground layer. In mid to late seral stands the fruticose lichens in the Cladinae are the most prevalent, and thus are the predominant lichens of interest in this study. Lichens have successional patterns that occur within the larger disturbance patterns found on the boreal/montane landscape. Scotter (1967) documented three recovery stages after fire in a Saskatchewan lichen woodland (which was modified from Ritchie 1958). The first stage, year one to year ten, was dominated by acrocarpous mosses and vascular shrubs. Stage two, year eleven to year fifty, was dominated by the faster growing *Cladonia* (horn and cup shaped lichens). The third stage, year fifty-one to year one hundred and twenty, is dominated by the slower growing *Cladina*, with *C. stellaris* (Opiz) Pouz. & Vezda and *C. rangiferina* (L.) Hoffm. (fruticose growth form) being the most common towards the end of the 120-year period. In northern Alberta, *Cladina mitis* is the climax phase lichen, found in more abundance than *C. stellaris* and *C. rangiferina* (Carroll and Bliss 1982).

According to Ahti (1961), Cladinae prefer acidic humus of podzolic soils over calcareous soils to germinate from propagules. In contradiction to Ahti (1961), Robinson *et al.* (1989) found members of the Cladinae on calcareous soil in the Canadian subarctic. Soil pH may not have much of an effect on mature lichens, with little substrate attachment, but may have a greater influence on propagules and/or juveniles that have more contact with the soil (Robinson *et al.* 1989). Pioneering lichen species must be able to physiologically tolerant and successfully survive in a setting of immense thermal stress (i.e., desert-like conditions (Kershaw 1977)), confirming Grime's (1979) view that lichens, as a whole, are *S*-strategists or stress tolerators. After a fire, Yarranton (1975) reported that it takes around 14 years for

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the soil and the humus layer to return to the pre-fire conditions which must occur, through the process of facilitation, before late successional species such as *Cladina stellaris* can become established in any great number. After fire, ground lichen colonization rates depend upon their primary method of dispersal; sorediate lichens (many *Cladonia* spp.) invade and increase at a faster rate than lichens that reproduce by thallus fragments (*C. mitis* and *C. rangiferina* (Honegger 1996)) (Johnson 1981). Carroll and Bliss (1982) found 71% of the soil-dwelling lichens sampled in the mid to late-seral stage forests of the Athabasca Plains region of northern Alberta and Saskatchewan were either *Cladonia* or *Cladina* (*C. mitis, C. rangiferina, C. stellaris*), with *C. mitis* dominating the lichen mat at 63% cover.

1.9 Ground layer habitats

Regional precipitation and moisture levels affect growth rate of ground layer lichens. Local habitat factors such as surrounding vegetation and light levels control wetness of the lichen mat (Kershaw and Rouse 1971, Yarranton 1975, Johnson 1981). Working in the Northwest Territories, Robinson *et al.* (1989) found *Cladina mitis* preferred dry habitats and Johnson (1981) reported that *Cladina rangiferina* favored mesic habitats. Yarranton (1975) described *Cladina* lichens growing on mesic sites being overtaken by fast growing carpets of *Pleurozium schreberi*. He also stated that in northern Ontario there is competition with *P. schreberi*, ericaceous shrubs like *Ledum groenlandicum*, and other *Cladina* and lichen species, all of which compete for the same habitat, reduce light intensity, or disrupt the podetia. In a study of acid rain tolerance *Cladina stellaris* and *C. rangiferina* better tolerated the acid rain treatments than did the moss *Pleurozium schreberi* (Scott and Hutchinson 1987, Hutchinson and Scott 1988). When fruticose lichens have the correct substrate, light, and conditions of moisture, they can and do become the dominant life form in the montane forest ground layer. With cyclic fire, reduction of over-foraging, and decrease in competitors, lichen patches can be maintained, perhaps indefinitely. Key roles of bryophytes and lichens in the boreal forest include the following:

sequestration of nutrients, winter forage for woodland caribou, amelioration of the microclimate, increased litter layer, and increased biomass (when compared to the other components of the ground layer).

1.10 Limiting factors

There are abiotic and biotic limiting factors that affect ground layer bryophytes and lichens. Abiotic factors are moisture levels (evaporation rates and relative humidity), temperature, light, and litter (Damman 1976, Proctor 1982, Frego and Carleton 1995). In this system, feather mosses (*Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis*) and lichens (*Cladina mitis, Cetraria ericetorum, Cladonia gracilis*) are poikilohydric (not having a mechanism to prevent becoming dehydrated) (Hosokawa *et al.* 1964) and have the ability to only metabolize when wet (Proctor 1972, Gaio-Oliveira *et al*. 2006), so water is a principal limiting factor. Moisture rates can be influenced by air temperatures, as temperature increases can cause drying and may spur formation of wind further desiccating the local environment. Light directly impacts a large range of processes such as photosynthesis, evapotranspiration, germination, growth and survivorship (Larcher 1980). Canopy or microsite litter impacts the ground layer as it retains moisture, provides cover, and releases nutrients through breakdown. Each of these factors impacts the meso- and micro-scale. Physical processes as well as physiology can be affected by these factors which can ultimately impact establishment and colonization rates. Tree removal and the loss of canopy (Chen *et al.* 1993) impact the forest floor by causing changes in perception of these factors in the understory and ground layer. There are also biotic components that can affect the definitive location of mosses and lichens in the ground layer. The biotic component is movement and availability of diaspores (Furness and Hall 1981, Smith 1987, Frego 1996, During 2001, Ross-Davis and Frego 2004). These small

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fragments or spores proliferate future generations on the forest floor and without ample

production and movement for establishment and/or colonization the effects of abiotic factors

impact little.

1.11 Nutrients

Nutrients, especially in terrestrial boreal systems, are limiting. The most limiting nutrient for

tree growth is nitrogen (Van Cleve and Zasada 1976, Van Cleve and Viereck 1981) and so more

emphasis is placed on this nutrient, though *Pinus contorta* and *Picea glauca* have lower nitrogen

requirements and thus slower growth with higher rates of nitrogen retention in photosynthetically active

needles (Chapin *et al.* 1986). According to Kukkola and Saramäki (1983), addition of nitrogen to

conifers in mineral soil increased tree biomass, but in natural systems much of the nitrogen gets

sequestered by ground layer plants. This sequestration of nutrients is an essential role of bryophytes and

lichens in the ground layer. Elements, available in ionic form, such as N, P, Ca, and Mg can be derived

from precipitation, leaf wash, and throughfall (MacLean and Wein 1978) and are absorbed and retained

by bryophytes (Tamm 1953, Foster and Morrison 1976, Van Cleve *et al.* 1983, Bates and Farmer 1990,

Brown and Bates 1990, Vitt 1990). Moss carpets can act as a reservoir by holding large proportions of

the ecosystem's available nutrients (Van Cleve *et al.* 1983, Carleton and Read 1991, Eckstein 2000).

Chapin *et al.* (1987) looked at biomass in Alaskan black spruce forests, calculating mosses at 6%, but

reported their greater importance as a nutrient reservoir. Throughfall elements are directly available to

plants because they are frequently ionic in form (Foster and Morrison 1976). Around 75% of the

nitrogen is water soluble, found in organic form, and may be released upon rewetting of the moss

(Carleton and Read 1991). In addition, living shoots of *Pleurozium schreberi* contain approximately

1.5-2.5% nitrogen. Symbiotic relationships, between cyanobacteria and feather mosses, reveal the

symbiotic is a notable contributor to ground layer nitrogen accumulation and cycling (Deluca *et al.*

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2002, Zackrisson *et al.* 2009). In peatlands, bryophyte nitrogen accumulation in ground layers is greater taken up through the leaves, over that of vascular plants, due to their unistratose leaves with limited cuticle (Li and Vitt 1997) which allows for greater absorption. In a boreal forest ground layer study with simulated nitrogen deposition, short term effects find bryophytes (*Dicranum majus* Sm., *P. schreberi*) contained the highest concentrations of fertilizer derived nitrogen (Nordin *et al.* 1998). Bråkenhielm and Liu (1998) reported that long-term effects of clear-cutting may release nitrogen into the system only to be taken up by the understory and ground layer. The potential for nutrient release from lichens owing to the wetting and drying cycles has been shown to be significant by Dudley and Lechowicz (1987). Bryophytes in the ground layer are clearly involved in nitrogen production (with the aid of cyanobacteria) and sequestration. The literature supports that mosses can sequester nutrients from the larger system. Nitrogen may be the most important limiting nutrient in boreal forests, but external saturation (i.e. fertilizer) is most likely deleterious to ground dwelling moss species (Mäkipää 1994).

1.12 Ground layer moisture

Studies show that when bryophytes are wet they can ameliorate the microclimate (Price *et al.* 1997, Betts *et al.* 1999, Cleavitt 2002, Mills and MacDonald 2005). Price *et al.* (1997) found evaporation from ground layer bryophytes was 35% of the total evapotranspiration in a spruce woodland, including interception by the canopy. Betts *et al.* (1999) also examined ground layer moisture levels and found that when bryophytes were hydrated, there was a 50% increase in evaporation. Cleavitt (2002) and Mills and MacDonald (2005) stated that terrestrial mosses are invaluable for their water holding and releasing abilities, in these systems. Lichens also play a role in boreal forest moisture levels, Kershaw and Field (1975) reported that soil moisture was increased in areas where lichen mats were well developed. Water levels at the ground layer are controlled by the

moss and lichen mat and dominate the flux of moisture in the forest climate. These moisture changes at

the microclimate scale affect the whole of the understory.

1.13 Litter

Understory litterfall is an important component of ground layer biomass that can have an acute

impact on the system. Ground layer litter holds moisture and increases shade at the microhabitat level

(Foster and Morrison 1976, De Grandpré *et al.* 1993; Coxson and Marsh 2001) and contributes to humus

formation. Changes in litter accumulation may have impacts at the ground layer (Anderson *et al.* 1969).

Increasing amounts of litter also negatively affects species richness of forest floor bryophytes,

conversely, litter removal boosts species richness (Dzwonko and Gawronski 2002, Startsev *et al.* 2008).

Forest litter is variable and comes from different forest strata. The majority of litter is coniferous tree

debris (needles, cones, bark, twigs) with the balance being formed from the field and shrub layer, and

ground layer bryophyte self-litter (Rincon 1988). Lichens can also comprise forest litter, but Sulyma

and Coxson (2001) found moss-dominated sites contain more litter than lichen only sites. Litterfall and

its microbial breakdown is the most important measurable avenue for nutrient transfer of N, P, K, Ca,

and Mg in boreal forests (Foster and Morrison 1976, Bonan and Shugart 1989, Brown and Bates 1990,

Frego and Carleton 1995). Litter decomposition not only releases nutrients, but produces an acidic layer

of organic material at the mineral soil interface. Litter, within denser coniferous forest canopies,

intercepts a larger proportion of throughfall, raising moisture levels over areas with less dense canopies

(Anderson *et al.* 1969), so litter helps modify climate at micro-scale. Removal of litter was found to

impoverish the soil and resulted in a marked increase in acidophilus vegetation (Dzwonko and

Gawroński 2002). These authors also reported an increase in establishment of bryophytes, in litter

removal plots, due to their light anemochores (small, light spores) that are easily transported via wind.

In deciduous forests litter is also a factor, and was found to be a major dynamic in determining plant

community differences within pit and mound (windthrow) microsites (Beatty and Sholes 1988). Litter, in this system, forms a mor humus type (2-5 cm thick) which creates a well-defined layer of unincorporated, matted organic material that rests directly on the mineral soil.

1.14 Diaspores

Lichens and mosses also persist in the soil under the living ground layer and duff in the form of spores (sexual) and fragments (asexual). Many authors refer to numerous different terms interchangeably, e.g. a pool of buried spores, diaspores, and propagules, in this thesis I choose the term diaspore for clarification. This term will be used to represent spores, asexual propagules (gemmae, rhizoids), and stem fragments for both mosses and lichens.

Diaspores are so prolific that soil samples taken from bryophyte populated habitats often contain viable fragments and diaspores (During and ter Horst 1983, Bisang 1996, During 1997, During 2001, Hock *et al.* 2004). The importance of the soil diaspore bank for colonization and establishment of bryophytes can be considered equivalent to the seed bank of vascular plants (Furness and Hall 1981, During *et al.* 1987, Smith 1987), but has not been studied as extensively as the vascular seed bank (Jonsson and Esseen 1990, Rydgren and Hestmark 1997, During 2001, Ross-Davis and Frego 2004). Soil diaspore bank diversity is often more species rich than the existing above ground mosses and lichens, with diaspores of the extant vegetation being absent or rare (Jonsson 1993, Ross-Davis and Frego 2004). After a disturbance event, the diaspore bank plays an important role in reestablishment of the ground layer as has been demonstrated in chalk grasslands (During and Ter Horst 1983), peat samples (Clymo and Duckett 1986), and a reservoir margin (Furness and Hall 1981). After a disturbance 21 new species appeared that were not previously present these were from the diaspore bank (Fenton *et al.* 2003). The diaspore bank is known to increase species numbers in relation to dispersal (During 2001). Moss diaspores in the soil have longevity (remaining ungerminated) and are persistent

for many (10+) years, remaining *in situ* until disturbance brings them to the surface and exposure to light (Jonsson 1993), During *et al.* 1987, During 1997). Considering only spores, Miles and Longton (1992) found that most bryophyte spores fell within 30 cm of the source colony, and are dispersal limited (Fenton and Frego 2005). Many authors agree that small moss spores (<20 μm), are lighter and have the ability to travel farther on the wind (During and van Tooren 1987, Ross-Davis and Frego 2004), and thus are not dispersal limited. Further supporting lack of bryophytes being dispersal limited, spores occur at arctic latitudes, where wind acts as an agent of aerial diaspore rain (Miller and Ambrose 1976). Wind was also responsible for the dispersal of bryophyte propagules (mostly gametophyte fragments) in mountain snowbeds (McDaniel and Miller 2000).

Lichens and bryophytes often form dense patches on the forest floor. These patches can be spatially separate or inter-mixed, as found in late successional stands. Interspecific competitive interactions occur between the mosaic of habitat patches (Rydin 1985, Marino 1991a, b, c) of bryophytes and lichens. These patches are frequently homogenous within the patch but compose a heterogeneous landscape. A variety of disturbance types can create areas available for colonization in the ground layer and thus initiate localized succession. Post disturbance, substrates are exposed and available for establishment and colonization from the available diaspore bank (During 1997, 2001), which may contain fragments of surrounding bryophytes (Longton and Schuster 1983) and lichens (Kershaw 1977).

1.15 Woodland caribou

Use of west-central Alberta as woodland caribou habitat has been documented over the past 40 years (Bjorge 1984, Edmonds and Bloomfield 1984, Edmonds 1988). Locally the terrestrial fruticose lichen component (*Cetraria*, *Cladonia* spp. and *Cladina* spp.) serves as winter fodder for these caribou (Edwards and Ritcey 1960, Scotter 1967, Bergerud 1972, Edmonds 1988, Coxson *et al.* 1998); the

epiphytic species *Alectoria* spp. and *Bryoria* spp. (Bergerud and Nolan 1970, Fancy and White 1985) are consumed in lesser amounts. This winter lichen forage accounts for 50 – 75 % of their diet (Arseneault 1997). Arseneault *et al.* (1997), working in Québec, reported that caribou removed more lichen than was replaced annually. Messier *et al.* (1988) supported this finding and argued that caribou herds can progressively deplete continental lichen dominated regions. In areas where caribou populations are high and abundance of lichen mats is low, overfeeding could reduce terrestrial lichen rich winter feeding grounds.

Due to their branched growth, increased biomass, and dense mat formation, *Cladina* lichens are eaten with more efficiency than the horn or cup-shaped earlier successional lichens (Arseneault *et al.* 1997). These late successional *Cladina* (*C. mitis, C. rangiferina, C. stellaris*) lichens are very palatable to the caribou (Palo 1993). Woodland caribou, in west-central Alberta, spend summers at the higher elevations of the Rocky Mountains and the herds relocate to the lower elevations (Upper Foothills Natural Subregion) when the snow pack becomes too deep (Edmonds 1988). At lower elevations the snow is shallower and terricolous lichens can be more easily accessed. Currently, the herd population is stable to declining (Natural Regions Committee 2006) and is listed as "Threatened" by the Committee on the Status of Endangered Wildlife in Canada and the Alberta Government. In the mid-1970s, Kershaw (1977) reported that there are too few animals to adequately use low elevation lichen populations. Lack of major forest disturbance leading to canopy closure in late stages of succession (Kershaw 1977) will further increase loss of the ground layer lichen, which will negatively affect availability of winter feeding grounds. Without canopy disruption feather mosses will dominate and caribou winter forage will continue to be diminished in the foothills. Management of forests for caribou habitat needs to be carefully engineered, as Stepaniuk (1997) could not document caribou crossing any clear-cut forest block. Chubbs *et al.* (1993), over a span of four years, found caribou avoided clear-cut

areas during the summer season. Avoidance of areas with distinct boundaries, diverse habitat types, and clear-cut regions (or related disturbance) was reported by Stuart-Smith e*t al.* (1997) and Smith *et al.* (2000). Careful construction of a land-use strategy will be necessary for success in maintaining or increasing local lichen feeding grounds for woodland caribou herds.

1.16 Disturbance

In most forest ecosystems, natural disturbances are essential in shaping vegetation composition at the local and landscape level (Pickett and White 1985). Disturbance can then be defined as a discrete event in space and or time that causes abrupt changes to communities or populations (Pickett and White 1985). The regime of disturbance acts to set back the successional clock, allowing early successional species to establish and resetting the colonization and establishment process. The disturbance frequency, time between disturbance events, affects composition of the community. If this frequency is high, then late (or slower) successional species will be denied the opportunity for colonization, keeping diversity at a low level. If the disturbance frequency is low then later long-lived successional species will have time to colonize and displace the earlier species, diversity will once more remain low. If the frequency is in-between, early species and late species can colonize with the pressure from competition being reduced, and species diversity is increased. This previously described (section 1.7) pattern of increased diversity at intermediate levels of disturbance was described by Horn (1975) and further amplified by Connell (1978, 1979) as the intermediate disturbance hypothesis. Disturbance events that are frequent can retard establishment of species that colonize slowly and lower species diversity by exclusion of long-lived, competitive species. Infrequent disturbance regimes also reduce diversity by promoting small numbers of long-lived species. Therefore, moderate or intermediate disturbance levels allow opportunity for increased species diversity by lessening pressure of highly competitive species and giving advantage to a wider variety of species establishment.

Boreal forests are dynamic ecosystems that experience continual change through disturbance. The major driving force behind temporal and spatial heterogeneity in the structure of forested communities is disturbance, and these act as agents of natural selection (Spurr 1952, Sousa 1985). Together with climate and soil type, disturbance acts as an additional component that can drive vegetation configuration (Thonicke *et al.* 2001). Disturbance regimes vary depending on the system. Size, magnitude (severity and intensity), frequency, predictability, and rotation period are all facets of disturbance (West *et al.* 1981, Sousa 1985, Peterson and Campbell 1993, Jonsson 1993, Coxson and Marsh 2001). Fire, wind, and insects are the principal natural agents of disturbance in boreal forests (Sousa 1985, Angelstam 1998) with anthropogenic disturbances such as forest harvest becoming increasingly more common on the landscape. This study uses selective mechanical thinning in order to research effects of canopy change on bryophytes, lichens and vascular plants that constitute the forest floor.

1.16.1 *Fire*

Fire is the primary natural disturbance in the boreal forest of North America (Rowe and Scotter 1973, Thonicke *et al.* 2001). Large scale fire is an important agent for stand disturbance (Ahlgren 1960, Ahlgren and Ahlgren 1965, Kuuluvainen *et al.* 1998) and is pervasive in montane systems (De Grandpré *et al.* 1993). It is well established that fire is an important ecological component that controls various functional and structural properties in boreal and montane forests (Maikawa and Kershaw 1976, Kershaw 1977, Johnson 1981, Sousa 1984, Foster 1985, Morneau and Payette 1989, Bergeron 1991, Coxson and Marsh 2001). Foster (1985) reported that the vegetation in fire-prone boreal regions is stable and uniform, which supports the view that the vegetation is adapted to fire as an integral ecological factor. In their study on subalpine and boreal forest fires, Nash and Johnson (1996) stated that the majority of large scale fires are ignited by lightning, the ignition agent alone is only one

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component in a larger complex set of interactions that leads to fire. Flannigan *et al.* (1998) provide a list of these complex interactions: precipitation, relative humidity, wind speed, temperature, topography, condition of fuels and ignition agent.

Wildfires can vary in severity, intensity, and behavior and can affect the stage of succession (stand development) by pushing it back (Coxson and Marsh 2001). Byram (1959) defines intensity as "energy output rate per unit length of the fire front". Forest fires can be placed into two classes in relation to intensity: 1) lethal- intense fires that kill the majority of the trees and 2) non-lethal-less intense fires that kill some trees with remaining trees that are untouched or only scarred (Bergeron 1991, Van Wagner 1983). Lethal- intensity fires allow for a large amount of succession post-fire, whereas non-lethal intensity fires cause partial openings and may permit limited regeneration. Intense, severe crown fires can cause increased death of canopy trees, opening up the forest floor for reestablishment of woody, non-woody vegetation, and the bryophyte and lichen mat. The incinerated canopy begins succession on the forest floor by increasing light and decreasing humidity. Low intensity crown fires may only damage specific areas and the effect to the ground layer may be reduced, however, Canadian boreal fires are typically high-intensity surface fires or crown fires that restart secondary succession (Bergeron 1991; Bergeron and Dansereau 1993). An intense, severe surface fire can destroy understory trees the shrub and ground layer, burning to the mineral soil (Dyrness and Norum 1983; Schimmel and Granstrom 1996). This can reset ground layer succession and place dependence for regrowth on the diaspore bank. A less intense surface fire may only burn the top stratum of the ground layer, scorching or lightly burning bryophytes and lichens, affecting only the ground layer. Schimmel and Granstrom (1996) found that survival of ground layer species depends on the diaspore bank, which they report, may receive little to no direct influence from the heat of a surface fire with low intensity. The quantity of energy that enters the soil during a fire depends on the burning duration and energy output, but, most

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commonly, only a modest amount of heat is transported into the soil (Rowe 1983, Bonan and Shugart 1989, Johnson 1992). All fires are dependent on fuel load and moisture levels within the forest (Dyrness and Norum 1983, Angelstam 1998). Johnson (1981) stated that post fire regeneration in the Northwest Territories of Canada comes from three sources: 1) vegetative reproduction 2) buried viable seeds 3) propagule invasion. However, he does not take the diaspore bank of mosses and lichens into account in his study. Fire frequency in boreal forests ranges from infrequent in wet areas, to more frequent in dry lichen-rich areas (Angelstam 1998). Fire, then, is an important ecological component for maintenance of open park-like woodlands that support ground layer lichens from northern Canadian boreal forests (Maikawa and Kershaw 1976) to the tundra region (Kershaw 1978).

Fire is cyclical on the landscape and can vary due to forest composition, location, and many other factors. Fire cycle, as defined by Johnson and Van Wagner (1985), is the number of years required to burn an area equal to the surveyed area. Boreal coniferous forests can have cyclic burning in the form of crown fires and/or severe surface fires have a return interval of ±50 - 100 years (Sousa 1985, Bonan and Shugart 1989, Coxson and Marsh 2001), these are necessary for maintaining diversity and canopy openness that supports lichen ground cover. Drier upland sites is where *Pinus contorta* is found to be the dominant tree, usually forming relatively uniform stands similar in size and age (Dix and Swan 1971, Carleton and Maycock 1978, Cogbill 1985, Larsen 1997). These boreal pine forests burn more regularly than boreal spruce forests, because dry sites are more vulnerable to fire than mesic sites (Cogbill 1985, Bergeron 1991). Depending on the frequency, boreal fire initiates development of the stand and sets restrictions on succession, and can continue to reset establishment at the stand and ground level (Foster 1985, Foster and King 1986, Morneau and Payette 1989). The burned ground layer can be divided into a stepwise establishment sequence, post-fire (Foster 1985). These phases range from initial establishment of lichens to the later successional stages of bryophyte homogeneity, where the ground

layer is almost completely dominated by a carpet of feather mosses. The literature mostly agree on four

phases beginning with establishment of (1) acrocarpous mosses (e.g. *Polytrichum* spp.), (2) crustose or

horned lichens (e.g. *Cladonia* spp.), (3) fruticose lichens (e.g. *Cladina* spp.), and finally (4)

pleurocarpous mosses (e.g., *Pleurozium schreberi*) (Ahti 1959, Bergerud 1971, Maikawa and Kershaw

1976, Foster 1985, Morneau and Payette 1989, Coxson and Marsh 2001). These phases are based on

increasing shade created by the slow closure of canopy over time post-fire disturbance.

Since the middle of the last century, forest management practices often involve fire suppression

on the landscape (Johnson *et al.* 2001). Boreal systems are not immune to this practice. In some

systems, suppression has led to increased (or "unnatural") fuel buildup on the forest floor (e.g. *Pinus*

ponderosa P. & C. Lawson ecosystems) which over time has changed the fire regime (Shinneman and

Baker 1997). Fire suppression may cause changes to the natural fire regime, but Johnson *et al.* (2001)

reported that this idea of atypical fuel buildup from fire suppression in boreal systems is invalid, and

does not affect fire frequency or cycle.

1.16.2 *Treefall gaps*

Wind creates canopy gaps of various sizes within a forest by blowing down all or parts of trees

(Sousa 1985; Peterson and Campbell 1993) and increases coarse woody debris (Jonsson 2000) on the

forest floor. The largest gaps are created when multiple whole trees fall (Schaetzl *et al.* 1989), this

action can cause a local domino effect (Sousa 1985). Naturally, windthrow would increase during

seasons with strong or gusting winds, with the addition of increased precipitation, softening the soil,

these actions could be enhanced. When windthrow occurs, the oldest and tallest trees are the most likely

to be affected because of their loss of flexibility (Sousa 1985, Mayer 1989). Topography, soil type, and

depth (Sousa 1985), can influence windthrow potential. Steepness of terrain can add to the risk of blow

downs. Trees in sandy, thin soils that are shallow rooted (lowering root anchoring strength) (Mayer

1989), are more at risk for the effects of windthrow. This describes the *Pinus contorta* forests of the

Upper Foothills, as shallowly rooted trees growing in sandy, thin soil are more vulnerable to windthrow.

Windthrow can vary seasonally and also with anthropomorphic activities. Any activity that removes

trees can produce abrupt and abundant forest edges, with these edges being more susceptible to wind

stress. Waters and Quesnel (2001) found that when harvesting smaller patches (1-2 hectares) of timber,

windthrow was not significant, rates did vary annually based on allogenic factors.

Operating at the small group or individual tree level of windthrow, these smaller, fine-scale

perturbations are important for maintenance of spatial heterogeneity. Treefall canopy gaps are one of

the most important types of local disturbance (Moore and Vancat 1986, Schaetzl *et al.* 1989, Jonsson

and Esseen 1990, Peterson and Campbell 1993). Treefall not only opens the canopy but also produces

root upheaval, creating soil depressions and elevations (pits and mounds) (Moore and Vancat 1986;

Peterson and Campbell 1993) that can last for centuries (Beatty and Stone 1986). Creation of this pit-

and-mound microrelief exposes a number of substrate types, e.g. the root mat, bare mineral soil, stones,

and humus, which results in increased habitat heterogeneity (Beatty and Stone 1986), as well as mixing

the soil horizons (Schaetzl *et al.* 1989). It is at these relatively small spatial scales ($< 1m^2$) and longer

temporal scales ($< 10yr$) that produce large changes in species abundance at the ground layer (Halvorsen

and Eilertsen (1996). These small scale, uninhabited substrates are exposed, waiting for colonization or

reestablishment by the diaspore (spores and asexual propagules- tubers and gemmae) bank, aerial

diaspore rain, and or surrounding ground layer (Putz 1983, Peterson and Campbell 1993). Continuance

of high levels of bryophyte colonization and diversity in boreal ecosystems is dependent on these

disturbances (Jonsson and Esseen 1990, Ross-Davis and Frego 2002). Many bryophyte species move

into and inhabit non-competitive environments like these disturbed areas (Slack 1982). Jonsson and

Esseen (1990) and Fenton (2001) note that little attention has been given to bryophytes and lichens that have been affected by treefall disturbance.

1.16.3 *Tree removal*

Since canopy thinning through anthropogenic tree removal is the basis for this thesis the following is included as a disturbance. One-third of the earth's forests are boreal and they provide around 20-50% of pulp, paper, and wood products (Reich *et al.* 2001), however, land use history of boreal regions is much shorter when compared to broad-leaved temperate forests of central Europe (Angelstam 1998). Modern man has a tremendous impact on boreal forested systems (Burton *et al.* 2003) and tree removal, as with any disturbance, influences diversity. With suppression of fire and intensified forestry, e.g. clear-cutting, man has become the major boreal disturbance (Hansen *et al.* 1991). It appears modern forestry techniques may not be as detrimental to the ecosystem as Delong and Tanner (1996), studying forest harvest, stated that tree harvest could mimic the outcome of natural fire regimes due to similarities in the effects of fire and harvest. In agreement, Johnson *et al.* (1998) found modern forest harvesting practices are similar to the results of natural fire. Effects on diversity by logging and wildfire, in southern boreal forests, have revealed that severe crown fires are equal to or greater than logging disturbance (Reich *et al.* 2001). They also found that both disturbances were very similar in nutrient cycle disruption. With any disturbance, all components of the ecosystem are affected, Niemelä *et al.* (1993), studying beetles in western Canadian clear-cut stands, found generalists increased in newly cut stands, but noted that specialists were uncommon. Tree removal, in any form, affects the ecology of the system, and drives edaphic and biotic changes. Between 1975 and 2001, 18.7 million hectares of forest was harvested in Canada (National Resources of Canada 2004). Harvest techniques such as site preparation, planting, spacing, and thinning as well as harvest methods as clear-cutting and

partial cutting all affect how much and what type of material is removed from the site and have significant influences on post-harvest site structure and function.

1.17 Study area

The study area is located in the Upper Foothills Natural Subregion of the eastern slope of the front ranges of the Rocky Mountains of western Alberta, Canada. Walter (1979) classified the region containing the study area in the Boreal Zonobiome VIII. This zonobiome type has a cold-temperate climate and is primarily composed of coniferous forests. The Natural Regions Committee (2006) further classifies the study area as being included in the Boreal-Cordilleran transitional Ecoclimatic Province. This Foothills Natural Region occurs on undulating terrain from the Bow River north to the Grande Prairie area (Natural Regions Committee 2006) (Fig. 1.1). The elevation of the Region ranges from 900 m to an upper limit of 2,000 m. The Upper Foothills Natural Subregion can be described as having high rounded hills and deep valleys that are forested to their summits with conifers (Rowe 1972). Much of the area is underlain with calcareous bedrock overtopped by medium textured cordilleran morainal deposits and colluvial material. Soils of the lower elevations are typically gray luvisolics or podzolic (Rowe 1972). Higher elevations typically have brunisolic luvisols covered by a narrow, acidic layer of needle litter (Natural Regions Committee 2006).

The climate is boreal with the coldest temperatures in January and warmest in July. The growing season is only around three months (June – August) and the annual precipitation is high due to elevation and climatic weather patterns. Fires are common based on geography, climate, and forest type. The research area is dominated by *Pinus contorta*, approximately 100 years of age with an average elevation of about 1,300 m (Pharo and Vitt 2000) and is located about 50 km southeast of Grande Cache and 80 km north-west of Hinton, Alberta and nForth of the Berland River and headwaters of the Little Smoky River ($53^{o}45$' and $53^{o}55$'N latitude and $118^{o}18$' and $118^{o}30$'W longitude) (Fig. 1.2).

As part of a forest thinning/ lichen abundance project established in 1997 (see Pharo and Vitt 2000), the study area sites were selected by industry ecologists of Alberta Newsprint Company (ANC), Weldwood Canada (WEL), and Weyerhaeuser Canada (WEY) to include undisturbed forest that was within suitable distance to current logging and mill operations all within a 375 km^2 area. Nine stands within this area were selected within the experimental thinning region (Pharo and Vitt 2000). Further experimental design and setup were also determined by Vitt and Pharo.

WEY
Pierre Grey's Lakes
Recreation Area

Grande
Cache

40

Little Smoky River

N

ANC
Cabin Creek

Hendrickson Ck.

WEL

Berland River

Hinton

WEY- Weyerhaeuser Canada
ANC- Alberta Newsprint Company
WEL- Weldwood Canada
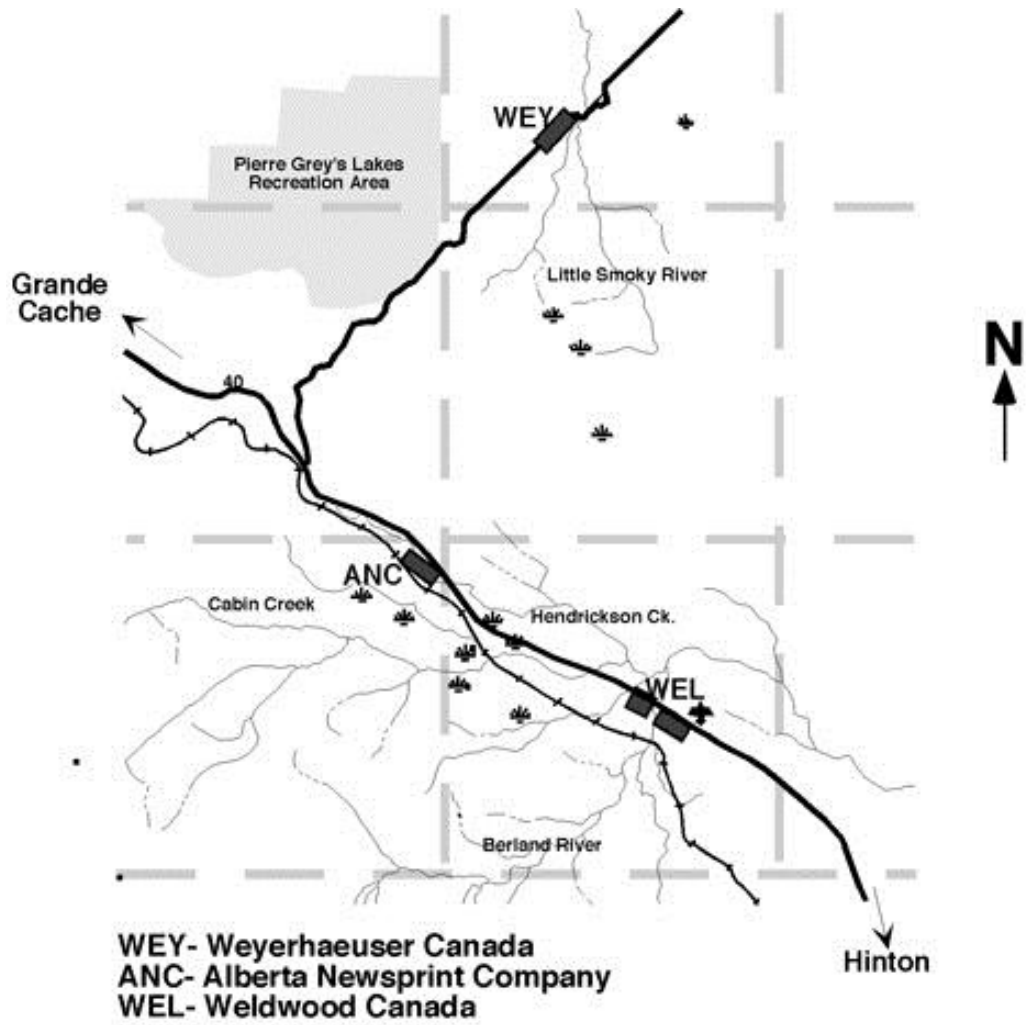
Figure 1.2. Map of the study area, black boxes indicate actual research sites, located along Highway 40, between Grande Cache and Hinton, Alberta.

The late seral ground layer mosaic of mosses and lichens, prolific throughout both the montane and boreal regions, is a dynamic forest stratum. This layer is diverse despite dominance of a few moss and lichen species. The forces of light, water, and temperature are a few of the fundamental factors that take part within this hundred year old mosaic. Equally important are biotic components that also affect life at the micro-scale. Disturbance, natural or otherwise, directs many changes in the ground layer. This study looked at canopy cover reduction and its effects at the macro- and micro-scale. With the combination of impacts largely unknown for ground layer bryophytes and lichens in this system, I addressed the following questions:

Chapter 2) What are the effects of thinning on canopy cover variability?

Chapter 3) What effect did thinning have on abundance and diversity of the ground layer?

Chapter 4) What was the importance of abiotic factors, scale and diaspore availability relative to the occurrence of ground layer mosses and lichens?

Chapter 5) Do a) substrate disturbance, b) pre-disturbance vegetation, c) canopy opening, and/or d) species interactions limit ground layer establishment of *Cladina mitis* or *Pleurozium schreberi*?

