TERRESTRIAL LICHEN ABUNDANCE IN RELATION TO STAND STRUCTURE AND SILVICULTURAL HISTORY

ROBIN KUZYK

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TERRESTRIAL LICHEN ABUNDANCE IN RELATION TO STAND STRUCTURE AND SILVICULTURAL HISTORY

By

Robin Kuzyk

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ABSTRACT

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Key Words: Woodland caribou (*Rangifer tarandus caribou* Gmelin), terrestrial lichen, stand structure, prescribed burning, mechanical site preparation.

Terrestrial lichen has been identified as an important factor contributing to suitable woodland caribou (*Rangifer tarandus caribou*) winter habitat. Conservation efforts to maintain viable populations of woodland caribou in areas where forest management activities take place will require an understanding of the forest conditions that promote suitable habitat characteristics.

Two studies were conducted for this thesis. In the first study, terrestrial lichen abundance and stand structure of naturally disturbed and previously harvested forest stands in northwestern Ontario were measured. Terrestrial lichen abundance (% cover) was relatively low and highly variable, but significantly higher in conifer-dominated (4.28 ± 6.83%), than in deciduous (0.60 ± 1.51%) or mixedwood (0.62 ± 1.01%) stands. No significant difference in lichen abundance was found between naturally disturbed (3.14 ± 5.77%) and previously harvested stands (3.41 ± 6.53%). Lichen abundance was significantly greater in stands with non-organic (5.71 ± 7.75%), rather than organic (2.07 ± 4.14%) soil textures. Among non-organic conifer-dominated stands, negative relationships were observed between lichen abundance and canopy closure, basal area, tree height and crown height.

In the second study, terrestrial lichen abundance was compared in twenty-four 20 to 40 year-old stands, previously treated with prescribed burning (PB) or mechanical site preparation (MSP). T-test and Mann-Whitney U test results indicated no strong difference in terrestrial lichen abundance between PB (8.95 ± 8.45%) and MSP (2.37 ± 2.03%) treatments, though confounding effects of dominant tree species composition may have contributed to this result. Among the stand structural characteristics measured, canopy closure exhibited the strongest negative relationship with lichen abundance. Negative relationships were also observed between lichen abundance and crown height and basal area.

The results of this study indicate that terrestrial lichen abundance is difficult to predict in conifer-dominated stands of northern Ontario. Terrestrial lichen abundance is strongly correlated with overstory structural attributes, which suggests that forest management activities could potentially influence terrestrial lichen abundance by manipulating stand structure to create understory light conditions that are favourable to terrestrial lichen establishment and growth.

CHAPTER ONE: INTRODUCTION TO THESIS

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1.1 INTRODUCTION

The occupation of forests in northern Ontario by woodland caribou (*Rangifer tarandus caribou* Gmelin) has declined significantly since European settlement (Vors et al., 2007). In Canada, the boreal population of woodland caribou was designated as threatened in May of 2000 and re-confirmed in May of 2002 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). In Ontario, woodland caribou are also listed as a threatened species under the *Endangered Species Act* (2007, c.6, Sched. 4).

Habitat alteration due to forest operations is cited as a factor contributing to the decline of woodland caribou (Courtois et al., 2008) and the development of strategies to sustain woodland caribou populations in commercial forests continues to be a major challenge in forest management (Cumming, 1992; Ontario Woodland Caribou Recovery Team, 2008). The ability to understand and identify caribou habitat requirements is essential to caribou conservation in managed forests (Sorensen et al., 2008; Johnson et al., 2003).

Woodland caribou prefer stands of mature to old forest (Hins et al., 2009; Sorensen et. al., 2008) and are unique from other ungulates in that their winter diet consists significantly of lichens (Johnson et al., 2001; Storeheier et. al., 2002). Lichens account for approximately 90 percent of caribou diet during winter, and up to 50 percent of caribou diet during the summer (Brodo et al., 2001). Many lichen species of importance to woodland caribou are considered more abundant in older forest conditions (Arseneault et al., 1997; Rolstad et al., 2001; Boudreault et. al., 2002), and are associated with coniferous forests in particular, where they constitute a large portion of the total understory biomass (Pharo & Vitt, 2000). The abundance of lichen species, both terrestrial and arboreal, has been described as an important, and even critical component of the winter habitat of *Rangifer* species throughout the northern hemisphere (Terry et al., 2000; Serrouya et al., 2007; Storeheier et al., 2002; Sulyma & Alward, 2004). Observed behaviour of

woodland caribou indicates a preference for forest types that support abundant lichen communities (Johnson et al., 2001; Briand et al., 2009).

Winter foraging behaviour of woodland caribou varies across North America (Cumming, 1992) and is likely a function of forage abundance and accessibility (Johnson et al., 2001). In western Canada, observations of woodland caribou indicate foraging of both arboreal and terrestrial lichen species, the preference for which is partly dependent on snow conditions (Johnson et al., 2001). Deep snow limits foraging of terrestrial lichen, and in such conditions caribou may feed more often or exclusively on arboreal lichens (Kinley et al., 2003). In eastern Canada, woodland caribou have been observed to select habitats with higher terrestrial, rather than arboreal, lichen abundance (Briand et al., 2009). This difference in forage preference may be due to increased accessibility to terrestrial lichen in eastern Canada, where average snow depth is more shallow (National Climate Data and Information Archive, www.climate.weatheroffice.gc.ca), or may simply be due to higher available biomass of terrestrial lichen relative to arboreal lichen in eastern Canada (Briand et al., 2009). In Ontario, observations of woodland caribou seem to indicate a preference for terrestrial lichen, even in areas where both arboreal and terrestrial lichen are abundant (Ahti & Hepburn, 1967).

Several lichen species have been identified as being of particular importance to woodland caribou diet. Terrestrial lichen species commonly referred to as "reindeer lichens" or "caribou lichens" include species of *Cladina*, such as *C. arbuscula*, *C. mitis*, *C. rangiferina* and *C. stellaris*. Species of *Cladonia*, where abundant, are also considered important grazing material for woodland caribou (Brodo et al., 2001). These species include *C. amaurocraea*, *C. gracilis*, and *C. uncialis* (Brodo et al., 2001; Colpaert et al., 2003). Foam lichens – species of the genera *Stereocaulon* – are an important part of caribou winter diet, particularly in parts of the boreal forest where they replace *Cladina* species as the dominant ground cover (Brodo et al., 2001). In addition to the terrestrial lichen species mentioned, species of *Cetraria*, *Peltigera*, and *Thamnolia* have also been observed in relation to woodland caribou forage selection (Johnson et al., 2001). Arboreal lichen

species considered most important to woodland caribou include pendent, hair-like species that grow on tree branches and trunks. These include species of the genera *Usnea*, *Evernia*, *Alectoria* and *Bryoria* (Cumming, 1992; Colpaert et al., 2003; Johnson et al., 2001; Serrouya et al., 2007). Of lesser importance to caribou, but worthy of mention are foliose lichens including *Hypogymnia physodes*, *Tuckermannopsis ciliaris*, and *Lobaria pulmonaria* (Brodo et al., 2001).

Numerous studies have been conducted throughout the world in attempts to understand the relationships between forest conditions and the abundance or diversity of terrestrial and arboreal lichen species. The focus of the research described in this thesis is to understand how forest stand structure is related to terrestrial lichen abundance in northern Ontario, and how forest management can alter the stand structural attributes considered important to terrestrial lichen. Recent radio-collar location data collected by the Ontario Ministry of Natural Resources, and reports from forest users (Racey et al., 2008, unpublished) indicates the re-occupation of woodland caribou in previously harvested stands. This suggests there are important characteristics in these areas and that there is potential for forest management activities to create stand structural conditions favourable to woodland caribou habitat. Forest management activities including silviculture could have a positive influence on the abundance of terrestrial lichen and hence increase the habitat value of previously harvested forest stands.

The general approach to this research was:

i. to examine terrestrial lichen abundance in relation to a variety of stand structural attributes in stand types representative of northern Ontario, and

ii. to explore whether forest management activities can have an effect on the regeneration of terrestrial lichen at the stand level through the application of silvicultural treatments.

The following includes a summary of existing literature pertaining to these subjects and descriptions of two projects that were undertaken to meet the objectives of the study.

1.2 Objectives of the Study

The first objective of this research was to identify stand structural characteristics associated with terrestrial lichen abundance and to understand the relative importance of these characteristics in contributing to this particular habitat value. To meet this objective, stand structural characteristics were measured in stands either previously harvested or naturally disturbed from two study areas located east of Lake Nipigon and northwest of Pickle Lake, in northwestern Ontario. These characteristics were compared with stand-level estimates of terrestrial lichen abundance to determine whether relationships existed between the variables. Terrestrial lichen abundance was compared between previously harvested and naturally disturbed stands, and compared among conifer, deciduous and mixedwood cover types.

The second objective of this research was to investigate the impact of different silvicultural treatments on abundance of terrestrial lichen in order to explore whether silviculture could be used to promote the establishment and persistence of terrestrial lichen communities. To meet this objective, terrestrial lichen abundance was measured and compared in forested stands previously treated with mechanical site preparation and prescribed burning in a study area located east of Lake Nipigon. Measured stands were also described in terms of their stand structural characteristics in order to help explain any observed differences in terrestrial lichen abundance between the two treatment types.

1.3 Literature Review

A review of the literature was conducted to identify the stand structural attributes associated with terrestrial lichen abundance. Many studies have investigated the forest stand structural characteristics associated with the biomass (Stone et al., 2008), abundance (Price & Hochachka, 2001) or diversity (Moning et al., 2009) of lichen species. Although this particular research project pertains to the stand structural conditions affecting the establishment of terrestrial lichen species, relevant literature contributions regarding arboreal lichen should be

mentioned as these help to highlight the full range of stand level factors important to lichen establishment and growth. Available literature on studies of the effects of forest management, silvicultural practices and fire disturbance on terrestrial lichen abundance was also reviewed. Knowledge gaps in the existing literature are addressed in this review.

1.3.1 Terrestrial Lichen in Relation to Stand Structure

For this research project, stand structure is the term used to describe a range of aspects of the stand environment, including the composition and structural characteristics of forested stands, and biotic and abiotic characteristics that may have a relationship or association with terrestrial lichen abundance. These aspects may include stand level characteristics such as stand age or time since disturbance and the extent to which residual trees, or patches of trees within stands are fragmented or retained after such disturbances. Elements of stand structure also include individual tree characteristics such as tree species composition, density and basal area; and structural attributes such as the amount and quality of dead wood in the form of snags, stumps and logs. Site characteristics including canopy closure and cover of understory vegetation are also used to describe stand structure. Forest floor attributes such as soil texture and moisture conditions are stand structural elements that may be estimated through ecological land classification measurements. Attributes such as site quality, topography, climate, and microhabitat characteristics may also be considered components that may influence terrestrial lichen abundance and be used to characterize stands.