Chapter 6) A summary of my results and their implications to management of these forested foothills.

The data chapters in this thesis are written in manuscript format. Therefore, there is some amount of overlap in introductory and methodical descriptions between chapters 3 – 5.

CHAPTER 2

EFFECTS OF THINNING ON POST-HARVEST CANOPY COVER

VARIABILITY

2.1 Introduction

Canopy cover can be defined as the proportion of tree crowns that cover the sky and regulate levels of sun (and shade) that reach the ground. Therefore, removal of canopy trees, in forested communities, produces almost immediate effects on understory and ground layer vegetation by directly increasing light levels and indirectly by increasing evapotranspiration. Thomas *et al.* (1999) reported that the effects of canopy thinning, depending on the magnitude, result in dominance of a few species (decreasing species richness) or may increase diversity among forest floor species, in accordance with the level of light. Besides increases in light, canopy removal also changes litterfall totals that has an affect nutrient cycling (Klemmedson *et al.* 1990, Kim *et al.* 1996), which is also tied to understory (and ground layer) diversity and site productivity (Beatty and Sholes 1988), as well as soil moisture (Kelliher *et al*. 1993). Mechanical selective tree removal in order to increase light to the ground layer is the basis for this study as a whole.

Manipulation of the canopy by thinning into three degrees (or light levels) was key for understanding its effects on the ground layer bryophyte and lichen communities. Eight years had passed between the initial creation of the canopy thinning treatments by the timber companies (see study area) and final data collection. During this time in the forests of the study area, notable natural disturbance, such as windfall, occurred and caused changes within the established canopy removal by volume thinning treatments (see treatment groups). Review of canopy cover

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data and field observations lead to the questions associated with the following objectives: 1) determine if canopy cover in the three treatment regimens was comparable between 1997 and 2005 2) examine the percent canopy cover change for each of the three removal by volume (RV) treatment groups and 3) compare any differences in removal by volume and establish new ranked canopy groups.

2.2 Methods

2.2.1 *Study area*

As part of a forest thinning/ lichen abundance project established in 1997 (see Pharo and Vitt 2000), the study area was selected by industry ecologists of Alberta Newsprint Company (ANC), Weldwood Canada (WEL), and Weyerhaeuser Canada (WEY) to include undisturbed montane forest that was within reasonable distance to current logging and mill operations all within a 375 km^2 area. Nine stands within this study area were selected by within the experimental thinning region (Pharo and Vitt 2000). Further experimental design and setup were determined by Vitt and Pharo.

The study area is in the Upper Foothill Natural Subregion (Natural Regions Committee 2006) of the eastern front ranges of the Rocky Mountains of western Alberta, Canada. The climate is boreal, having short, cool, moist summers and long, cold, and snowy winters. The January daily mean minimum temperature is ca. -11.1 ^{o}C and in July is ca. +15.1 ^{o}C (Leith *et al.* 1999). The growing season length is around 165 to 170 days and the annual precipitation (for the Ecoclimatic Province) can range from 500 to 800 mm, with an average annual precipitation of 632 mm (Natural Regions Committee 2006). Due to climate, elevation (approximately 1,300 m), and landscape location fires are common place. The prevailing tree species comprising the forests is *Pinus contorta* Dougl. ex Loud. (lodgepole pine), which is considered by Walter (1979)

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as a post fire subclimax dominant species. At this elevation and geographical location, *Pinus contorta* forms sparsely mixed stands with *Picea glauca* (Moench) Voss (white spruce) (Smithers 1961, Rowe 1972, Beckingham *et al.* 1996). This study area is located about 50 km southeast of Grande Cache and 80 km north-west of Hinton, Alberta and north of the Berland River and headwaters of the Little Smoky River (53^o45' and 53^o55'N latitude and 118^o18' and 118^o30'W longitude).

For the Upper Foothills, Beckingham *et al.* (1996) classified the soils as acidic, well drained, and having a poor nutrient content with little variation throughout the area. In 2000, Pharo and Vitt examined the soil pH and texture and found that the mean pH was 4.88, varying from 4.83 to 4.92 (unpublished data). No significant differences were reported between soil samples of the nine stands. Soil texture ranged from loamy sand to sandy loam. The moisture regime is generally classified as mesic.

2.2.2 *Experimental design*

2.2.2.1 *Forest stands*

Nine stands of approximately 30 to 40 ha were selected by Dale Vitt and Emma Pharo in 1997 from a 375 km^2 area along highway 40. These stands in each forest management area were chosen using four criteria: 1) dominance of *Pinus contorta*, 2) at least 30% moss and lichen cover in the ground layer, 3) initially undisturbed forest tracts, all about 100 years old, and 4) proximity to access road.

2.2.2.2 *Treatment areas*

Each of the nine stands was divided into a control and three treatment areas which were based on tree removal by volume (RV); control (0% removed), treatment 1 (~20% RV), treatment 2 (~40% RV), treatment 3 (~60% RV). These 10 ha treatment areas were located

randomly within each stand (Fig. 2.1). Treatment areas were harvested during the 1997-1998

winter as to reduce negative impact of logging equipment on the ground layer.
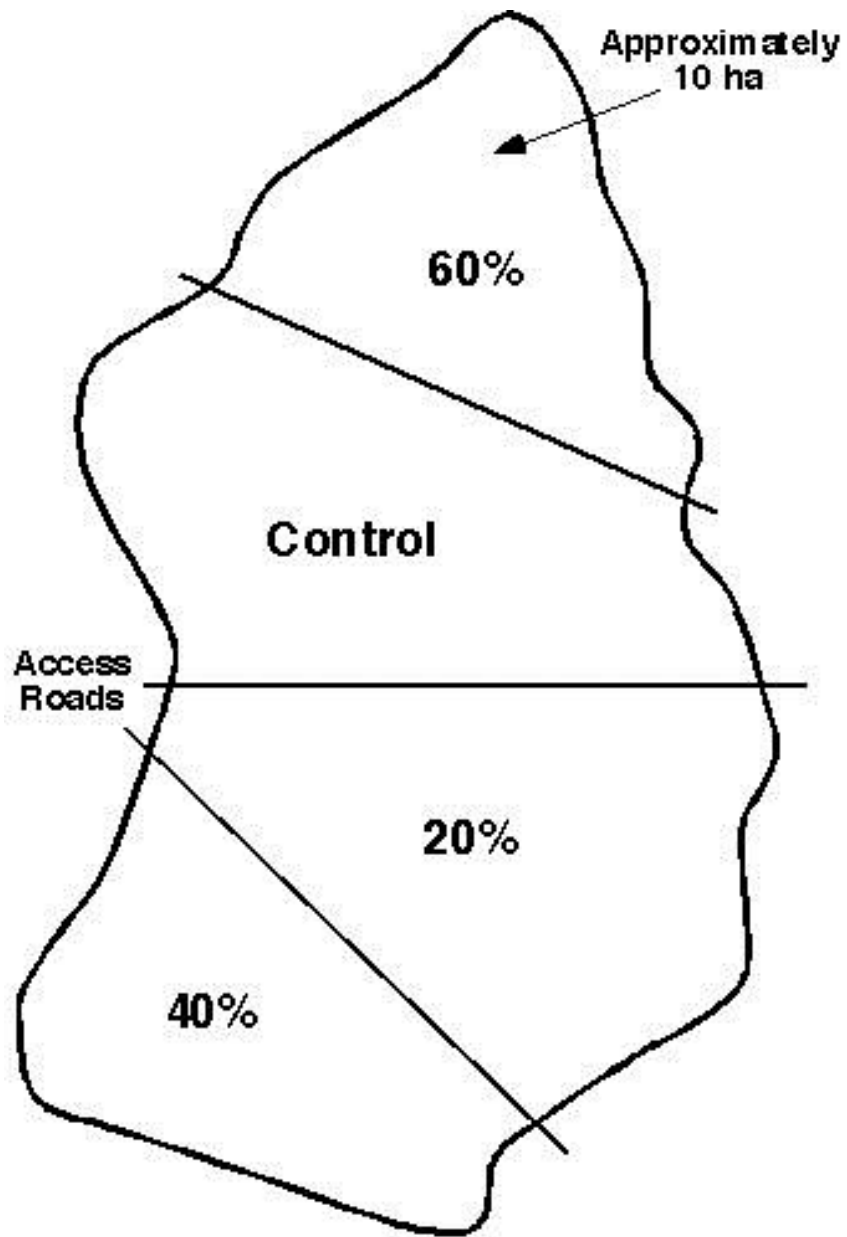
Figure 2.1. A forty hectare stand divided up into 10 ha treatment areas with ~20%, ~ 40%, and ~60% tree removal by volume, plus a control.

Between 1997, the original date of thinning, and 2005, the final collection of canopy data, differences were noted between the original experimental treatment groups and thus the canopy groups were re-measured. Over the period of eight years windthrow (loss of whole trees, lateral branches, and crowns) had increased the canopy openness in the treatment areas so the assigned percentages for the groups had changed with time. In 1997 and 2005 canopy cover was estimated ocularly with a spherical concave densiometer (Lemmon 1956) that was held one meter above and parallel to the ground. Four readings were taken from each direction pivoting off the rebar rod in the northwest corner of each plot, the average of these constitutes the canopy cover (further explained below).

2.2.2.3 *Plots*

In the summer of 1997, for each treatment area, a baseline was randomly placed on the long axis and extended across the entire distance of the area. This baseline was used to divide the treatment area into five equal segments. Plots were first randomly positioned within each segment, and randomly placed along a perpendicular line that extended to the plot boundary (Fig. 2.2).

A metal rebar rod was then driven into the northwest corner of each plot and tagged with the plot number. From this corner facing east, a 6.5 x 6.5 m permanent plot was established. Five of these 6.5 x 6.5 m plots per each treatment area were laid out for a total of 20 plots per stand. The nine stands were divided evenly among tree lumber companies (three per company). The accidental plot removal by one company (WEY 59) led to the creation of extra plots by another (WEL 63), with 182 plots in total.
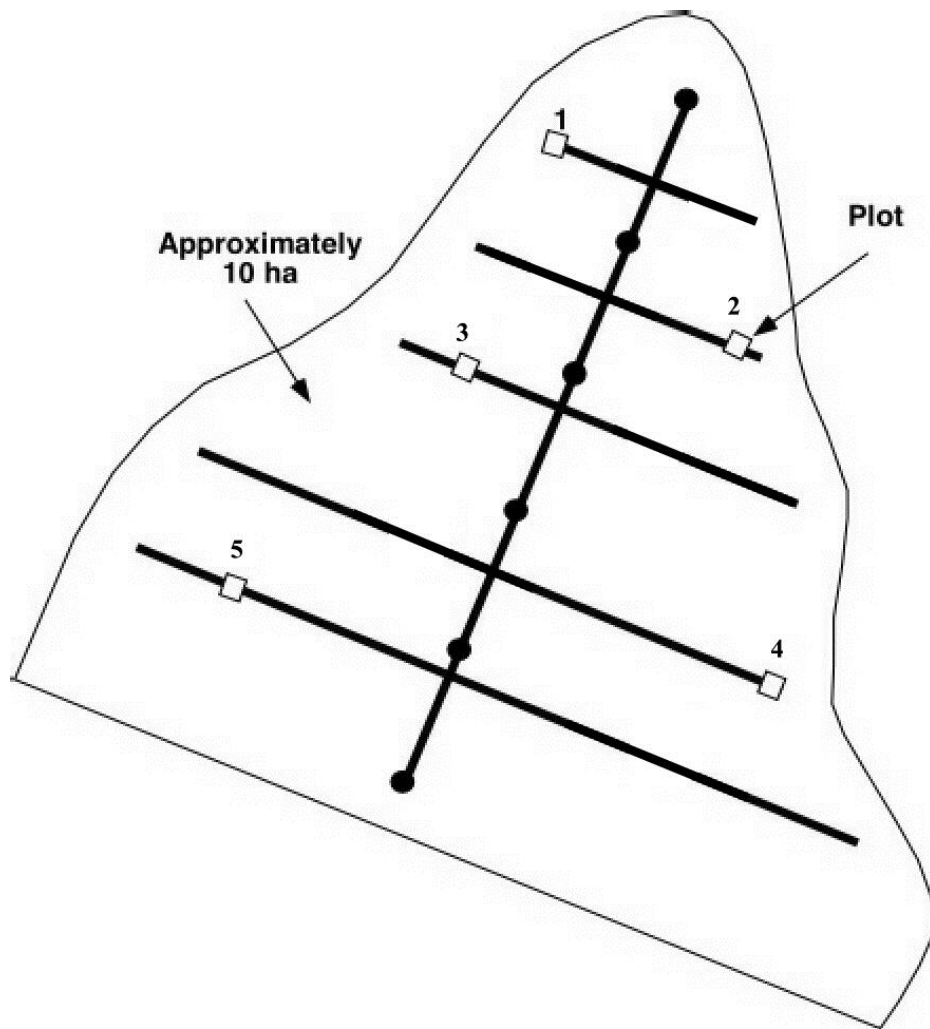
Figure 2.2. A treatment area partitioned with five randomly assigned 6.5 x 6.5 m plots.

Plot with subplot location

1	2	3	↓ 1.5 m ↑
6	5	4	↕ 1 m / 6.5 m
7	8	9	
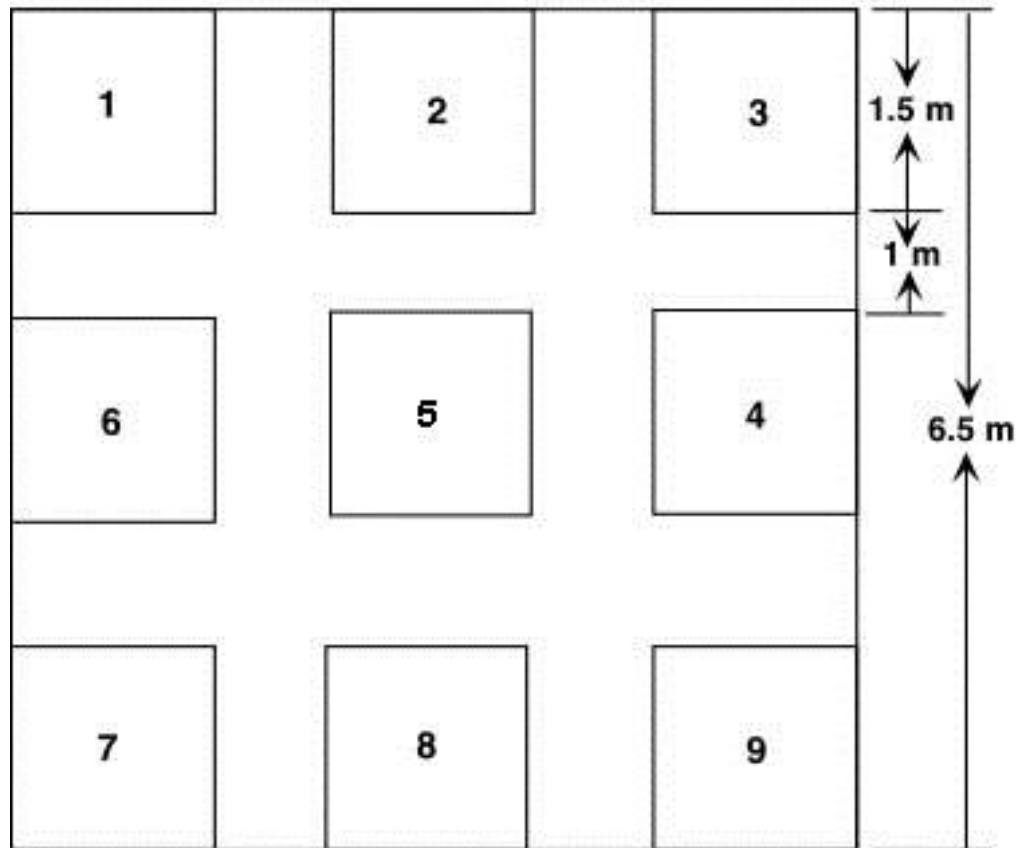
Figure 2.3. Division of the 6.5 x 6.5 m plot, showing number assignments for each of the nine subplots.

2.2.2.4 *Subplots*

Plots were divided into a grid of nine 1.5 x 1.5 m (based on herb layer measurement (Cain and Castro 1959)) permanent subplots with a 1 m walkway in between. Beginning at the northwest corner rod moving east, these are numbered 1-9 traveling in a Z pattern (Fig. 2.3).

2.2.3 *Data analysis*

A one-way analysis of variance (ANOVA) (SAS 2008) was used to establish statistical significance between pre-harvest canopy groups (1997). Tukey's Honestly Significant Difference (HSD) (SAS 2008) was used post hoc to determine which treatments differed significantly ($p = 0.05$). Percent canopy cover change was calculated by subtracting one from, pre-harvest canopy cover minus post-harvest canopy cover. A one sample t-test (R 2011) used to test whether the observed canopy cover change differed from expected canopy cover change (% RV) for each of the thinning treatments.

2.3 Results and Discussion

2.3.1 *Canopy cover*

Under pre-harvest conditions, canopy cover of the individual plots range anywhere from 45.3 to 87.0 % (Fig. 2.4). Before mechanical thinning, there was natural variation in the canopy cover for the plot locations, with mean canopy cover in the control area being lower. However, overall pre-harvest canopy cover means for four treatments ranged only from 58 to 63% (Fig. 2.5). Canopy means of the control and the removal by volume (RV) treatment groups were (control – 58.2, 20% RV- 63.4, 40% RV – 62.3, 60 % RV – 62.3).
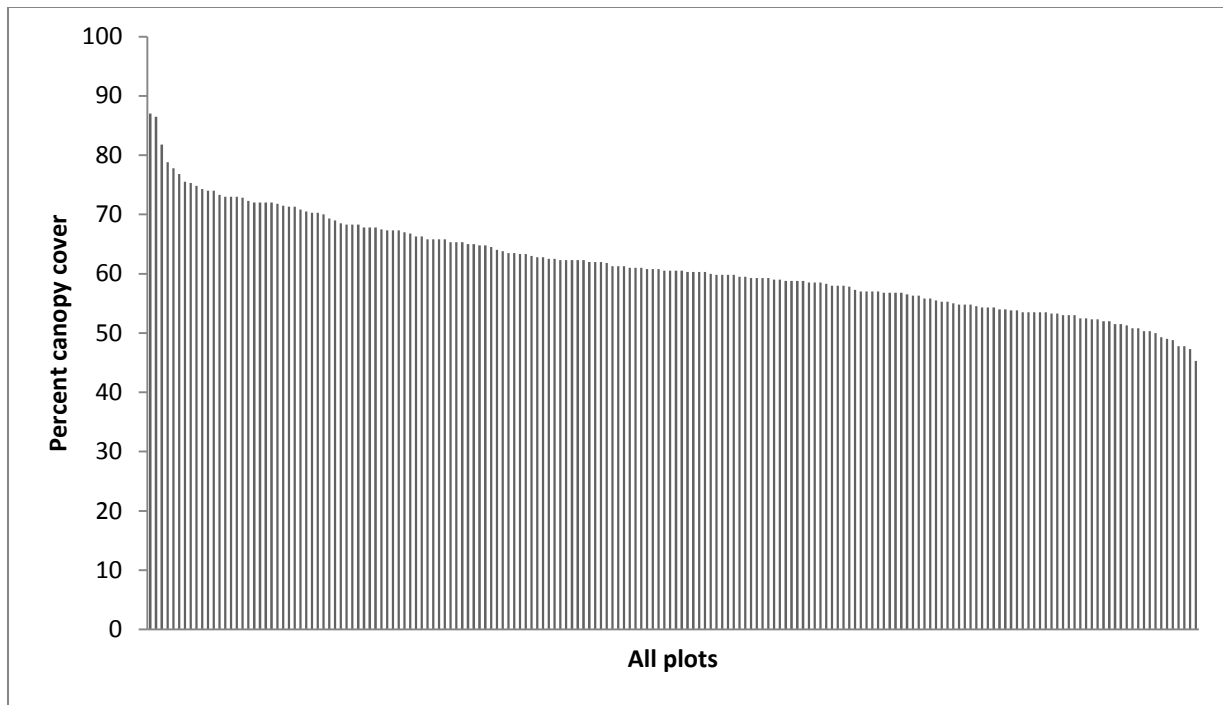
Figure 2.4. Pre-harvest variation in canopy cover (1997) for each of the 182 plots.

The three timber companies were to thin each of their three stands to conform to experimental treatment removal by volume of ~20%, ~40%, ~60%. These 20/40/60 volume removal treatments, upon inspection, did not correspond with the associated thinning regime. This may well be due to differences in canopy cover in pre-treatment stands, to post-harvest wind fall, or differences in thinning techniques by each of the timber companies. Further examining this variation, I plotted percent canopy cover change (post-harvest % canopy cover/pre-harvest % canopy cover -1) for each of the 182 plots by RV at the stand level (Figs. 2.6 – 2.8). Thinning by all three lumber companies had a wide range of canopy change across all three experimental groups. For the 20% RV treatment only 3 out of 43 (or 7%) of the plots were within ±0.05% of the 0.2 percent canopy change level (Fig. 2.6). For the 40% RV treatment 9 out of 44 of the plots (or 20%) were within ±0.05% of the 0.4 percent canopy change level (Fig. 2.7). For the 60% RV treatment 14 out of 47 plots (or 30%) were within ±0.05% of the 0.6 percent canopy change level (Fig. 2.8). A one sample t-test reveals that the actual canopy cover change for the 20% RV group was significantly different than the observed canopy cover change ($t(42) = 11.2$, $p < 0.0001$). The observed canopy change mean of 58.2 was different than the expected 20% RV group. The 40% RV group was also different from the observed canopy change ($t(43) = 4.59$, $p < 0.0001$) with a mean of 55.9 for the observed canopy cover change. The 60% RV group was not different ($t(46) = -0.732$, $p = 0.467$). There was no difference between the observed canopy mean of 57.9 and the 60% RV group. The means for the observed canopy change groups differed only by approximately two percent, and two out of the three groups were significantly different from the removal by volume groups.
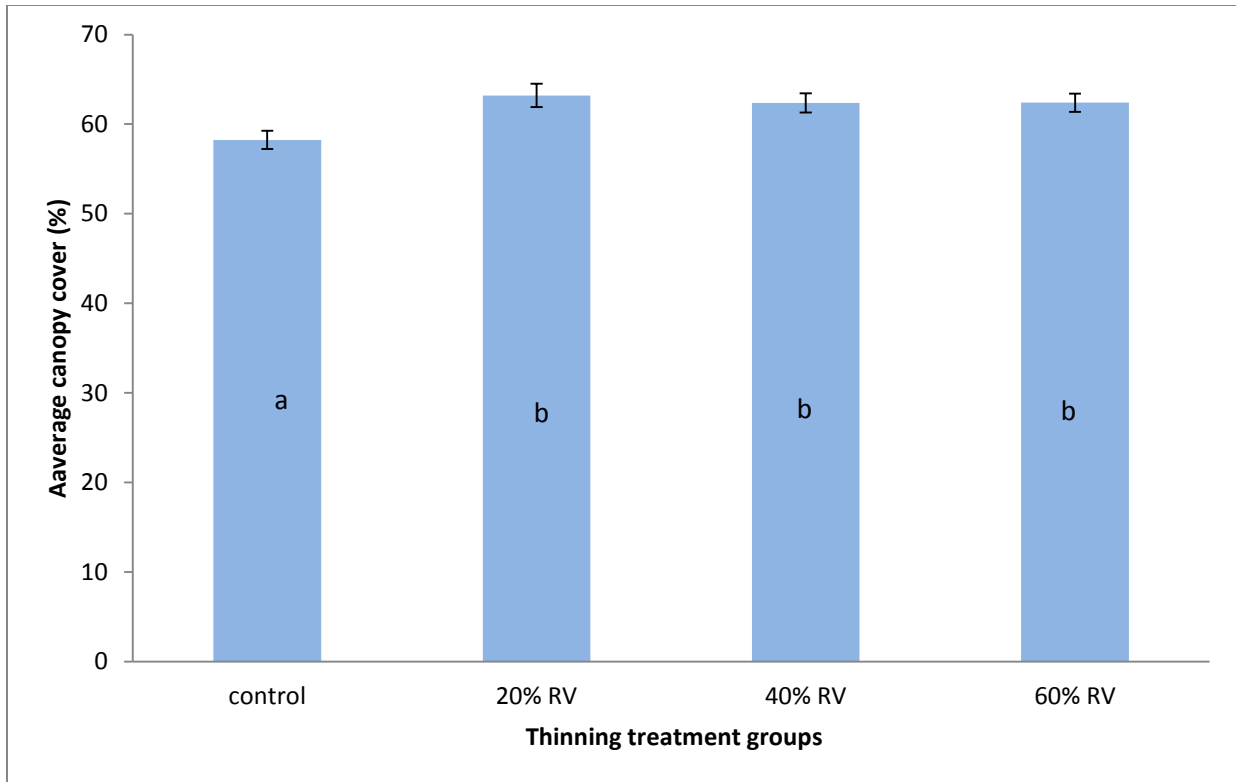
Figure 2.5. Pre-harvest canopy cover (1997) for control and removal by volume (RV) thinning treatment groups (Tukey Post Hoc $p < 0.0064$). Error bars are standard error. Different letters indicate significance ($p < 0.05$).
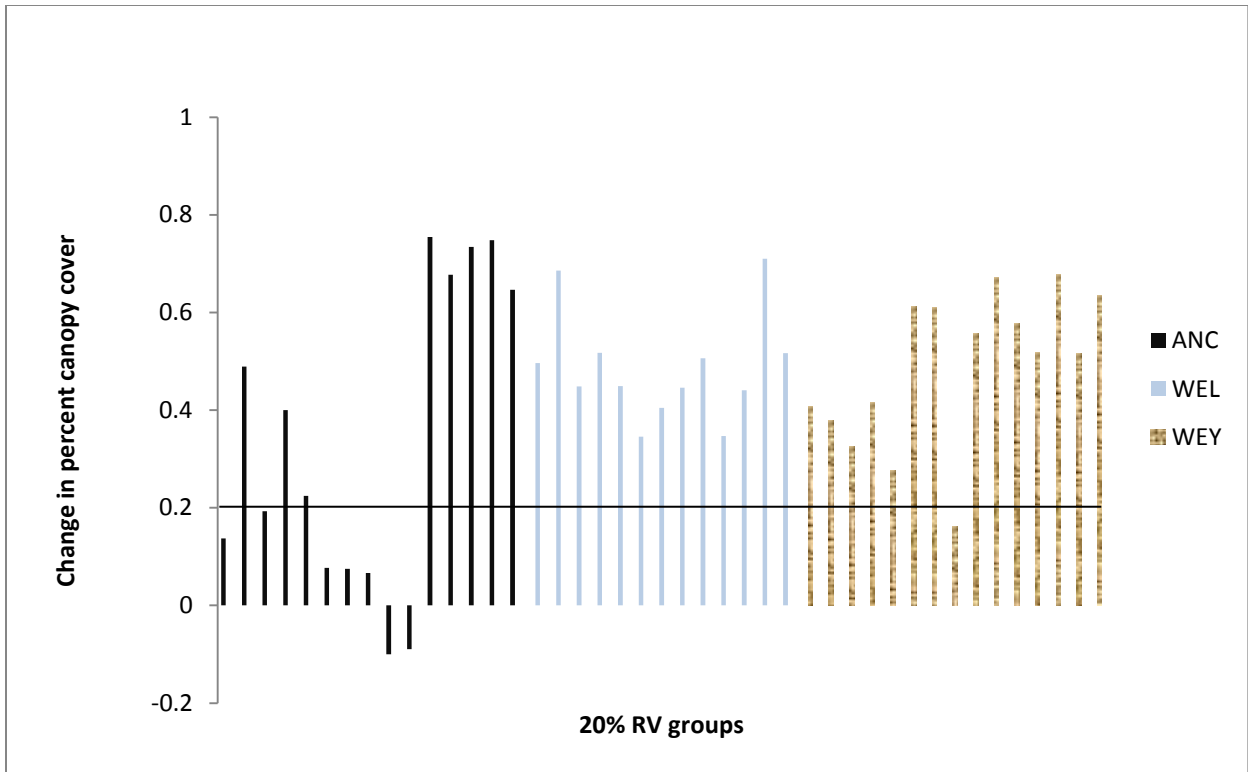
Figure 2.6. Change in percent canopy cover for all 20% RV plots. The solid line marks 20% canopy. Negative numbers represent increases in canopy.
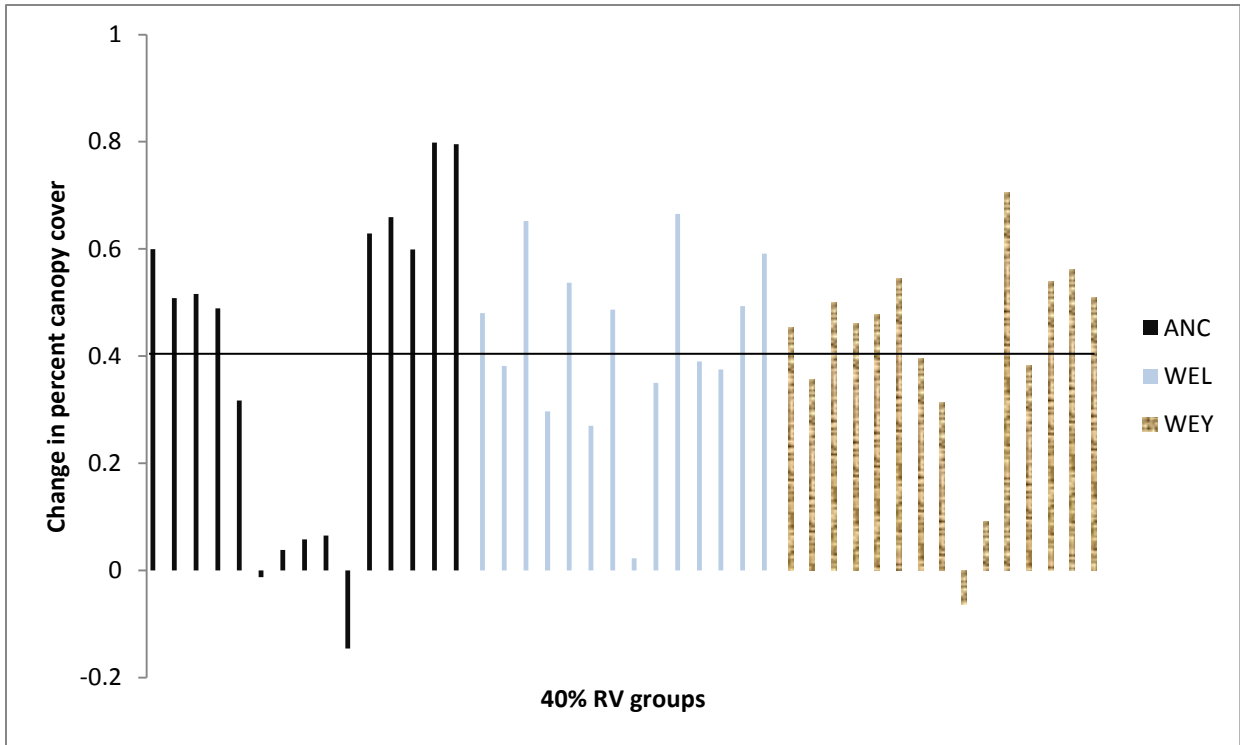
Figure 2.7. Change in percent canopy cover for all 40% RV plots. The solid line marks 40%

canopy. Negative numbers represent increases in canopy.
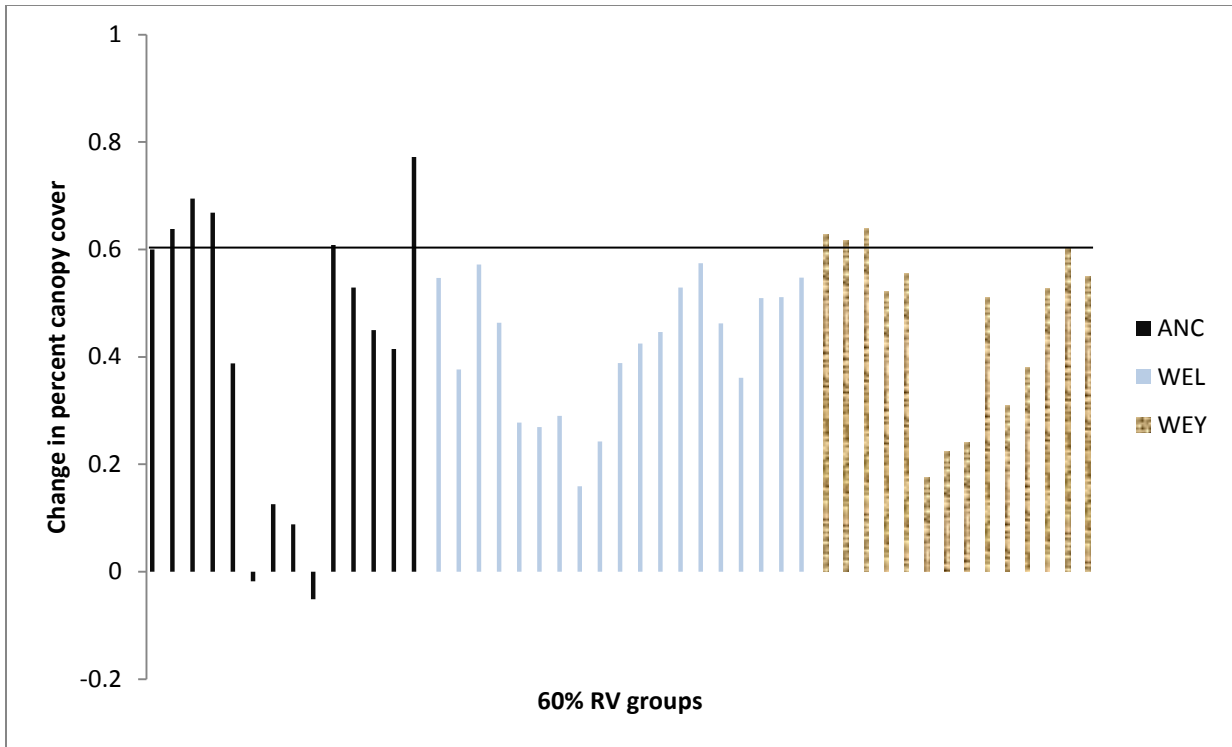
Figure 2.8. Change in percent canopy cover for all 60% RV plots. The solid line marks 60%

canopy. Negative numbers represent increases in canopy.

In conclusion after eight years post-thinning, the 20/40/60 removal by volume treatments did not result in significantly different treatments for the stands. Despite the lack of treatment effect organized by treatment area, large differences in percent cover change were present ranging from +10% more cover to 80% canopy cover reduction (Fig. 2.9). Since differences between RV groups was lacking, in order to test ground layer response to canopy cover change I ranked all post-harvest canopy change (2005) thinned plots from highest to lowest percent canopy cover change (Fig. 2.9). These 120 plots were then divided the into three ranked groups: group 1 - least removed, mean 18% removed – ranging from 0 – 38 %, group 2 – moderate amount removed, mean 46% removed – ranging from 38 – 53 %, group 3 - most removed, mean 66% removed – ranging from 54 – 79%. Regrouping the thinning treatments by percent canopy cover change created distinguishable groups based on cover removal. The effect of using this ranked approach is to establish actual percent canopy cover removed, 18%, 46%, and 66% - very close to the original design of volume removal (20/40/60). These new treatment groups will be used throughout Chapter 3.
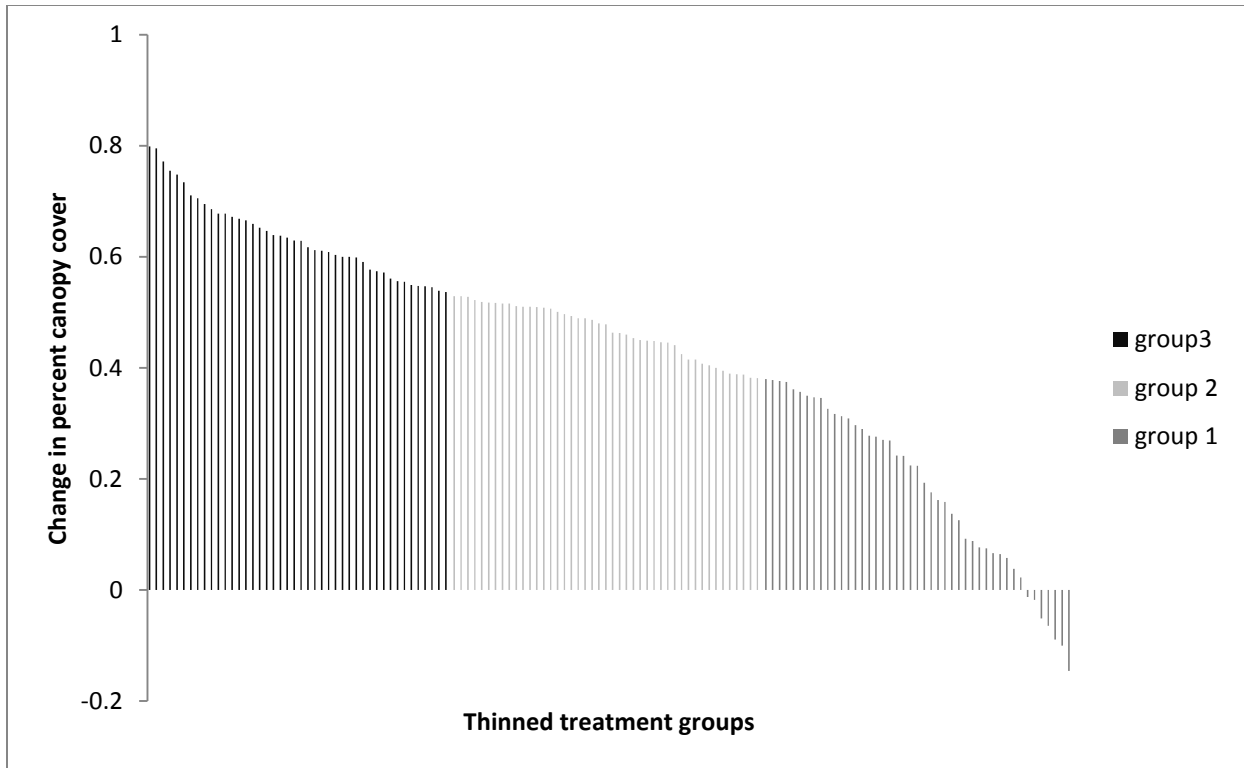
Figure 2.9. Ranked post-harvest (2005) change in percent canopy cover for thinned stands

divided into new arbitrary groups. These new groups replace the original 20% RV, 40% RV,

and 60% RV groups. Negative numbers are increases in canopy from the initial 1997

measurements.

CHAPTER 3

SELECTIVE TIMBER HARVEST EFFECTS ON ABUNDANCE AND DIVERSITY OF GROUND LAYER BRYOPHYTES AND LICHENS

(A version of this chapter will be submitted to *The Bryologist* for publication.)

3.1 Introduction

The ground layer in the Upper Foothill Natural Subregion of Alberta (Natural Regions Committee 2006) is primarily a mosaic of mosses and lichens. The spatial heterogeneity, or patchiness, of the ground layer may be due to the disturbance regime of the past and/or to local edaphic and climatic differences of the present. The bryophytes and lichens that comprise these forest floor patches, although small in stature, constitute a large proportion of the total biomass of the forests (Busby *et al.* 1978, Rieley *et al.* 1979, Pharo and Vitt 2000, Fenton 2001). The seemingly homogeneous patches of bryophytes can contribute a level of species richness that is comparable to vascular plants (Steel *et al.* 2004, Grytnes *et al.* 2006). Due to their diminutive size these ground layer components have often been overlooked in studies dealing with diversity (Slack 1977, Mills and Macdonald 2004). In fact, for some systems they may constitute a major component of total species richness and ground layer abundance. Regardless of size, these forest floor bryophytes and lichens can have high abundance and diversity.

When evaluating the forest floor, several factors including structural elements (Lee and La Roi 1979a, Vitt *et al.* 2001), light dynamics (Ipatov and Kirikova 1981; Ipatov and Tarkhova 1983), and moisture regimes (Vitt and Pakarinen 1977; Lee and La Roi 1979b), have been shown to be beneficial when trying to understand development and structure of the ground layer. The mechanisms, especially light and moisture, drive the occurrence of mosses and lichen

morphotypes on the forest floor, which are ultimately under the broader control of the trees, in terms of canopy density. Reduction in canopy, whether anthropogenic or natural in origin, influences changes in the ground layer microclimate. Canopy loss can effect moss and lichen morphotypes differently as increased light can cause localized extinctions, introductions, and shifts in current patches. For example; increased light levels, reduced moisture, and lower humidity can decrease log decay which directly affects xylicolous bryophytes (Humphrey *et al.* 2002) and over time can cause loss of ground layer moss and lichen populations. Modern forest management techniques (i.e., involving disturbance) disrupt ground layer communities and have prompted scientific study of timber-harvested forests. Studies from all over the globe (e.g., Vellak and Paal 1999, Newmaster and Bell 2002, Ross-Davis and Frego 2002, Fenton *et al.* 2003, Fenton and Frego 2005) provide evidence that support diversity decline of bryophytes, based on sensitivity to changes in their particular environment. Conversely, many types of fruticose lichens often thrive in these types of disturbances (Harris 1996, Miège *et al.* 2001).

Intensity of available light, from canopy to forest floor, is a vital resource. Whittaker (1972), when examining light in the forest, stated that light goes through a "logarithmic extinction" which is the interception of light by the foliage of various plants from the top of a forest downward. The amount of canopy openness ultimately has bearing on the composition of the ground layer. It is this light (or lack of) that strongly affects moss and lichen abundance and diversity in late seral coniferous forests. It is also this light that contributes to the integrity of the forest system as a whole. As life on this planet is constrained by solar radiation, in this system its accessibility is the main driver of this study, being tied directly to selective mechanical removal of trees (and subsequent canopy) and the increased light that follows.

Functionally, mosses are involved in nutrient cycling and carbon storage for many boreal and arctic ecosystems (Longton 1992, Vitt e*t al.* 1995), including those of the montane-boreal region (O'Neill 2000). The importance of bryophytes in wet ecosystems is well-documented for their contributions to nitrogen and carbon pathways (Granhall and Selander 1973, Gorham 1991, Aerts *et al.* 2001, Turetsky 2003). Mosses are also becoming recognized as important players in drier ecosystems for these same biogeochemical cycling processes (DeLuca *et al.* 2002, Zackrisson *et al.* 2009). The feather mosses, *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis* (DeLuca e*t al.* 2002, Zackrisson *et al.* 2009, Houle *et al.* 2006), have all been found to harbor epiphytic cyanobacterial associates that fix nitrogen (N) in montane-boreal systems. Deluca *et al.* (2002), under ultraviolet-fluorescence micrography, found both motile and colonization stages of *Nostoc* spp. living within the incurved leaves of *Pleurozium*. Zackrisson *et al.* (2009) found N-fixing activity associated with moss leaves decreased during June and July. It is postulated that this drop may be due to higher summer temperatures (Markham 2009) or mid-seasonal drying conditions (Chapin *et al.* 1991). Since processes such as these can be limited by water, distinctive adaptations that influence water-use efficiency (i.e., lack of cuticle) are associated with bryophytes. In a *Picea mariana* forest in Manitoba, bryophytes intercepted 23% of throughfall, versus 15- 60% for the forest overstory (Price *et al.* 1997). This water gain in mosses is due to the lack of an outer epidermis which enables the entire colony surface to act as a single "leaf" (Proctor 1990) and allows bryophytes to have a high leaf area index (Bond-Lamberty and Gower 2007). The ability of water to penetrate the moss permits amelioration of the local microclimate.

Fruticose lichens are ground layer pioneer species that establish post-disturbance in areas of heat stress (Kershaw 1977) and high light. They produce small amounts of self-litter, when

compared to mosses (Sulyma and Coxson 2001, Sedia and Ehrenfeld 2003). In dense, compact, and well developed lichen mats litter additions (self or other) benefit the soil as moisture levels are elevated (Kershaw and Field 1975), and this aids in amelioration at the micro-climate scale. Lichens, like mosses, do not have a cuticle and thus can quickly become wet or dry. For lichens, periods of dryness are beneficial (Fraser 1956) as metabolic processes may occur more efficiently.

Diversity of a system has more than one facet, thus vegetation composing the forest floor can be measured in several ways. Species abundances at the ground level can be summarized by the use of cover-abundance scales, to determine the relative area covered by individual species in an area. If measuring spatial variation in a heterogeneous environment or monitoring variation on a long-term temporal scale then broad cover-abundance scales will provide adequate data. Finer-scale measurements need more precise cover-abundance scales to more accurately convey species importance. Whittaker (1972) described three simple diversity measurements that encompass the range of species abundances over spatial scales; these are alpha (α), beta (β), and gamma (γ). Alpha diversity is expressed as species richness (or number of species) of a particular area or site. Beta diversity is a comparison of species diversity between sites, and is often represented as an index of the rate of increase of α diversity as determined by the amount of species change between sites along a habitat gradient. Gamma diversity, or total diversity, is an overall measure of species richness within a larger region. Hunter (2002) defines it as "geographic-scale" diversity. Although these indices of richness are fundamental in providing convenient comparisons of biological structure of communities within a region, the incorporation of both abundance and richness is necessary. The use of diversity indices to compare diversity among areas (Whittaker's β diversity, β_w), to take rare species into account (Shannon-Weiner H),

and to incorporate equitability (Shannon's E) all enhance understanding of the pattern of species occurrence on the landscape.

The unique properties of mosses and lichens deem them valuable components of the larger forested ecosystem. With continued increases in disturbance to the ground layer their losses may have serious impacts. This is the first study to address the relationship between ground layer response to canopy opening in the form of selective timber harvest on the eastern slope of the Canadian Rockies (Natural Regions Committee 2006). The overall objective of this study is to determine what effect the three degrees of thinning had on abundance and richness of mosses, lichens, and vascular plants that occur on the forest floor. I approached this with an examination of the relationship between species abundances and richness and percent canopy cover removed utilizing measures of species diversity in the form of α, β (β_w), γ, and evenness.

3.2 Methods

3.2.1 *Study area*

As part of a forest thinning/ lichen abundance project established in the winter of 1997/ 1998 (see Pharo and Vitt 2000), the study area in the Upper Foothills was selected by industry ecologists of Alberta Newsprint Company (ANC), Weyerhaeuser Canada (WEY), and Weldwood Canada (WEL) to include undisturbed forest that was within suitable distance to current logging and mill operations all within a 375 km^2 area. Nine stands within this study area were selected within the experimental thinning region (Pharo and Vitt 2000). Further experimental design and setup were determined by Vitt and Pharo.

For the Upper Foothills, Beckingham *et al.* (1996) classified the soils as acidic, well drained, and having a poor nutrient content with little variation throughout the area. In 2000, Pharo and Vitt examined the soil pH and texture and found that the mean pH was 4.88 , varying

from 4.83 to 4.92 (unpublished data). No significant differences were reported between soil samples of the nine stands. Soil texture ranged from loamy sand to sandy loam. The moisture regime is generally classified as mesic.

3.2.2 *Perimeter transects*

Abundance in terms of cover was estimated from perimeter line transects (see Chapter 2). At the start of this project in the summer of 1997, pre-harvest cover data were collected by E. Pharo; final measurements (post-harvest) were done by R. Mooneyhan McClelland in the summer of 2003. Due to differences between 1997 and 2003 cover assessment, these data were not comparable. The 2003 cover data were collected by placing a meter tape along the outside perimeter of each of the 182 plots, each singular plot totaling 2,600 cm in length. To better comprehend the intertwined components of the forest floor, the vegetation was divided into two synusiae (or layers) for greater understanding of the local community components (Whittaker 1965, 1972; Achuff and La Roi 1977; McCune and Antos 1981); 1) the small shrub/herb layer and 2) the moss and lichen layer. Cover of all components of these layers (shrubs, herbs, and graminoids; bryophytes and lichens) and duff/bare ground was measured and recorded.

3.2.3 *Species richness and diversity*

Species richness and diversity were measured at the subplot (see Chapter 2) level. For each of the nine stands, approximately half of the plots (94) were chosen at random for collection of these data. Five of the nine 1.5 x 1.5 m subplots (1, 3, 5, 7, 9) were chosen to adequately represent species composition in control and thinned areas (~11 plots per treatment area type per stand). These data were collected in the summer of 2005. Due to limited time available to document and sample five subplots within each of the 94 plots, spread out randomly over an area greater than 320 ha, each subplot species (bryophyte, lichen, or vascular plant-including small

trees) was recorded and abundance was estimated visually by using a cover-abundance score

from 1 to 4: 1-rare, found only once or few individuals present, no more than 5%; 2-locally

abundant, 5-25% ; 3-abundant, 25-50%; 4-very abundant, 50-100%. The cover-abundance

scores used here are scaled down from Braun-Blanquet (1932) (who used 6 cover classes). Since

the fidelity of vegetational units and associations have already been established for the region

(Beckingham *et al.* 1996) a broader scale was chosen as this was a long term project with a

heterogeneous ground layer. To assess biodiversity of the community, in controls and three

canopy cover change groups, the commonly used diversity measures of species richness

(represented as mean alpha), beta (comparison of species between canopy groups), and gamma

(total number of species per canopy group) were used. To better quantify species diversity for

the purposes of comparison the index Shannon-Weiner H was used to characterize species by

abundance and Shannon-Weiner Evenness (E) was used for equitability. Shannon-Weiner H

takes both evenness and richness into consideration and is a measure of uncertainty, whereas

Shannon-Weiner Evenness measures the relative abundance of individuals between the species.

3.2.4 *Post harvest canopy groups*

Using a spherical concave densiometer (Lemmon 1956) to estimate total overstory

percent canopy cover, the 182 individual plots ranged from 45.3 to 87.0% cover under pre-

harvest conditions. The three timber companies each thinned three areas to conform to an

experimental treatment removal by volume of ~20%, ~40%, ~60%. Due to windfall, differences

in thinning procedures, and loss of whole and partial trees over eight years post-harvest a

reassessment of the removal by volume groups was necessary. Using 2005 densiometer

readings, three experimental canopy cover groups were delineated based on change in percent

canopy cover (from 1997 to 2005): group 1 – least change– ranging from 0—38% canopy cover

change, average of ~18%; group 2 – moderate change– ranging from 38—53% canopy cover

change, average of ~46%; and group 3 - most change — ranging from 54—79% canopy cover

change, average of 66% canopy cover change. These canopy removal groups, along with the

uncut controls, are used throughout this chapter.

Ground layer vascular plants, terrestrial lichens (not including uncommon crustose

lichens), and bryophytes were all identified to species level. Vascular plant nomenclature

follows Gleason and Cronquist (1991), nomenclature for mosses follow Anderson *et al.* (1990),

for liverworts follow Stotler and Crandall-Stotler (1977), and Esslinger and Egan (1995) for

lichens.

3.2.5 *Data analyses*

For plot perimeter transect data, linear regression was used to model relationships

between change in percent canopy cover (independent variable) and perimeter vegetation cover

(dependent variable). Regressions were performed using Sigma Plot (2008). A non-metric

multidimensional scaling (NMDS) ordination was conducted in which distances between sample

variable pairs (canopy groups) are ranked in order of agreement with dissimilarities in species

organization (ground layer species) (McCune and Grace 2002). The Bray-Curtis Index (Bray

and Curtis 1957) was used to calculate dissimilarities in community, and 1 to 6 dimensions were

used to perform the analysis. Stress versus the number of dimensions, represented in a scree

plot, was used to determine dimensionality. To determine degree of correlation for plots within

the ordination, vector fitting was used for variables relating the character of the plot, canopy

cover and species diversity. Analysis of Similarity (ANOSIM) (Clarke 1993) was then used to

make pair-wise comparisons among the canopy cover groups to uncover if they occupy different

positions, Bray-Curtis (1,000 permutations) generated an R value between +1 and -1, with zero

representing the null hypothesis of no separation. Values of R near 1 represent similarities within groups and separation of sample groups. All NMDS, ANOSIM, and vector fitting analyses were performed using the DECODA® software package (version 3.00 b 38; Southern Illinois University, Edwardsville, Illinois).

For species richness, values are given as mean α (richness plot level), β (species turnover between plots), and γ (richness at the group and plot level). Canopy cover group plots (control, groups 1-3) were summed for mean abundance and a total abundance value. Whittaker's beta diversity (β_w) was used to indicate the proportion of species common between combinations of sites (control vs. group 1, group 1 vs. group 2, group 2 vs. group 3, group 3 vs. control). The equation

$$\beta_w = \gamma/\mu(\alpha)$$

where γ is the total number of species shared by the two groups; μ is the mean of α; α is the species richness. Species diversity was calculated using Shannon-Weiner H as this measurement takes subspecies proportion of richness and evenness into account. The equation

$$H = -\sum_{i-1}^{S} (p_i) ln(p_i)$$

where S is the number of species, ln is the natural log, and P_i is the proportion of individuals found in the ith species for the total sample. To calculate equitability the Shannon-Weiner Evenness (E) index was used. The equation

$$E = H/ln(S)$$

where H is the species diversity value, ln is the natural log, S is the number of species. A value between 0 and 1 is produced, where 1 is completely even.

3.3 Results

3.3.1 *Perimeter transects*

3.3.1.1 *Vegetation responses to canopy opening*

Mean shrub abundance of the combined thinned plots as measured in 2005 was 25% of the cover in the control plots (percent cover calculated from data in Appendix I). Shrub cover was reduced with increasing loss of canopy cover (Fig. 3.1a). Approximately 30% of the variation in shrub cover can be explained by canopy cover change ($r^2 = 0.287$, $p < 0.0001$). Cover of shrubs begins to decline in canopy cover group 1 and continues to decline throughout the next two canopy cover groups (2 and 3). Cover of *Cornus canadensis* (the dominant herbaceous perennial) averaged highest for control plots, with 2.4% cover. Cover of *Cornus* decreased as canopy cover changed with roughly 15% of the variation being explained by changes in the canopy ($r^2 = 0.137$, $p < 0.0001$) (Fig. 3.1b). This herbaceous cover decline also exhibited increasing incidence of an absence of *Cornus* beginning around 20% canopy reduction (group 1) and continuing in frequency with greater canopy loss. There was no relationship between generic herb cover and canopy change ($r^2 = 0.0155$, $p = 0.094$).

Generic lichen (all lichens except *Cladina mitis*) cover was not associated with canopy cover change ($r^2 = 0.0189$, $p = 0.064$). Cover of the fruticose lichen, *Cladina mitis*, also is not related to canopy change ($r^2 = 0.0008$, $p = 0.706$).
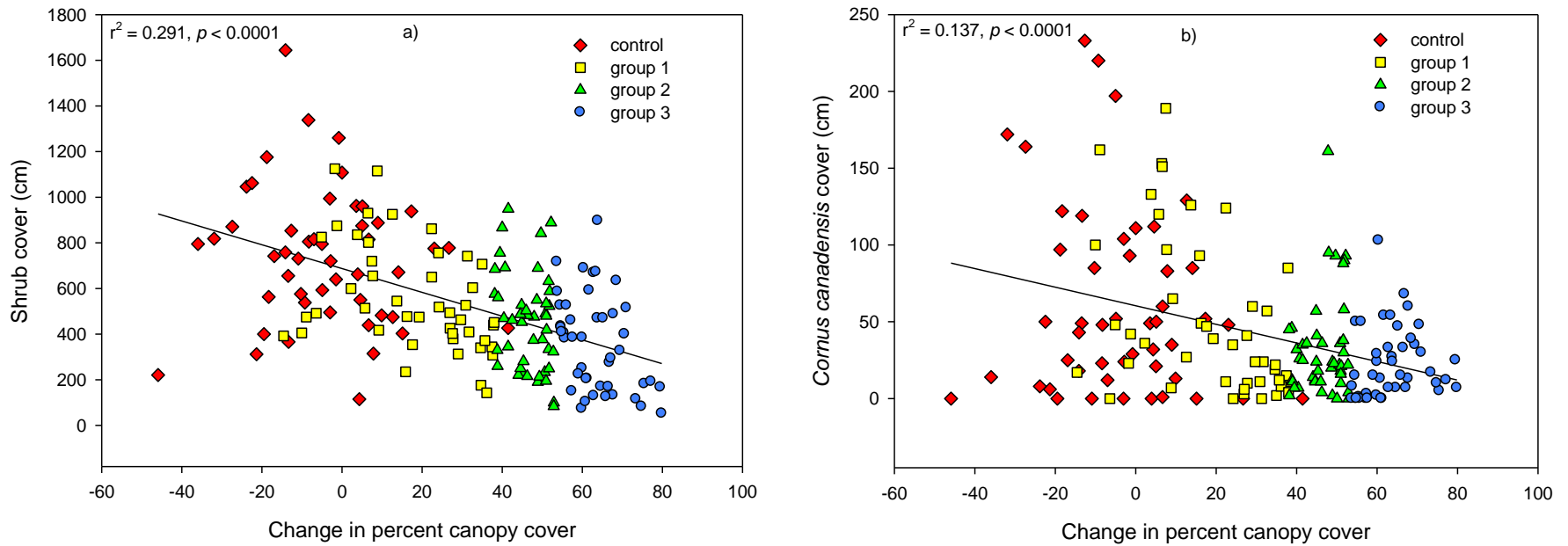
Figure 3.1. Relationship between a) shrub and b) *Cornus canadensis* cover (cm) and change in percent canopy cover for 182 plot perimeter transects divided into a control (uncut), group 1 (canopy change average of 18%), group 2 (canopy change average of 46%), and group 3 (canopy change average of 66%). Standard error of estimate for shrubs is 235.8 and 44.09 for *Cornus*.

Generic bryophyte cover (all bryophytes excepting the three dominant feather mosses) decreased with increasing canopy cover change ($r^2 = 0.118$, $p < 0.0001$) (Fig. 3.2 a). Roughly 12% of bryophyte cover reduction can be explained by canopy loss. Loss of generic bryophyte cover increases beginning in canopy cover group 1 and continues to decline in groups 2 and 3. Each of the three feather mosses have decreases in cover in relation to increasing canopy change. The relationship between *Pleurozium* cover and change of canopy cover ($r^2 = 0.422$, $p < 0.0001$) is strong (Fig. 3.2b) with ~40% of the variation explained. *Pleurozium schreberi*, most abundant of the three dominant feather mosses, has the highest cover (21%) in control plots. *Pleurozium* cover declines sharply in group 1 and continues to little cover remaining in group 3. *Hylocomium splendens*, the second most abundant feather moss, had mean cover of 0.75% in control plots. The decrease in *Hylocomium* cover is positively associated with increasing canopy cover change ($r^2 = 0.0909$, $p < 0.0001$) (Fig. 3.2c). Cover of *Hylocomium*, like that of *Pleurozium*, is most strongly reduced beginning in group 1 and dwindles to almost no cover in group 3. The least common feather moss, *Ptilium crista-castrensis*, had an overall cover of 0.64% in control plots. Being affected similarly by canopy opening, *Ptilium* cover is linked to canopy cover change ($r^2 = 0.123$, $p < 0.0001$) (Fig. 3.2d), with the greatest reduction in *Ptilium* cover evident in group 1. All feather mosses, as they are late successional species and thrive in the shade of closed canopy, have the largest amount of cover losses at the lowest level of canopy change (group 1).
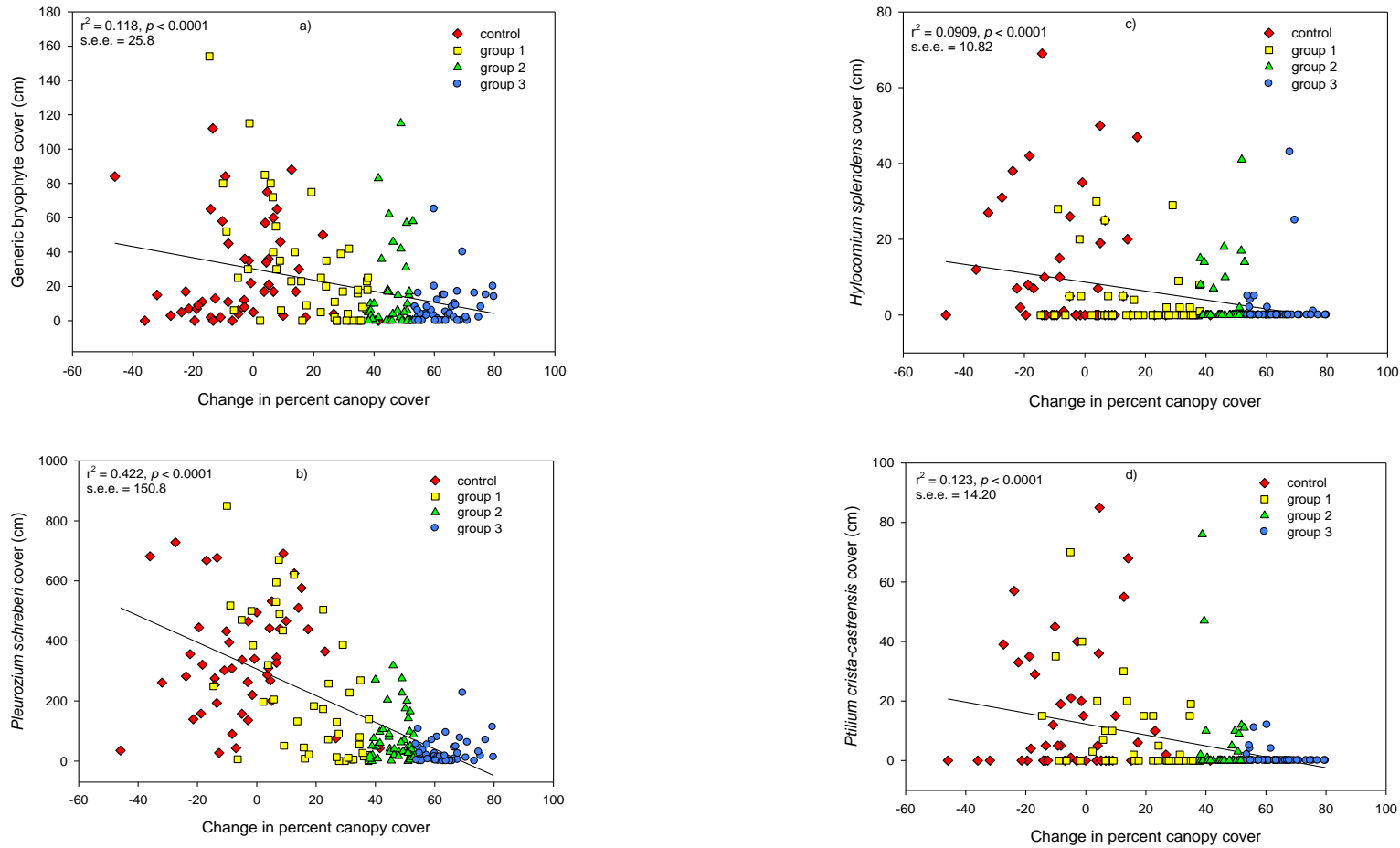
Figure 3.2. Relationship between a) generic bryophyte, b) *Pleurozium schreberi*, c) *Hylocomium splendens*, and d) *Ptilium crista-castrensis* cover (cm) and change in percent canopy cover for 182 perimeter transects. Standard error of estimate is denoted as s.e.e..

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Grass cover was positively correlated with change in canopy cover ($r^2 = 0.0215$, $p = 0.048$) (Fig. 3.3a). Grass cover in control plots is low and rapidly increases with the lowest canopy change, group 1. The cover of dead moss increased in association with increases in canopy cover change ($r^2 = 0.108$, $p < 0.0001$) (Fig. 3.3b). As the canopy was opened, moss cover in general decreased resulting in increases in cover of dead moss (and bare ground). There is a strong positive correlation of bare ground to change in canopy cover ($r^2 = 0.413$, $p < 0.0001$) (Fig. 3.3c). Duff/bare ground (including any plant material that was not recognizable) represented about 30.8% cover in control areas. Between groups 1 and 2 bare ground begins to steadily increase as bryophyte death occurs. Over the span of seven years, increases in bare ground present opportunities for recolonization by incoming species.
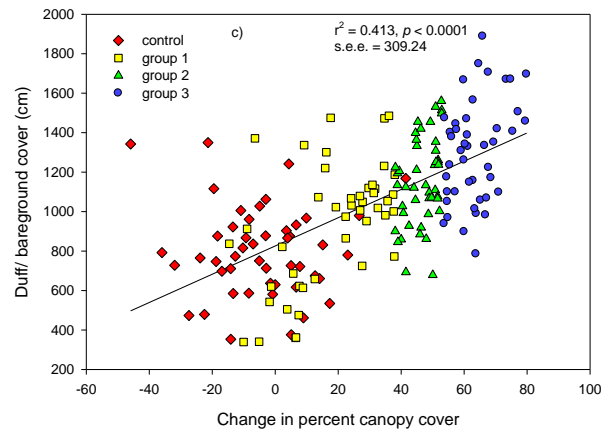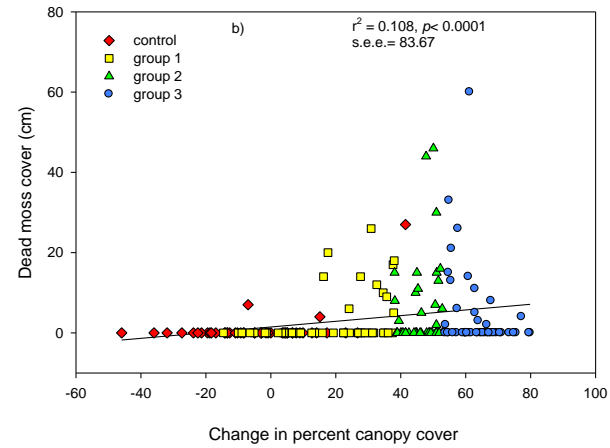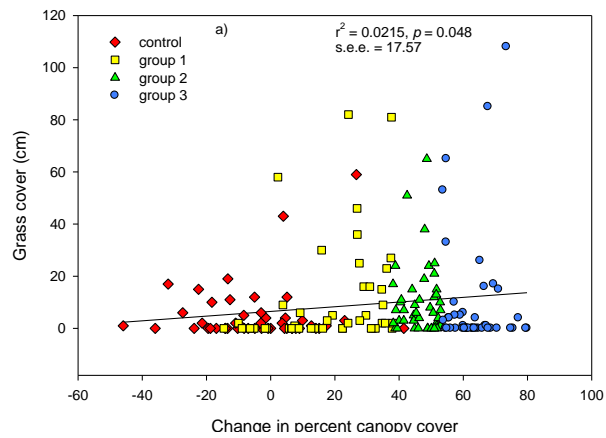
Figure 3.3. Relationship between a) grass, b) dead moss, and c) duff/ bareground cover (cm) and change in percent canopy cover for 182 plot perimeter transects. Standard error of estimate is denoted as s.e.e.

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Although there is considerable overlap betwee the four canopy cover groups ((Fig. 3.4), they are significantly different ANOSIM (R: 0.1801, $p = < 0.0001$, Table 3.1)) and their centroids form a progression from control through canopy cover group 1, then 2, and finally 3, suggesting greater differences as canopy cover change increases. Vectors for species diversity and change in canopy cover show that both canopy cover and species diversity are highest in the control and group 1 and decrease across groups 2-3.

a)
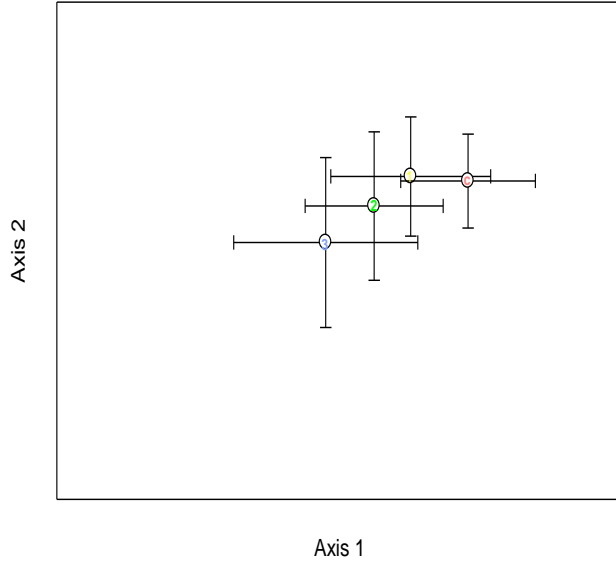
b)
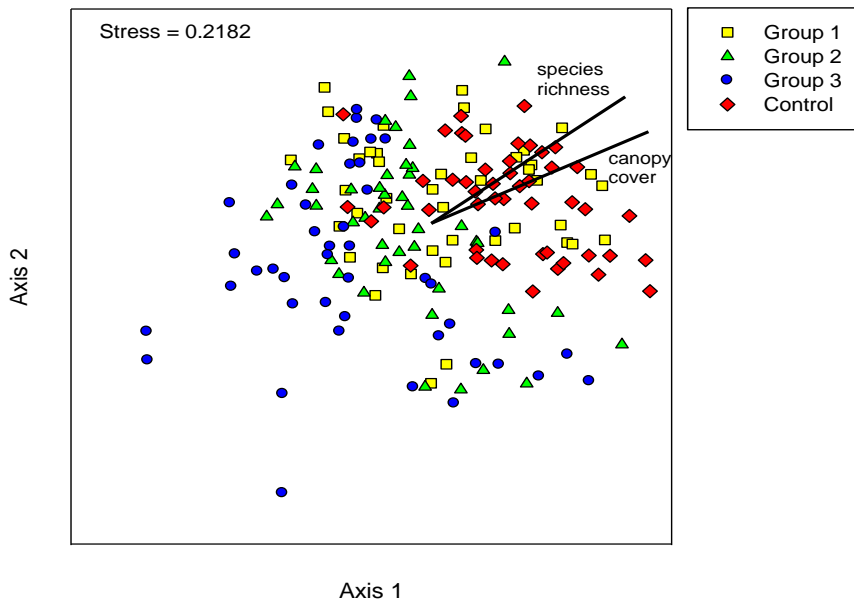
Figure 3.4. a) Centroids (mean sample scores +/- standard deviation); c = control, 1 = group 1, 2

= group 2, 3 = group 3. b) Two-dimensional NMDS ordination of change in percent canopy

cover groups based on ground layer perimeter cover. Significant vectors are canopy cover (r =

0.6862, $p < 0.0001$) and species richness (r = 0.8552 , $p < 0.0001$).

Table 3.1. Results of ANOSIM statistics for pair-wise comparisons involving change in percent canopy cover (control = uncut, group 1 = light canopy removal, group 2 = moderate canopy removal, group 3 = heavy canopy removal).

Group Comparison	R statistic	p value
Control-Group 1	0.0807	< 0.0001
Control-Group 2	0.2806	< 0.0001
Control-Group 3	0.4219	< 0.0001
Group 1-Group 2	0.0558	0.002
Group 1-Group 3	0.1782	< 0.0001
Group 2-Group 3	0.0496	0.005

3.3.2 *Species richness and abundance*

3.3.2.1 *Species diversity responses to canopy change*

The 2005 sampling recorded 124 species (Appendix I) of which 23% were bryophytes, 39% lichens, and 38% vascular plants. Overall, the 15 most abundant species were the bryophytes *Pleurozium schreberi, Dicranum polysetum, Ptilium crista-castrensis, Hylocomium splendens*, and *Ptilidium pulcherrimum*; the lichens *Cladina mitis, Cetraria ericetorum, Cladonia gracilis, C. ecmocyna, Peltigera aphthosa*, and *P. malacea*; and the vascular plants *Empetrum nigrum, Linnaea borealis, Vaccinium vitis-idaea, V. membranaceum*, and *Cornus canadensis*. When canopy group 3 is compared with the control, these most abundant species show an overall decrease of 11% in abundance, however bryophytes decrease 40%, vascular plants decrease 5%, while lichens increase 4% (calculated from data in Table 3.2). Likewise, overall abundance of all species show quite similar trends; with bryophytes steadily decreasing, vascular plants remaining nearly constant, and lichens increasing with increases in canopy change (Table 3.2).

Table 3.2. Mean abundance of bryophytes, lichens, and vascular plants across the control and three canopy change groups. Values are sums of abundance ranks (1-4) for the five subplots analyzed for 94 plots (see methods). Parentheses contain standard error.

	Control	Group 1	Group 2	Group 3
All species	135.2	154.7	130.1	120.1
	(0.20)	(0.20)	(0.17)	(0.18)
Bryophytes	38.5	33. 4	25.8	23.0
	(0.52)	(0.47)	(0.30)	(0.36)
Lichens	53.3	70.7	60.9	55.7
	(0.26)	(0.30)	(0.29)	(0.29)
Vascular Plants	43.5	50.6	43.4	41.4
	(0.35)	(0.34)	(0.29)	(0.29)

Mean α-diversity (number of species at the group level) for bryophytes remained constant with a drop in group 3, lichens (highest alpha) had a slight increase in groups 1 and 2, while vascular plants fluctuated only slightly with increased canopy cover change (Table 3.3). In all cases, canopy group 1 had the greatest species richness, suggesting that minor changes in canopy cover may play a role in improving diversity. Beta diversity in the form of Whittaker's beta (β_w) (species turnover between groups) was similar for morphotype groups, especially for lichens and bryophytes with a high amount of constancy between plots (Fig. 3.5). Vascular plants showed higher turnover especially in the control plots that overall had lower richness but were individually more different (Table 3.3).

Species losses within the thinned stands were few, only four bryophytes, two lichens, and four vascular plants were present in the control and not in one or more canopy groups, however four bryophytes, 11 lichens, and seven vascular plants appeared in thinned plots but were not present in the controls (data in Appendix II).