In this study, stand structural characteristics were distinguished into two groups based on the capacity for forest management activities to have an influence on them. Characteristics such as stand age, tree species composition and basal area were considered to be attributes that can be manipulated by forest management through such measures as length of harvest rotation, tree species planted, and amount of structural retention post-harvest, respectively. Characteristics such as climate, topography, and microhabitat features such as percent cover of bedrock are considered to be attributes that cannot be manipulated or adjusted through forest

management activities. These types of attributes therefore represent limitations with respect to the extent that forest management can influence terrestrial lichen abundance in managed stands.

1.3.1.1 Canopy Structure and Composition

Lichens function in much the same way as green leafy plants in that they require light in order to photosynthesize and grow (Brodo et al., 2001). Perhaps the most important factor governing the understory light conditions available to terrestrial lichen species is the forest canopy. Forest canopy structure controls light quantity and quality, and plays an important role in determining moisture and temperature conditions at the forest floor (Jennings et al., 1999). Canopy structure is thus a major factor in determining the habitats of lichen species since optimal light levels for photosynthesis vary from species to species (Brodo et al., 2001).

Canopy closure and canopy cover are two common indicators of canopy structure; with direct and indirect methods for their measurement having been developed for each (Jennings et al., 1999). A study conducted by Gauslaa et al. (2007) involved image analysis of hemispherical digital photographs in order to quantify canopy cover indirectly. In this study, the influence of canopy cover on the growth of old-forest lichen species was investigated. They found that the foliose lichens *Lobaria pulmonaria* and *Pseudocyphellaria crocata* exhibited limited growth in low light conditions with *L. pulmonaria* showing the fastest growth in forests with more open canopies. This study also showed that for the arboreal lichen species *Usnea longissima*, mean dry matter gain was close to zero in shadiest forest conditions but showed an increase in more open conditions. Most terrestrial lichen species of importance to woodland caribou are associated with open canopy conditions, many of which are found to occupy sites exposed to full sunlight (Brodo et al., 2001). Pharo and Vitt (2000) found significantly greater terrestrial lichen cover among the 10% most open sites, compared with the 10% most dense sites measured in *Pinus contorta* stands of Alberta. With respect to caribou winter habitat in Ontario, satisfactory lichen supplies are thought to occur in stands with canopy closure values of 70% or less (Racey et al., 1991).

Canopy light conditions have also been shown to affect lichen species diversity. In the Bavarian Forest National Park in southeastern Germany, Moning et al (2009) found that open canopy structures affected total diversity of lichen species positively. The authors of this study provided management recommendations to create a considerable number of stands with a canopy cover of less than 50% in order to maintain lichen diversity in that forest. In spruce and pine plantations in Britain, lichen species richness was negatively correlated with the vertical cover index, a unified measure of stand structure that takes into account the percent cover of the various vegetation strata (Humphrey et al., 2002).

Stand density, the number of standing trees per hectare, is a major aspect of canopy structure and has been observed to have a strong relationship with terrestrial lichen abundance (Dettki and Esseen, 1998). The measure of stand basal area is related to stand density (Husch, Miller & Beers, 1982) and is also a function of tree size distribution. In general, basal area per hectare increases with stand age (Hilmo et al., 2009) while stem density tends to decrease over the rotation age of the stand (Coxson & Marsh, 2001). Both metrics have an obvious influence on forest canopy closure as they affect the amount of light penetration to the forest floor. Many studies have used such canopy characteristics as a means to explain the observed variability in terrestrial and arboreal lichen abundance and diversity. In a study conducted in lodgepole pine forests of British Columbia, Coxson and Marsh (2001) found the stand structural factors that best correlated with terrestrial lichen mat development were tree density, basal area and canopy cover. In their study, *Cladonia* species showed their greatest percent cover in stands aged 0 to 50 years old – a time frame during which stands thin and light reaches the forest floor (Coxson & Marsh, 2001). A study conducted by Lesmerises et al. (2011) in spruce-dominated stands of northern Quebec found that lichen occurrence was negatively correlated with stand age and tree density. The observed decrease in lichen occurrence was attributed to light reduction at the ground layer and the accumulation of organic detritus (Lesmerises et al., 2011). In the pine-lichen woodlands of north-central British Columbia, Sulyma and Coxson (2001) found higher reindeer

lichen cover on microsites with lower leaf area index (LAI) values. The LAI values were highly correlated with stand structural variables including basal area (Sulyma & Coxson, 2001). Humphrey et al. (2002) also found negative correlations between lichen species richness and the stand structural attributes, height to live crown and LAI. In contrast to these studies, Dettki and Esseen (1998) found positive correlations between lichen abundance and estimates of stem density and basal area. They suggested confounding effects of elevation and tree species composition between study sites as a potential explanation for this result.

Terrestrial lichen is associated with other structural elements of the canopy including height of overstory trees and height to the lowest live tree branches, or crown height. Lesmerises et al. (2011) found a negative relationship between lichen occurrences and stand height in boreal spruce forests of Quebec. Lower lichen cover associated with reduced light conditions in dense stands also coincided with an increase in the height of live crown in *Picea abies* forests of central Norway (Hilmo et al., 2009). Remote sensing techniques have also incorporated measurements of canopy height to estimate lichen and feathermoss cover, as demonstrated by Peckham et al. (2009) who found feathermoss and lichen communities to be associated with a specific foliage height profile.

Tree species composition has been shown to influence the occurrence of lichen species in forested stands. Moning et al (2009) found that the availability of sycamore maple in the Bavarian Forest National Park in southeastern Germany had a positive effect on lichen diversity. In black spruce stands in the Abitibi region of Quebec , lichen richness was found to be higher in sites where trembling aspen and jack pine were present (Boudreault et al., 2002). Spruce trees served as the main substrate for macrolichens in Norwegian coastal spruce forest, however *L. pulmonaria*, *L. scrobiculata*, and *Nephroma* spp. preferred deciduous trees in that particular forest type (Rolstad et al., 2001).

1.3.1.2 Stand Age

Stand age, or time since harvest or fire disturbance, is recognized as having a strong relationship with the abundance of lichen in forested ecosystems (Arseneault et al., 1997; Hilmo et al., 2011; Lesmerises et al., 2011). Lichens are characteristically slow-growing organisms (Kumpula et al., 2000), with growth rates of some species amounting to only a few millimetres each year (Brodo et al., 2001). Since stand-replacing disturbances such as forest harvest and fire often destroy terrestrial lichen communities (Morneau & Payette, 1989; Arseneault et al., 1997) it is understood that old-growth forests can often support a higher abundance of, and more diverse lichen communities than younger forests (Rolstad et al., 2001).

Berryman & McCune (2006) found that biomass of arboreal lichen in forests of western Oregon was lowest in even-aged young stands and highest in mature stands with remnant trees and in old growth. In a study conducted in stands aged 80 to greater than 200 years old, Boudreault et al. (2002) found that epiphytic lichen abundance increased with stand age. Pharo and Vitt's (2000) study conducted in *Pinus contorta* stands in the eastern Rocky Mountains of Alberta also found there to be an association between caribou lichen cover and older trees. Stand age was a significant factor governing probability of lichen species occurrence in *Picea abies* forests of central Norway, though relationships with time since disturbance differed by lichen species (Hilmo et al., 2011). In a quantitative review of studies on lichen response to disturbance, Johansson (2008) found that lichen recovery following disturbance differed by lichen functional group. High abundances of cyanolichens were generally found to not occur for more than 300 years, while alectorioid lichens appeared to take 200-300 years before reaching high abundances following disturbance (Johansson, 2008). In his review Johansson postulated that time since disturbance is often confounded with disturbance type, as older forests often represent those originating from natural disturbance, while previously harvested forests often represent the younger early successional forests studied.

Structural attributes that vary with stand age and disturbance may explain why some studies have found older forests to be no more abundant or diverse in terrestrial lichen than younger forests (Lesmerises et al., 2011). Lõhmus and Lõhmus (2007) found no significant difference in lichen community characteristics between first-generation afforested lands and managed long-term forest lands in Estonia. This was partly attributed to the relatively low cutting intensity in the new forests, aiding in the retention of old-forest substrates available for lichens. Lower lichen cover observed in late successional forests in central Norway was thought to be due to reduced light conditions in the canopies of older stands (Hilmo et al., 2009). The results of this study indicated foliose lichen cover to have a nearly unimodal response to stand age, with middle-aged plantations having the highest cover of epiphytic lichens.

Lichen species richness is not necessarily always greater in older forests (Johansson, 2008). In planted spruce and pine forests in Britain, early successional stands were found to have the highest lichen species richness due to the presence of stumps found important to *Calicium* and *Cladonia* species (Humphrey et al., 2002). In mature to old-growth forests in Ontario and Quebec, Boudreault et al. (2002) found that old growth forests had no more species than younger forests. In their study, availability of microhabitats suitable for lichen colonization was observed to decrease with time since fire, possibly as a result of paludification. Lichen species composition appears to follow a successional sequence after disturbance, with dominant species being replaced with more competitive species over time (Morneau & Payette, 1989; Arseneault et al., 1997). Morneau and Payette (1989) found crustose lichens to be among the first lichens to colonize post-fire spruce stands in northern Quebec. Fruticose lichens including species of *Cladonia* and *Cladina* then gradually increased in coverage, with *Cladina mitis* reaching maximum coverage 65 years after disturbance, and *Cladina stellaris* eventually dominating stands about 130 years after disturbance. Similar post-disturbance patterns were observed by Arseneault et al. (1997), who found cup-shaped lichens of the genus *Cladonia* to be frequent in stands aged 1 to 30 years. Species including *Cladonia crispata*, *Cladina mitis* and *C. stellaris* dominated stands 31 to 50

years of age, and after 90 years *C. stellaris* became the most important part of the lichen mat (Arseneault et al., 1997).

1.3.1.3 Understory Structure and Composition

Associations between terrestrial lichen abundance and other vegetation have been observed. Certain lichen species demonstrate a preference for the unique habitat niche provided by younger shrub vegetation found in the understory. Alder, for example, was the preferred substrate of *L. pulmonaria*, *L. scrobiculata*, and *Nephroma* spp. in a study conducted in central Norway (Rolstad et al., 2001). In a study conducted in the Scottish highlands, Fryday (2001) found terricolous lichen vegetation to be associated with specific heath communities, but noted that lichens are generally sparse in homogeneous stands of vascular plant vegetation whereas lichen-rich areas are often associated with sparsely distributed vascular plants.

In forested ecosystems, the amount and composition of understory cover can have an inhibiting effect on the presence of terrestrial lichen. In the Castlewood Lake area in northern Ontario, higher abundances of terrestrial lichen were observed under shrub layers that were sparse, with less balsam fir and ericaceous species (Racey et al., 2008, unpublished). Pharo and Vitt (2000) found the strongest predictor of terrestrial lichen cover to be bryophyte cover. In their study, lichen cover was found to have a strong negative relationship with bryophyte cover; this was attributed to higher competition with bryophyte species under lower light conditions due to increased canopy density. Similar observations were made by Sulyma and Coxson (2001) who determined that competitive interactions between lichen and feather moss mats were linked to canopy structural variables, which govern light and moisture conditions at the forest floor.

Understory species composition can contribute to further ecological interactions, with consequences on the population dynamics of wildlife species such as woodland caribou. A study conducted in the Laurentian hills of Quebec found that regenerating stands (6-20 years old) rich in fruit-producing vegetation were frequently selected by black bears (Brodeur et al., 2008). The

authors posed this as a concern for forest-dwelling woodland caribou given that black bears are opportunistic predators of this species.

1.3.1.4 Forest Floor and Microhabitat Characteristics

Microhabitat characteristics at the forest floor level are important correlates of terrestrial lichen abundance, with most lichen species showing specific preferences for certain soil, moisture and substrate conditions (Brodo et al., 2001).

Soil texture – used to describe classes of soils based on proportions of sand, silt and clay – is directly related to soil drainage, with coarser textured soils such as sands able to drain water more rapidly than finer textured soils such as clays (OMNR, 2010). Lichen-rich forests in northwestern Ontario are generally associated with sites that have shallow soils or well-draining soil textures such as coarse to fine sands (Harris, 1996). In sub-boreal spruce forests of central British Columbia however, terrestrial lichen cover was found significantly higher on fine-textured soils than on coarse-textured soils, possibly due to the fact that the fine-textured sites had shorter canopies and less shrub cover than coarse-textured sites (Botting & Fredeen, 2006). Land cover associations between terrestrial lichen cover and drier, sandy, upland locations have been detected at a sub-metre scale using satellite-based remote sensing technology (Rapalee et al., 2001). Soil and organic depth may be suitable indicators of terrestrial lichen abundance given that these characteristics represent the historical accumulation of organic litter from vascular plants which would compete with lichen for growing space and light. In the Castlewood Lake area of northern Ontario, a lower incidence of terrestrial lichen was found on moderately deep soils (30-70 cm) which had balsam fir, ericaceous shrub and broadleaf litterfall (Racey et al., 2008, unpublished). In mature and old growth spruce stands of northern Ontario and Quebec, lichen species *Cladina rangiferina* and *C. stygia* showed a preference for sites with high organic matter depth, however these sites were also among the oldest measured (Boudreault et al., 2002). Site productivity may be another factor related to terrestrial lichen abundance, as lichens are poor competitors compared to vascular plants, and are generally not found on richer sites (Harris,

1996). In aspen stands of northeastern British Columbia, Boudreault et al. (2008) found epiphytic lichen diversity to be related to a site productivity gradient, with less productive sites dominated by crustose lichens, and more productive sites dominated by mosses.

Lichens grow on a wide variety of substrates including wood, rock, soil and other vegetation. Substrate characteristics considered to be most important to lichen establishment include texture, moisture retention, and chemistry (Brodo et al., 2001; Nascimbene et al., 2008; Leppik et al., 2011). Lichens are able to persist in a diversity of habitats and have the ability to occupy substrates that are generally unsuitable for other plant species. In the Auden Forest of northwestern Ontario, stands with extensive rock outcrops were among those with the highest cover of *Cladina* spp. in previously harvested stands (Harris, 1996). Other terrestrial lichen species of importance to woodland caribou that are known to inhabit rock substrates include *Cladonia uncialis* and certain species of the genus *Stereocaulon* (Brodo et al., 2001).

Several studies have found dead wood in the form of standing dead trees (snags) or coarse woody debris at various stages of decay, to be related to lichen abundance or diversity. Rheault et al. (2009) demonstrated that forest structure is a good indicator of lichen species diversity in old growth forests, with the association of epixylic lichens being mainly due to better moisture conditions and the presence of greater amounts of coarse woody debris. Similar findings were reported by Moning et al. (2009), who found structural features such as the availability of dead wood to be most important in enhancing lichen diversity. Berryman & McCune (2006) found that stands with remnant trees had greater arboreal lichen biomass than even-aged stands. Different lichen communities are found in association with coarse wood of different decay classes. Lichen communities found on moderately decayed logs tend to be the most diverse (Bunnell et al., 2008; Caruso & Rudolphi, 2009; Nascimbene et al., 2008; Pharo & Vitt, 2000). The presence of stumps, in particular seems to have a strong association with the diversity of lichen communities. Humphrey et al. (2002), found stumps to be of special importance to *Cladonia* and *Calicium* lichen species in a study conducted in planted and

unmanaged forests in Britain. Caruso & Rudolphi (2009) found increased lichen richness on taller stumps and stumps that had more surface structural variety.

1.3.1.5 Topography

Topographical features such as slope, aspect and elevation also influence terrestrial lichen abundance, with *Cladina* spp. in northern Ontario often found in great abundances on upper slopes with south-facing exposures (Harris, 1996). Slope and elevation were among the variables measured by Berryman & McCune (2006) in a study that found cyanolichen biomass to be highest at low elevations, while forage lichen biomass was higher at high elevations. In a coastal spruce forest in central Norway, lichen species *F. ahlneri* and *P. crocata* were found significantly more abundant in ravine bottoms, while *Platismatia norvegica* was more abundant on slopes and plateaus (Rolstad et al., 2001). Pharo and Vitt (2000) found greater lichen cover at sites of higher elevations, while Lesmerises et al. (2011) found that lichen biomass was partly a function of altitude. Factors related to local climate may also influence lichen communities. Lichen species richness was found to be greater in northern and western stands that were more moist, compared with drier, more southerly stands in spruce and pine plantations in Britain (Humphrey et al., 2002).

1.3.2 Terrestrial Lichen in Relation to Forest Disturbance

Several studies have investigated the response of lichen communities to forest management-related disturbances including forest harvest and silviculture operations (Coxson & Marsh, 2001; Roturier et al., 2011), as well as their response to natural disturbances such as fire (Morneau & Payette, 1989; Johansson et al., 2006). The boreal forest is characterized as a fire-driven ecosystem (Klein, 1982; Mack et al., 2008), and natural disturbance-based management strategies applied in the boreal forest attempt to emulate fire disturbance as a means of sustaining natural ecosystem function (Kuuluvainen & Grenfell, 2012). With respect to woodland caribou, large-scale disturbances are generally considered to have a negative impact on winter habitat since terrestrial lichens are extremely vulnerable to mechanical damage (Courtois, 2008) and

burning (Morneau & Payette, 1989; Cumming, 1992); not to mention the effects these disturbances have on the spatial configuration of habitat types that affect populations at the landscape scale (Hins et al., 2009; Courtois et al., 2007). On the other hand, fires are natural processes (Arseneault et al., 1997) that control long-term productivity of the boreal forest, which is also considered essential to caribou conservation (Klein, 1982). In light of this, the merits of using prescribed burning as a means of mimicking natural fire processes to improve caribou habitat have been debated in the literature (Cumming, 1992; Harris, 1996; Racey et al., 1996).

With recent evidence of woodland caribou re-occupation of previously harvested stands (Antoniak, 1993), it is important to understand how both harvest and fire disturbances impact the stand structural conditions important to terrestrial lichen abundance.

1.3.2.1 Forest Harvest and Silviculture

Many studies relating forest management activities to lichen communities have dealt with various aspects of overstorey tree removal, including timing of harvest, frequency of harvest (or rotation age), and amount of biomass removed during harvest. Esseen et al (1996) suggested that an extension of the rotation age could lead to an increase in epiphytic lichen biomass in managed stands, as this would allow more time for lichens to colonize and grow. A prolonged rotation was also suggested by Hilmo et al. (2011), as this would increase the probability of lichen recruitment and promote dispersal to nearby regenerating forest.

Abundance of epiphytic chlorolichens was found to vary by species and by logging strategy in a study conducted by Hilmo et al. (2005). The lichen species *Cavernularia hultenii* was found most vulnerable to logging, with significantly lower abundance in logged versus control areas. In northern Sweden, both lichen species richness and abundance were negatively correlated with the number and basal area of cut stumps in harvested stands (Dettki & Esseen, 1998). Rolstad et al. (2001) found no significant effect of harvest volume on post-harvest lichen abundance, but suggested that the impacts of logging could have been mitigated by pre-harvest conditions that facilitated lichen dispersal, such as the amount of older forest and availability of

remnant trees in logged areas. Harris (1996) made a similar conclusion that recovery of *Cladina* spp. biomass was due to the presence of residual lichens post-harvest in Ontario. Different harvest systems were found to have various impacts on terrestrial lichen cover 3 years post-harvest in boreal Manitoba, with both cut-to-length and full-tree systems resulting in lower lichen cover than the control (unharvested) treatment (Kembel et al., 2008).

Variable retention harvests have been proposed as possible means to retain the structural features necessary to promote the establishment and persistence of lichen (Rolstad et al, 2001; Lohmus & Lohmus, 2008; Pharo & Vitt, 2000). Different methods of tree harvest such as partial harvest and single tree selection harvest can alter light conditions and promote increases in dead wood volumes, resulting in forest floor conditions that are favourable to terrestrial lichen establishment (Harris, 1996; Humphrey et al., 2002). A study conducted in balsam fir stands on Québec's Gaspé Peninsula indicated that logging activities resulted in direct losses of arboreal lichen biomass, but that careful selection cutting techniques could retain substantial lichen biomass post-harvest (Stone et al., 2008). In British Columbia, Coxson et al. (2003) compared arboreal lichen abundance among stands treated with group selection, single-tree selection and partial cut harvests. They found that partial cut treatments did not have a significant effect on lichen abundance suggesting that such treatments can maintain short-term lichen and associated forage values for caribou. In west-central British Columbia, terrestrial lichen abundance was compared among group selection, and whole-tree and stem-only shelterwood treatments (Waterhouse et al, 2011). In that study, terrestrial lichen under the group selection treatment recovered to pre-harvest amounts, while lichen in shelterwood treatments recovered to about 70% after 9 years. Caruso (2008) investigated the effects of whole-tree harvesting on lichen diversity in a study conducted in south central Sweden. He found that the majority of lichen species assessed were found more frequently on stumps, highlighting possible implications on biodiversity that could result from stump removal in harvesting systems.

Many studies have suggested the application of pre-commercial harvest strategies as a means of retaining the stand structural conditions required for lichen growth. In jack pine and black spruce stands of northwestern Ontario, Harris (1996) looked at effects of pre-commercial thinning (PCT) on the cover of *Cladina* lichen species. He found lichen stocking and cover to be higher in sites subjected to PCT compared to that of unthinned portions of the same stand. The author suggested that canopy closure contributed to this observed difference. Similar conclusions were reached by Coxson and Marsh (2001), who postulated from their data on winter harvest plots that lichen succession to feathermoss mats could be reversed or slowed down by the removal of the overstorey canopy. Based on observations of abundant terrestrial lichen in open, undisturbed forests, Pharo and Vitt (2000) hypothesized that selective harvesting could succeed in producing greater abundance of caribou lichen by opening the canopy enough to cause substantial mortality of feather-mosses.