Diversity and evenness across the canopy cover groups is not markedly different for any vegetational type (Table 3.4). Of the morphotypes, lichens not only have a greater number of species present, and species are distributed more equitably among plots. Bryophytes and vascular plants have lesser numbers of species, with vascular plants having the least in the control and group 1.

Table 3.3. Mean alpha (number above) with standard error in parenthesis, below is beta diversity represented as species differences between groups (Control is C vs. G1, Group 1 is G1 vs. G2, Group 2 is G2 vs. G3, Group 3 is G3 vs. C) with β_w in parenthesis, brackets contain rare species (species recorded only once) for bryophytes, lichens, and vascular plants in all canopy cover groups. .

	Control	Group 1	Group 2	Group 3	Total No. of Species (gamma)
All	31.0 (1.5) 33 (3.62) [2]	35.7 (1.3) 39 (3.33) [11]	32.8 (1.4) 19 (3.02) [1]	29.0 (0.97) 23 (3.37) [2]	124
Bryophytes	8.1 (0.91) 7 (3.2) [1]	8.3 (0.80) 7 (3.36) [1]	8.0 (1.1) 5 (3.12) [0]	6.7 (0.65) 9 (3.9) [0]	29
Lichens	15.5 (0.54) 8 (2.83) [0]	18.8 (0.56) 9 (2.55) [1]	16.6 (0.57) 5 (2.6) [0]	15.3 (0.50) 5 (2.62) [0]	48
Vascular Plants	7.2 (0.44) 18 (5.62) [1]	8.6 (0.48) 23 (5.09) [9]	8.2 (0.42) 8 (3.76) [1]	7.8 (0.50) 11 (4.07) [2]	47
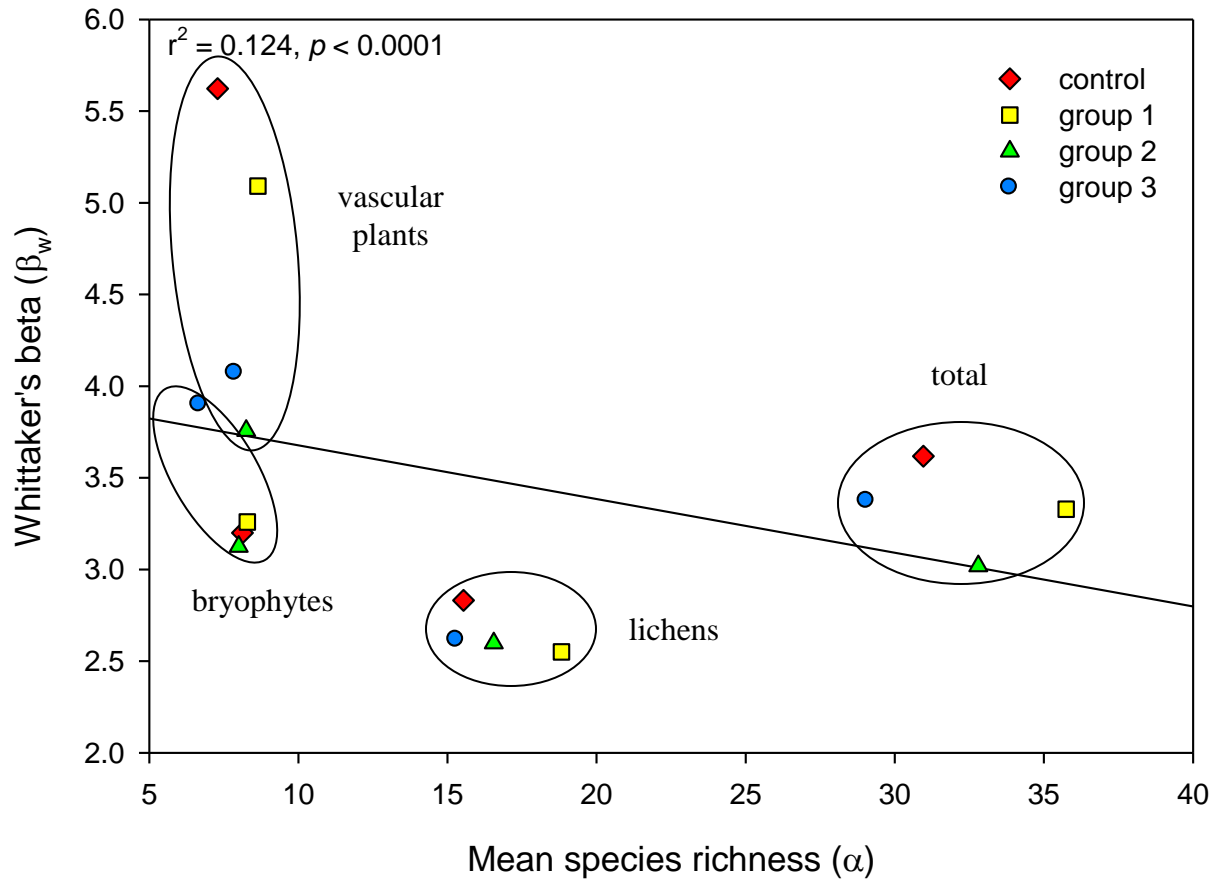
Figure 3.5. Relationship between mean species richness at the group level and calculated Whittaker's beta diversity (β_w) scores. Circles encompass plant groups. Standard error of estimate is 0.834.

Table 3.4. Diversity indices for richness (Shannon-Weiner H , top) and evenness (Shannon-Weiner Evenness, bottom).

	Control	Group 1	Group 2	Group 3
All	3.60	3.79	3.74	3.60
	0.81	0.81	0.83	0.81
Bryophytes	2.21	2.21	2.44	2.08
	0.72	0.71	0.77	0.68
Lichens	2.97	3.11	3.00	2.92
	0.82	0.82	0.80	0.80
Vascular Plants	2.21	2.54	2.43	2.37
	0.69	0.69	0.75	0.71

3.3.2.2 *Species rarity*

Out of the 124 species recorded, two mosses, one lichen, and 13 vascular plants were found only on one occasion in the study area (see Appendix II). Thirteen percent of the total species are locally rare (7% of bryophytes, 2% of lichens, and 28% of vascular plants). Canopy group 1 (lowest canopy change) contained the most locally rare species with 11 that were not found anywhere else (19% of the vascular plants, 2% of the lichen, and 3% of the bryophyte flora). It is not unreasonable to assume that these nine vascular plant species (excepting *Geum aleppicum* and *Pedicularis groenlandica* that prefer more moist areas), which are common in open locations (i.e. road sides), would be found growing as early successional species within the lowest thinning regime. The uncut control, group 2 (moderate canopy cover), and group 3 (least canopy cover and highest canopy change) all contained the least amount of locally rare species. The control contained a moss and vascular plant, group 2 contained only one vascular plant, and group 3 had two locally rare vascular plants. Seven years post-harvest, increased locally rare vascular plants are present in the lowest thinned plots as rarity greatly decreases in the moderate to heavily thinned plots.

3.3 Discussion and Conclusion

What effect does canopy opening have on a) species diversity and b) vegetation seven years after thinning treatment?

For this study area, overall species richness remained more or less constant over the canopy cover change groups (increasing only slightly in groups 1 and 2). Increases in bryophyte richness levels have been associated with moisture (Gradstein *et al.* 1990, Frisvoll and Prestø 1997) and elevation (Lee and La Roi 1979a, Stark and Castetter 1987). Bryophyte richness in the controls was substantially less (mean of 8.1), for this lower elevational site, than what Lee

and La Roi (1979a) reported (mean of 26) for *Pinus contorta* forests in Jasper National Park, Alberta. This difference is most likely due to scale, as this study is based on small plots and Lee and La Roi (1979a) used much larger transects. The group 1 increase may well be explained by Sollows *et al.* (2001), who found that colonial growth, in some bryophytes, may protect interior shoots and thus allow increased survival in unfavorable sites, as well as the work of Hosokawa *et al.* (1964) who observed that both live and dead moss cushions held similar amounts of extracellular water, both would be necessary for poikilohydric life forms. Increases may also be explained by appearance of mosses that better tolerate drier conditions (i.e. *Dicranum undulatum* and *Polytrichum piliferum*). According to Tinya *et al.* (2009), Mills and MacDonald (2004), and Humphrey *et al.* (2002), they all found no correlation between light and bryophyte species richness.   Increases in light due to canopy opening, then, may have no direct bearing on bryophyte diversity. The findings of this study uphold their reports but contradict work at the fine spatial scale by Moora *et al.* (2007), who found that species richness did increase with light, which was in partial agreement with Mills and MacDonald (2004) who reported that light is more important at the fine scale. Looking only at scale, Mills (2001) working in a conifer-dominated boreal forest at the microsite scale, found bryophytes have increased species richness. Most studies from forests lacking widespread disturbance reveal increases in richness associated with increasing forest age.

Patterns of species richness and species turnover follow morphotypes rather than canopy group. Each of the three main morphotypes have distinctive patterns of diversity, for example bryophytes have both low plot richness and low species turnover yielding overall low diversity. Lichens have high plot diversity but low turnover, thus overall richness is high and individual plots are relatively similar. Vascular plants have low plot diversity, but high turnover between

plots, thus achieving a relatively high species richness (Fig. 3.5). These differences lead to lichens (through high richness) and vascular plants (through high turnover values) maintaining species richness over this disturbance regime, while bryophytes (having neither high plot richness nor high turnover of species between plots) lose some species as disturbance increases.

Exposure to increased solar radiation and associated effects due to canopy removal can affect species differently. Changes in environmental conditions can cause reductions in species numbers and induce rarity. Rarity can be an issue of scale. Vitt (1991), Vitt and Belland (1995), and Newmaster (2000) agree that the greater part of species found on a landscape are infrequent. Following the previous authors, rarity can be described as species (common or uncommon) that on a small spatial scale in the landscape are scarce, and thus considered locally rare. All of the rare species in this study area can be found over the greater montane/boreal region, so in the study area they are locally rare. Several of the species may be rare because the location is near the edge of their ranges (e.g. *Solorina crocea*, *Dicranum acutifolium*). A few of the locally rare species are considered weedy (e.g. *Ceratodon purpureus*, *Achillea millefolium*) and are infrequent in these mature stands of forest. Before tree removal took place, local rarity in the native forest may have been due to a number of reasons like small local population sizes (Rabinowitz 1981) or lack of specialized substrates (Wiklund 2004). Having data available on local rarity before and after mechanical thinning sheds light on the impacts of canopy removal on the ground layer. Comparing pre-harvest (1997) (see Pharo and Vitt 2000) to post-harvest (2005) rarity levels, reveals 16 species, that were (1997) then listed as locally rare, as absent in 2005. After seven years of open canopy effects on the forest floor, five bryophytes, three lichens, and nine vascular plants that were considered locally rare have disappeared from the study area. In 1997, locally rare species constituted 14% of the total species richness, in 2005

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that number is similar at 13%. The story is not always one of loss, in 1997 one moss (*Buxbaumia aphylla*), two lichens (*Cladonia pleurota*, *Peltigera leucophlebia*) and one vascular plant (*Pyrola asarifolia*) were listed as locally rare, as of 2005 they occurred more frequently and were identified multiple times. One would then conclude that after seven years, species richness (and locally rare species) bryophytes, lichens, and vascular plants respond somewhat differently to removal of the canopy, with bryophyte responses being the strongest. Overall species rarity remains relatively constant with a few extinctions countered by several additions to the flora.

As opposed to the lack of α-diversity changes, both vegetational and dominant species changes are dramatic. Abundance of shrubs, herbaceous perennials, and bryophytes, including all three dominant feather mosses, decrease along the canopy cover groups and all are different from the control group (Fig. 3.2). Lichens remain constant. More canopy openness positively correlates with the amount of grass, dead moss, and duff/bare ground all increasing with percent canopy cover change. The most dramatic effects in bryophyte cover decline are seen between the control and group 1, this indicates that moss abundances (especially the dominant feather mosses) are affected even at the lowest canopy removal levels. This trend is firmly correlated for the amount of dead moss in relation to canopy loss, where substantial increases occur in group 1. However, shrubs and the herb *Cornus* continue to decline under the more severe canopy removal. Overall, vascular plants are most infrequent, with group 1 containing the majority. In conclusion, changes to the moss and vascular plant vegetation are evidenced at even the lowest canopy cover regimes, lichens remain unaffected, and as result bare ground and dead moss both increase. Seven years after manipulation of the forest canopy reveals that vegetation, as a whole, is affected but species diversity remains relatively constant.

3.3.1 *Successional processes*

The temporal conciseness of this study on effects of canopy opening on the ground layer fails to provide definitive results on larger successional concepts such as Egler's (1954) initial floristic composition or relay floristics. Within the canopy change groups, only early successional species and a few residuals of the previously dominant late successional species (feathermosses) continue to persist. Past successional studies suggest that forests in early-successional states should have a lower beta diversity than stable, mature forests (Christensen and Peet1984). They postulated dispersal, chance establishment, and reduction of competition in these early-successional communities are more important in shaping composition and therefore β-diversity is higher than that of mature communities. For this study, the procession of succession has only just been initiated in this forest so it could be assumed that thinned areas would have lower β-diversity, but currently this is not the case as these areas had higher β than the other groups. Due to climate, elevation, and landscape disturbance patterns (fire and timber removal) being separated by 80 to 100+ years, this study area will need to be examined for a longer period to establish if the species at the population or community level can be predicted by vital attributes such as shade tolerance and longevity to see if they would equate to a particular model. The evaluation of systems over extended periods of time (Loucks 1970, Bergeron and Dubuc 1989) provides greater insight into successional processes when contrasted to short term studies.

CHAPTER 4

THE IMPORTANCE OF ABIOTIC FACTORS, SCALE, AND DIASPORE AVAILABLITY RELATIVE TO THE OCCURRENCE OF GROUND LAYER MOSSES AND LICHENS

4.1 Introduction

Limiting factors ultimately control spatial location of bryophytes and lichens in the ground layer. Four of the most important microclimate environmental abiotic factors that are limiting, affecting lichens and bryophytes are; moisture, light, temperature, and litter (Damman 1976, Foster and Morrison 1976, Proctor 1982, Frego and Carleton 1995). These factors affect species physiology as well as physical processes that can have an impact on colonization. These factors, especially on the forest floor, are influenced greatly by tree removal and canopy loss (Chen *et al.* 1993). In addition to these limiting factors there is a biotic component, diaspore availability and movement can affect the spatial pattern and occurrence of mosses and lichens in the ground layer (Furness and Hall 1981, During *et al.* 1987, Smith 1987, Frego 1996, During 2001, Ross-Davis and Frego 2004). Without ample diaspores and their movement, environmental limiting factors are, in effect, meaningless.

A fundamental component for growth and development of all plant life, especially for bryophytes, is water. The dominating feather mosses (*Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis*) and lichens (*Cladina mitis, Cetraria ericetorum, Cladonia gracilis*) in this montane system are poikilohydric, not having a mechanism to prevent drying out, (Hosokawa *et al.* 1964) and metabolize only when wet (Proctor 1972, Gaio-Oliveira *et al.* 2006), so water is a principal limiting factor. Busby *et al.* (1978) and Vitt (1990) address the

negative impacts of excess dryness on the growth rates of bryophytes and found that growth is restricted when water is unavailable. Other authors have also conducted studies on the relationship between water and mosses (Busby and Whitfield 1978, Dilks and Proctor 1979, Ipatov and Trofimets 1988, Proctor 1990, Li and Vitt 1995, Price *et al.* 1997, Hylander *et al.* 2002). Due to the ease at which mosses dry out they are usually found in shady areas (During 1992) and microhabitats that are sheltered from high wind speeds. Most lichens need less water than do mosses and many montane species prefer mesic to xeric habitats (Kershaw and Rouse 1971a, Johnson 1981, Robinson *et al.* 1989). Fraser (1956) noted the value of lichens undergoing periods of complete dryness. These fruticose lichens execute metabolic processes better in drier, compared with moister, conditions as long as the microclimate does not get too dry for too long or change (increase in wind or light) too quickly (Esseen 2006).

Moisture in the environment can be directly affected by light availability. In montane systems, feather mosses such as *Pleurozium schreberi* and *Hylocomium splendens* are abundant based on many factors, one key factor is light. *Pleurozium* is a genus characteristically found in closed (late successional) boreal forests (La Roi and Stringer 1976, Foster 1985, Bond-Lamberty and Gower 2007), but *Pleurozium* rarely occurs in northern tundra situations and *Hylocomium* can be found in more northern regions only as *H. splendens* var. *alaskanum* (Steere *et al.* 1977). Tamm (1953) reported that the distribution of *H. splendens* is based on low light levels created by high levels of canopy cover. Busby *et al.* (1978) observed high mortality of *H. splendens* due to elevated light in clear-cuts. Change in existing light can produce shifts in mosses and lichens in the ground layer. Morneau and Payette (1989) and Økland and Eilertsen (1993) agree that high light intensity, which can lead to lowered moisture levels, can lead to a transferal in dominance from moss to higher lichen abundance. Canopy reduction due to forest thinning has

been documented as stimulating lichen community growth (Söderström 1988, Sulyma and Coxson 2001). Ground layer lichens prefer higher light levels, but very high levels of solar radiation are able to increase lichen death (Smith 1962) probably owing to long periods of drought.

Bryophyte growth is usually associated with precipitation levels, but some studies delineate air temperature as being the factor driving growth (Bates 1989, Zechmeister 1995). Air temperatures can have direct and indirect effects on other environmental factors. Increases in temperature can cause drying of the ground layer, thus reducing moisture available for mosses. Rises in temperature can also spur winds that may further dry out the forest floor. Lower surface temperatures may also have the opposite effect by reducing moisture losses through respiration (Dynesius *et al.* 2008), often resulting in significantly lower surface temperatures.

Litterfall, from canopy rain and from the ground layer itself, has an impact on species as litter retains moisture, provides cover, and its slow decomposition releases nutrients. Litter can come from various sources depending on species and stand structure of the local environment. Litterfall biomass for different types of forests has been studied extensively by Bray and Gorham (1964). Emphasis is also being placed on litterfall in relation to mineral elements in nutrient cycling (Switzer and Nelson 1972, Foster and Morrison 1976). In this system, litterfall input provides organic material for the formation of mor humus. Litter can also increase shade on the ground layer and thus limit bryophyte growth (Rincon 1988, Startsev *et al.* 2008). Økland *et al.* (1999), working in a Norwegian boreal spruce forest, found needle litter amplified density-independent mortality for mosses. Frego (1996) reported that coniferous needle litter can provide substrate for bryophyte colonization. Self-litter in moss-dominated mats is greater than in their lichen-dominated counterparts (Sulyma and Coxson 2001). Sedia and Ehrenfeld (2003)

also found, when studying moss and lichen mats in New Jersey, that the underside of moss mats contained high amounts of self-litter, whereas lichen mats were low in litter and had little to no organic material. Working in a coniferous forest, Anderson *et al.* (1969) measured precipitation in areas with more dense canopies and reported that the increased litter intercepted more throughfall and thus held more moisture at the ground layer. Also, the microbial breakdown of litter is an important avenue for nutrient transfer (N, P, K, Ca, and Mg) in boreal forests (Foster and Morrison 1976, MacLean and Wein 1978, Bonan and Shugart 1989, Brown and Bates 1990, Frego and Carleton 1995). In general, litter can contain elements of overstory trees, ground layer components, invertebrates, and debris. Collecting litter at the ground layer can reveal primary sources, shed light on movement, as well as, quantity of bryophyte and lichen fragment diaspores. These factors are the driving force behind litter collection in this study.

Diaspore availability and movement are beneficial for establishment and colonization of the forest floor. The importance of diaspore banks has been considered equal to the value of vascular plant seed banks (Furness and Hall 1981, During *et al.* 1987, Smith 1987). Reproduction in bryophytes can be sexual (spores) or asexual (fragmentation). Dispersal of spores via wind has captivated plant biologists for decades (see van Zanten and Pócs 1981). According to Miles and Longton (1992) and Fenton and Frego (2005) bryophyte spores are dispersal limited as they mostly fall <30 cm from the source colony. During and van Tooren (1987) and Ross-Davis and Frego (2004) reported that small light spores (<20 μm) can be carried farther. For some montane bryophytes, distance may be limited for larger asexual fragments (e.g. *Mnium arizonicum*, Cleavitt 2004). Frego (1996), when looking at bryophyte colonization, found that fragmented *Pleurozium schreberi* shoots grew, but more slowly than those remaining attached to a colony. Lichens can also reproduce via fragmentation (e. g., species of Cladonia,

Ahti 1982), with the fragments carried by the wind (Heinken 1999) or animals. Harris (1996) noted *Cladina* fragments were moved by logging activities and were found on stumps and dead feather moss beds. He also reported that ground layer lichens fully recovered from logging activities within 11 years. If diaspores are available, microenvironmental conditions are within acceptable ranges, and there is ample disturbance, bryophytes and lichens should be able to establish and colonize soon after disruption (Longton and Schuster 1983, Rincon 1988, Harris 1996, During 1997, Coxson *et al.* 1998). This calls the question, are spores and fragments that are needed for establishment, abundant enough post-disturbance.

The microenvironmental variables (water, light, temperature), along with litter and diaspore traps, were chosen because they are linked to community structure and distribution on the forest floor. The objectives of this study were to provide evidence on environmental and biotic limiting factors that affect ground layer bryophytes and lichens. In order to meet this objective the following avenues were pursued. 1) Determine the availability of diaspores for colonization in the form of asexual propagules or spores at the ground layer, and 2) Measure and investigate at what scale environmental factors (moisture, temperature, light) are likely to affect the local distribution of lichens and bryophytes. These objectives are organized into the following questions: 1) What is the availability of diaspores for colonization in the form of asexual propagules or spores at the ground layer? 2) At what scale do environmental factors (light, temperature, moisture) affect the local distribution of ground layer lichens and bryophytes?

4.2 Methods

4.2.1 *Study area*

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As part of a forest thinning/ lichen abundance project established in the winter of 1997/ 1998 (see Pharo and Vitt 2000), the study area was selected by industry ecologists of Alberta Newsprint Company (ANC), Weyerhaeuser Canada (WEY), and Weldwood Canada (WEL) to include undisturbed forest that was within suitable distance to current logging and mill operations all within a 375 km^2 area. Nine stands within this study area were selected within the experimental thinning region (Pharo and Vitt 2000). Further experimental design and setup were determined by Vitt and Pharo (see Chapter 2 for more information on study area).

Soils throughout the area are classified as luvisolics and brunisolic (Corns and Annas 1986). They are well drained, acidic, and have poor nutrient content (Beckingham *et al.* 1996). In 2000, Pharo and Vitt found the average pH was 4.88 with little variation. Soil texture ranged from loamy sand to sandy loam. The moisture regime of the area is generally considered mesic. The humus form of the area is mor, having a distinct boundary between the organic and mineral layer (Beckingham *et al.* 1996).

Temperatures for the summer growing season (June-August) of 2005 were compared to 30 year means from 1971-2000 (National Climate Data and Information Archive) for the same months to ensure that the study season was within the limits of normal temperature and precipitation data (Table 4.1). Jasper and Grande Prairie, Alberta, were the two weather stations used for comparison, as my study area lies between these two locations. Elevational differences are as follows: Jasper 1,003 m, Grande Prairie 669 m, study area 1,300 m.

Temperatures for 2005 were slighly lower for the three month growing season (13.0 ^{o}C and 14.0 ^{o}C for 2005 versus 14.1 ^{o}C and 15.0 ^{o}C for the 30 year average for Jasper and Grande Prairie, respectively. The 2005 growing season was drier compared to the 30 year long-term average, with precipitation for 2005 averaging between 15 and 32% lower (Jasper and Grande Prairie, respectively) than the 30 year long-term average.

Table 4.1. Thirty year seasonal, summer (June – August) and 2005, temperature averages with total precipitation for Jasper and Grande Prairie, Alberta. Temperatures are ^{o}C and precipitation is mm.

	Jasper, AB				Grande Prairie, AB			
	30 year average		2005 average		30 year average		2005 average	
	Mean Temperature	Total Precipitation	Mean Temperature	Total Precipitation	Mean Temperature	Total Precipitation	Mean Temperature	Total Precipitation
June	12.9	91.5	12.5	66.6	14.1	76.5	13.7	71.4
July	15	93.7	13.8	56.4	15.9	70.4	14.9	69
August	14.3	89.5	12.8	65	14.9	61.8	13.3	37

4.2.2 *Experimental design*

The Weldwood Canada Ltd. (WEL) study area (see Chapter 2) was chosen for

measurement of microclimate environmental parameters for relative humidity, light, evaporation

rates, temperature, litter fragment abundance, and diaspore movement on distribution of

bryophytes and lichens. Ten plots, five control plots (WEL 9, 21, 31, 32, 53) with ~60% canopy

cover and five experimental plots (WEL 10, 25, 29, 43, 60) with ~40% canopy cover, were

randomly selected for data collection. For each of the plots three separate plant microsite types

were delineated; a feather moss (*Hylocomium splendens* and/or *Pleurozium schreberi*) dominated

area, a fruticose lichen (*Cladina mitis*) -dominated area, and an approximate equal mix of feather

moss and fruticose lichen (moss, lichen, 50/50). Dominance of moss and lichen plots were based

on percent cover, these were chosen if there was 60% or greater ground cover of the morphotype.

A 10 x 10 cm^2 area of moss, lichen, and 50/50 were chosen and marked with flags. These

located no closer than five meters and no farther than ten meters from the perimeter of the 6.5 x

6.5 m permanent plot boundary (to lessen impact on the permanent plot). All measurements

were carried out in these 10 plots except temperature that was measured by two temperature

sensors (HOBO$_®$), one at control plot WEL 21 and one at experimental plot WEL 29.

Temperature data were collected for the 2005 growing season, June through August. These data

were collected from the same moss, lichen, and mix canopy areas as the other environmental

parameters.

Relative humidity. Measuring water vapor content at the microclimate level, a relative

humidity meter (Extech Hygor-Thermometer Model RH101, ± 3.5% accuracy) was used to take

measurements at each of the ten plots. The tip of the meter was placed vertically in the top five

cm of the moss or lichen mat. Readings were taken only in the all moss and all lichen-dominated

mats of the microclimate plots mentioned above. Measurements were taken in the morning

(between 9 and 11 am) of June 3, 9, and 15 of 2005.

Photosynthetically active light. Following Friend (1961) and Sullivan and Mix (1983)

light levels at the micro-environmental scale were measured using photosensitive Diazo

blueprint paper (Western Diazo, Blue 5/Reproblue) (Cleavitt 2002). This paper was used to

create inexpensive photometers used for field measurements. All activities involving the

creation of the photometers using photosensitive paper were performed in a dimly lit room. A

stack of 30 papers, one by one inch, of diazo blueprint paper were sandwiched between same

sized black paper squares. A standard office hole punch was used to create a hole in the top

black paper square to allow for light exposure in the field. The edges of the stack were then

completely covered with black electrical tape, to protect from side exposure. The light box unit

was secured with tape to the bottom of a 100 x 15 ml round, clear Petri dish. Electrical tape

around the sides of the dish created a water barrier. A black paper cover was used to shield the

light box from accidental exposure until placement in the field. Once collected, the Petri dishes

were placed in a black plastic bag until the exposed sheets were counted. The number of sheets

(three quarter, one half, to as low as one quarter partial sheets) exposed were recorded and used

to indicate the cumulative photosynthetically active light (Friend 1961, Cleavitt 2002) at the

ground layer. These photometers were placed at the same ten control and thinned microclimate

plots in a moss, lichen, and half lichen and half moss dominated microsite canopy on the forest

floor. The light boxes were placed and retrieved four times (June 5, 15, 30, and July 15) in 2004,

and were allowed 15 days exposure.

Moisture rates. To examine evaporation rates with local moisture availability in

morphotype ground layer canopies using dry and wet sponges an inexpensive nylon sponge was

cut into cubes weighing 0.77 g each. For each site, two cubes, one dry (control) and one wetted, with approximately 2.45 ml of water added (to measure water loss), were weighed using an electronic balance having a 150 g capacity. A wind shield was used to get accurate readings in the field, weights were recorded, and the cubes immediately set into place in the morphotype canopies of moss, lichen, and mix areas. Initial weight was recorded for the two sponge cubes, they were again weighed twice more approximately two and a half and five hours apart (Cleavitt 2002). These data on local moisture rates were measured on an average sunny day under normal summer conditions four times (same dates as light box pick up and replacement) in 2004. Between water loss measurements, sponges were set in the sun to completely dry and stored in an air tight plastic bag.

     Litter fragment abundance. Following Rincon (1988), Frego and Carleton (1995), Waters and Quesnel (2001), and Coxson and Marsh (2001) who used litterfall traps to sample actual litter and moss and epiphytic lichen dispersal. For this study, litter traps were seated slightly into the ground layer mat on the forest floor to collect falling litter, as well as, ground moving diaspores (fragments of moss and lichen). The collection devices were 215 mm round and 38 mm deep aluminum pans perforated for drainage. These were placed at each of the ten plots in the moss, lichen, and mixed areas and affixed to the ground with ten centimeter long wooden skewers inserted at an angle into the soil. Litter traps were set in place at the moss, lichen and mixed areas during the first visit to the plots and collected on the last visit, for summer 2004 (3 months), 2005 (2 months), and fall 2005 (2 months). Traps were individually bagged and marked. Collected debris was dried, identified, counted, and recorded at Southern Illinois University Carbondale, Illinois (SIUC).

Diaspore traps. Following Miles and Longton (1992) to trap airborne diaspores (spores), two petroleum jelly covered square 13 x 13cm gridded Petri dishes were placed – one at ground level and one at 0.5 m above ground level. The ground layer traps were placed to collect diaspores moving low across the ground layer canopy, the half meter traps were for collection of aerial diaspores moving on air currents just above the ground layer. These "sticky traps" were placed in the moss, lichen and mix areas. Ground layer traps were fixed to the forest floor with "L" shaped wire pins on each corner. Construction of the half meter traps involved drilling a hole in the center of the Petri dishes and fastening the dish (sides facing down) with a stainless steel screw into a 0.75 m long wooden stake. The stake was set into the ground for 0.25 m. These traps were left in place for 14 days at a time, and collected and replaced three times during the summer of 2004. Once collected, they were marked and boxed until identification at SIUC in the fall of 2004. A dissecting scope, set to 40x magnification, was used to make counts for pine pollen, moss spores, fungal spores, debris, and other pollen. Pine pollen is easily distinguished from all other pollen due the prominent appearance of a pair of wings or bladders attached to the pollen grain. Round, non-trilete moss spores were assumed to be from the 89% of *Pleurozium schreberi*, 3.2% *Hylocomium splendens*, and 2.8% of *Ptilium crista-castrensis* that annually produce sporophytes with capsules, and form a dense carpet on the forest floor (percentages are from Chapter 3 perimeter data). Fungal spores, smaller than moss spores, were not identified beyond initial recognition. Trilete marks identified *Sphagnum* spores. Ten random squares of the grid were counted and recorded.

Air temperature. HOBO® temperature sensors with four 2.5 m leads were used to collect streaming temperature data at the microclimate level for one growing season (June -August 2005). Two plots, WEL 21 (control plot) and WEL 29 (thinned plot), were randomly chosen to

have a HOBO® affixed. At each of these plots, one probe was placed parallel to the ground in the top centimeter of a 90% feather moss mat, fruticose lichen mat, and in a ~50/50 mix area. Due to the denseness of the ground layer the probe on the end of the lead was not visible to the sun, when viewing from above or from the side.

Terrestrial foliose and fruticose lichens (due to rarity, no crustose species were included), mosses, and liverworts, were identified to species. Nomenclature for vascular plants follows Gleason and Cronquist (1991), Anderson *et al.* (1990) for mosses, Stotler and Crandall-Stotler (1977) for liverworts, and Esslinger and Egan (1995) for lichens.

4.2.3 *Data analysis*

For relative humidity, photosynthetically active light, water loss, and litter fragment abundance a three-way repeated measures analysis of variance (ANOVA) (SAS 2008) was used to test the equality of means accounting for the repeated factor in each variable that are affecting the distribution of bryophytes and lichens in the ground layer. This mixed model ANOVA was performed using canopy cover group (60% and 40%) by microsite vegetation type (bryophyte, lichen, and/or 50/50% mixed sampling areas) with time (three or four repetitions)as the repeated measure. For the high and low diaspore traps the test is the same as above (three-way repeated measures ANOVA) except position (low, high) replaced time as the repeated measure. For all of the above analyses the method used to compute denominator degrees of freedom (ddfm) was Kenwardroger (kr) (Kenward and Roger 1997) as this adjustment reduces the potential for Type I error with mixed model repeated measure analyses.

A repeated measures two-way ANOVA with fixed effects, for site, was used on minimum and maximum temperatures measured via HOBO® devices. These tests were performed with 60% and 40% canopy cover group by microsite vegetation type (moss, 50/50

mix, lichen) with time as the repeated measure. The Satterthwaite option was used to compute ddfm for all temperature data.

For all ANOVAs that produced statistically significant results, a Tukey Honestly Significant Difference (HSD) (except photosynthetically active light, minimum, and maximum temperatures where contrast was used to more closely examine differenced among means) (SAS 2008) was used post hoc to determine which treatments differed significantly ($p = 0.05$) for the canopy cover groups of 60% and 40%, vegetation type, position, and time. For each statistical analysis the best covariance matrix was chosen using AIC, with a first-order autoregressive structure (ar (1)) being the best fit over unstructured covariance (un) and compound symmetry (cs) in all cases. Data appeared normal and were not transformed.

4.3 Results

Outcomes of the statistical tests, in the form of ANOVA tables, for environmental parameters, measurements of litter, and diaspores are in Appendix III.