The impact of forest management activities on terrestrial lichen abundance appears to depend partly on the degree of soil disturbance that occurs during forest operations. Soil disturbance could potentially have an even greater impact on regenerating understory communities than canopy structure (Fleming & Baldwin, 2008). Harvesting during winter months may help to minimize negative impacts of soil disturbance (Sulyma & Alward, 2004; Harris, 1996). Terrestrial lichen cover in *Pinus contorta* stands in British Columbia was found higher in winter-harvested stands, than in summer-harvested stands presumed to have undergone greater soil disturbance (Coxson & Marsh, 2001). Activities that reduce the depth of the organic soil layers could also promote the establishment of terrestrial lichen. In previously harvested stands near Lucy Lake, Ontario, terrestrial lichen was found most prevalent on the tops of cut stumps, and on tertiary haul roads where the humus layer had been scraped clear to facilitate truck access (Racey et al., 1996). Organic mat displacement was thought to be one potential advantage of summer harvests that could contribute to longer-term establishment of lichen communities (Sulyma & Alward, 2004).

Mechanical site preparation (scarification) is a common practice used to facilitate regeneration by reducing vegetative competition and increasing mineral soil exposure after harvest (Sutherland & Foreman, 1995). This type of disturbance may favour the establishment of species better adapted to exposed mineral soil, and reduce the abundance of terrestrial lichen (Kembel et al., 2008). Light scarification methods which minimize disturbance of the soil surface have been recommended in order to protect terrestrial lichen. Harris (1996) suggested the use of a spiked anchor and chains or Bracke, as opposed to using barrels which were considered to cause more damage. In a study conducted in *Pinus*-lichen stands in northern Sweden, effects of disc-trenching were compared with a "HuMinMix" treatment that mixed upper soil layers with the existing lichen mat (Roturier et al., 2011). The "HuMinMix" treated stands exhibited higher re-establishment rates of reindeer lichen species, owing to the effectiveness of the treatment to immobilize lichen fragments for dispersal.

1.3.2.2 Fire

Since fire plays a major role in the succession of unmanaged boreal forests (Boudreault et al., 2009), it is logical that post-fire stand structure and composition is often compared to that which is generated post-harvest in boreal forest ecosystems. With respect to terrestrial lichen, the literature suggests the role of fire can be either beneficial or detrimental to lichen communities depending on ecosystem type and fire characteristics. Klein (1982) made the distinction between short- and long-term effects of fire on lichens as caribou forage; arguing that in the short-term, fire indeed has detrimental effects on forage lichens but that in the longer term fire is essential in maintaining ecological diversity and forage production for caribou. Existing literature reveals that factors such as time since fire, fire intensity and other indirect effects of fire related to changes in the understory all have effects on terrestrial lichen communities. Attributes such as lichen growth form, dispersal mechanism and habitat preference also govern post-fire abundance or diversity of lichen species (Johansson et al., 2006).

In the peatlands of northern Alberta, terrestrial lichen recovered relatively quickly after fire disturbance, with comparable cover estimates observed in mature (> 70 years) sites and those aged only 40 years (Dunford et al., 2006). This recovery rate was attributed to higher than average lichen growth rates that the authors suggested was a function of an elevated peat substrate thought to provide a drier, more favourable microsite condition for lichen growth. In southeastern Manitoba, recently burned habitats exhibited a decline in the quality of *Cladina* spp. lichens compared to old-growth (90 years) stands (Schaefer & Pruitt, 1991). Morneau and Payette (1989) found most lichen species to recover only 14 years after fire, though *Cladina* spp. did not begin to dominate the understory until 38 years after fire in their study in northern Quebec.

Johansson and Reich (2005) found post-fire cover of lichen to be a function of fire intensity. In their study, post-fire cover of *Cladonia* lichen species was higher in areas that had experienced lower-intensity fires, while high mortality rates were experienced above a so-called fire intensity threshold.

Fire disturbance creates stand structural conditions much different from those that result from conventional harvest activities (Bergeron et al., 2002). Increased organic debris remaining after fire (McRae et al., 2001) may have an inhibiting effect on terrestrial lichen establishment by occupying growing space and reducing available light (Waterhouse et al., 2011). Certain terrestrial lichen species however, show a preference for burned habitats and the structures left after fire. Johansson et al. (2006) found habitat preference to be an important factor in post-fire lichen community composition, with fire-favoured species characterized as having a preference for dead wood. In their study, 32 lichen species were also found on charcoal.

Fire disturbance has different effects on the regenerating understory plants than certain types of harvest disturbance. Fire-origin stands in northern British Columbia had lower occurrences of vascular plants than similar-aged harvested stands, though this may have been partly related to the season of harvest (Coxson & Marsh, 2001). Contrasting observations were made in black spruce stands in Interior Alaska, where moss and lichen richness significantly

decreased post-fire, while no net change was observed in vascular plant richness (Mack et al., 2008). In that study, post-fire species occurrence was suggested to be a function of life history strategy, with species that regenerate from seed found in burned sites but absent in unburned sites. Many woody vascular plants with buried rhizomes, as well as burnt stumps, are able to resprout after fire, whereas lichens have few penetrating structures and are often destroyed by burning (Holt et al., 2008).

In some ecosystems, the extended absence of fire can cause succession to closed-canopy forests, favouring the establishment of bryophytes such as *Pleurozium schreberi* (Foster, 1985) which out-compete terrestrial lichen species including *Cladina* spp. under shaded conditions (Sulyma & Coxson, 2001). Intense fires are assumed to greatly reduce the humus layer of soils, which could help sustain lichen communities in areas that would otherwise succeed to those dominated by feathermoss (Racey et al., 1996). This may be one reason why prescribed burning has been discussed as an option to maintain long-term supplies of terrestrial lichen for caribou. In the shorter-term however, most authors agree that applying burn treatments to caribou wintering areas would be disastrous (Cumming, 1992; Morice & Lakes IFPA, 2003) and such treatments should be focussed on mesic sites where slash reduction is an objective (Harris, 1996). A prescribed burn study conducted in Banff National Park showed substantially less terrestrial lichen cover in 7-year old burn sites, compared with unburned, mature sites (Sachro et al., 2005). In a grassland ecosystem in Oregon, prescribed burning was found to benefit vascular plants, but was found harmful to terricolous lichen communities, with reduced lichen abundance and diversity observed in burned sites (Holt & Severns, 2005).

1.3.3 Knowledge Gaps in Existing Literature

Although much work has been published on the topic of lichen and its relationships with stand structure and disturbance, some gaps in the existing knowledge are evident. For example, much of the existing literature has focussed on the importance of arboreal lichen to caribou habitat, while relatively fewer studies have been published concerning the importance of

terrestrial lichen. Although arboreal and terrestrial lichen species share the same types of requirements for light and moisture, the stand structural conditions necessary to provide species-specific requirements may be fundamentally different between the two life forms.

Many studies concern the mountain caribou ecotype, or caribou habitat in jurisdictions such as British Columbia or Scandinavia, while relatively fewer studies seem to have been published that deal specifically with woodland caribou habitat in northern Ontario. Winter habitat of *Rangifer* species consists significantly of abundant lichen resources throughout the species range; however other jurisdictions are characterized by different forest types and disturbance histories, which may have inherently different consequences on the abundance of terrestrial lichen. Terrestrial lichen communities in other areas may also be subject to other pressures that are not as prevalent in boreal Ontario, such as grazing by domesticated reindeer.

Much of the available literature pertains to studies of lichen diversity, as opposed to lichen abundance. Both measures are important in maintaining overall ecosystem function, however, in the interest of sustaining focal species such as woodland caribou in northern Ontario, abundance of terrestrial lichen may be a more limiting habitat requirement than terrestrial lichen diversity. Finally, few studies exist regarding the long-term impacts of forest management activities on terrestrial lichen abundance, due to both the length of time required for lichen communities to reach peak abundance, and to the relative amount of historical harvest data that is available for analysis.

Through the research described in this thesis, I hope to address some of the existing gaps in knowledge regarding terrestrial lichen abundance in relation to the structure of managed and natural forest stands of northern Ontario.

2.1 INTRODUCTION

Forest stand structure is recognized as being important to the abundance and diversity of lichen species throughout the world (Humphrey et al., 2002; Moning et al., 2009). Stand structural conditions may vary depending on factors such as disturbance history (McRae et al., 2001), time since disturbance or stand age and forest cover type (Price & Hochachka, 2001). Many stand structural characteristics of importance to terrestrial lichen can be manipulated through forest management activities (Stone et al., 2008; Roturier et al., 2011). These include overstory characteristics such as tree species composition, tree density, stand age and structural features such as dead wood. Forest management decisions can also have impacts on understory characteristics, including understory species composition (Kembel et al., 2008). Terrestrial lichen abundance is related to factors that cannot be altered by forest management as well, such as topography and ecosite characteristics which are inherent in a stand's geographical location and geologic history (Rolstad et al., 2001; Botting & Fredeen, 2006).

The purpose of this study is to identify the stand structural characteristics most important to terrestrial lichen abundance in northern Ontario in order to understand the extent to which forest management can help improve woodland caribou winter habitat in managed forests. Stand characteristics important to terrestrial lichen are measured and compared with estimates of terrestrial lichen abundance in both naturally disturbed and previously harvested stands in northwestern Ontario. The relative importance of these characteristics to terrestrial lichen abundance is analysed using a variety of parametric and non-parametric statistical tests. The results of this study are interpreted in terms of the local context and knowledge gained from field observations, and are compared with results of similar studies. Based on the results of this study, recommendations for forest management and further research are made.

2.2 METHODS

2.2.1 Study Area Description

Data were collected from forested stands in two study areas (18,202 km^2 each) located in Ontario's Boreal Forest region (Figure 2.1). The Auden study area is located east and northeast of Lake Nipigon and encompasses administrative forest management units of the Lake Nipigon, Kenogami, and Ogoki Forests. This study area is generally characterized as being previously disturbed through anthropogenic activities such as forest harvesting. The Pickle Lake study area is located west and northwest of the community of Pickle Lake and is largely situated north of the Area of the Undertaking (AOU, where forest management activities are permitted). This study area is generally characterized as being disturbed naturally through stand-replacing fires. The two study areas represent a broad range of forested stand types dominated by black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.) and balsam fir (*Abies balsamea* (L.) Mill.). Stands occur in various combinations of mixed-species to pure species with diverse understory plant communities. Ecosite conditions vary across both study landscapes– from sandy uplands to lowlands with finer-textured mineral and organic soils. Drier ecosites tend to be dominated by jack pine while lowlands tend to be spruce-dominated. Both study areas are interspersed with poplar and birch stands of pure or mixedwood condition, these generally being on finer textured soils and most common in southern portions of the Auden study area. A range of successional stages is represented; the youngest measured stand was aged 3 years and the oldest measured stand was aged 153 years.

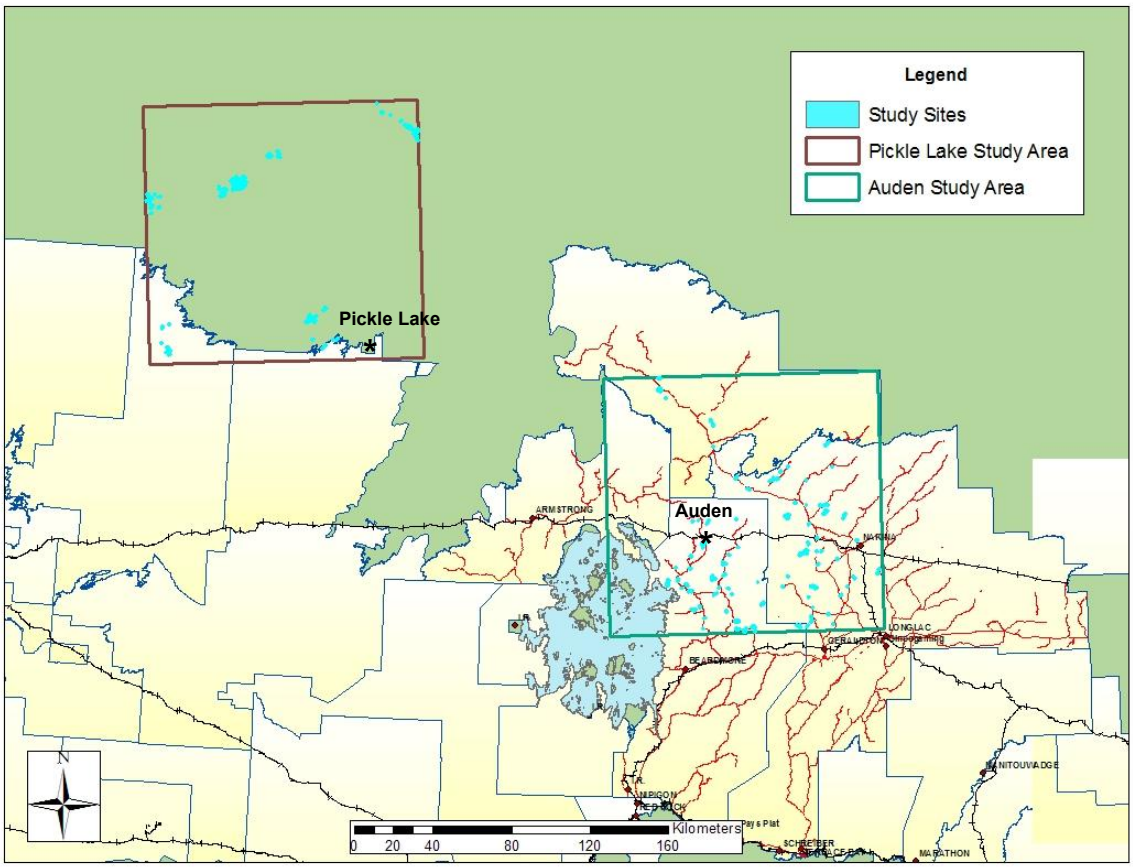


Figure 2.1. Map showing the Auden and Pickle Lake study areas and study sites visited for field data collection. Yellow shaded sections represent Forest Management Units (FMUs) with the Area of Undertaking (AOU).

2.2.2 Experimental Design

Using ArcGIS™, the study areas were mapped by converting Ontario Land Cover (OLC, http://geogratis.cgdi.gc.ca) raster data into polygons (25 m pixel size) according to cover type. Potential study sites were selected randomly from all accessible polygons among coniferous, deciduous, mixedwood and sparse forest cover types. Stands were thus selected to represent the range of forest conditions within the two study areas, and represented the land cover types that are generally considered in forest management planning in Ontario. Each polygon was evaluated to ensure that as much as possible current conditions represented the definition of the OLC class represented. Data from the 2010 Ontario Forest Resources Inventory (FRI) were available for the Auden study area and the southern portion of Pickle Lake study area. Where FRI data were

available, it supplemented reconnaissance observation of stand conditions to confirm forest cover type. Any stands with historical record of harvest activity having taken place were considered previously harvested, while stands with no record of harvest were considered to have been naturally disturbed. Replication was sought in each OLC cover type across 3 age classes for natural- and harvest-origin stands (Table 2.1). The age classification scheme represents broad age classes defining young, mature and old-forest successional stages. The upper age limit of harvested stands is based on available records of harvest disturbance that occurred in the Auden study area in the 1940's. In total, data from 54 harvest-origin stands, and 104 natural-origin stands were used for analysis. Table 2.1 provides the sampling matrix used to select stands for measurement:

Table 2.1. Sampling matrix used to select stands according to stand origin, Ontario Land Cover (OLC) Class and Age Class.

Stand Origin	Natural				Harvest			
OLC Class	Conifer	Deciduous	Mixedwood	Sparse	Conifer	Deciduous	Mixedwood	Sparse
Age Class	10 to 29	10 to 29	10 to 29	10 to 29	10 to 29	10 to 29	10 to 29	10 to 29
	30 to 69	30 to 69	30 to 69	30 to 69	30 to 49	30 to 49	30 to 49	30 to 49
	70+	70+	70+	70+	50 to 72	50 to 72	50 to 72	50 to 72

2.2.3 *Sampling Strategy*

Replicate stands were randomly selected from the current OLC GIS (Geographic Information System) layer, with candidate stands restricted to those accessible[1] by available road networks, float plane or by boat. Where possible, forested sample units within the Auden study area were further restricted to OLC polygons that fell within a single FRI polygon that had a species composition consistent with the corresponding OLC definition. Where FRI data were available this allowed sample units to be characterized by designated standard forest units as well. Selected stands from each study area were at least 10 ha in size and met geographic shape requirements to allow for the placement of five ($100m^2$) sample plots within the stand, at least 50 metres from the stand boundary and 100 metres apart from one another.

[1] Accessible stands were defined as those within 2km of a road or trail, or a lake >100ha in size where no roads were available.

2.2.4 Field Data Collection

A minimum of 3 sample points were measured in each stand. At each point, tree-level attributes of stand structure were estimated from circular fixed-area plots 100m^2 in size. A complete census of all live trees greater than 2 cm in diameter at breast height (dbh) was conducted. Tree species was recorded and the diameter of each tree was measured to the nearest 0.1 cm. In each plot, one representative tree of each species was selected and used to measure tree height, crown height and stand age. The crown class of each tree species representative was recorded. Tree height and crown height data were collected using a laser hypsometer (Impulse-200, Lasertech Inc., USA). Tree age was estimated at breast height (1.3m) from increment cores by counting the number of annual rings in the field.

Understory vegetation was measured by establishing circular fixed-area plots 50 m^2 in size. These plots were located outside the fixed area tree plots to avoid trampling of plants by crew members. The centre of each vegetation plot was located approximately 10m away from the tree plot on a bearing perpendicular to the bearing of travel to the tree plot. Understory vegetation was classified as belonging to the "ground layer" if it measured 40 cm or less in height, or to the "shrub layer" if measured greater than 40 cm and up to 2 metres in height (Rodgers et al., 2008). Ground and shrub vegetation was identified to species; or to genus where field identification to species was not possible. Terrestrial lichen genera measured included *Cladina* spp., *Cladonia* spp., *Cetraria* spp., *Stereocaulon* spp., and *Peltigera* spp. Percent cover of vegetation in each layer was estimated visually. Consistency among visual estimates by crew members was achieved by having the same individuals estimate the percent cover values, and by sub-dividing the fixed area plot into 4 smaller sections. A percent cover class scheme with 1% intervals for species occurring at abundances of less than 5%, and at intervals of 5% for species occurring at abundances of ≥ 5% (i.e. 1, 2, 3, 4, 5, 10, 15…90, 95, 100%) was used. Species occurring in abundances of <1% were recorded as "present". Trees and shrubs greater than 2 metres in height but having a portion of their live foliage within the 0.4 to 2m height range were

included in the shrub percent cover estimates. The portion of foliage occurring within the 0.4 to 2m range was included in the percent cover estimate. Mean height of vegetation in the shrub layer was recorded by species to the nearest 0.1 m.

At each plot, ecosite characteristics were measured according to Ontario's provincial Ecological Land Classification Guide (OMNR, 2009). A Dutch auger was used to sample soil cores as near as possible to the centre of the fixed-area tree plot, to determine soil texture and moisture regime based on substrate condition. Substrates were characterized as described in the "Field Guide to Substrates of Ontario" (OMNR, 2010). For mineral substrates, effective soil texture[2] was determined by conducting diagnostic tests on soil originating from the appropriate horizon of the soil profile. For organic substrates, the von Post scale of decomposition was used to classify organic 'textures'. Moisture regime was assigned at each plot using moisture regime keys in the Guide (OMNR, 2010; Figures 21-24). In deep soils, moisture regime was determined by assessing the depth in centimetres to continuous mottles within the soil profile. For these sites, moisture regime was recorded as the numeric code corresponding to the appropriate depth class, and ranged from "θ" which represented very rapidly draining substrates, to "9", which represented very wet substrates. For non-standard situations, such as very shallow soils (≤ 5 cm of mineral material over bedrock), moisture regime was assigned based on site characteristics including proximity to water, percent of direct shading and substrate texture. For these sites, moisture regime was recorded as being xeric ("X"), saturated ("S"), or humid ("H"). Ecosite was determined by using the dichotomous keys in the field guides, which assign an ecosite code based on the particular combination of dominant soil texture, moisture regime and overstorey tree composition. Soil depth was measured in centimetres and was recorded as belonging to a soil depth class depending on the depth to bedrock, as per Table 2.2. Shallow soils could be

[2] In non-stratified mineral material and mineral substrates with a depth ≤ 60cm, the effective texture is the substrate texture that comprises most of the profile (Figure 19 in OMNR 2010). In stratified mineral substrates it is determined using the effective texture chart (Figure 20 in OMNR 2010). In deep organic peats the surveyors recorded the degree of decomposition of the middle tier, in folics and very shallow organic substrates the surveyors recorded the degree of decomposition of organic material making up >50% of the sampled profile (OMNR 2010)

further qualified as a shallow peat or shallow folic, and deep soils could be further qualified as a deep peat or deep folic, depending on the nature of the soil. The organic depth was recorded in centimetres and represented the measured sum of the depth of the organic horizons.

Table 2.2. Soil depth classes used to characterize stands based on depth (cm) to bedrock.

Depth to Bedrock:	Class:
< 5 cm	Rock
> 5 to <= 15 cm	Very Shallow
>15 to <= 30 cm	Shallow or Shallow Peat
> 30 to <= 60 cm	Moderate
> 60 to <= 120 cm	Moderately Deep
> 120 cm	Deep or Deep Peat or Deep Folic

Canopy closure was measured using a convex spherical densiometer (Forest Densiometers, Model A; Lemmon, 1956). Canopy closure readings were taken at least 20 times, every 20 metres along the bearing travelled between plots in each stand. Canopy closure was also measured at the centre of each fixed-area vegetation plot, resulting in at least 23 canopy closure readings per stand.