4.3.1 *Relative humidity*

Measurements of relative humidity show a higher order interaction between canopy cover groups (60%, 40%) and time (1,2,3) ($F_{2,28.3} = 52.39$; $p = 0.0176$) (Fig 4.1) Relative humidity levels for canopy groups are dependent upon the date on which they were collected, with times 1 and 3 having similar Rh values; however, at time 2 Rh is much lower at 40% cover group compared to the 60% cover group. Despite this interaction of time and cover group, moss and lichen microsite types are different ($F_{1,25.4} = 16.56$; $p = 0.0004$) (Fig. 4.2). Relative humidity in the lichen-dominated canopy was, 6.9% lower compared to the moss-dominated canopy; however, Rh differences are highly variable over time.
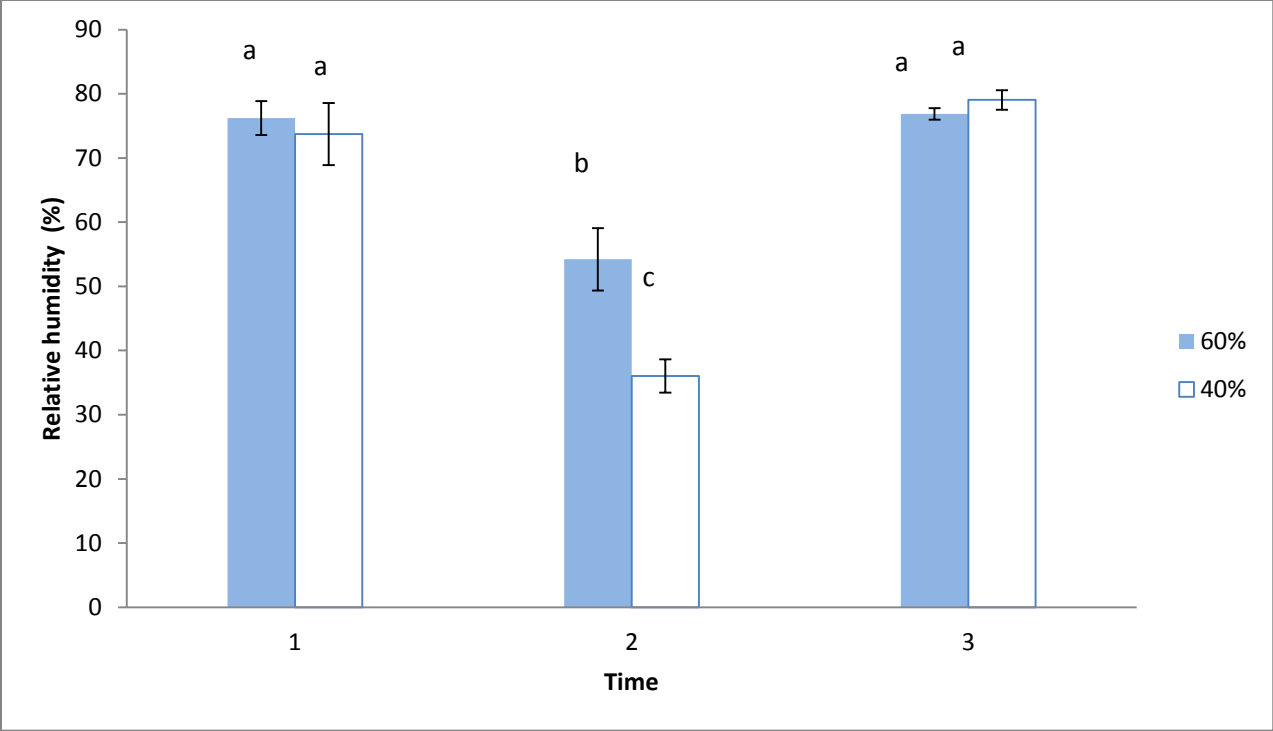
Figure 4.1. Relative humidity (%) levels for canopy cover group versus time (n=10). Mean humidity readings (± standard error). Different letters indicate significance $p = 0.05$ using Tukey HSD test.
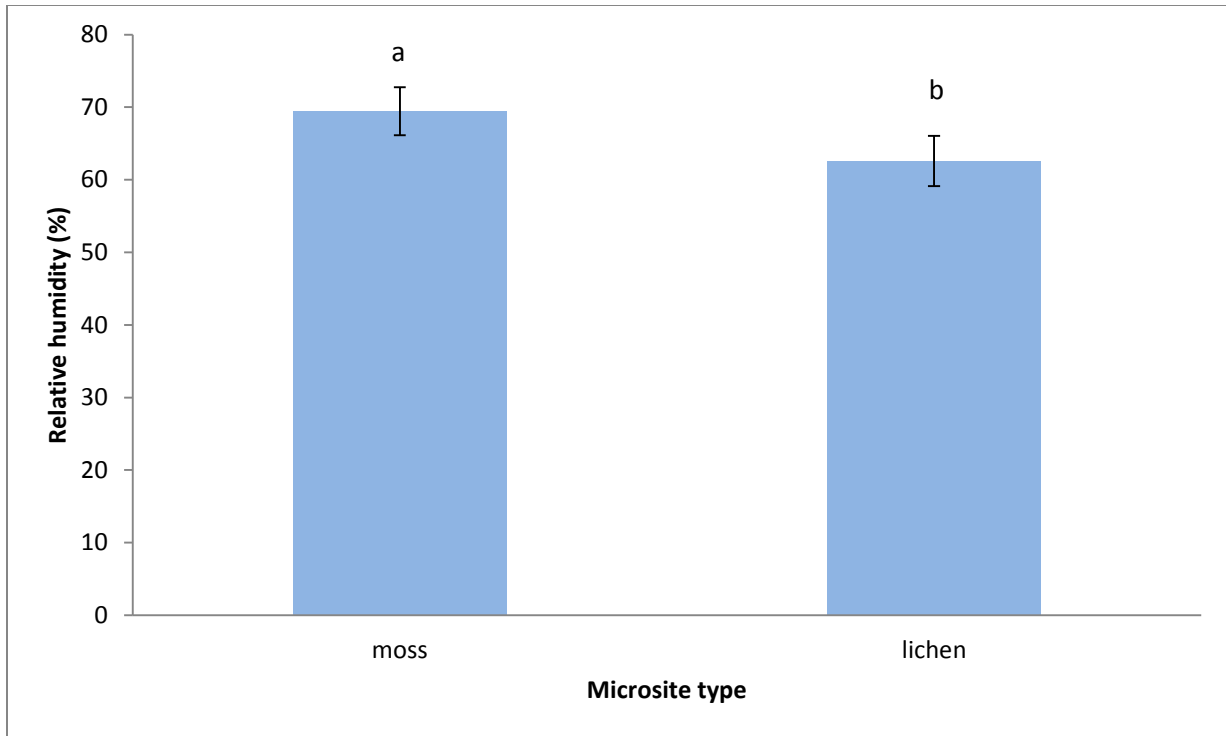
Figure 4.2. Microsite relative humidity (% water vapor) (2005) for two ground layer microsites (n=30). Different letters indicate means with significance at $p = 0.05$ using Tukey HSD test. Error bars are standard error.

4.3.2 *Photosynthetically active light*

Measurement of light levels reaching the forest floor revealed differences between meso-scale control and treatment canopy types ($F_{1,8.31} = 25.36$; $p = 0.0009$) (Fig. 4.3) and also between the ground layer microsites ($F_{2,20.3} = 4.79$; $p = 0.0197$) (Fig. 4.4). The effect of time also has variation ($F_{3,66.6} = 4.88$; $p = 0.004$)(not graphed), due to increased day length as the summer season progressed. Canopy group light levels for 40% treatment area are 11.7% higher than those of the 60% controls. At the microsite level, the moss sites are different from the lichen sites (Tukey HSD $p = 0.0150$), with the 50/50 mix in the middle. Lichen mat light levels were increased 7.5% and 50/50 mix areas were 5.6% higher than moss dominated areas. Thus more light is available for lichens, irrespective of canopy cover type.
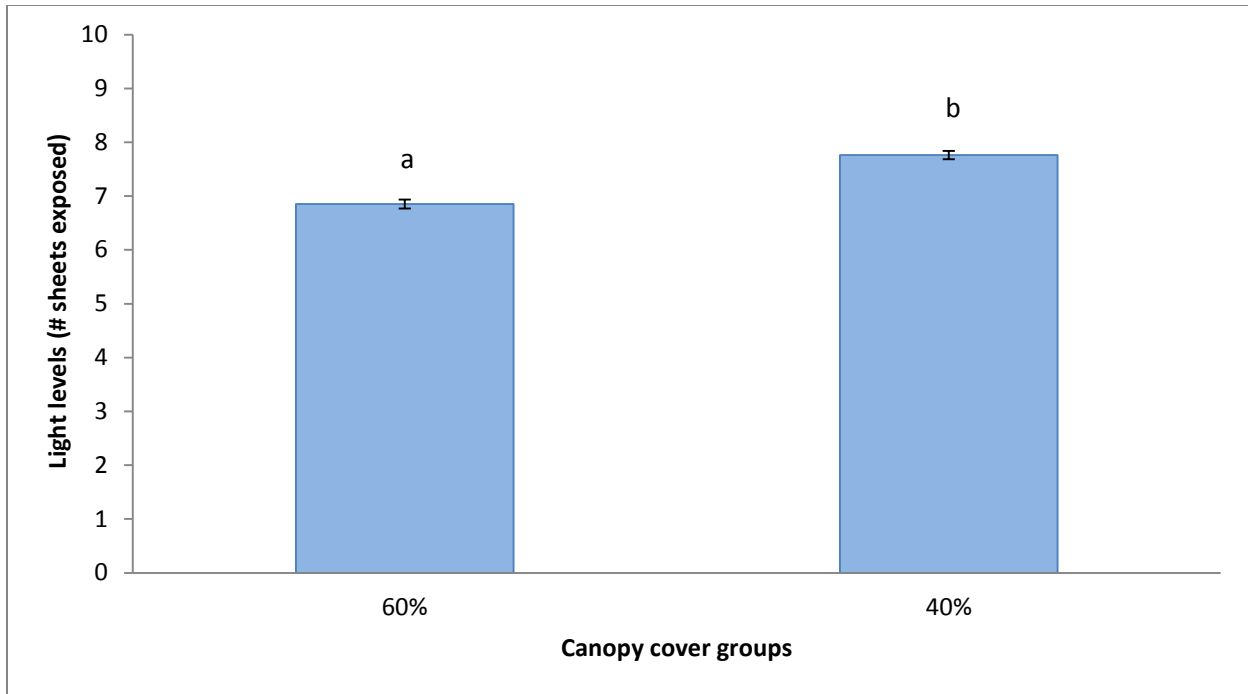
Figure 4.3. Photometer readings (2004) measuring mean photosynthetically active light (# of exposed sheets) for canopy cover groups (n = 60). Higher numbers of exposed sheets equate to increased cumulative light for that group. Different letters indicate means with significance at *p* = 0.05 using Tukey HSD test. Error bars are standard error.
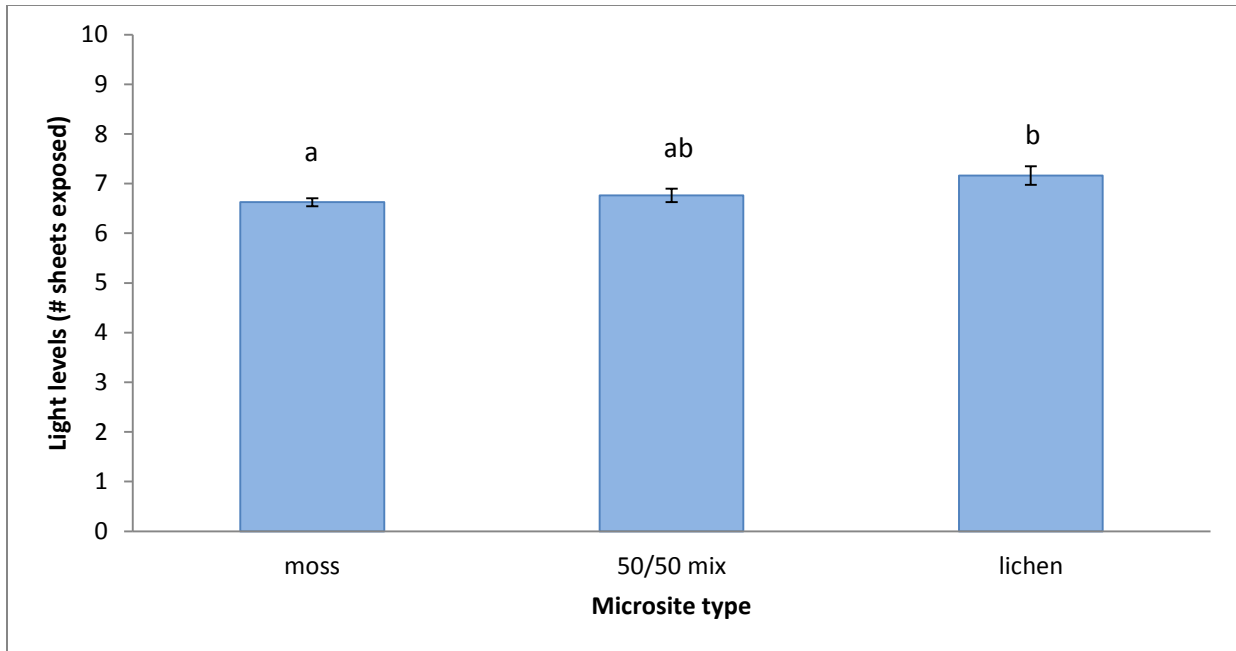
Figure 4.4. Photometer readings (2004) measuring mean photosynthetically active light (# of exposed sheets) from three microsites (n = 20). Higher numbers of exposed sheets equate to increased cumulative light for that microsite. Different letters indicate means with significance at $p = 0.05$ using Tukey HSD test. Error bars are standard error.

4.3.3 *Moisture*

Water loss from moistened sponges was different between the two canopy cover groups ($F_{1,8.15} = 5.81$; $p = 0.0419$) (Fig. 4.5). Loss of water from the 40% canopy group was greater than that of the 60% group by 16.9%. The effect of collection time was also a factor ($F_{3,64.9} = 13.6$; $p < 0.0001$) (not graphed), as conditions on individual days varies depending on weather patterns. Water loss when compared at the microsite level showed little variation and water loss values were almost equal (data not shown).
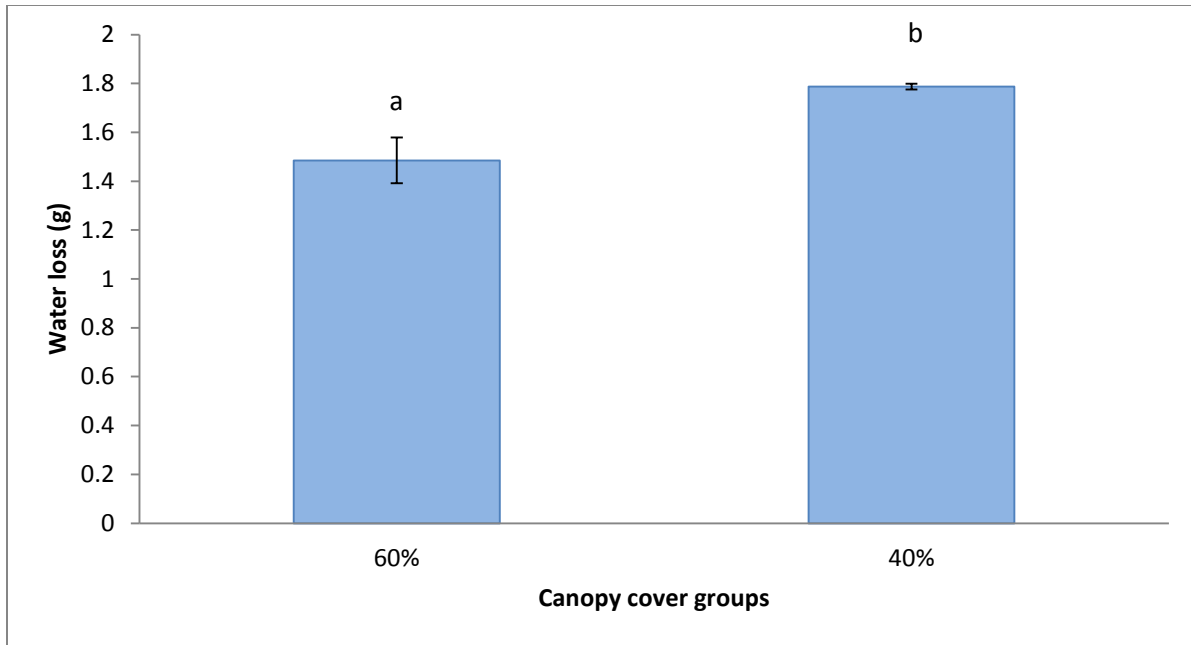
Figure 4.5. Evaporation of wetted sponges (g) (2004) for overall canopy cover groups (n = 60).

Different letters indicate means with significance at $p = 0.05$ using Tukey HSD test. Error bars

are standard error.

4.3.4 *Air temperature*

Daily minimum temperatures (June – August 2005) for the 60% canopy cover group range from 0.3 to 7.8 ^{o}C in the moss mat, 0.7 to 8.2 ^{o}C in the 50/50 mixed area, and -0.2 to 8.2 ^{o}C in the lichen mat (Fig. 4.6). The minimum temperature span for the 60% canopy site is 8.4 degrees. The 40% canopy cover group minimum temperatures range from -3.8 to 7.4 ^{o}C in the moss mat, -2.9 to 7.4 ^{o}C in the 50/50 mix, and -0.2 to 7.8 ^{o}C in the lichen mat (Fig. 4.7). The minimum temperature span for the 40% canopy site is 11.7 degrees.

Daily maximum temperatures for the 60% canopy cover group (June – August 2005) range from 7.0 to 46.9 ^{o}C in the moss mat, 7.4 to 26.7 ^{o}C in the 50/50 mixed area, and 7.4 to 34.8 ^{o}C in the lichen mat (Fig. 4.9). The maximum temperature span for the 60% canopy cover group is 39.9 degrees. Maximum temperatures for the 40% canopy cover group range from 8.6 to 42.5 ^{o}C in the moss mat, 8.2 to 41.0 ^{o}C in the 50/50 mix area, and 8.2 to 44.4 ^{o}C in the lichen mat (Fig. 4.10).

Minimum temperatures for all three microsite types do not differ within the 60% canopy cover group ($F_{2.134} = 10.34$; $p < 0.0001$) (Fig. 4.8), but the 50/50 and moss microsites become much different within the 40% cover group (Fig. 4.8). It appears that minimum temperatures for microsites with mosses are much more affected by open canopies than are the lichen microsites. When maximum temperatures are examined temperatures differ only between the canopy cover types ($F_{1,77.6} = 27.87$; $p < 0.0001$) (Fig. 4.11), with no differences at the microsite level ($F_{2,77.6} = 2.04$; $p = 0.1373$).
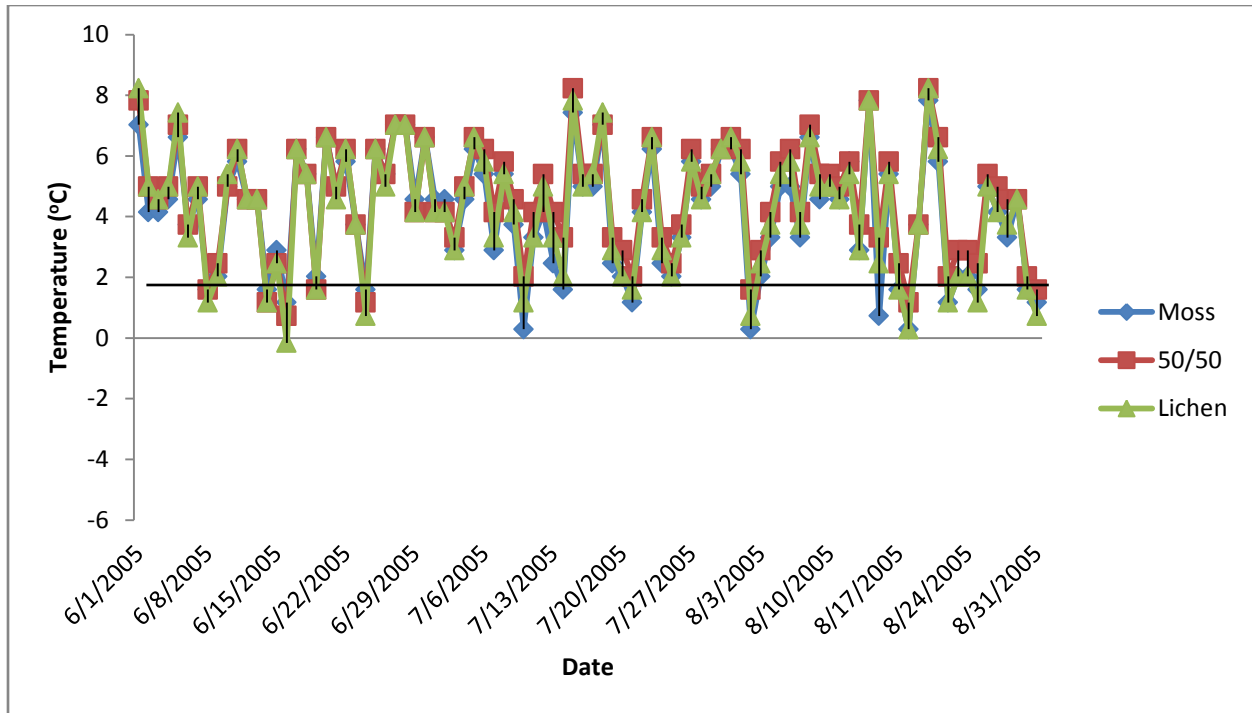
Figure 4.6. Minimum daily temperatures for 60% canopy cover site (Weldwood 21) during the

2005 growing season (June - August). The solid line is the minimum average, 4.3°C.
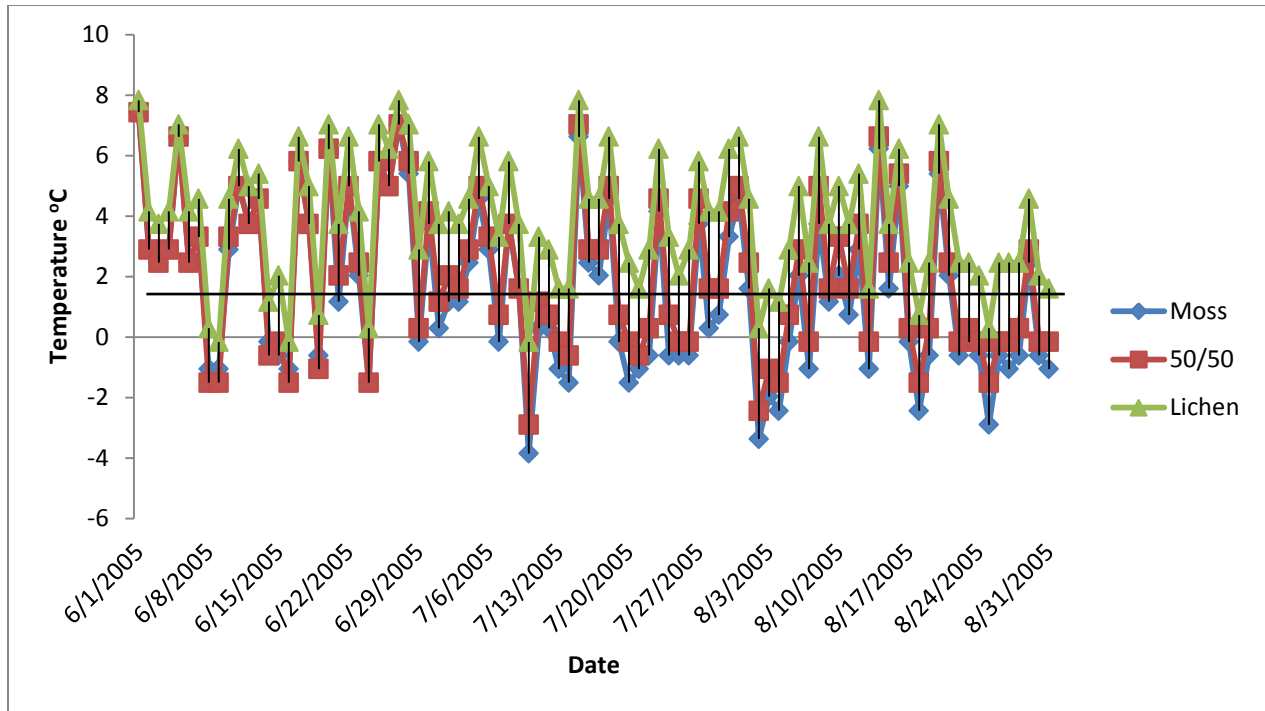
Figure 4.7. Minimum daily temperatures for 40% canopy cover site (Weldwood 29) during the

2005 growing season (June - August). The solid line is the minimum average, 2.5°C.
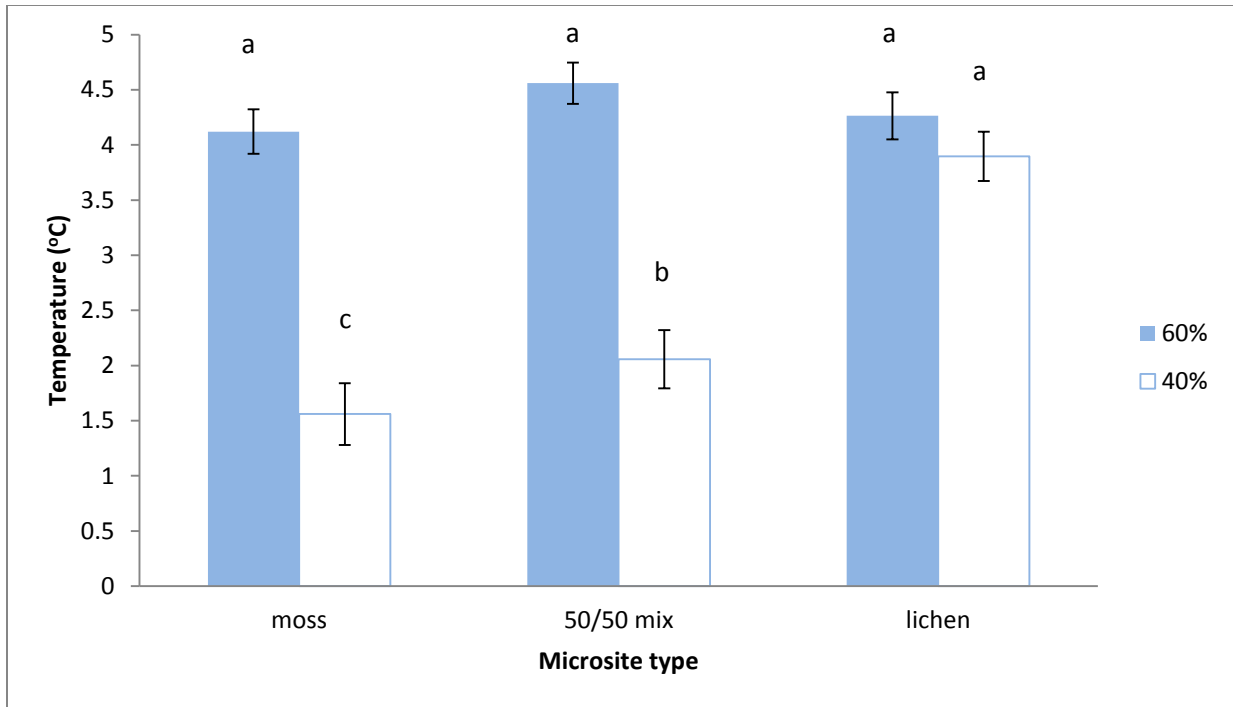
Figure 4.8. Average temperature minima for two canopy cover groups (60% and 40% cover) by microsite type (June – August 2005) (n = 92). Error bars are standard error. Different letters represent significance $p = 0.05$ using Tukey HSD test.
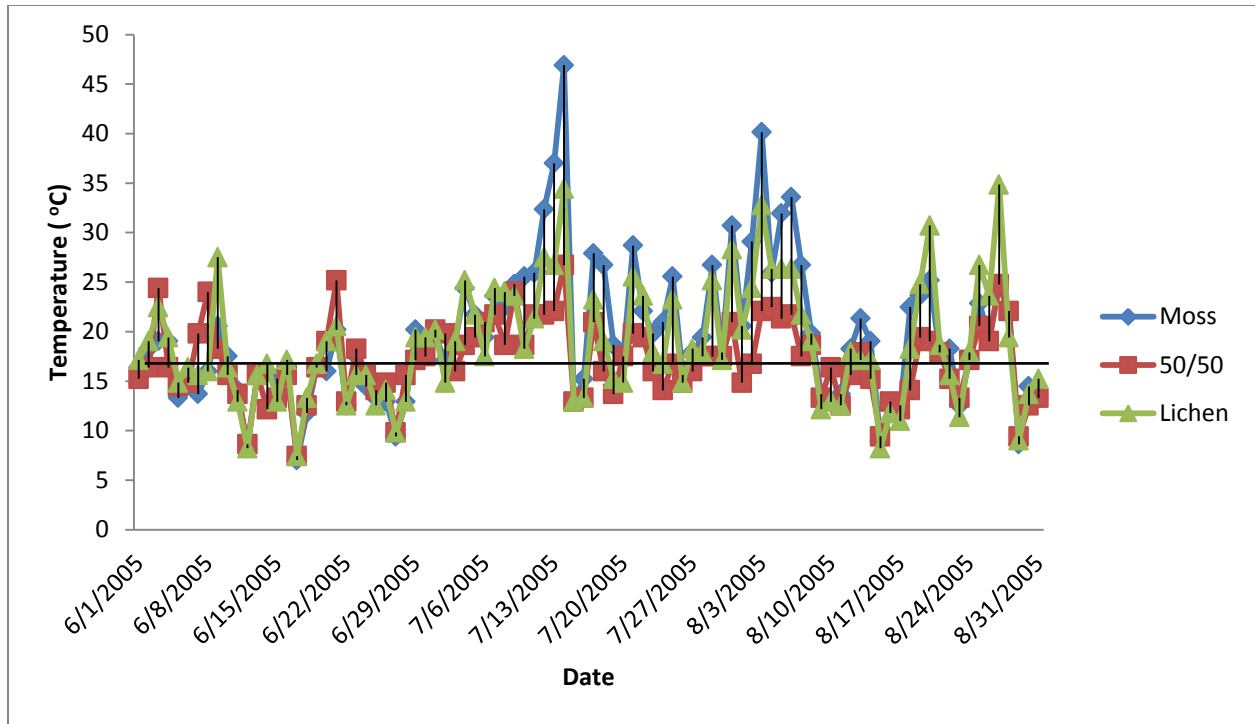
Figure 4.9. Maximum daily temperatures for 60% canopy cover site (Weldwood 21) during the

2005 growing season (June - August). The solid line is the maximum average, 18.5°C.
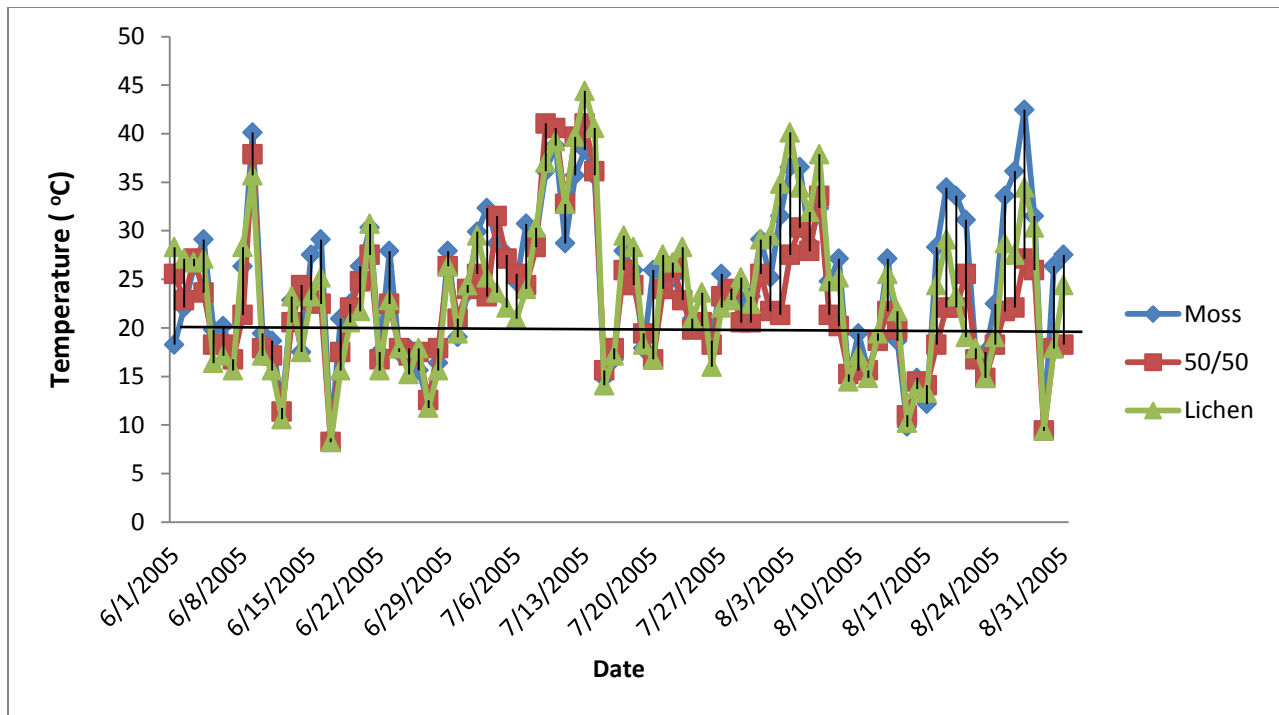
Figure 4.10. Maximum daily temperatures for 40% canopy cover site (Weldwood 29) during the

2005 growing season (June – August). The solid line is the maximum average, 23.5°C.
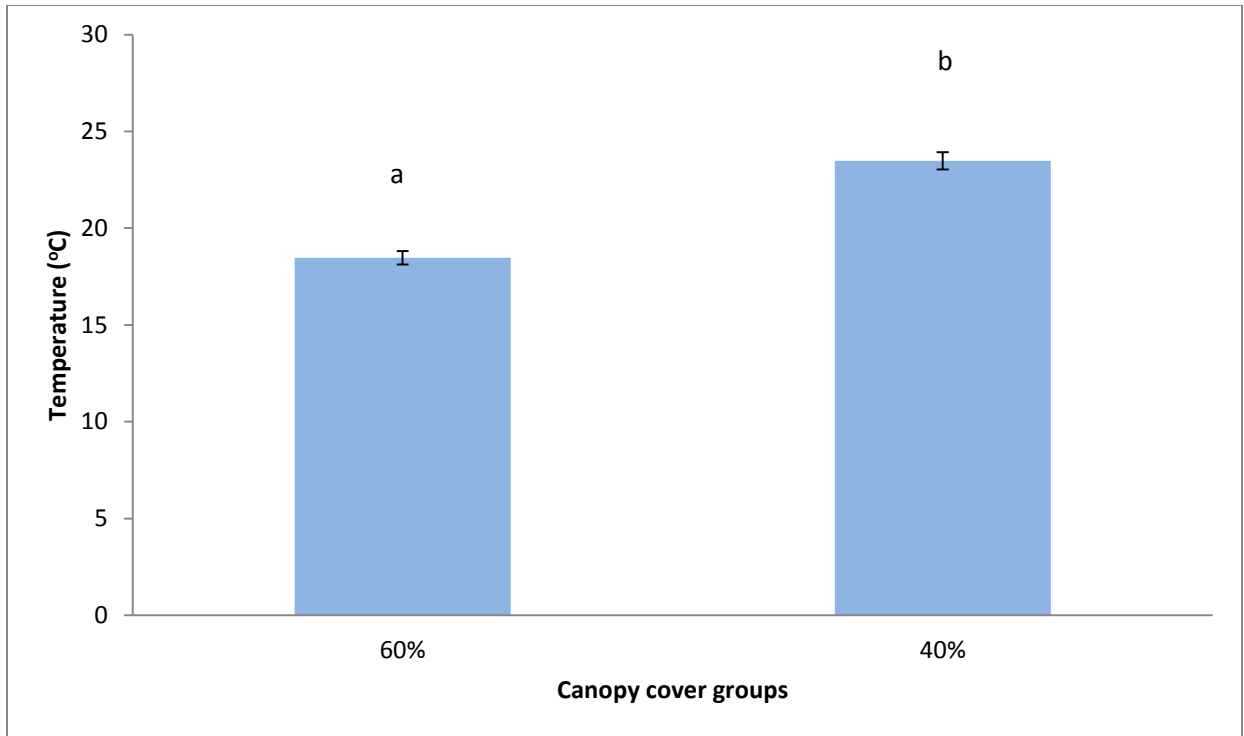
Figure 4.11. Average temperature maxima for two canopy cover groups (60% and 40% cover) (June –

August 2005) (n = 92). Error bars are standard error. Different letters represent significance $p = 0.05$

using Tukey HSD test.

4.3.5 *Litter*

Though these litter traps were lightly placed into the ground layer mat, it was not possible to adequately measure the low-growing, dense shrub patches as the litter collecting trap was not directly beneath the small shrubs. These woody plants do contribute to litter on the forest floor but are not included here due to sampling technique. Of captured material, ground layer litter traps for pine litter reveal a higher order interaction between canopy cover groups (macro-scale) over time ($F_{2,46.7} = 8.30$; $p = 0.0008$) (Fig. 4.12). The amount of pine litter is dependent on the canopy group type (60% control and 40% treatment) and time of year. Pine litter was by far the most abundant litter collected and is highly variable over time but always in greater abundance in the control stands. It is 48.4% higher in the control (60%) canopy cover groups than in the thinned treatment (40%) groups.

Lichen and moss litter, although not significantly different, are both lower in control areas (data not shown), whereas debris is almost equal across the two canopy cover groups (data not shown). At the micro-scale, moss litter is significantly different between microsite types ($F_{2,21.4} = 4.70$; $p = 0.0204$) (Fig. 4.13). More moss litter was found in moss-dominated microsites. Moss litter levels declined by 48.3% between moss and 50/50 mix and by 80.6% between moss and lichen mats. Debris is different for each of the three collection times ($F_{2,39} = 7.40$; $p = 0.0019$) (Fig. 4.14),with the most debris accruing in late summer 2004.