2.2.5 Data Compilation Methods

2.2.5.1 Tree Data

Tree diameter data from the fixed-area plots in each stand were used to calculate the basal area of each live tree (BA/tree) using the formula:

$$BA/tree\ (cm^2) = \Pi\ (dbh/2)^2$$

Basal area per tree was converted to units of square metres and was summarized by species for each stand. This value was divided by the total number of plots measured in each stand to obtain the mean total BA per plot for each tree species. Total BA per hectare (m^2/ha) for each species was then calculated by multiplying the average plot basal area by 100 (each plot represented 0.01 hectares). Total BA per hectare in each stand was calculated as the sum of the basal area per hectare of all tree species.

Stand level tree height, crown height and age were calculated using the mean values of representative trees measured at each plot. Only trees belonging to the "dominant" or "co-dominant" crown classes were considered, while data from trees designated as "understory", "intermediate", "anomaly" or "overtopped/suppressed" were omitted from stand level calculations for these parameters. In pure or nearly pure stands, the data used for these calculations were further limited to data from the most dominant tree species – those representing at least 70 percent of the total basal area. In these types of stands, the parameters tree height, crown height, and stand age were assumed to be best represented by data from the most dominant species in typically even-aged stand conditions common in the boreal forest (Bergeron et al., 2002).

Based on the analysis described above, stands were assigned a dominant cover type as a general description of tree species composition. Stands were described as having a conifer (CON) cover type if at least 70 percent of their total basal area was composed of coniferous tree species, and were described as having deciduous (DEC) cover type if at least 70 percent of their basal area was composed of deciduous tree species. The remaining stands that did not meet either of these definitions were designated as having mixedwood (MIX) cover type.

Stands were also assigned a standard forest unit designation based on their tree species composition and ecosite. The Northwest Regional Standard Forest Unit definitions (OMNR, 2010, unpublished) were used to characterize sampled stands in terms of how they are recognized in the Ontario Forest Resources Inventory (FRI) and in forest management planning in northwestern Ontario. This provides a mechanism to link this work to the forest management planning process, and potentially provide direction where terrestrial lichen is a management objective.

2.2.5.2 Terrestrial Lichen and Understory Vegetation Data

Stand-level terrestrial lichen abundance was calculated by summing the percent cover estimates of all terrestrial lichen species observed in each plot, and dividing by the number of plots measured in each stand. Total ground vegetation cover was calculated in a similar way to represent the mean total percent cover of all vegetation (excluding terrestrial lichen species) within the ground layer of each stand. Total shrub cover in each stand was calculated by summing the mean percent cover of all shrub species and overstorey tree foliage observed in the shrub layer of each plot. Mean shrub height was calculated from the height estimates of all shrub and tree species having foliage within the shrub layer, weighted by the proportion each species contributed to total percent shrub cover.

2.2.5.3 Ecosite Data

Effective soil texture of each plot was classified as belonging to a particular texture family (Table 2.3) as defined in the Field Guide to Substrates of Ontario (OMNR, 2010). The "Sandy" texture family includes textures ranging from very coarse sands (vcS) to loamy fine sands (LfS); the "Coarse Loamy" texture family includes textures ranging from silty very coarse sands (SivcS) to very fine sands (vfS); and the "Fine Loamy" texture family includes textures ranging from sandy clay loams (SCL) to silty clay loams (SiCL). The "Silty" and "Clayey" texture families represented less frequently in the stands sampled, included textures ranging from silty (Si) to silty loams (SiL), and silty (SiC) to sandy clays (SC), respectively. Plots recorded as having organic effective texture or that were described with a von Post decomposition code were combined into a general "Organic" texture family. Stand level estimates of texture family were decided by assigning stands the most frequently occurring texture family that was observed in each of the plots measured. No texture family was assigned to stands for which a most frequently occurring plot-level estimate of texture family could not be determined.

Table 2.3. Texture families assigned to plots according to effective textures (Field Guide to Substrates of Ontario, OMNR 2010). The Organic texture family includes sites identified as 'peat' or 'folic'.

ELC Texture Family		Effective Texture(s)
Sandy	S	vcS, LvcS, cS, LcS, mS, LmS, fS, LfS
Coarse Loamy	cL	SivcS, SicS, SimS, SifS, SivfS, vcSL, mSL, fSL, vfSL, L, LvFS, vfS
Silty	Si	Si, SiL
Fine Loamy	fL	SCL, CL, SiCL
Clayey	C	SiC, C, SC
Organic	OG	sites designated with von Post code

Moisture regime was characterized in the field using both numeric and character-labelled codes. To determine stand-level average moisture regime, a numeric moisture regime code was assigned that corresponded with the moisture regime data recorded for each plot (Table 2.4). Moisture regime was thus considered an ordered variable, with values of "X" (xeric) representing the driest sites and values of "9" representing the wettest sites. The moisture regime coding system was used to facilitate the calculation of a mean moisture regime for each stand based on the plot data. It was also used for statistical analysis as it could be easily recognized as a ranked categorical variable in the statistical software used, R version 2.15.1 (R Development Core Team, 2012).

Table 2.4. Moisture regime codes used for calculation of stand-level values for moisture regime and for statistical analysis.

Moisture Regime	Moisture Regime Code
X (xeric)	0
H (humid)	1
θ	2
0	3
1	4
2	5
3	6
4	7
5	8
6	9
7	10
8	11
9	12

Soil depth measured at each plot was converted from soil depth class to a corresponding soil depth estimate which represented the midpoint of each soil depth class in centimetres. Deep soils were assigned a soil depth of 120 cm as they represented sites that were at least 120 cm deep. The midpoint numbers for the other soil depth classes were used to calculate the mean soil depth of each stand from the plot level data. Table 2.5 shows the midpoint values used for these calculations. Mean organic depth for each stand was calculated as the average of the organic depth data collected from each plot.

Table 2.5. Soil depth midpoint values used to calculate stand-level soil depth (cm) based on soil depth classes recorded in field measurements.

Soil Depth (cm)	Class	Soil Depth Midpoint (cm)
< 5	Rock	2.5
> 5 to <= 15	Very Shallow	10
>15 to <= 30	Shallow, Shallow Peat	22.5
> 30 to <= 60	Moderate	45
> 60 to <= 120	Moderately Deep	90
> 120	Deep, Deep Peat, Deep Folic	120

2.2.5.4 Canopy Closure Data

Stand level canopy closure was calculated as the mean of all densiometer readings taken in each stand. Canopy closure was analyzed as a continuous variable for regression analyses, and as a categorical variable to compare stands with ≥ 80% and < 80% canopy closure using parametric t-tests and non-parametric Mann Whitney U-tests. The measure of 80% was chosen as a conservative threshold based on literature that suggests lichen abundance is greater in areas with less than 70% canopy closure (Racey et al., 1991) and less than 50% canopy closure (Moning et al., 2009).

2.2.6 Statistical Analysis

All analyses were completed using the statistical computing software R, version 2.15.1 (R Development Core Team, 2012). Both the base package and the Vegan: Community Ecology package (Oksanen et al, 2012) were used to analyze the relationships between the dependent variable, terrestrial lichen abundance, and the independent variables. All test results were

considered significant at a $p < 0.05$. Standard boxplots were used to display comparisons among categorical data, with the horizontal line in each boxplot representing the median of each dataset.

2.2.6.1. Disturbance History and Cover Type Analysis

Preliminary analysis of the data was done to identify the broad-scale forest conditions most important to terrestrial lichen abundance. First, a two-way analysis of variance (ANOVA) was conducted on data from all 158 stands to determine the significance of the effects of disturbance history (harvested or natural) and cover type (conifer, deciduous or mixedwood) on terrestrial lichen abundance. The Bartlett test was used to determine homogeneity of variance among samples. Tukey's HSD (Honestly Significant Difference) test was used to identify significantly different means.

2.2.6.2. Analysis of Conifer-Dominated Stands

The results of the two-way ANOVA were used to guide subsequent statistical analyses aimed at narrowing the list of independent variables to those that were most important to terrestrial lichen abundance at the stand scale. The subset of the data representing conifer-dominated stands (n = 105) was analyzed separately, as terrestrial lichen was found to be most abundant in stands of this cover type. The independent variables used in the initial analyses were stand age, canopy closure, total basal area of trees per hectare, percent conifer, tree height, crown height, percent cover of ground vegetation, percent cover of shrubs, shrub height, texture family, moisture regime, soil depth, and organic depth. Independent variables were first considered individually in relation to terrestrial lichen abundance.

All variables were tested for normality using the Shapiro-Wilk normality test. Variables that did not satisfy assumptions of normality were transformed to achieve normality where possible. The most appropriate option among Box-Cox, log, logit and arc sin square-root transformations was selected for each non-normal variable. Despite best efforts to achieve normality, this was not always possible. For variables that could not be normalized, the data transformation that produced the closest to a normal distribution of the data was selected. These

were transformations that maximized the p-value obtained in the Shapiro-Wilk normality test and appeared normal on visual inspection. Data for the dependent variable, terrestrial lichen abundance, had the most normal distribution using a Box-Cox transformation (Figure 2.2b), but did not satisfy assumptions of normality (Shapiro-Wilk's test, p = 5.072e-05).

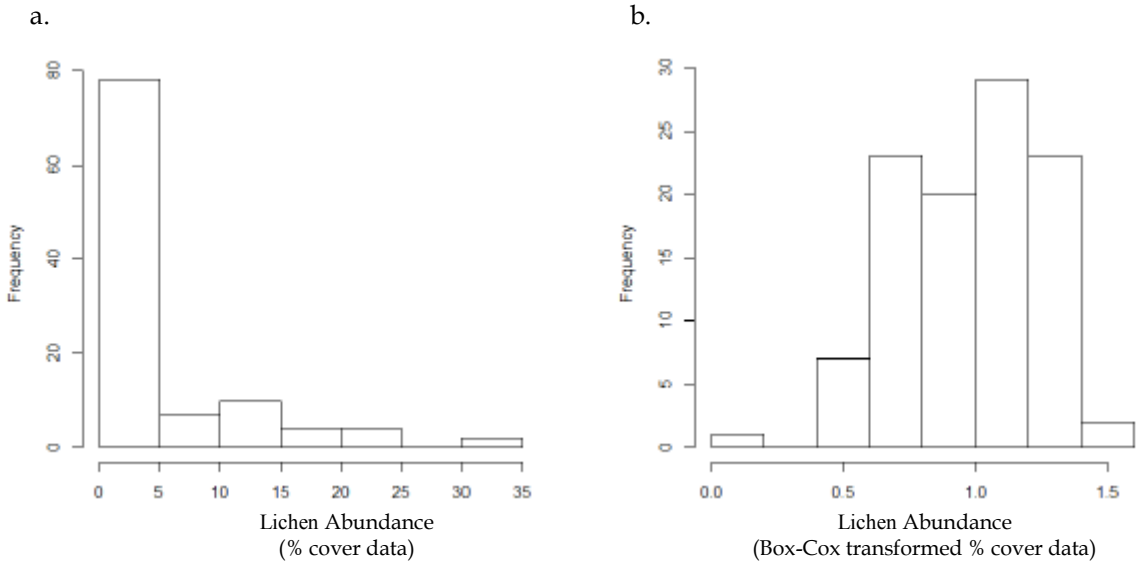


Figure 2.2. Frequency distributions of (a) original (untransformed) terrestrial lichen abundance data (% cover) and (b) transformed terrestrial lichen abundance data (Box-Cox transformed, $y^{0.15}$).