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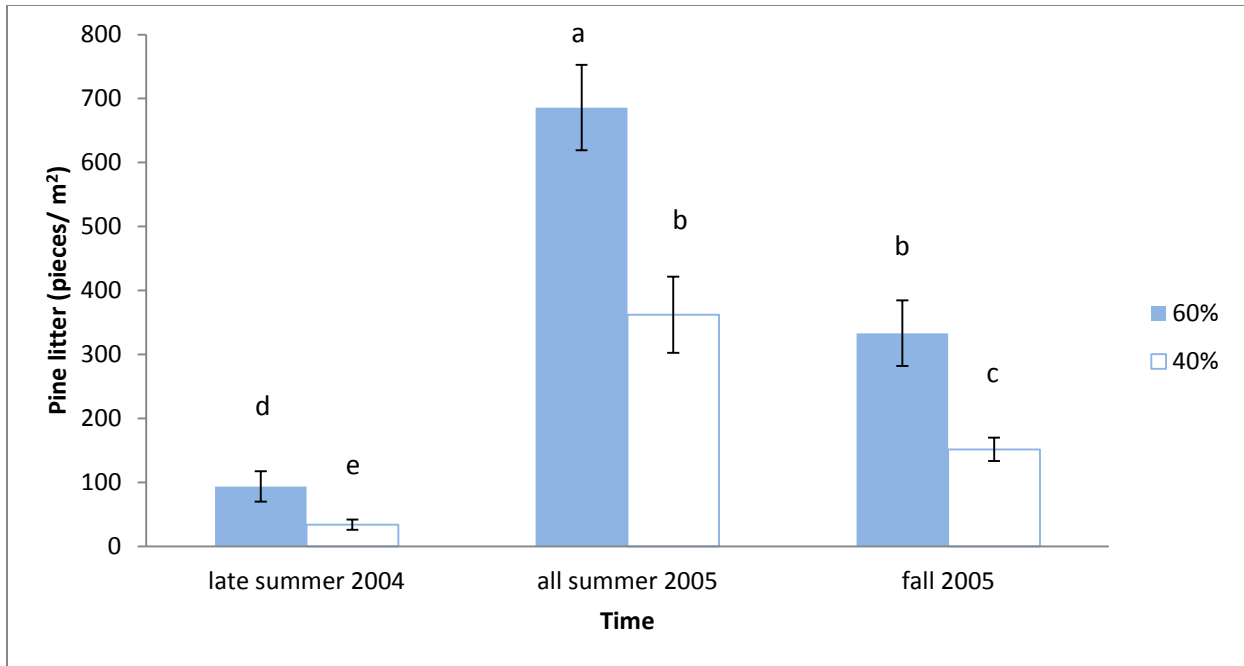
Figure 4.12. Pine litter (pieces/m^2) collected from litter pans (2004-2005) for 60% and 40% canopy cover groups over time (n = 15). Mean number of litter fragments (± standard error). Different letters indicate significance *p* = 0.05 using Tukey HSD test.
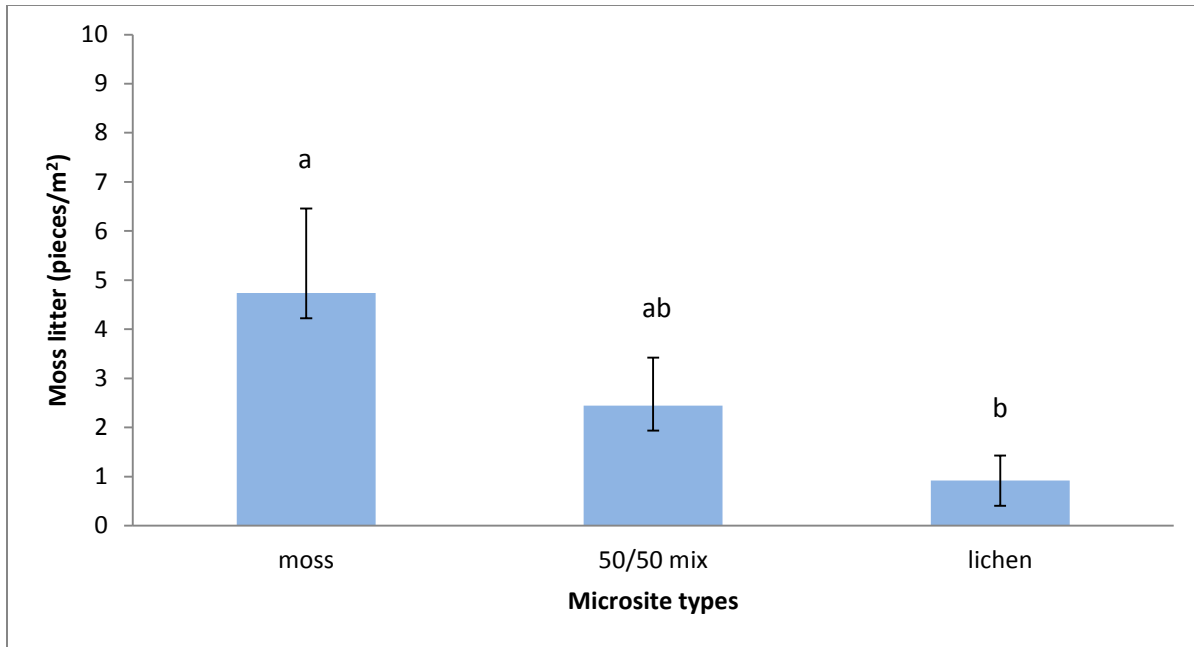
Figure 4.13. Moss litter (pieces/m^2) collected in litter pans (2004-2005) in three microsite types (n = 30). Mean number of litter fragments (± standard error). Different letters indicate significance *p* = 0.05.
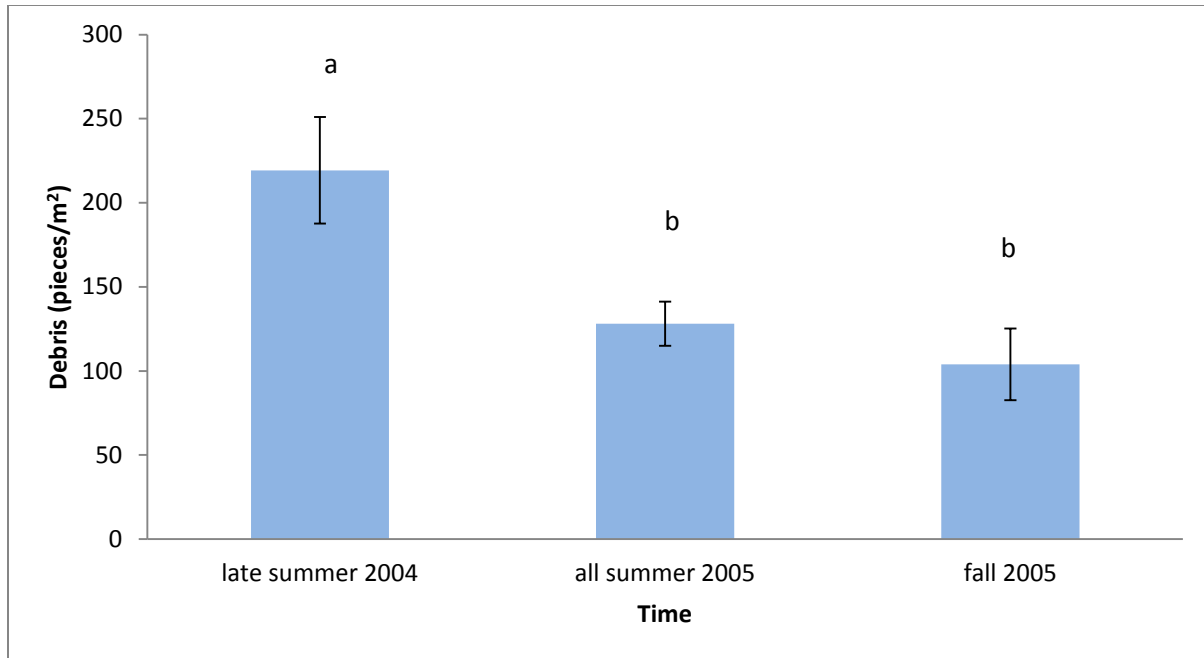
Figure 4.14. Debris (pieces/m^2) collected in litter pans (2004-2005) for three collection times (n = 30).

Mean number of debris pieces (± standard error). Different letters indicate significance $p = 0.05$.

4.3.6 *Diaspore traps*

Pine pollen counts are different based on position (low, high) ($F_{1,92.3} = 28.47$; $p < 0.0001$) (Fig. 4.15), as was debris ($F_{1,76} = 13.65$; $p = 0.0004$). Pine pollen is also different based on canopy cover group ($F_{1, 60.2} = 4.16$; $p = 0.0457$) (Fig. 4.16). Pine pollen levels are highest on ground level (low) traps and in 40% canopy cover areas. Low traps contain approximately 80% more pollen than high traps. Moss spores do not vary with time, trap position, or canopy cover. Fungal spores reveal a higher order interaction between canopy cover groups and microsite type ($F_{2,52} = 3.39$; $p = 0.0412$) (Fig. 4.17), where spore abundance at the micro-scale is dependent on the macro-scale. Fungal spores in low traps in 40% canopy groups are higher by 17.9%, high trap fungal spores in the 40% canopy group are 25.7% greater than the 60% canopy group.
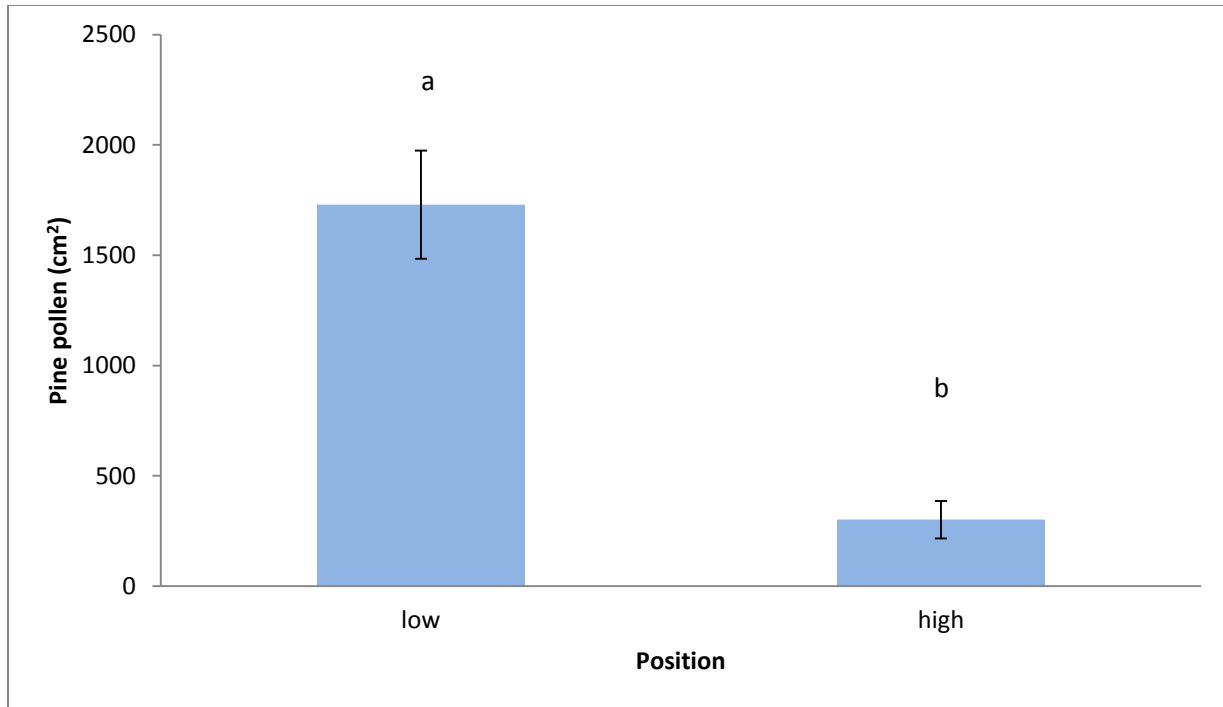
Figure 4.15. Pine pollen (cm^2) diaspore traps (2004) for two height positions (n = 90). Error

bars are standard error. Different letters indicate significance.
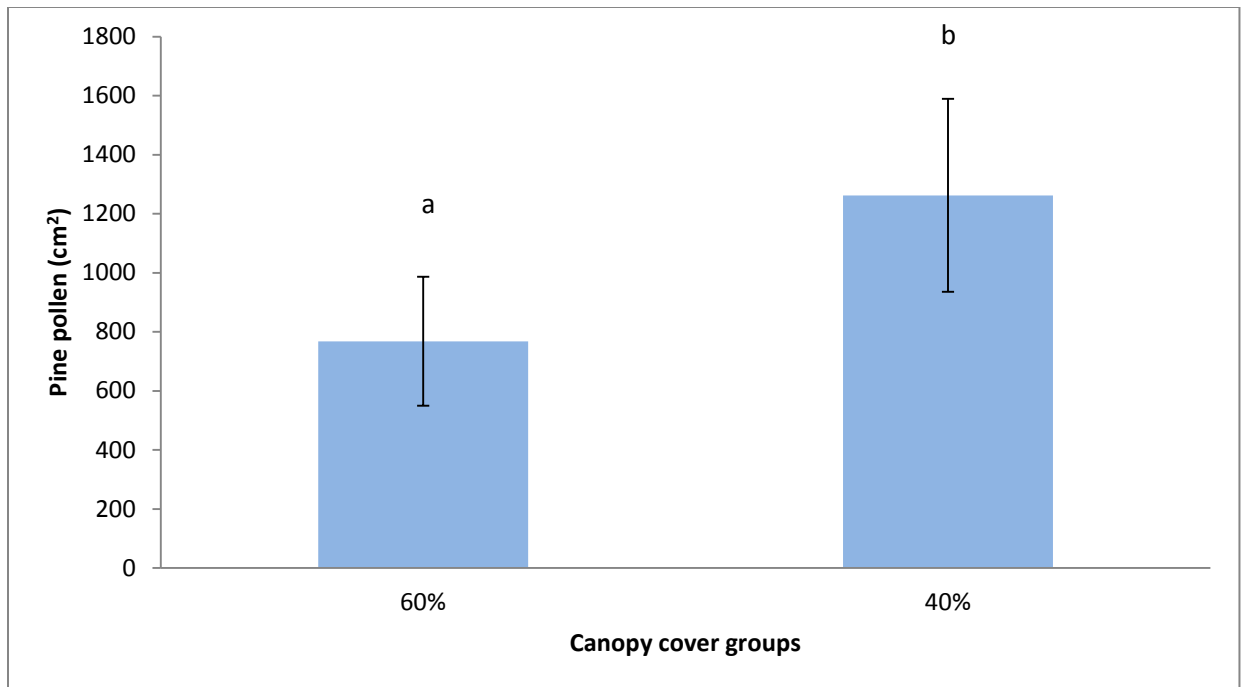
Figure 4.16. Pine pollen (cm^2) diaspore traps in canopy cover groups (n = 90). Error bars are standard error. Different letters indicate significance.
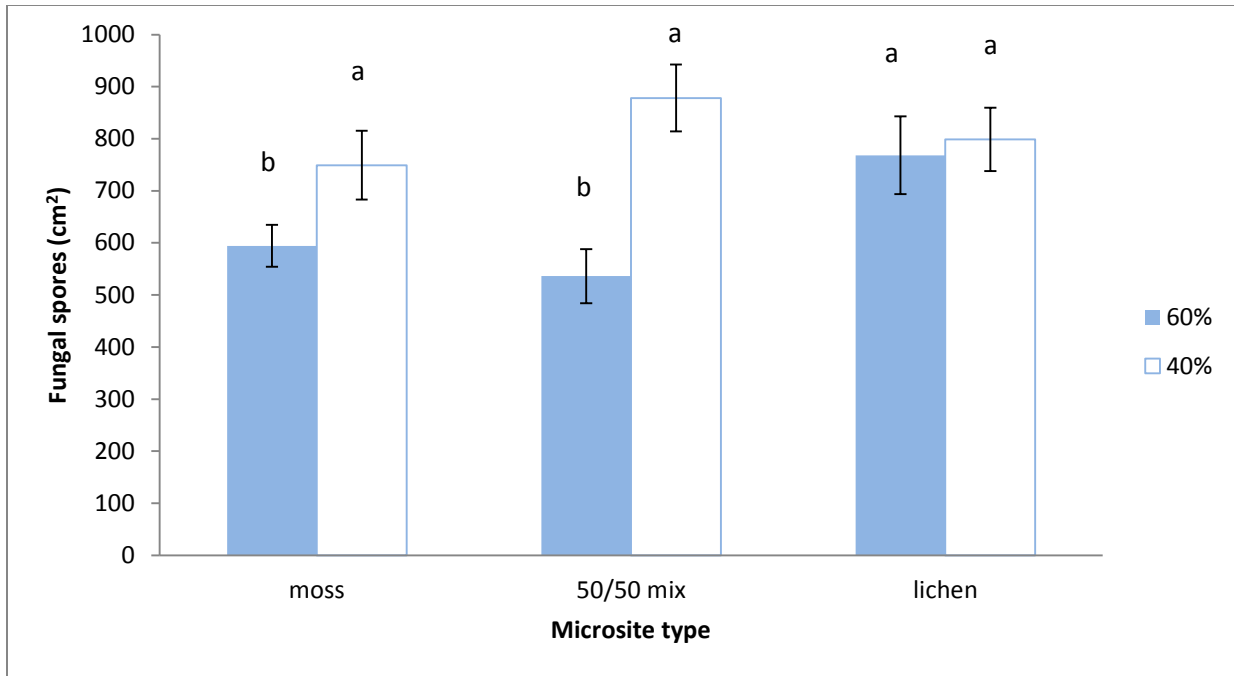
Figure 4.17. Fungal spore (cm^2) diaspore traps (2004) for canopy cover groups (60% and 40%) by microsite type (n=30). Mean number of fungal spores (± standard error). Different letters indicate significance at $p = 0.05$ using Tukey HSD test.

4.4 Discussion and Conclusion

1) What is the availability of diaspores for colonization in the form of asexual propagules or spores at the ground layer?

This study revealed, at the macro-scale, abundance of pine litter is directly tied to increased overstory canopy. High litterfall, under tree crowns, can influence survival of bryophytes by increasing density-independent mortality (Tamm 1953, Økland *et al.*1999), but according to Bray and Gorham (1964) and Cole *et al.* (1975) conifer leaf litterfall rates become constant in closed canopy forests older than 30-40 years (MacLean and Wein 1978). Litter at the micro-scale reveals moss fragments have little movement outside areas dominated by moss, whereas lichen fragments are found with more equal frequency (Fig. 4.18). At the larger scale, both lichen and moss diaspores were abundant with 10-20 fragments per square meter.

Sticky traps containing airborne pollen/spores for the ground layer and half a meter above revealed that pine pollen was higher at ground level and in the 40% canopy plots. Increased levels of pine pollen in the canopy removal plots may be due to increases in air movement due to more open space, lower Rh, and elevated temperatures. Moss spores were collected with equal frequency in all areas as they were not different at the meso- or micro- scale. Fungal spores were measured and analyzed, but there is no evidence that these spores produce lichens in this system.

Sticky traps revealed abundance of moss spores in native (60%) and thinned (40%) canopy groups. Actual litter fragments revealed lichens are abundant throughout, but at the micro-scale, feather mosses are dispersal limited to moss-dominated areas (Fig. 4.18). I presume, for this system, that the biotic factors in the form of both moss and lichen diaspores are available and are not limiting in either canopy cover group.

2) At what scale do environmental factors (light, temperature, moisture) affect the local distribution of ground layer lichens and bryophytes?

All abiotic factors (with the exception of relative humidity) were higher at the meso-scale level in the 40% canopy treatment plots. It is reasonable to assume that opening up the canopy would produce such effects. A reduction of ~20% canopy (difference between 60% control and 40% treatments) increased light, temperatures, and evaporation rates. For native conifer stands in boreal regions, canopy architecture differs by having smaller LAI (leaf area index), when compared to non-conifers, (Gower *et al.* 1999) and clumped foliage (Chen *et al.* 1997). Light reaching the forest floor is also influenced by stand density, structure, solar angle, and sky conditions (Anderson 1964, Ipatov and Kirikova 1981, Constabel and Lieffers 1996, Rambo and Muir 1998). Messier *et al.* (1998) demonstrated that light reaching the forest floor in native stands is increased in forests with shade-intolerant conifer species, but understory vegetation plays a large role in interception of that light. Other studies (Béland and Bergeron 1993, Parent and Messier 1996) measured less light than Messier *et al.* (1998) in similar closed canopy coniferous forests but agree that dense understory vegetation reduces light reaching the forest floor. In a Hungarian mixed-wood forest, Tinya *et al.* (2009) found that increases in relative diffuse light conditions positively correlate with increases in cover of the mosses *Hylocomium splendens* and *Pleurozium schreberi*. The native 60% canopy plots may receive more light due to the nature of needle leaved coniferous overstory, even with understory interception, diffuse light is benefiting the ground layer. The 40% canopy plots with reduced overstory, as well as decreased understory vegetation (see chapter 3), light levels are much higher. This benefits ground layer lichens that prefer higher light levels (Sulyma and Coxson 2001) and for both 60%

and 40% canopy plots at the microscale lichen-dominated areas received more light than moss-dominated areas (Fig. 4.18).

Additional sunlight can result in a rise in air temperatures. At the meso-scale this is the case for the 40% canopy plots, as there is both higher minimum and maximum temperatures. Additionally, removal of 20% of the canopy has resulted in greater air temperature measurements with higher minimum temperatures at the micro-scale for lichen microsites (Fig. 4.18). Fan *et al.* (1995) found air temperatures were increased in a boreal lichen woodland that contained a sparse canopy. Increases in light levels directly affect temperatures which can have an effect on moisture levels (evaporation and humidity). At the meso-scale, canopy removal escalated evaporation in the 40% canopy cover plots. Relative humidity is the only abiotic factor that has delineation only at the micro-scale. Moss-dominated areas have higher relative humidity levels than either mixed or lichen-dominated sites. This is in agreement with Söderström (1988) and Sulyma and Coxson (2001) who found connections with canopy opening equating to increased light and reduced humidity (which may benefit lichen mat formation).

Variability at the microsite level may also influence the distribution of moss and lichen populations. Within the natural (60%) canopy cover group, moss-dominated plots are more shaded and have greater humidity than do lichen-dominated plots (Fig. 4.18). Thus moss dominance is strongly associated with a suite of micro-scale environmental features that are closely tied to density of available canopy cover and increased mor humus formation. When the canopy is opened, this combination of factors leaves behind a legacy of environmental factors (background patterns) that are retained to a large extent in the thinned forest most of which are maintained at the micro-scale.

Distribution of mosses and lichens within this system support individualistic action of species to their environment, presented by Gleason (1926). This community of existing ground layer species form as a consequence of requirements and tolerance levels to exogenous abiotic (light, moisture, temperature) and endogenous biotic (diaspore dispersal) components. These vegetational forms also correspond to Connell and Slatyer's (1977) life history strategies. Their model of tolerance encompasses both mosses and lichens, in this system. This model is based on an interaction between life history characteristics and competition, emphasizing the start of succession, tolerance to change, and dispersal. Here, success of these mosses and lichens to establish and persist is based on these perturbations.

From these results, I conclude that given adequate abundances of diaspores, lichens and mosses will preferentially continue to exist and colonize suitable sites at the local-scale, as they always have. These preferences produce a mosaic of moss and lichen-dominated microsites. Characteristics of the microsites are a combination of local-scale environmental factors that persist through disturbance coupled with an overall abundance, but differential pattern of diaspores. Lichen fragments are more widespread than those of mosses and more tolerant of the changing conditions of the opened canopy. Mosses are limited by both legacy environmental conditions especially local climatic factors and surficial edaphic features, coupled with the more restricted occurrence of diaspores.
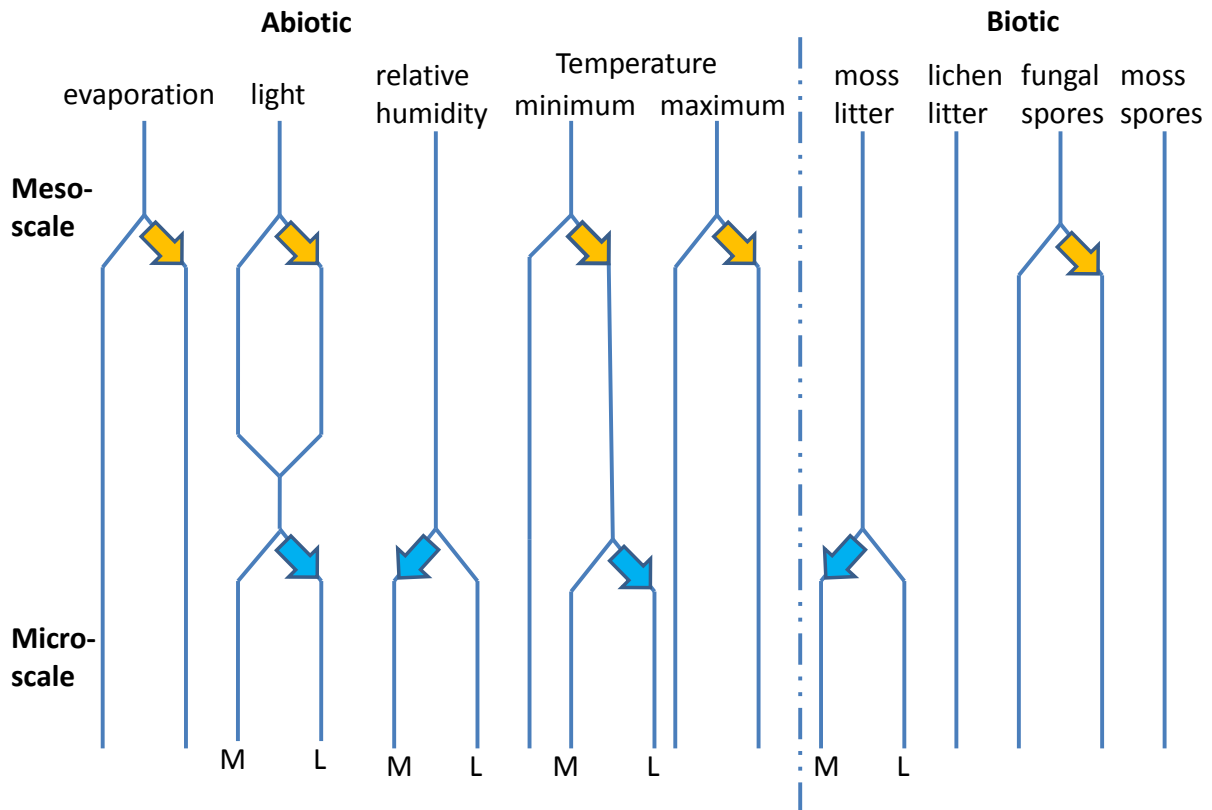
Figure 4.18. Diagram of abiotic and biotic factors at the meso- and micro-scale and their influence on ground layer mosses (M) and lichens (L). First division at the meso-scale level is 60% canopy (left) and 40% canopy group (right). Arrows show significant differences and point toward increase in parameter.

CHAPTER 5

ESTABLISHMENT OF MOSSES AND LICHENS

5.1 Introduction

When a moss or lichen diaspore lands on appropriate substrate, establishment of that

species may occur, but since many species are substrate specific this becomes a key topic for

understanding distribution. Edaphic features, such as substrate, are a principal determinant of

species abundance (Vitt *et al.* 1995). Robinson *et al.* (1989) concluded in Canadian forest-

tundra zone that lichens and bryophytes are influenced by pH, latitude, and soil texture.

Preferences in chemical differences in substrate, especially calcareous versus non-calcareous

(Brown and Bates 1990), suggest that this is a significant factor for bryophyte location (Bates

1979, Bates and Farmer 1990). Bayfield (1976) grew some common Scottish bryophytes on

assorted substrates and found nutrient solution had no effect on establishment, but found that

water relations between substrate and fragment germination were more important than originally

thought. This study revealed the strong influence of substrate on young mosses. Bates and

Bakken (1998) further reinforced the critical nature of the establishment phase for bryophytes, as

their study lent more support for edaphic factors exerting strong effects on feather mosses (e.g.

Pleurozium schreberi) during establishment. Lichens also must have suitable substrates for

establishment (Bailey 1976), and if lacking, colonization may lag or not occur after disturbance.

A study on epiphytic lichens found that if appropriate substrate was not available in young

forests lichen colonization is limited (Esseen *et al.* 1996). Muir *et al.* (2006) reported similar

findings while working with epiphytic mosses and lichens influenced by overstory removal. For

fruticose lichens, Harris (1996) noted establishment and re-colonization of *Cladina* spp. on

disturbed mineral soil in a clear cut Ontario forest. Establishment of *Cladina* spp. on mineral

soil has also been noted by other studies (Christensen 1988, Boudreau and Payette 2004). Soil

texture has been determined to be an important factor for terrestrial lichen establishment (Sulyma

2001). He found that smaller particles (clay and silt sized) held more moisture than larger sized

(sand) particles, so lichens perform better in the drier areas containing the larger sized substrate.

Since these late seral lichens need a dry cycle (Fraser 1956), course soils drain better due to

amplified inter-particle spaces, and provide an improved habitat. Sedia and Ehrenfeld (2003),

studying in New Jersey pinelands, reported both mosses (*Polytrichum juniperinum*) and lichens

(*Cladonia*) initially prefer bare substrate, with moss litter forming a rich organic layer. These

studies reveal that substrate is an important feature for establishment.

Several establishment studies have been conducted using transplants and artificial

dispersal, both epiphytic bryophyte studies (Hazell and Gustafsson 1999, Muir *et al.* 2006) and

epigeic lichen studies (Fink 1917, Christensen 1988, Roturier *et al.* 2007, Hylander 2009,

Roturier 2009) have shown success in moss and lichen colonization. A study in old growth

forests, found that epiphytic moss and lichen transplants in tree removal areas had high

survivorship (Muir *et al.* 2006). Using "cup shaped" lichens, Fink (1917) "pounded" several

species of *Cladonia* and spread the fragments on a moss matt and found after four years the

lichens were full sized, and after eight years two species dominated the quadrat. More recently,

Roturier *et al.* (2007) artificially dispersed lichen fragments and found establishment occurred

best on mineral soil and moss substrate in clear cut areas. Studying *Cladina* spp., Webb (1998)

reported that before lichen fragments begin to grow they have to be able to anchor to suitable

substrate. In order to predict ecological elasticity of mosses and lichens to periodic disturbances,

it is critical to understand factors involved in recolonization and establishment (Bengtsson *et al.* 2003), such as edaphic limitations.

This study takes a late successional forest species (moss) and an early, but persistent, successional species (lichen) that both produce prolific mats commonly found in the ground layer, and examines establishment of each morphotype (separately and together) based on soil substrate, light, and previous vegetational occupant. The objective of this study was to answer the question: Do a) substrate disturbance, b) pre-disturbance vegetation, c) canopy opening, and/or d) species interactions limit ground layer establishment of *Cladina mitis* or *Pleurozium schreberi*? In order to meet this objective establishment plots were created and revisited and measured four years later.

5.2 Methods

5.2.1 *Study area*

As part of a forest thinning/ lichen abundance project established in the winter of 1997/ 1998 (see Pharo and Vitt 2000), the study area in the Upper Foothills Forest Section was selected by industry ecologists of Alberta Newsprint Company (ANC), Weyerhaeuser Canada (WEY), and Weldwood Canada (WEL) to include undisturbed forest that was within suitable distance to current logging and mill operations all within a 375 km^2 area. Nine stands within this study area were selected within the experimental thinning region (Pharo and Vitt 2000). Further experimental design and setup were determined by Vitt and Pharo.

For the Upper Foothills, Beckingham *et al.* (1996) classify the soils as acidic, rapidly drained, and having a poor nutrient content. In 2000, Pharo and Vitt examined the soil and found that the average pH was 4.88 with little variation. Soil texture ranged from loamy sand to sandy loam. The moisture regime is generally classified as mesic.

5.2.2 *Experimental design*

In August of 1999, one of the nine stands was selected based on having clearly differentiated moss- and lichen-dominated plots. Within this stand, 12 plots were selected from among the permanent ones established in 1997, six in the control and six in the thinning regime. Mean canopy cover, measured in 2003, was 62% for the control and 31% for the thinned area. Within each of the control and thinned areas, three, out of the six, plots were chosen because they were moss-dominated and three because they were lichen-dominated. These establishment plots were gridded at one and half by one meter, and were separate from the permanent plots used in other parts of this study. Each of these plots were pretreated by a) one half of the plot having complete removal of above ground vascular plants and complete moss/lichen mats including the duff layer down to the mineral soil (mineral) and b) removal of only the living moss/lichen biomass (organic) on the remaining half of the plot (Fig. 5.1). Within an establishment plot, three half-meter square subplots were established in each of the 12 plots. A randomized reciprocal treatment was carried out with 1-2 cups of lichen fragments (*Cladina mitis*), 1-2 cups of moss fragments (mostly *Pleurozium schreberi*), and 1-2 cups of 50/50 mix of lichen and moss fragments spread on one third of each of the 12 subplots; six originally moss-dominated, six originally lichen-dominated and these distributed equally within control and thinned areas. Fragment sizes were approximately 2-4 mm for both mosses and lichens.

In June 2003, four years after fragment initiation, establishment of moss and lichen individuals was assessed using a point sampling method. A point quadrat frame, 0.75 x 0.75 m, containing a double 10 cm grid of strings, for a total of 100 points, was used. A sharp pencil was positioned at the intersection of strings and moss, lichen, or nothing was recorded.

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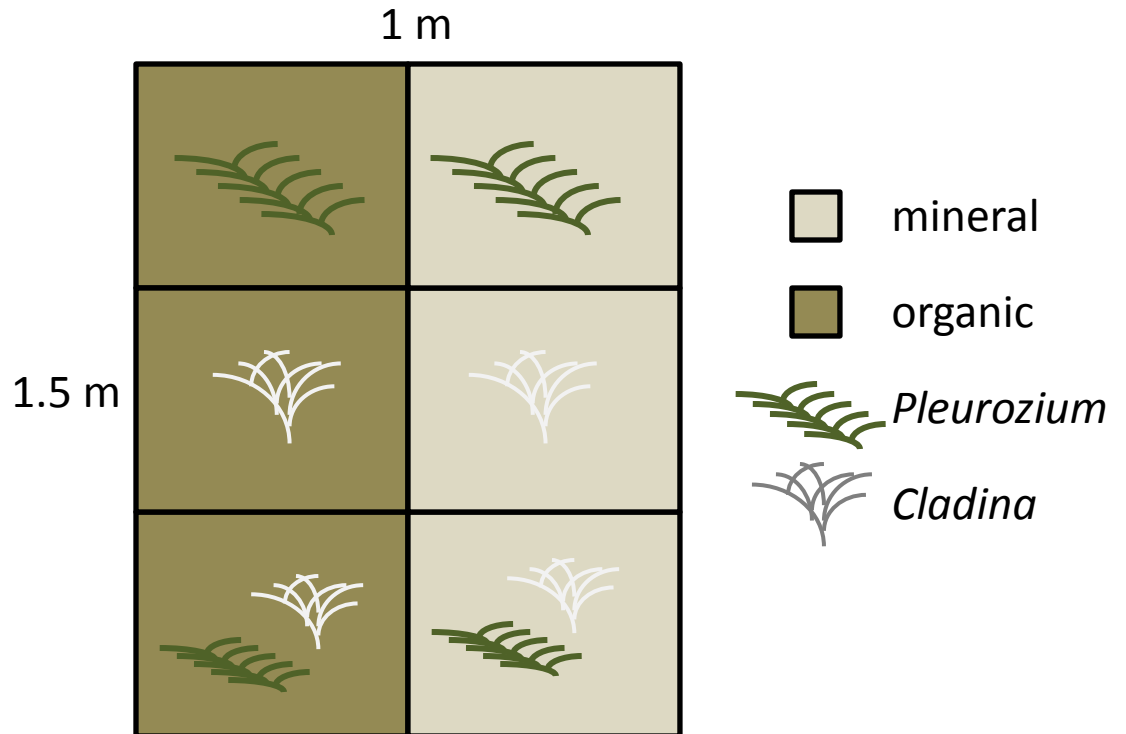
Figure 5.1. Experimental plot design showing the substrate treatment and addition of moss, lichen, and a 50/50 mix. For each plot, the fragments were added to the subplots randomly. Three of these are in lichen-dominated control areas, three in moss-dominated control areas, three in lichen-dominated thinned areas, and three in moss-dominated thinned areas.

5.2.3 *Data analysis*

A two-way analysis of variance (ANOVA) (SAS 2008) was used to test the effects of canopy thinning treatment on canopy cover in the lichen and moss establishment plots. A split-split plot ANOVA was used to analyze establishment of moss and lichen germinants for two canopy regimes (native uncut control, thinned areas) that were subdivided into to two pre-existing ground layer dominants (moss and lichen), which were divided into subunits of two types of substrate (organic, mineral) with three types of propagule treatments (moss, lichen, 50/50 mix). A Tukey's Honestly Significant Difference (HSD) (SAS 2008) was used post hoc to determine which treatments, or combination of, differed significantly ($p = 0.05$). Moss and lichen establishment data was log transformed.

5.3 Results

Outcomes of statistical tests, in the form of ANOVA tables, for all moss and lichen establishment data, are located in Appendix IV.