Shapiro-Wilk's normality test results (Appendix 1a) indicated that only tree height data met assumptions of normality at the desired significance level of $p < 0.05$. Arc sin square-root transformations of canopy closure and percent conifer data improved the distribution of the data but did not allow it to meet assumptions of normality. Log-transformation resulted in a normal distribution for shrub height data, and improved normality of organic depth data but did not allow it to meet normality assumptions. Data for all other variables (stand age, crown height, basal area, moisture regime, soil depth, ground vegetation cover, and shrub cover) did not improve with transformations, and were analyzed using original units.

Both parametric and non-parametric tests were used, given that most variables did not meet assumptions of normality. Continuous variables including stand age, canopy closure, basal area, tree height, and crown height, ground vegetation cover, shrub cover, shrub height, moisture

regime, soil depth, and organic depth were analyzed using both parametric simple linear regression and the non-parametric Spearman rank correlation test.

Canopy closure was analyzed as both a continuous and a categorical variable. As a categorical variable, stands were sorted into two classes – those with less than 80%, and those with greater than or equal to 80% canopy closure. Assumptions of normality among canopy closure class data were tested using Bartlett's and Shapiro-Wilk's tests. Variances of the two classes were found to be approximately equal (Bartlett test, $p > 0.05$). A Box-Cox transformation ($y^{0.15}$) of the total lichen abundance data improved the normality of both sample distributions; however Shapiro-Wilk's test indicated that data from each sample did not meet assumptions of normality at the desired significance level ($p > 0.05$). The parametric Welch two-sample t-test and the non-parametric Mann-Whitney U-test were used to analyze differences in terrestrial lichen abundance between canopy closure classes.

Standard forest unit (SFU) was analyzed as a categorical variable. One shallow jack pine stand (PjSha) was omitted from the analysis as it was the only stand representing that SFU. Bartlett's test indicated homogeneity of variances among the remaining standard forest units ($p = 0.7741$). Box-Cox transformations of the total lichen data for each SFU resulted in approximately normal distributions with the exception of the balsam-fir mixedwood (BfMx1) SFU. One-way ANOVA and the Kruskal-Wallis rank sum test were used to test for differences in lichen abundance among SFUs.

Texture family was also analyzed as a categorical variable. One Fine Loamy stand was omitted from the texture family analysis as it represented the only stand of that texture family. Bartlett's test indicated homogeneity of variances among the remaining texture families (Coarse Loamy, Sandy and Organic, $p = 0.637$). Box-Cox transformations of lichen abundance data (by texture family) improved the respective distributions of these data, but data for Coarse Loamy and Sandy texture families did not meet assumptions of normality using Shapiro-Wilk's test. A one-way ANOVA and a post-hoc Tukey HSD test were used to identify significant differences in

mean lichen abundance among texture families. The non-parametric Kruskal-Wallis rank sum test was also used to test for differences in median lichen abundance among texture families. Organic and non-organic (Fine Loamy, Coarse Loamy, and Sandy) textured stands were subsequently compared using both a t-test and a Mann-Whitney U-test. Bartlett's test indicated homogeneity of variance among these two sample groups, and though a Box-Cox transformation improved normality of lichen abundance data, data for the non-organic stands did not meet assumptions of normality at the desired significance level.

2.2.6.3. Analysis of Non-Organic Conifer-Dominated Stands

The dataset was further partitioned based on the results of the texture family analysis. Stands with organic 'texture' were omitted from further analysis as they generally represented stands with much lower terrestrial lichen abundance, compared with non-organic (mineral) textured stands. Organic stands also represented the majority (31 of 34) of the spruce lowland (SbLow) stands measured; a SFU type which is generally treated differently with respect to silviculture. The remaining non-organic conifer-dominated stands (n = 71) thus represented stands with higher potential for management of terrestrial lichen. Independent variables, with the exception of texture family and SFU, were again examined individually using the same procedures described above to determine whether their statistical significance changed when organic stands were removed from the dataset.

Both parametric and non-parametric tests were used, as the distribution of the data for total lichen abundance and other variables could not be normalized through various data transformations (Appendix 1b). Data for stand age, tree height, crown height and basal area met assumptions of normality at the desired significance level of $p < 0.05$. Total terrestrial lichen abundance data was Box-Cox transformed to improve its distribution; however it did not meet assumptions of normality according to Shapiro Wilk's normality test. The same was true for canopy closure data, which was logit transformed to improve normality. An arc sin square-root transformation improved normality of percent conifer data, however it did not meet normality

assumptions at the desired significance level. Log transformations of both organic depth and shrub height data resulted in normal distributions. Data for moisture regime, soil depth, ground vegetation cover, and shrub cover did not improve with transformations, and were analyzed using original units.

Canopy closure was again analyzed as both a continuous and categorical variable. Bartlett's test indicated homogeneity of variance between canopy closure classes ($p = 0.465$), and arc sin square root transformations of the total lichen abundance data within canopy closure classes improved normality of the sample distributions; however samples did not meet assumptions of normality (Shapiro-Wilk's test $p = 0.01345$).

Multi-collinearity among independent variables, with the exception of texture family, was identified prior to multivariate analyses using Pearson's product-moment correlation test. Variables with correlation coefficients of 0.7 or greater were considered collinear. Collinear variables were excluded from further analyses based on the strength of their relationship with terrestrial lichen abundance. Tree height was found to be correlated with crown height and age, and was removed from the list of independent variables used in further analysis. The remaining independent variables used for multivariate analyses were canopy closure, stand age, total basal area of trees per hectare, crown height, percent conifer, moisture regime, soil depth, organic depth, texture family, percent cover of ground vegetation, percent cover of shrubs, and shrub height.

2.2.6.4. Non-Metric Multi-Dimensional Scaling

Non-metric multi-dimensional scaling (NMDS) was used to illustrate potential ecological separation among sampled stands in terms of their abundance of terrestrial lichen. NMDS is an indirect ordination technique in which species abundance data are ordinated independently of available environmental data, and subsequent analyses are used to correlate environmental variables to the distribution of species data (Kent & Coker, 1992). The metaMDS function in R (Vegan package; Oksanen et al, 2012) uses an iterative process of calculating an optimal solution

that best relates distances in the ordination plot to dissimilarities in species data among sampled units – in this case, sampled stands.

Abundance data of the three most commonly occurring genera of terrestrial lichen were used in the NMDS ordination. The lichen genera considered were: *Cladina* spp., *Cladonia* spp., and *Peltigera* spp. The Bray-Curtis distance measure was used to calculate the dissimilarity matrix from Box-Cox transformed terrestrial lichen abundance data in the 71 non-organic conifer-dominated stands. Data were centred and scaled prior to ordination. The metaMDS function in R also rotated the configuration of ordination objects to maximize the variance of points along the first dimension NMDS1.

A stable solution was reached after 8 iterations. Two dimensions were selected for the final NMDS ordination. The scree plot in Figure 2.3 shows that higher dimensions did not provide substantially greater reductions in stress; hence a two-dimensional solution was selected to facilitate interpretability of the final ordination diagram.

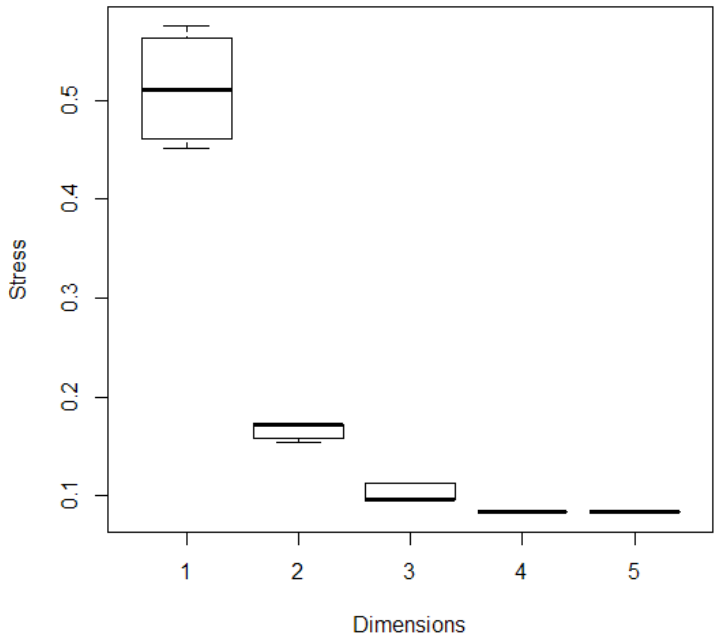


Figure 2.3. Scree plot of stress by dimensionality showing that stress is most reduced with the first two dimensions of the final ordination solution.

The stress of the final solution was approximately 0.1362, indicating relatively low stress (McCune & Grace, 2002). A Shepard plot (Appendix 6) was used to interpret the measure of stress representing a goodness of fit or match between the inter-site distances and the equivalent values for stands and species in the dissimilarity matrix (Kent & Coker, 1992). Non-parametric regression was applied to the resulting line of best fit, and residuals were used to evaluate stress. The non-metric fit r^2 (0.981) is analogous to the proportion of variance represented by each ordination axis (Oksanen, 2012).

The independent environmental variables were then fit to the NMDS ordination diagram to show the relative associations between the environmental variables and the ordination diagram. To do this, the envfit (Vegan) function was used to fit vectors of continuous variables and centroids of levels of class variables onto the ordination plot (Oksanen, 2009). The fit of the environmental variables to the ordination was used to infer the explanatory value of each independent variable on the distribution of terrestrial lichen species and sampled stands in ordination space.

A second NMDS ordination was done using the independent environmental variables to plot stands based on similarities in environmental characteristics. Texture family was removed as a variable for this analysis, as these data represented categorical data that poorly reflected ecological gradients in the ordination space. Abundance data for the terrestrial lichen genera (*Cladina* spp., *Cladonia* spp. and *Peltigera* spp.) were then fit to the environmental ordination diagram to determine whether certain lichen genera showed correlation with particular types of stands.

2.2.6.5. Multiple Linear Regression

Backward stepwise multiple linear regression was used to build a predictive model for terrestrial lichen abundance. An initial model including all independent environmental variables was first computed using the lm (base package) function in R (R Core Team, 2012). The step function was then used to carry out backward elimination of environmental variables until an

optimal model was reached. Akaike's Information Criterion (AIC) was used to select a model that best explained variance in terrestrial lichen abundance with the fewest possible environmental variables. At the final step the model produced an AIC of -157.86; removing additional variables did not result in any further reduction in AIC. The results of the final model were summarized and compared to those of the previous statistical analyses.