5.3.1 *Canopy cover for establishment plots*

Overhead canopy cover, measured in 2003 when plots were assessed for propagule establishment, showed significant variation between the six control and thinned plots ($F_1=153.49$, $p <0.0001$) (Fig. 5.2). There was no difference in canopy cover between control plots that were originally dominated by lichens compared to those originally dominated by mosses, and the same was true in the thinned plots (Fig. 5.2). As a result, there were no significant differences between moss- and lichen-dominated experimental plots when substrate pre-treatment and subsequent moss and lichen fragments were initiated. Mean post-harvest canopy cover for the control plots was: moss-dominant 62% , lichen-dominant 61%. The thinned plot post-harvest canopy cover was: moss-dominant 33%, lichen-dominant 29%.
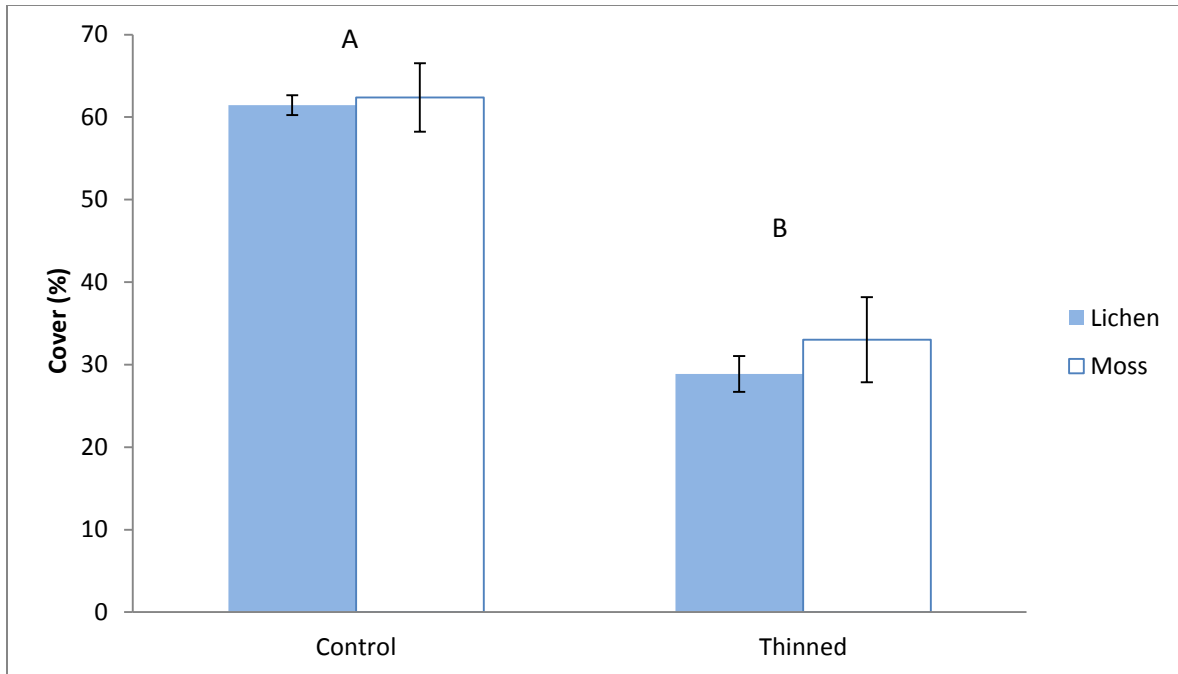
Figure 5.2. Mean overhead canopy cover (2003) for lichen- and moss-dominated reciprocal transplant establishment plots in control and thinned stands. Within control stands, three lichen-dominated and three moss-dominated plots (same for thinned plots) were used to assess establishment (n=6). Capital letters indicate significance for canopy cover group. Error bars are standard error.

5.3.2 *Total moss and lichen establishment*

A total of 2,655 established diaspores ('=germinants') were found during point-quadrat sampling. Forty-six percent of the established germinants occurred in the control plots, while 54% occurred in the thinned plots. Seventy-seven percent of the germinants were lichens, while 22% were mosses. Moss germinants were two times more abundant in the controls compared with the thinned plots, whereas lichen germinants were about one and a half times as abundant in the thinned plots when compared to the controls. However, what is most striking is that of the 2,058 lichen diaspores that established, 60% established in the thinned plots (Table 5.1).

5.3.3 *Canopy, propagule, and substrate effects*

Moss establishment numbers reveal a significant interaction between canopy cover groups (control and thinned) and substrate (organic and mineral) ($F_{1,8.18} = 6.09$; $p = 0.0382$) (Fig. 5.3). Moss germinants in the canopy groups are bound by substrate specificity. Moss germinant counts were greater for the controls, when compared to the thinned areas ($F_{1,17.4} = 18.39$; $p = 0.0005$) (Table 5.2). Added propagule type (moss, 50/50 mix, or lichen) also differed in number of moss germinants ($F_{2,13.5} = 30.26$; $p < 0.0001$) (Fig. 5.4), with moss establishment being greater where moss propagules were spread. Mosses also had higher rates of success on previously moss dominated plots ($F_{1,17.4} = 16.38$; $p = 0.0008$) (Fig. 5.5).

Lichen establishment germinant numbers reveal that there is an interaction between substrate (organic and mineral) and added propagule types (moss, 50/50 mix, and lichen) ($F_{2,23.6} = 4.35$; $p = 0.0247$) (Fig. 5.6). Lichen establishment on specific substrate type is coupled with added propagule type. Lichen germinants were more abundant in the thinned areas ($F_{1,16}=23.76$; $p = 0.0002$) (Fig. 5.7). Lichens had better rates of establishment on areas previously dominated by lichens ($F_{1,16} = 5.31$; $p = 0.0349$) (Fig. 5.8).

Overall, substrate (mineral versus organic) had a profound effect on germinant establishment for both morphotypes. Mosses were more frequent on organic material in native canopy sites ($F_{1,8.18} = 6.45$; $p = 0.0342$), whereas lichens occurred with greater frequency on mineral soil ($F_{1,4.7} = 66.25$; $p = 0.0006$) in both canopy types (Figs. 5.6 and 5.7). Increased lichen establishment occurred on previously lichen-dominated plots in thinned areas on mineral substrate. Lichens established efficiently, but were least abundant in moss-dominant controls on organic soil. Mosses established best in moss-dominant controls on organic substrate, and most poorly in lichen-dominant plots in the thinned area on organic soil (Table 5.2).
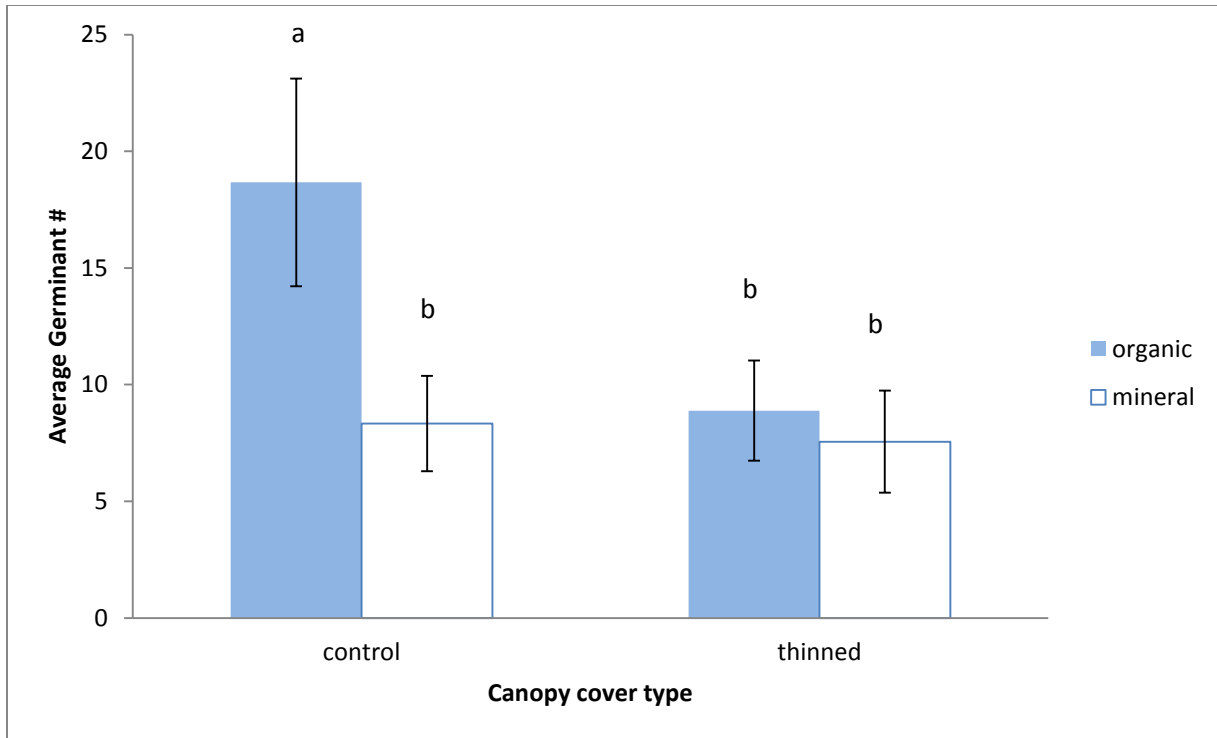
Figure 5.3. Moss establishment of two different substrates (organic and mineral) in two canopy cover types (control and thinned) by moss germinants (n=9). Mean number of germinants (± standard error). Different letters indicate significance at $p = 0.05$ using Tukey HSD test.

Table 5.1. Total number of established diaspores. $n = 6$, cc = mean canopy cover.

	Control cc=62%	Thinned cc=31%	Total
Lichen	831	1227	2058 (77%)
Moss	396	201	597 (22%)
Total	1227 (46%)	1428 (54%)	2655 (100%)
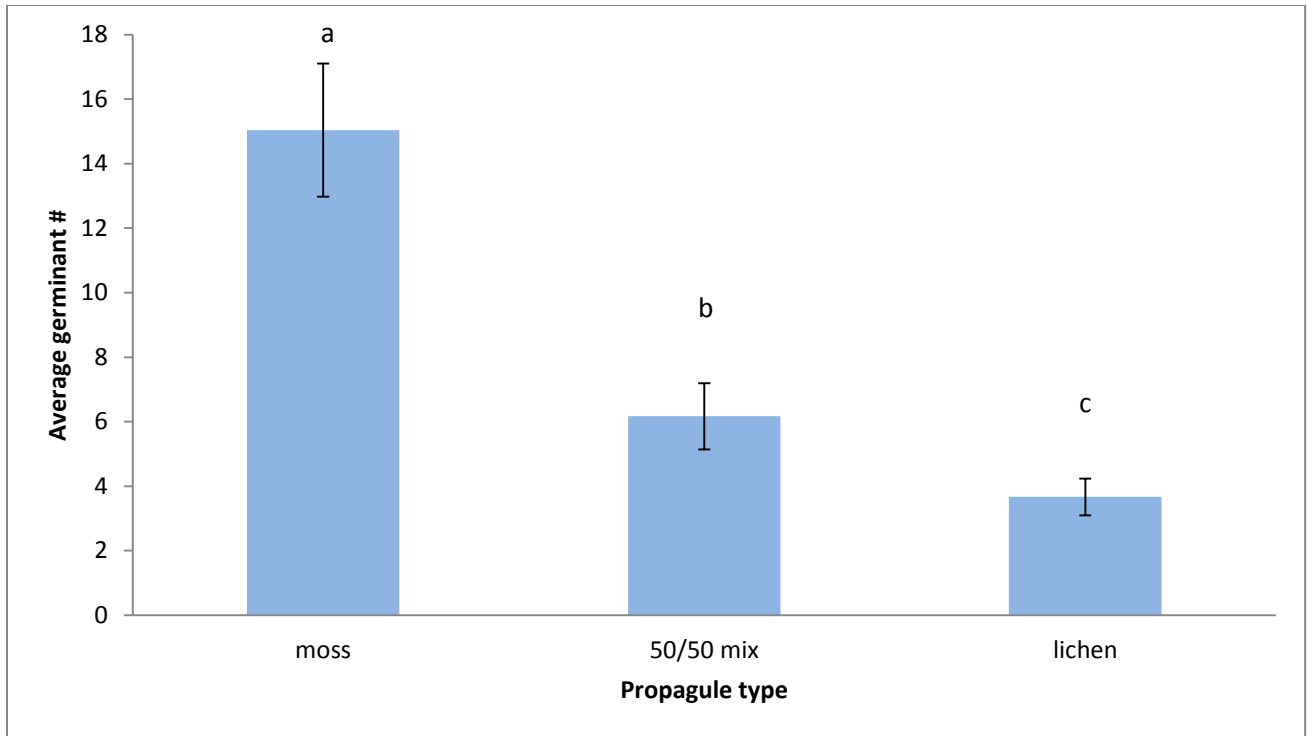
Figure 5.4. Average number of moss germinants for type of propagule added (n=24). Different letters indicate significance at $p = 0.05$ using Tukey HSD test. Error bars are standard error.
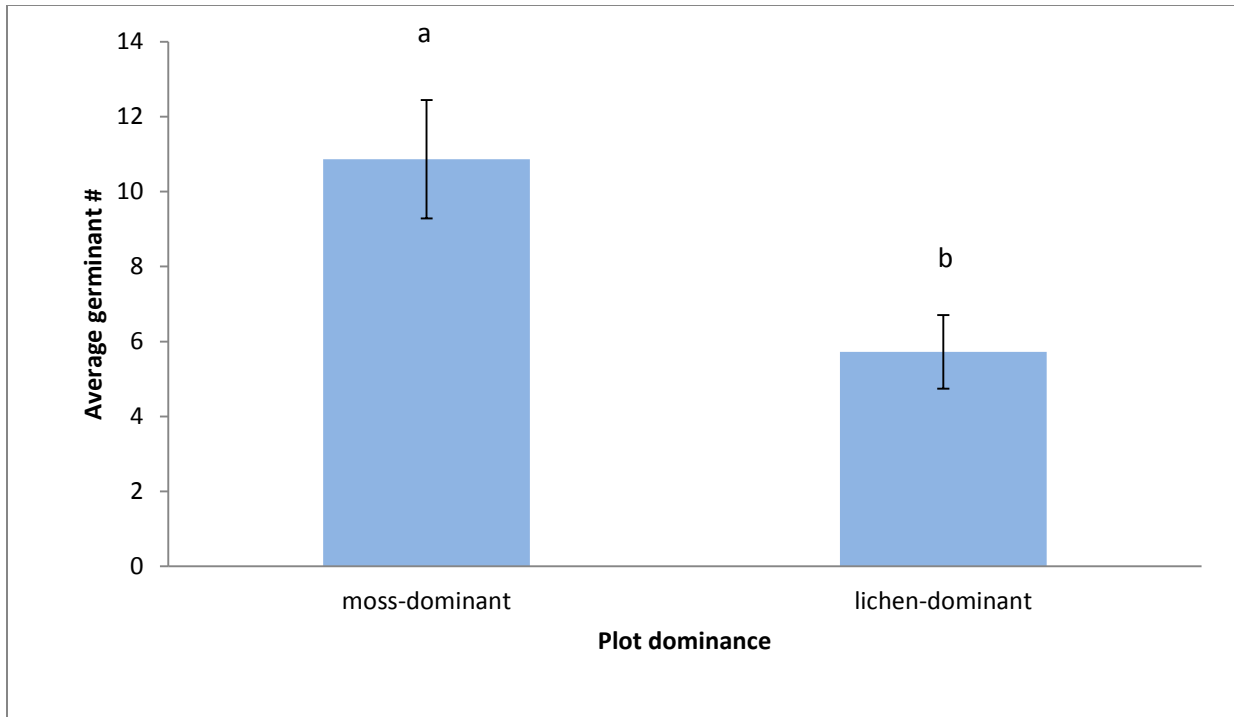
Figure 5.5. Average number of moss germinants for previous vegetational plot dominance (n=36).

Different letters indicate significance at $p = 0.05$ using Tukey HSD test. Error bars are standard error.
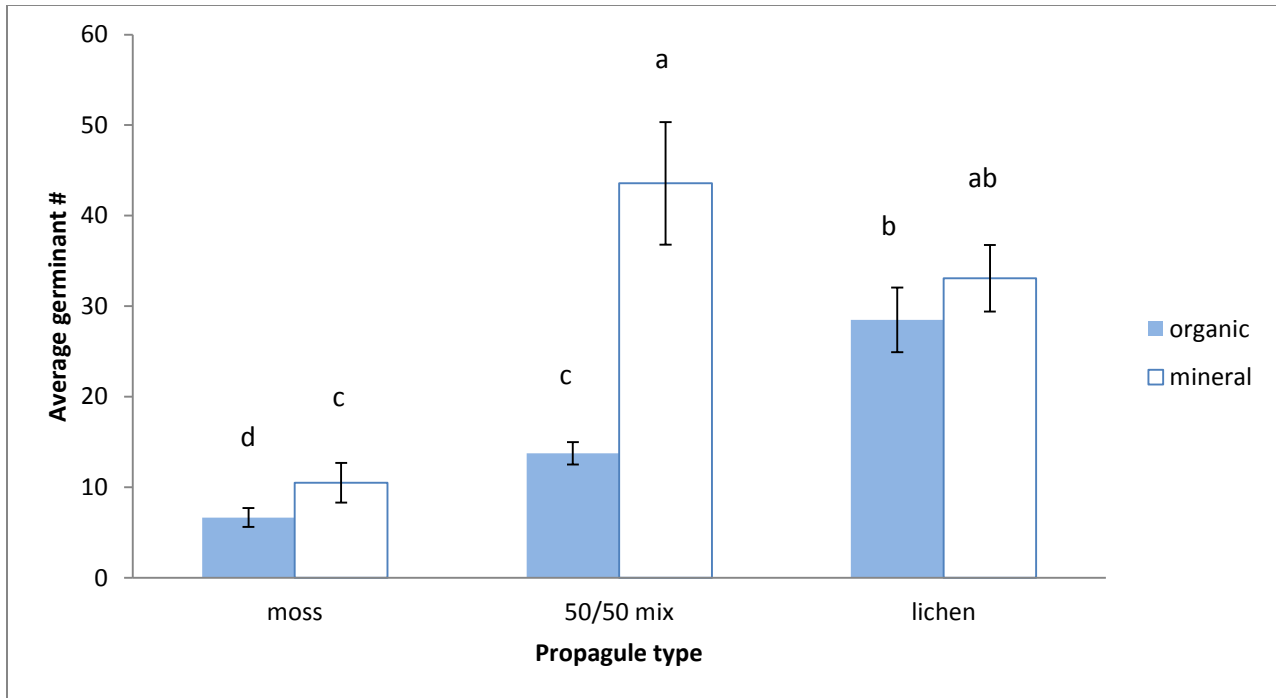
Figure 5.6. Lichen establishment of two different substrates (organic and mineral) in areas sowed with propagules (moss, 50/50 mix, lichen) by lichen germinants (n=12). Mean number of germinants (± standard error). Different letters indicate significance at $p = 0.05$ using Tukey HSD test.
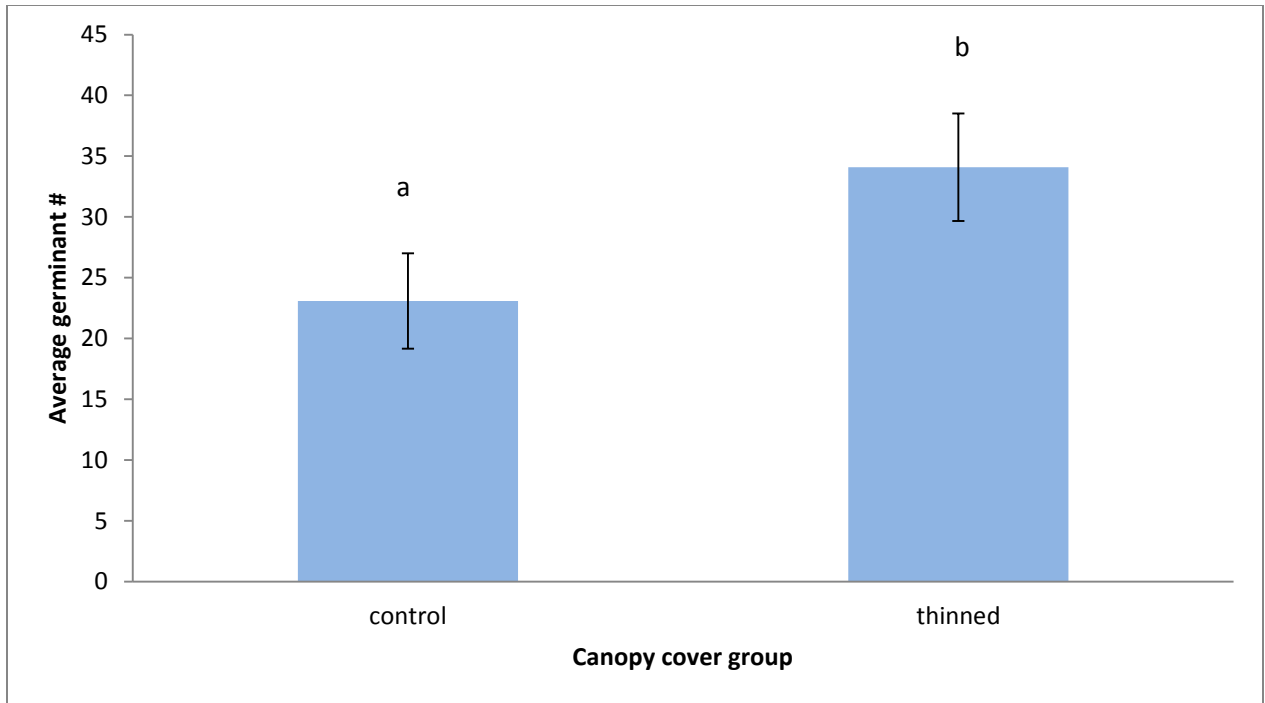
Figure 5.7. Lichen establishment in the two canopy cover types. Mean number of germinants (±

standard error). Different letters indicate significance at $p = 0.05$ using Tukey HSD test.
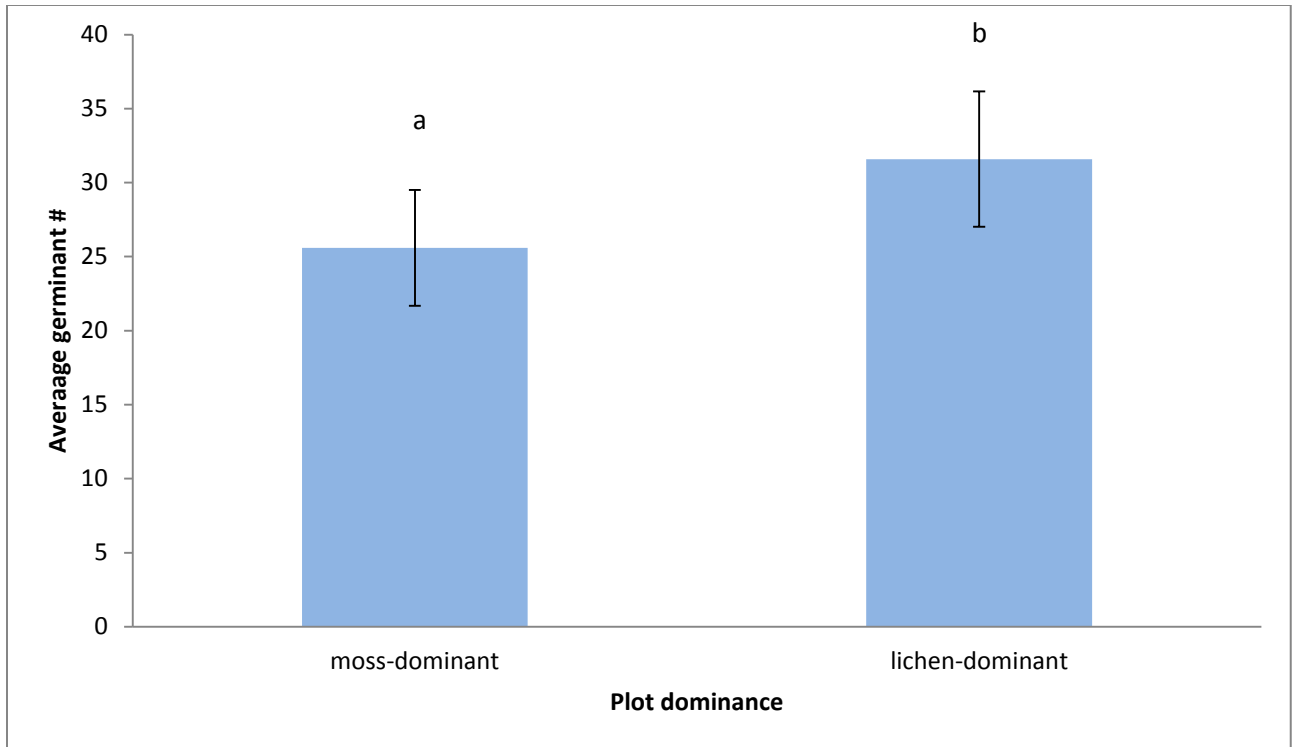
Figure 5.8. Average number of lichen germinants for previous vegetational plot dominance (n=36). Different letters indicate significance at $p = 0.05$ using Tukey HSD test. Error bars are standard error.

Table 5.2. Number of established germinants on substrate type, in six thinned and six control plots, separated by plot dominant species.

		Moss- dominant Plots				Lichen-dominant Plots			
		Control		Thinned		Control		Thinned	
		Moss	Lichen	Moss	Lichen	Moss	Lichen	Moss	Lichen
Substrate Type	Organic	168	92	80	175	96	138	22	182
	Mineral	75	239	68	415	57	362	31	455
Total		243	331	148	590	153	500	53	637

5.3.4 *Lichen establishment dynamics*

When lichen propagules were introduced to either control or thinned plots, irregardless of whether the original plots were lichen- or moss-dominated, lichens established well (Table 5.3 – percent germinants found ranging from 18 to 98%). When moss propagules were added to originally moss-dominated plots under control conditions only 18% of the germinants were lichens, however under all other conditions of moss additions (including 50/50 mix), between 31 and 76% were lichens. When lichen fragments were added to originally lichen-dominated plots under control conditions 98% of the germinants were lichens, however under all thinned conditions where lichens were added (including 50/50 mix), lichen germinants were between 87-97%.

Table 5.3. Lichen establishment (not including 50/50 mix propagule additions). Data are percent of established lichen germinants for plots, ($\pm$ s.d.), $n = 3$, cc = mean canopy cover.

	Control (cc = 62%)		Thinned (cc = 31%)	
	Lichen-dominant	Moss-dominant	Lichen-dominant	Moss-dominant
Lichen Introduction	98 (29.3)	87 (18.5)	97 (28.6)	94 (21)
Moss Introduction	31 (5.3)	18 (1.2)	76 (9)	31 (2.8)

5.3.5 *Moss establishment dynamics*

When lichen propagules are added to originally lichen dominated plots under thinned conditions only 3% of germinants were mosses, however under all other conditions of lichen addition, between 6 and 13% were mosses (Table 5.4). When moss diaspores were introduced to control plots that were originally moss-dominated 82% of the germinants were mosses, with moss germinant numbers for all other conditions ranging from 24-69% of the total established germinants. Mosses established most efficiently in uncut controls where mosses were added, they did not establish well in lichen-dominated, thinned areas where lichens were added. When lichens are introduced, moss establishment ranged between 3 and 13% of the total germinants. When mosses are introduced, moss establishment ranged from 24 to 69%.

These data suggest that when lichen propagules are introduced to plots, under either control or thinned conditions they establish well, and even when only moss propagules are added to the plots lichen germinants account for about 39% of the established germinants. Only under control conditions, in plots that were originally dominated by mosses and that moss fragments were added, do mosses establish well. Thinned plots that were originally moss-dominated (Fig. 5.9) perform similarly to control plots that were originally lichen-dominated.

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Table 5.4. Moss establishment (not including 50/50 mix propagule additions). Data are percent

of established moss germinants for plots (± s.d.),*n* = 3, cc = mean canopy cover.

	Control (cc = 62%)		Thinned (cc = 31%)	
	Lichen – dominant	Moss-dominant	Lichen dominant	Moss-dominant
Lichen Introduction	8 (3.6)	13 (3)	3 (4.3)	6 (4.3)
Moss Introduction	69 (7)	82 (12.3)	24 (1.3)	69 (2.5)

Figure 5.9. Photograph of a moss-dominant plot in the thinned area. On the left, only the living layer has been removed leaving the organic substrate. On the right, the living layer and humus have been removed down to the mineral soil. Established lichen germinants appear white.

5.3.6 *Species interactions*

When a mix of 50% lichen and 50% moss fragments are introduced to plots, lichens perform better than mosses in all situations (Table 5.5). Lichen germinants accounted for between 62 and 94% of all germinants, whereas moss germinants ranged from 6 to 38%. It is especially noteworthy that lichen germinants made up 62% of the total for control plots that were originally moss-dominated, whereas for the reverse (control plots that were originally lichen-dominated) only 20% of the germinants were mosses. When introduced to common plots lichen establishment is greater than that of mosses. Under control conditions and in 50/50 propagule mixes, mosses essentially do not establish as quickly as lichens in four years.

Table 5.5. Established germinants in areas where a 50/50 propagule mixture was introduced.

Data are percent of established germinants for plots, ($\pm$ s.d.), $n = 3$, cc = mean canopy cover.

	Control (cc = 62%)		Thinned (cc = 31%)	
	Lichen – dominant	Moss- dominant	Lichen dominant	Moss- dominant
Lichen germinants	80 (22.2)	62 (14)	94 (20)	87 (29)
Moss germinants	20 (3)	38 (6.2)	6 (0.9)	13 (4.1)

5.4 Discussion and Conclusion

The purpose of this study was to provide answers to the question: Do a) substrate disturbance, b) pre-disturbance vegetation, c) canopy opening, and/or d) species interactions limit ground layer establishment of *Cladina mitis* or *Pleurozium schreberi*? Both types of fragments did establish under all conditions. About equal numbers of diaspores established in controls, versus thinned plots though lichens established about four times more frequently than mosses. Lichen fragments established with greater frequency in the thinned plots and mosses established less often. Mosses favored previously moss-dominated, organic substrate of native control sites over any other condition.

Substrate type (mineral or organic) was the dividing line for establishment of moss and lichen germinants. Moss fragments performed better on organic soil, whereas lichen establishment occurred at greater frequencies on mineral substrates. Generally, lichens were less particular about substrate type and were found in greater numbers than moss germinants on both types of substrate. Harris (1996) described late successional lichens (i.e., *Cladina*) as having a low frequency when re-colonizing logged areas with more developed organic soils, which is supported by increased lichen numbers in areas of mineral soil. Roturier *et al*. (2007), in a three year artificial dispersal study of *Cladina mitis*, found greater establishment on mineral soil and prepared (ground up) feather moss substrate. For *Pleurozium* and other feather mosses, the initial stage of establishment is where the moss has the most contact with the soil, because of this physical connection the substrate can exercise its most influential effects (Bates and Farmer 1990, Bates and Bakken 1998). Kimmerer (2005) also found increased establishment of moss fragments on humus substrate in areas of forest disturbance. This study supports these studies, as mosses established less frequently on mineral soil.

These data suggest that when lichen propagules are introduced to plots, under either canopy condition, they establish well, and even when only moss fragments are added to the plots, lichen germinants account for about 18% of established germinants. Under control conditions on organic substrate mosses are the most frequent, but moss germinants are found on both mineral and organic substrate. This is in agreement with Frego (1996), who found that *Pleurozium* establishment was unaffected by native substrate type *in situ* (e.g. humus, needles, dead moss). For mosses, originally moss- dominated thinned plots perform similarly to control plots that were originally lichen-dominated.

There are important differences in the ability of lichens to establish compared to those of mosses. According to this study, lichens establish more frequently than mosses after four years. Moss propagules do establish better in native forest habitats, while lichens are found in greater numbers on mineral substrates in both thinned and control areas. These findings, then, presume that when lichen propagules are introduced, they should establish well under both native and thinned regimes (if time is included as a factor), which agrees with Crittenden (2000) and Roturier *et al.* (2007). In areas where species interactions were measured and a 50/50 propagule mix was added, lichen germinants were more abundant than moss germinants in all cases. Lichens, also, perform better than mosses under all conditions in these trials except under control conditions that were originally dominated by mosses, this is also the situation for the 50/50 mix areas. Consequently, moss occurrence may partially be a reflection of the history of the habitat, whereas lichen occurrence is strongly influenced by stochastic events.

In this system, it appears that mosses are limited by pre-disturbance vegetation (moss-dominated areas), reflections of their past substrates (buildup of organic material), canopy opening, and species interactions. Lichens have some limitations when it comes to pre-

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disturbance vegetation, especially poor establishment in moss dominated areas and more germinants on mineral soil but canopy opening had less of an effect than on mosses, and species interactions did not hinder lichen establishment. Essentially lichens are able to establish under a wider variety of disturbance regimes and conditions than mosses. Currently, canopy removal (thinned) areas provide ample available disturbed substrate that could be colonized by local lichen and moss populations, over time, as diaspores (fragments or spores) appear not to be limiting in either thinned or native forest stands (see Chapter 4). This study, along with others, fully supports the finding that fragmented lichens can and do survive and establish (Fink 1917, Roturier 2009). Since these thinned areas have intensified disturbance at the ground layer (e.g. log harvesting equipment and effects of $\pm$ 30% more light), these results suggest that with increased time since disturbance, terricolous mat forming lichens will have an upsurge in establishment.

CHAPTER 6

SYNTHESIS AND GENERAL CONCLUSIONS

6.1 Introduction

In the pursuit of the initial question, "Why is it here and not there?", an evolution of fine-tuning occurred and two new questions emerged: 1) How do moss and lichen patches respond to disturbance resulting from changes in canopy cover? and, 2) do these patches move? To gain a better understanding, I pursued various avenues to untangle the underlying factors of ground layer dynamics. In Chapter 1, I gave an overview of the region, general vegetation, prevailing natural disturbance regime, community succession, and factors influencing life in the ground layer to provide a structural context for my research. In the second chapter, I evaluated the canopy effects of the three thinning regimes established seven years previously, determined the canopy variation that resulted from the thinning procedure, and ranked the plots by percent canopy cover, re-grouped them, to better understand effects of thinning on the ground layer. For Chapter 3, I presented the effects of canopy opening on diversity and abundance of dominant shrub, herb, and ground layer species. Physical environmental and biotic limiting factors affecting the ground layer were examined in Chapter 4. *Pleurozium schreberi* and *Cladina spp.* establishment was addressed in Chapter 5. This concluding chapter will cover disturbance, patch dynamics, results, implications for forest management, and suggestions for future research.

6.2 Disturbance

Disturbance has been defined in multiple ways (van der Maarel 1993), but regardless of the definition, it is ultimately the loss of biomass (Grime *et al.* 1987) releasing previously occupied space and resources for establishment and colonization by incoming species. Natural and anthropogenic disturbances drive composition and location of many components of the ground layer in this ecosystem.

These disturbance events reset successional processes, re-initiating movement into an area by new individuals. For these *Pinus contorta* forests, disturbance is primarily responsible for heterogeneity, both spatial and temporal (Spurr 1952). Natural disturbance agents in this system are principally fire, wind, and insects (Sousa 1985, Angelstam 1998), and vary with magnitude, size, frequency, and rotation time (Ahlgren 1960, West *et al.* 1981, Jonsson 1993, Coxson and Marsh 2001). Anthropogenic disturbances include timber harvest by clear-cutting or selective removal (Hansen *et al.*1991, Johnson *et al.* 1998). Disturbances, both anthropogenic and natural, generate different sized patches across a broad range of spatial and temporal scales. Various degrees of canopy change via selective mechanical harvest was the disturbance initiated for this study.

Hutchinson (1953) provided an early discussion linking species coexistence with disturbance. Here he described species coexistence in the context of space and time, relating that different species are found in newly disturbed patches versus older patches. Under the closing crown of late seral *Pinus contorta* forests, broad mats of mosses and lichens form a tightly intermixed ground layer, slowly establishing through the influences of light, moisture, temperature, and time. For these patches, a suite of environmental factors is tied to canopy opening and affects the ground layer at different scales (community or meso-scale versus population or micro-scale). Every component of the ground layer mosaic is affected differently and thus survives, thrives, or dies at that particular location for that moment in time. This cycle of survival continually shifts throughout time and space as disturbance, both large and small, is the common driver of location. The ground layer response to disturbance matters more than the actual disturbance itself (van der Maarel 1993), especially in this highly disturbance prone boreal forest.

6.3 Patch dynamics

Bormann and Likens (1979) first used the term "shifting mosaic steady state" to describe landscape scale patterns explaining changes in dynamics based on disturbance. This idea proposes that blocks within the landscape create a mosaic composed of individual patches (i.e., forest stands, openings in the forest), and these are dynamic. The different aged blocks are at various stages of succession creating diversity and heterogeneity at the landscape scale. The shifting mosaic model can be employed to illustrate patterns for large scales. In contrast, my research was focused at a finer scale (e.g., community and population levels), from the perspective of a single plot within a patch or group of patches. A patch, in this sense, is a spatially small area incorporating the basic structural and functional unit of the landscape (Forman and Godron 1986). Patch size ranged from 1.5 m^2 to 6.5 m^2, in a homogeneous 30-40 hectare area. Wu and Loucks (1995) noted the perception of ecological dynamics of smaller individual patches can be skewed by scale. However, diversity is dependent on scale and van der Maarel (1993) differentiates three levels, the smallest of these being patch. My research was concerned with changes in structure, function, and configuration of smaller individual patches over a short (eight year) interval.

The feather mosses (*Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis)* and the fruticose lichen (*Cladina mitis*) dominate the forest floor in these *Pinus contorta* forests and are small in scale (< 10 cm). These morphotypes form extensive, homogeneous patches that intermix in areas of differing amounts of canopy cover. This heterogeneous ground layer is cyclic in nature and driven by disturbance that dictates successional stage.

6.4 Synthesis

1) How do moss and lichen patches respond to disturbance in the form of canopy change?

The moss and lichen mosaic composing the ground layer is dependent upon amount of canopy cover, substrate, and the environmental factors of light, moisture, and temperature. Two "worlds" can be demarcated for establishment, colonization, and persistence of feather mosses and fruticose lichens within the constraints of the forest floor. Mosses prefer closed canopies, found in many parts of the native forest. These shaded microsites have higher relative humidity, reduced evaporation, lowered evaporation rates, and more moderate temperatures. For establishment, these late seral mosses favor organic substrates found in the native shaded control plots. Persistence of mosses may continue in areas of high light as long as moisture rates can be maintained, but are restricted primarily by canopy openness and substrate type, an effect of legacy. In part, these patterns of occurrence relate to the work of Williams and Flanagan (1998) who reported that feather mosses in closed canopy forests dominate because they have maximum photosynthetic capacity at low light levels. Based on this information, these mosses fit into Loucks (1970) definition of shade tolerant as they are prolific spore producers who are adapted to living in extreme low light. These mosses also fit into Grime's (1977) triangle as 'competitive' species due to persistence and longevity, and appear late in succession surviving only with environmental stability.

Lichens prefer more open canopies but are less constrained by edaphic and environmental conditions than mosses. Open areas are generally drier than closed areas, with lowered humidity levels and increased evaporation at the micro-scale. Edaphic factors have less of an impact on lichens as they establish extremely well on mineral substrates, but can also establish well on organic substrates. Perseverance of lichens is less constrained than those of mosses, with the closed canopy (i.e., reduced light, increased moisture, decreased temperatures) being the primary hindrance. These reindeer lichens with endurance for high light and dry conditions would be

classified by Loucks (1970) as pioneers, as they have the ability to maximize high light in open

areas and are competitive enough to establish and persist. According to Grime (1977), these

lichens are 'stress tolerators', with a less competitive ability in relation to disturbance. Fruticose

lichens in this system are early successional species that establish in disturbed, high light, dry

environments. Once establishment and colonization occurs, these mats persist until successional

changes (competition from the feather mosses) or disturbance force alterations.

2) Do these patches move?

Disturbance directly affects small scale dynamics through cyclic replacement (Watt

1947). Patches are opened through disturbance, developing habitable areas for fruticose lichens

that slowly cover the forest floor. Eventually conifers sprout, grow, and with expanding canopy

initiate changes in micro-site conditions in the ground layer. These new shaded, micro-climate

altered conditions are unsuitable to lichens, but are pristine for feather mosses that can encroach

upon the lichen mat, shifting patch dominance. Temporally and spatially patches of mosses and

lichens shift in this manner. In the previous scenario, disturbance was assumed to be of natural

origins, in this study selective thinning mimicked the natural disturbance regime, and created

unidirectional open canopy areas. When plots were "seeded" with moss and lichen fragments

there was establishment, but outside of that experiment only moss decline was found in thinned

areas with no rise in lichen abundance.

Conclusions are that increases in canopy opening have negatively affected vascular plant

and bryophyte ground layer components with little or no effect on the lichen component, and

have had little effect on overall species richness. Both lichen and moss diaspores are plentiful,

lichen diaspores are available in all microsites, while moss diaspores are primarily limited to

moss-dominated areas. With increasing change in canopy cover bare ground has increased, moss cover has decreased, but lichens remain constant and have not yet re-colonized available areas. Lichens appear more tolerant of changing environmental conditions, and with time are able to establish under varying conditions, however, organic substrates do hinder lichen establishment. Concerning environmental and edaphic conditions, feather mosses are more particular. Environmental conditions (i.e., relative humidity, light, temperature) inhibit moss occurrence, except in local areas where pre-existing substrates and canopy conditions have precluded lichen establishment. Some patches move more than others. Patches of mosses may degrade to open patches on mineral soil which in turn are colonized by lichens and eventually to moss-dominated patches; however, other moss patches are more stable and when degraded by disturbance retain their organic base and are recolonized by mosses. These 'habitat reserves' may parallel those proposed by Ghandi *et al.* (2001) for ground beeltes and are long term stable microsites and are key components of the natural conifer-dominated forest.

6.5 Implications for forestry management

For the goal of promoting caribou habitat in the form of terrestrial lichen patches in the ground layer, it appears that selective timber harvest removing between ~18 and 46% of the original canopy reduces bryophytes, shrubs, and increases duff/bare ground (without affecting lichen numbers). Measurements of light, moisture, and temperature in ~40% canopy cover areas revealed that changes in these abiotic factors directly influence the ground layer, making it uninhabitable for shade tolerant species. Over a period of four years, *Pleurozium* and *Cladina* establishment plots indicated that when diaspores are made available, lichens do establish. Even though lichens prefer high light and mineral soil, they did establish on more organic material. The selective thinning approach was also less detrimental to the ground layer as a whole. Past

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studies indicate that clear-cutting techniques cause: increased damage to fragile lichen thalli by machinery, lack of visitation of woodland caribou (Stepaniuk 1997), larger fluctuations in temperature in combination with high light levels leading to additional wind, increased ground layer desiccation, with the significance of these post-harvest effects lasting much longer (Kranrod 1996). Finally, the next generation of thinning practices should recognize the dynamic nature of moss and lichen patches, and that the distributions of these patches are controlled by a series of complex environmental and biotic factors operating at the microsite scale. Thinning of the canopy, although seemingly uniform at the stand scale, is remarkably non-uniform at the microsite scale.

6.6 Future research

Seven years post-harvest, this investigation uncovered many components affecting ground layer bryophyte and lichen abundance, diversity, and establishment. Another field season of data collection would produce vital information on the impacts of selective canopy removal on the major ground layer components. I recommended that a fifteen-year post-harvest follow-up study (for 2013) be undertaken to 1) ascertain if lichens have begun to establish in bare areas produced by moss death in thinned stands; 2) further examine the fate of the decreased vascular plant abundance in the understory of the canopy cover groups (or to record any increases); 3) to determine whether species richness continues to be unaffected and again evaluate local rarity; 4) revisit moss and lichen establishment plots to gage colonization.

Beyond the scope of this ground layer research, it would be useful to determine if local woodland caribou herds are utilizing any portion of the selectively harvest study area 15 years post-harvest.

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APPENDICES

Contains plot level perimeter transect data. Cover of understory vegetation and key species measured in 2005 from 182 plots. Data are cm

covered along a line transect of 2600 total cm.

Control	Shrub	*Cornus*	Other lichen	*Cladina*	Other bryophyte	*Pleurozium*	*Hylocomium*	*Ptilium*	Dead wood	Dead moss	Duff/bare ground
anc17	775	53	200	165	50	490	0	25	5	0	805
anc18	675	113	315	220	65	290	0	28	35	0	803
anc19	550	112	115	160	75	323	0	85	54	0	1040
anc20	475	129	107	185	88	685	5	55	13	0	804
anc21	320	88	230	349	65	456	0	0	140	0	902
anc32	1108	111	25	5	5	1272	0	0	61	0	5
anc33	1270	29	80	30	42	1265	60	40	38	0	0
anc34	465	31	107	105	43	637	135	0	93	0	970
anc35	778	18	163	337	80	405	0	10	55	30	724
anc36	655	49	70	267	137	338	0	0	83	0	943
anc41	865	53	69	189	50	220	10	5	33	0	1106
anc42	758	220	103	75	84	1025	0	5	95	0	234
anc43	576	85	143	130	58	432	0	45	112	0	1019
anc54	815	60	151	275	60	520	25	0	605	0	616
anc55	720	24	59	273	36	690	0	40	766	0	666
anc56	888	35	123	146	61	961	0	0	1022	0	292
wel9	960	50	233	277	21	662	34	0	17	0	325
wel18	853	233	293	189	13	47	0	0	14	0	932
wel19	1062	50	311	112	17	486	7	33	37	0	460
wel20	1184	97	82	65	7	183	8	35	34	0	901

wel21	938	52	265	158	2	455	47	6	16	0	655
wel22	795	197	139	169	4	159	5	1	7	0	920
wel23	837	172	303	50	15	335	39	0	2	0	801
wel31	366	119	208	54	5	732	10	5	392	0	666
wel32	563	122	239	103	9	409	64	4	40	0	992
wel33	487	13	129	115	3	533	0	25	130	0	1121
wel34	662	0	221	146	57	385	0	5	23	0	1005
wel35	495	104	180	141	8	146	0	0	213	0	1292
wel51	671	85	60	184	17	785	20	98	126	0	531
wel52	115	32	81	78	34	615	7	56	164	0	1362
wel53	778	0	139	91	4	101	0	2	167	0	1200
wel54	439	1	123	253	17	412	0	0	235	0	1081
wel55	731	0	94	61	2	497	0	17	101	4	1082
wey7	403	0	98	391	30	605	0	0	83	4	980
wey8	433	0	165	151	0	96	0	0	116	188	1401
wey9	824	12	74	343	0	110	1	0	199	28	991
wey11	1158	83	48	13	2	1058	157	0	65	0	4
wey12	748	25	138	23	15	1154	7	29	77	0	339
wey13	994	52	110	97	12	591	0	0	45	0	668
wey14	593	52	77	51	6	438	54	21	172	0	1134
wey15	962	49	37	103	17	647	0	10	34	0	729
wey16	795	14	32	30	0	933	26	0	44	0	724
wey17	400	0	32	81	0	445	0	0	237	0	1395
wey18	221	0	210	257	84	36	0	0	117	0	1673
wey19	312	6	152	148	7	215	11	0	138	0	1587
wey20	1338	25	47	67	11	937	96	19	43	0	7
wey21	871	164	70	11	6	892	44	39	66	14	407

wey22	1046	8	45	16	5	601	60	57	101	18	603
Group 1											
anc10	560	141	94	112	40	207	0	20	89	0	1283
anc12	410	24	130	520	47	5	0	0	84	10	1365
anc14	475	39	173	257	75	313	0	15	92	0	1128
anc16	650	124	30	101	25	719	0	45	73	0	831
anc22	875	42	155	127	115	675	5	40	81	0	485
anc23	836	133	165	180	85	450	30	20	171	0	501
anc24	514	120	235	145	80	205	0	7	436	0	858
anc25	930	153	190	119	72	565	0	10	126	0	435
anc26	432	22	285	156	164	259	0	18	153	0	1046
anc27	655	97	165	295	30	490	5	0	84	0	779
anc28	720	189	207	110	55	700	0	0	49	0	559
anc29	802	151	232	230	40	615	25	0	41	10	412
anc30	440	115	185	97	95	890	5	45	240	0	424
anc31	475	162	61	77	52	518	28	0	30	0	1141
anc37	1140	23	50	84	30	1030	20	0	110	0	93
anc38	925	27	30	15	23	1195	5	50	94	0	228
anc39	1120	12	30	75	80	1140	0	40	96	0	2
anc40	920	73	15	25	25	1025	65	145	53	35	214
wel10	489	57	280	258	40	73	0	0	40	68	1230
wel12	308	16	254	597	28	0	0	0	54	17	1215
wel13	340	19	210	68	16	60	0	15	287	20	1539
wel17	380	10	254	595	3	0	0	0	36	0	1293
wel25	494	3	283	215	2	13	0	0	192	0	1349
wel27	426	6	260	290	11	130	2	0	133	0	1258
wel29	603	36	151	75	0	197	0	3	401	10	1032

wel30	707	2	145	18	0	314	0	19	139	30	1197
wel36	313	60	335	126	39	397	29	0	92	2	1175
wel37	235	97	131	296	34	45	0	2	193	0	1511
wel38	524	0	116	119	35	258	0	5	121	0	1281
wel42	176	22	114	68	18	80	2	0	260	10	1841
wel48	349	15	167	208	7	30	0	0	292	80	1343
wel60	143	8	183	89	8	15	0	0	122	63	1857
wey2	440	85	210	250	18	179	11	0	217	272	853
wey3	604	57	65	374	0	5	0	0	193	51	1209
wey5	405	41	156	401	0	101	0	0	149	344	757
wey24	372	12	102	233	0	27	0	0	223	240	1312
wey33	477	49	20	37	0	13	4	0	180	240	1550
wey38	742	0	149	105	4	285	2	2	23	0	1280
wey39	492	0	164	180	6	6	0	0	38	0	1714
wey40	417	65	159	112	6	51	0	0	95	21	1666
wey41	354	47	101	74	9	22	0	0	39	62	1844
wey42	862	14	98	123	5	249	0	0	82	23	1118
wey43	771	35	116	92	20	164	0	0	109	30	1255
wey45	527	36	19	19	0	36	21	0	110	437	1344
wey56	451	4	87	42	25	3	1	0	269	236	1465
Group 2											
anc6	330	46	340	267	10	131	0	76	88	0	1282
anc8	533	36	115	266	57	50	0	0	155	0	1353
anc9	339	38	187	334	15	188	0	0	150	0	1347
anc11	275	2	62	120	130	387	0	0	154	60	1374
anc13	690	24	70	125	52	620	0	0	36	0	977
anc15	867	32	69	158	10	376	0	10	66	0	956

anc58	100	0	75	134	58	88	0	0	229	0	1892
anc59	330	50	42	175	72	67	0	0	137	65	1658
anc60	402	37	191	127	83	122	0	2	183	5	1405
wel1	847	93	39	33	8	130	15	35	161	0	1226
wel3	558	57	55	49	0	136	0	0	72	0	1630
wel4	523	58	154	75	0	68	0	0	94	10	1561
wel5	453	24	147	252	17	80	0	0	93	65	1447
wel6	476	95	296	441	15	115	0	0	79	30	966
wel7	611	45	202	281	27	7	15	0	112	35	1139
wel14	470	7	123	238	0	47	0	1	415	0	1284
wel16	482	36	238	259	46	40	10	0	202	115	1149
wel24	487	12	264	252	18	80	0	0	140	15	1323
wel28	550	20	305	229	2	62	0	5	110	0	1234
wel39	260	12	127	308	6	70	0	0	275	3	1435
wel40	462	36	301	215	36	116	7	0	187	23	1140
wel41	233	22	128	181	31	230	0	3	137	94	1515
wel43	221	14	166	78	0	244	0	0	227	234	1362
wel45	249	30	131	69	17	235	17	0	177	124	1475
wel47	576	11	166	45	3	20	0	0	587	80	1027
wel49	215	23	219	7	0	77	0	0	145	7	1821
wel56	250	11	124	156	17	105	0	0	129	52	1733
wel57	84	4	111	149	0	24	0	0	268	30	1872
wel59	216	4	144	177	4	20	0	0	209	15	1775
wel61	195	18	196	39	6	30	1	0	109	12	1914
wel62	419	21	104	51	10	157	2	0	97	121	1549
wey1	701	26	176	135	0	8	0	0	140	81	1197
wey4	952	25	63	133	2	181	0	0	92	564	531

wey23	281	18	98	116	0	1	0	0	187	37	1804
wey25	377	0	174	212	5	175	0	0	416	359	845
wey26	503	11	105	182	0	361	18	4	166	152	1055
wey27	376	164	91	168	6	26	0	0	163	99	1382
wey31	889	107	31	15	0	227	14	0	111	168	1009
wey37	756	7	57	35	1	178	14	52	56	46	1368
wey44	480	10	86	67	0	0	0	0	113	179	1636
wey47	588	90	0	19	0	20	41	12	175	140	1511
wey49	632	88	2	1	0	4	0	0	139	343	1231
wey52	685	2	31	40	0	27	8	2	96	138	1518
wey55	534	16	16	9	0	32	0	9	154	127	1671
wey57	323	22	10	54	0	21	14	21	44	186	1876
Group 3											
anc2	385	24	245	655	20	45	0	0	88	0	1102
anc3	470	27	305	625	5	115	0	0	55	0	981
anc4	327	35	90	60	44	454	25	0	111	0	1432
anc5	275	68	220	650	10	8	0	0	113	0	1228
anc7	265	29	42	347	81	15	0	0	168	16	1613
anc44	231	5	53	152	8	17	1	0	349	0	1758
anc45	132	13	2	30	17	4	0	0	175	10	2132
anc46	115	17	8	21	16	0	0	0	217	0	2087
anc47	82	10	38	198	2	30	0	0	139	10	2088
anc48	170	7	31	32	3	2	0	0	156	0	2186
anc49	139	7	56	187	15	15	0	0	206	10	1956
anc50	125	15	71	336	8	0	0	0	92	0	1953
anc51	74	2	68	245	3	3	0	0	130	0	2068
anc52	52	7	39	126	14	13	0	0	223	6	2120

anc53	167	25	79	156	20	113	0	0	195	10	1822
anc57	103	13	30	179	0	90	0	0	306	34	1827
anc61	192	12	65	52	15	80	0	0	278	4	1877
wel2	634	39	94	41	0	172	0	0	193	0	1369
wel8	470	47	370	212	4	0	0	0	62	10	1362
wel11	434	0	204	400	2	85	4	4	143	33	1258
wel15	460	0	212	323	4	20	0	0	175	0	1374
wel26	717	0	279	172	8	75	0	2	138	0	1149
wel44	515	30	164	137	0	162	0	0	182	0	1252
wel46	169	33	135	48	2	45	0	0	329	98	1690
wel50	239	19	63	170	6	70	0	0	273	25	1696
wel58	150	3	138	168	3	54	0	0	162	76	1780
wel63	429	50	145	300	21	0	0	0	206	0	1375
wey6	205	0	157	199	1	1	0	0	224	144	1662
wey10	204	0	83	53	12	46	0	0	256	196	1698
wey28	669	33	64	12	0	124	0	0	183	213	1280
wey29	592	54	77	4	0	40	0	19	151	232	1376
wey30	897	24	39	18	0	0	0	0	251	195	1128
wey32	428	1	154	132	4	16	0	0	113	166	1501
wey34	382	0	112	132	0	0	0	0	147	28	1751
wey35	294	7	65	15	9	48	0	0	412	376	1335
wey36	526	15	130	0	6	142	14	5	279	29	1420
wey46	385	0	60	74	8	6	0	0	164	120	1773
wey48	488	60	9	9	0	58	43	0	146	305	1465
wey50	676	54	4	3	15	36	0	0	454	112	1230
wey51	426	48	16	8	2	23	0	0	132	135	1765
wey53	586	8	4	26	0	3	5	0	67	30	1843

wey54	526	50	0	0	0	100	9	27	68	167	1499
wey59	689	103	12	0	0	2	2	12	24	29	1676
wey60	409	0	98	132	0	26	0	0	288	497	1143

APPENDIX II

Species richness data 2005. Numbers are rank abundances taken from cover-abundance classes 1-4. An asterisk (*) indicates local rarity.

	Canopy Group			
Bryophytes	**Control**	**1**	**2**	**3**
Aulacomnium palustre	0.04	0.07	0.05	0.13
Barbilophozia hatcheri	0.92	0.57	0.42	0.17
Barbilophozia lycopodioides	0.33	0.21	0.21	0.09
Bryum caespiticium	0.33	0.46	0.79	1.17
Buxbaumia aphylla	0.08	0.00	0.00	0.04
*Ceratodon purpureus	0.04	0.00	0.00	0.00
*Dicranum acutifolium	0.00	0.04	0.00	0.00
Dicranum brevifolium	0.00	0.00	0.32	0.04
Dicranum fragilifolium	0.00	0.11	0.00	0.00
Dicranum fuscescens	0.75	1.11	0.89	0.70
Dicranum muehlenbeckii	0.71	1.07	0.53	0.43
Dicranum polysetum	3.58	3.54	3.42	1.96
Dicranum scoparium	1.79	1.32	0.68	1.17
Dicranum spadiceum	0.00	0.00	0.26	0.04
Dicranum undulatum	0.00	0.14	0.21	0.00
Hylocomium splendens	2.79	1.25	1.53	1.00
Hypnum revolutum	0.04	0.00	0.05	0.00
Lepidozia reptans	0.00	0.00	0.05	0.04
Lophozia longidens	0.04	0.11	0.11	0.00
Lophozia ventricosa	0.71	0.68	0.63	0.39
Pleurozium schreberi	14.71	13.29	8.21	10.26
Pohlia nutans	1.71	2.07	1.74	1.09
Polytrichum commune	0.38	0.14	0.11	0.00
Polytrichum juniperinum	2.29	2.75	2.05	2.09
Polytrichum piliferum	0.00	0.14	0.58	0.13
Polytrichum strictum	0.04	0.11	0.00	0.00
Ptilidium ciliare	1.08	0.36	0.32	0.26
Ptilidium pulcherrimum	2.88	2.14	1.63	1.22
Ptilium crista-castrensis	3.21	1.71	1.00	0.61
Lichens				
Bryoria spp.	0.83	1.00	0.58	0.61
Cetraria ericetorum	3.29	4.93	5.32	6.17
Cetraria islandica	0.38	0.43	0.68	0.78
Cladina mitis	9.54	11.00	10.68	11.30
Cladina rangiferina	1.04	1.71	1.47	1.70
Cladina stellaris	0.08	0.21	0.26	0.17
Cladonia botrytes	0.25	0.18	0.32	0.35
Cladonia cariosa	0.00	0.00	0.16	0.00
Cladonia carneola	0.00	0.04	0.26	0.22
Cladonia cenotea	0.00	0.07	0.47	0.04
Cladonia cervicornis subsp. verticillata	0.21	0.43	0.05	0.09
Cladonia chlorophaea	0.96	1.11	0.84	0.26
Cladonia coccifera	0.04	0.32	0.32	0.22
Cladonia coniocraea	0.46	0.86	0.11	0.26
Cladonia cornuta	1.25	0.96	0.47	0.26
Cladonia crispata	2.33	2.64	0.89	0.78
Cladonia deformis	2.83	3.39	3.42	2.52
Cladonia ecmocyna	3.88	3.46	3.74	3.61
Cladonia fimbriata	1.08	2.04	1.11	1.09
Cladonia furcata	0.04	0.11	0.05	0.35
Cladonia gracilis	3.96	5.29	5.16	4.17

Cladonia multiformis	0.42	1.04	0.95	0.65
Cladonia pleurota	1.96	3.14	4.00	2.87
Cladonia pyxidata	0.00	0.07	0.00	0.00
Cladonia sulphurina	0.67	1.89	1.00	0.43
Cladonia uncialis	0.21	0.14	0.11	0.17
Dactylina arctica	0.00	0.00	0.05	0.04
Flavocetraria cucullata	2.46	3.64	3.26	2.83
Flavocetraria nivalis	0.58	0.75	0.63	1.09
Hypogymnia physodes	2.58	2.54	1.89	2.26
Icmadophila ericetorum	0.13	0.07	0.11	0.22
Letharia vulpina	0.04	0.11	0.05	0.00
Nephroma arcticum	0.00	0.14	0.00	0.00
Nephroma expallidum	0.04	0.18	0.11	0.00
Pannaria pezizoides	0.00	0.07	0.00	0.00
Parmeliopsis ambigua	0.75	1.29	0.68	0.74
Parmeliopsis hyperopta	0.50	0.86	0.53	0.26
Peltigera aphthosa	5.42	5.07	4.42	3.26
Peltigera leucophlebia	0.46	0.14	0.05	0.13
Peltigera malacea	1.00	3.68	1.84	1.22
Peltigera neopolydactyla	0.00	0.07	0.00	0.00
Psoroma hypnorum	0.00	0.14	0.11	0.00
Rhizocarpon geographicum	0.00	0.00	0.11	0.00
Solorina crocea	0.00	0.04	0.00	0.00
Stereocaulon alpinum	0.04	0.21	0.11	0.09
Stereocaulon tomentosum	0.79	2.14	1.89	2.17
Usnea spp.	0.46	0.21	0.16	0.13
Vulpicida pinastri	2.42	2.89	2.47	2.13

Vascular Plants

Achillea millefolium	0.00	0.04	0.00	0.00
Aconitum delphinifolium	0.00	0.29	0.00	0.00
Agoserus glauca	0.00	0.04	0.00	0.00
Arctostaphylos uva-ursi	0.29	0.46	0.00	0.17
Betula pumila	0.00	0.04	0.00	0.09
Calamagrostis canadensis	0.50	0.39	0.42	0.74
Campanula roundifolia	0.00	0.04	0.00	0.00
Cornus canadensis	7.17	7.61	6.26	6.09
Danthonia californica	0.04	0.36	0.53	0.17
Elymus innovatus	0.21	1.79	1.84	0.57
Empetrum nigrum	3.17	3.96	2.89	3.09
Epilobium angustifolium	0.00	0.11	0.16	0.04
Equisetum scirpoides	0.04	0.96	0.11	0.09
Festuca campestris	0.00	0.00	0.11	0.00
Galium boreale	0.00	0.04	0.00	0.00
Geum aleppicum	0.00	0.04	0.00	0.00
Graminoid sp. 1	0.04	0.00	0.00	0.00
Hedysarum alpinum	0.04	0.36	0.00	0.00
Hieracium umbellatum	0.00	0.00	0.05	0.00
Ledum groenlandicum	2.88	2.86	3.89	3.78
Linnaea borealis	3.54	4.64	5.00	3.61
Lycopodium annotinum	0.96	0.64	1.32	1.13
Lycopodium clavatum	0.04	0.04	0.00	0.04
Lycopodium complanatum	0.58	0.82	0.47	0.09
Orthilia secunda	0.00	0.21	0.05	0.09
Orysopsis pungens	0.00	0.21	0.26	0.35
Pedicularis groenlandica	0.00	0.04	0.00	0.00
Pedicularis labradorica	0.08	0.04	0.05	0.04
Petasites palmatus	0.17	0.54	0.00	0.00
Picea glauca	0.29	0.68	0.84	0.48
Pinus contorta	2.17	1.75	1.37	1.35
Potentilla diversifolia	0.00	0.00	0.05	0.43
Pseudotsuga menziesii	0.04	0.04	0.00	0.00
Pyrola asarifolia	0.29	0.00	0.16	0.04
Pyrola chlorantha	0.29	0.21	0.05	0.04

Rosa acicularis	0.29	0.32	0.47	0.48
Rubus acaulis	0.00	0.00	0.00	0.04
Rubus pedatus	0.00	0.07	0.00	0.00
Senecio sp.	0.00	0.04	0.00	0.00
Smilacina stellata	0.00	0.00	0.16	0.00
Spiraea alba	0.00	0.07	0.00	0.00
Vaccinium caespitosum	1.25	2.43	1.84	2.39
Vaccinium membranaceum	6.00	6.46	5.42	6.26
Vaccinium vitis-idaea	13.13	11.82	9.58	9.70
Veronica alpina	0.00	0.04	0.00	0.00
Viola adunca	0.00	0.04	0.00	0.00
Viola sp.	0.00	0.00	0.00	0.04

ANOVA results for environmental measurements.

Table 4.2. Results of repeated measures three-way ANOVA analysis for relative humidity percentages for three microsite plant types under two canopy regimes measured three times in 2005.

Error	Num df	Den df	F	p
Treatment	1	8.37	3.78	0.0860
Plant	1	25.4	16.56	0.0004
Treatment x plant	1	25.4	0.72	0.4048
Time	2	28.3	52.39	<0.0001
Treatment x time	2	28.3	4.63	0.0176
Plant x time	2	28.3	0.90	0.4174
Treatment x plant x time	2	28.3	0.78	0.4690

Table 4.3. Results of repeated measures three-way ANOVA analysis for diazo paper light boxes that measured photosynthetically active light for three microsite plant types under two canopy regimes measured four times in 2004.

Error	Num df	Den df	F	p
Treatment	1	8.31	25.36	0.0009
Plant	2	20.3	4.79	0.0197
Treatment x plant	2	20.3	0.21	0.8135
Time	3	66.6	4.88	0.0040
Treatment x time	3	66.6	1.18	0.3252
Plant x time	6	68.1	0.68	0.6654
Treatment x plant x time	6	68.1	0.59	0.7341

Table 4.4. Results of repeated measures three-way ANOVA analysis for wetted sponge water loss (g) for three microsite plant types under two canopy regimes measured four times in 2004.

Error	Num df	Den df	F	p
Treatment	1	8.15	5.81	0.0419
Plant	2	37.1	0.93	0.4032
Treatment x plant	2	37.1	0.17	0.8467
Time	3	64.9	13.60	<0.0001
Treatment x time	3	64.9	1.59	0.1995
Plant x time	6	69.1	0.48	0.8243
Treatment x plant x time	6	69.1	0.29	0.9400

Table 4.5. Results of repeated measures three-way ANOVA analysis for pine litter in litter traps (m^2) for three microsite plant types under two canopy regimes measured three times from 2004 to 2005.

Error	Num df	Den df	F	p
Treatment	1	7.74	5.82	0.0433
Plant	2	23.4	0.24	0.7876
Treatment x plant	2	23.4	0.99	0.38.75
Time	2	46.7	92.19	<0.0001
Treatment x time	2	46.7	8.30	0.0008
Plant x time	4	48.7	0.29	0.8839
Treatment x plant x time	4	48.7	0.23	0.9210

Table 4.6. Results of repeated measures three-way ANOVA analysis for lichen litter in litter traps (m^2) for three microsite plant types under two canopy regimes measured three times from 2004 to 2005.

Error	Num df	Den df	F	p
Treatment	1	22.3	1.58	0.2222
Plant	2	22.3	0.71	0.5024
Treatment x plant	2	22.3	1.34	0.2831
Time	2	43	1.90	0.1620
Treatment x time	2	43	1.37	0.2639
Plant x time	4	43.5	1.57	0.2114
Treatment x plant x time	4	43.5	3.25	0.0204

Table 4.7. Results of repeated measures three-way ANOVA analysis for moss litter in litter traps (m^2) for three microsite plant types under two canopy regimes measured three times from 2004 to 2005.

Error	Num df	Den df	F	p
Treatment	1	7.74	0.81	0.3941
Plant	2	21.4	4.70	0.0204
Treatment x plant	2	21.4	0.69	0.5115
Time	2	39	3.02	0.0605
Treatment x time	2	39	0.37	0.6921
Plant x time	4	40.9	0.96	0.4413
Treatment x plant x time	4	40.9	0.56	0.6948

Table 4.8. Results of repeated measures three-way ANOVA analysis for debris in litter traps (m^2) for three microsite plant types under two canopy regimes measured three times from 2004 to 2005.

Error	Num df	Den df	F	p
Treatment	1	8.32	1.26	0.2926
Plant	2	16.1	1.05	0.3719
Treatment x plant	2	16.1	0.99	0.3914
Time	2	39	7.40	0.0019
Treatment x time	2	39	0.37	0.6948
Plant x time	4	39.9	0.34	0.8523
Treatment x plant x time	4	39.9	0.42	0.7945

Table 4.9. Results of repeated measures three-way ANOVA analysis for pine pollen found on low and high diaspore traps (cm^2) for three microsite plant types under two canopy regimes measured in 2004.

Error	Num df	Den df	F	p
Position	1	92.3	28.47	<0.0001
Treatment	1	60.2	4.16	0.0457
Position x treatment	1	92.3	0.96	0.3300
Plant	2	60.2	0.01	0.9852
Position x plant	2	92.3	0.38	0.6840
Treatment x plant	2	60.7	0.66	0.5184
Position x treatment x plant	2	92.3	0.12	0.8833

Table 4.10. Results of repeated measures three-way ANOVA analysis for moss spores found on low and high diaspore traps (cm^2) for three microsite plant types under two canopy regimes measured in 2004.

Error	Num df	Den df	F	p
Position	1	76.7	0.15	0.6962
Treatment	1	7.79	0.75	0.4126
Position x treatment	1	76.7	1	0.3207
Plant	2	58.4	0.86	0.4300
Position x plant	2	76.7	0.43	0.6526
Treatment x plant	2	58.4	0.20	0.8186
Position x treatment x plant	2	76.7	1.01	0.3697

Table 4.11. Results of repeated measures three-way ANOVA analysis for fungal spores found on low and high diaspore traps (cm^2) for three microsite plant types under two canopy regimes measured in 2004.

Error	Num df	Den df	F	p
Position	1	87.9	1.35	0.2485
Treatment	1	7.99	8.03	0.0220
Position x treatment	1	87.9	0.32	0.5728
Plant	2	52	1.80	0.1753
Position x plant	2	87.9	2.14	0.1237
Treatment x plant	2	52	3.39	0.0412
Position x treatment x plant	2	87.9	0.45	0.6365

Table 4.12. Results of repeated measures three-way ANOVA analysis for debris found on low and high diaspore traps (cm^2) for three microsite plant types under two canopy regimes measured in 2004.

Error	Num df	Den df	F	p
Position	1	76	13.65	0.0004
Treatment	1	7.91	0.19	0.6750
Position x treatment	1	76	1.00	0.3195
Plant	2	52.8	0.08	0.9226
Position x plant	2	76	0.15	0.8645
Treatment x plant	2	52.8	1.37	0.2621
Position x treatment x plant	2	76	0.67	0.5167

Table 4.13. Results of repeated measures two-way ANOVA analysis for minimum temperatures for three microsite plant types under two canopy regimes measured in 2005.

Error	Num df	Den df	F	p
Treatment	1	134	64.71	<0.0001
Plant	2	134	10.18	<0.0001
Treatment x plant	2	134	10.34	<0.0001

Table 4.14. Results of repeated measures two-way ANOVA analysis for maximum temperatures for three microsite plant types under two canopy regimes measured in 2005.

Error	Num df	Den df	F	p
Treatment	1	77.6	27.87	<0.0001
Plant	2	77.6	2.04	0.1373
Treatment x plant	2	77.6	0.02	0.9840

ANOVA results for reciprocal transplants.

Table 5.6. Results of a two-way ANOVA for establishment canopy cover for moss and lichen dominated plots under two canopy regimes measured in 2003.

Source	df	SS	MS	F	p
Treatment	1	5755.77	5755.77	153.49	<0.0001
Plant	1	38.27	38.27	1.02	0.3244
Treatment x plant	1	15.73	15.73	0.42	0.5246

Table 5.7. Results of the split- split-plot ANOVA for moss establishment (log transformed) on two different substrates, with three propagule plant treatments, under two canopy treatment regimes in 2003.

Error	Num df	Den df	F	p
Dominance	1	17.4	16.38	0.0008
Substrate	1	8.18	6.45	0.0342
Sub x dom	1	8.18	2.02	0.1920
Propagule type	2	13.5	30.26	<0.0001
Prop x dom	2	13.5	2.42	0.1267
Sub x prop	2	20.3	0.49	0.6227
Sub x prop x dom	2	20.3	0.08	0.9257
Treatment	1	17.4	18.39	0.0005
Treat x dom	1	17.4	1.76	0.2017
Treat x sub	1	8.18	0.09	0.0382
Treat x sub x dom	1	8.18	0.18	0.6793
Treat x prop	2	13.5	1.05	0.3770
Treat x prop x dom	2	13.5	1.01	0.3913
Treat x sub x prop	2	20.3	0.70	0.5086
Treat x sub x prop x dom	2	20.3	0.01	0.9906

Table 5.8. Results of the split-split-plot ANOVA for lichen establishment (log transformed) on two different substrates, with three propagule plant treatments, under two canopy treatment regimes in 2003.

Error	Num df	Den df	F	p
Dominance	1	16	5.31	0.0349
Substrate	1	4.77	66.25	0.0006
Sub x dom	1	4.77	0.84	0.4028
Propagule type	2	8.38	111.17	<0.0001
Prop x dom	2	8.38	1.71	0.2380
Sub x prop	2	23.6	4.35	0.0247
Sub x prop x dom	2	23.6	1.62	0.2196
Treatment	1	16	23.76	0.0002
Treat x dom	1	16	0.18	0.6781
Treat x sub	1	4.77	0.26	0.6321
Treat x sub x dom	1	4.77	0.14	0.7269
Treat x props	2	8.38	1.20	0.3485
Treat x prop x dom	2	8.38	2.85	0.1134
Treat x sub x prop	2	23.6	0.92	0.4106
Treat x sub x prop x dom	2	23.6	0.15	0.8632

Table 5.9. Results of the split-split-plot ANOVA for total establishment (log transformed) on two different substrates, with three propagule plant treatments, under two canopy treatment regimes in 2003.

Error	Num df	Den df	F	p
Dominance	1	16	0.53	0.4770
Substrate	1	16	22.83	0.0002
Sub x dom	1	16	1.88	0.1896
Propagule type	2	32	42.28	<0.0001
Prop x dom	2	32	5.57	0.0084
Sub x prop	2	32	14.57	<0.0001
Sub x prop x dom	2	32	1.47	0.2441
Treatment	1	16	1.17	0.2951
Treat x dom	1	16	0.41	0.5302
Treat x sub	1	16	4.43	0.0514
Treat x sub x dom	1	16	0.03	0.8670
Treat x props	2	32	5.63	0.0080
Treat x prop x dom	2	32	1.53	0.2309
Treat x sub x prop	2	32	2.75	0.0787
Treat x sub x prop x dom	2	32	0.04	0.9565

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