2.3 RESULTS

2.3.1 Disturbance History and Cover Type

Harvested and naturally disturbed stands represented similar proportions of conifer (CON), deciduous (DEC) and mixedwood (MIX) stand types (Table 2.6), though harvested stands had slightly higher proportions of DEC and MIX. Harvested stands represented a higher frequency of younger (<40 years old) stands, while naturally disturbed stands represented a higher frequency of mature to old growth (>40 years old) stands (Figure 2.4).

Table 2.6. Proportion of cover types represented in harvested and naturally disturbed sampled stands.

	CON (%)	DEC (%)	MIX (%)
Harvested	63.0	20.4	16.7
Natural	76.0	11.5	12.5
Total	71.5	14.6	13.9

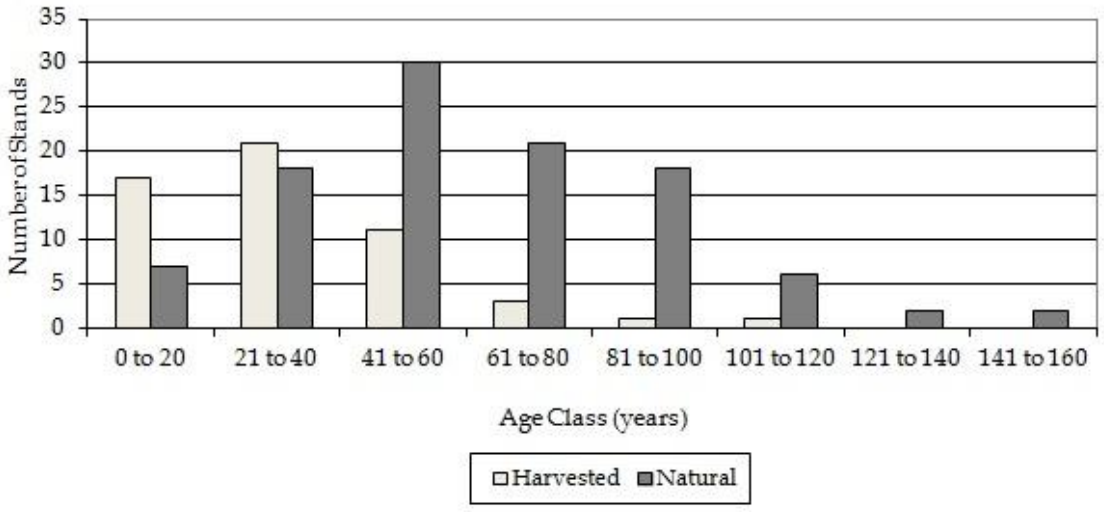


Figure 2.4. Frequency distribution showing number of sampled stands by disturbance history and age class; Harvested stands: n = 54, Natural stands: n = 104.

Two-way ANOVA confirmed no significant differences (p = 0.781) in mean terrestrial lichen abundance between naturally disturbed (3.14 ± 5.77%) and harvested (3.41 ± 6.53%) stands (Figure 2.5a) and no interaction effect between disturbance history and cover type. Dominant cover type had an effect (p = 0.0000336, F = 13.708, df = 2) with significantly higher lichen abundance in CON stands (4.28 ± 6.83%) than in DEC (0.60 ± 1.51%) or MIX stands (0.62 ± 1.01%; Figure 2.5b).

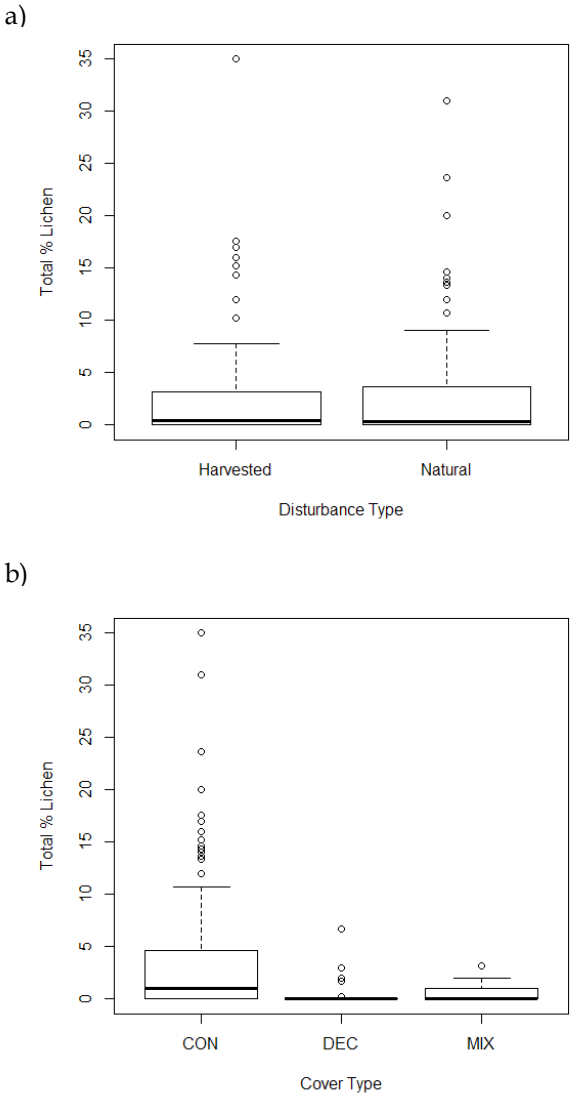


Figure 2.5. Standard boxplot of terrestrial lichen abundance (% cover) in (a) previously harvested (n = 54) and naturally-disturbed (n = 104) stands, and in (b) coniferous (CON, n = 113), mixedwood (MIX, n = 22) and deciduous (DEC, n = 23) stands.

2.3.2 Terrestrial Lichen in Conifer-Dominated Stands

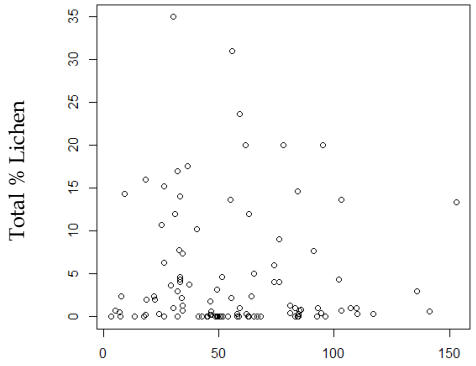
Based on the results of the previous analysis, further statistical analysis was conducted on a subset of the data representing 105 conifer-dominated stands as these stands had higher terrestrial lichen abundance relative to the other cover types measured. A summary of the results of parametric and non-parametric tests of independent variables is provided in Table 2.7 below.

Table 2.7. Results of parametric and non-parametric tests for continuous and categorical variables in relation to terrestrial lichen abundance in conifer-dominated stands (n = 105).

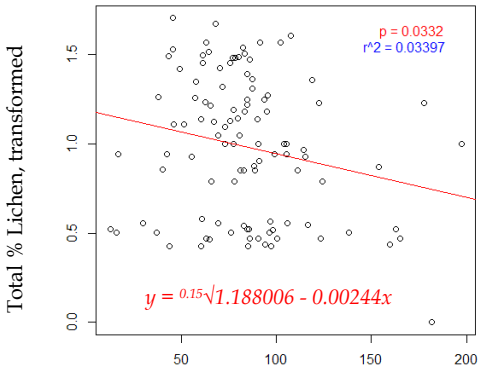
	Parametric		**Non-parametric**	
Independent Variable	Test	Result	Test	Result
Continuous				
Stand Age (years)	SLR*	ns (p = 0.781)	SRC**	ns (p = 0.507)
Canopy Closure (%)[1]	SLR	ns (p = 0.484)	SRC	ns (p = 0.479)
Basal Area (m^2/ha)	SLR	ns (p = 0.862)	SRC	ns (p = 0.853)
Tree Height (m)	SLR	ns (p = 0.696)	SRC	ns (p = 0.636)
Crown Height (m)	SLR	p = 0.085, r^2 = 0.019, df = 103	SRC	ns (p = 0.156)
Percent Conifer (%)[1]	SLR	ns (p = 0.312)	SRC	ns (p = 0.461)
Ground Vegetation Cover (%)	SLR	p = 0.033, r^2 = 0.034, df = 103	SRC	p = 0.029, rho = -0.213
Shrub Cover (%)	SLR	ns (p = 0.186)	SRC	ns (p = 0.263)
Shrub Height (cm)[2]	SLR	p = 0.034, r^2 = 0.034, df = 103	SRC	p = 0.017, rho = 0.233
Moisture Regime (code)	SLR	p = 0.012, r^2 = 0.051, df = 103	SRC	p = 0.007, rho = -0.263)
Soil Depth (cm)	SLR	p = 0.004, r^2 = 0.069, df = 103	SRC	p = 0.012, rho = -0.246
Organic Depth (cm)[2]	SLR	p = 0.034, r^2 = 0.034, df = 103	SRC	p = 0.0285, rho = -0.216
Categorical				
Canopy Closure (class)	t-test	p = 0.007, t = -2.831, df = 50.4	Mann-Whitney U	p = 0.007, W = 707
Standard Forest Unit	ANOVA	ns (p = 0.436)	Kruskal-Wallis	ns (p = 0.4321)
Texture Family (class)	ANOVA	p = 0.026, F = 3.789, df = 2	Kruskal-Wallis	P = 0.017, χ^2 = 8.13, df = 2
Texture Family Group (class)	t-test	p = 0.021, t = 2.352, df = 74.6	Mann-Whitney U	p = 0.016, W = 1560.5

[1] Arc sin square-root transformed * Simple linear regression ** Spearman rank correlation
[2] Log transformed

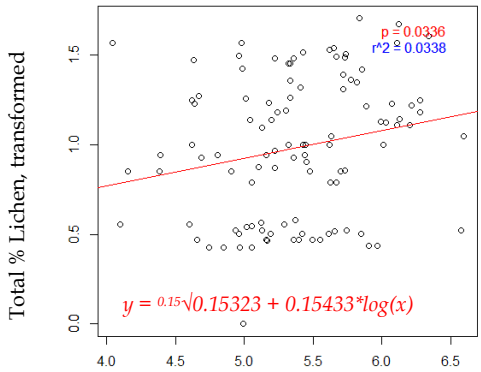
Results of parametric and non-parametric tests were generally consistent (Table 2.7). Statistically significant ($p < 0.05$) negative relationships were found between total lichen abundance (%) and ground vegetation cover, moisture regime, soil depth and organic depth (Figure 2.6). A weak negative relationship was found between lichen abundance and crown height using simple linear regression (Appendix 4), but no correlation was found between these two variables using Spearman rank correlation (Table 2.7). A statistically significant positive



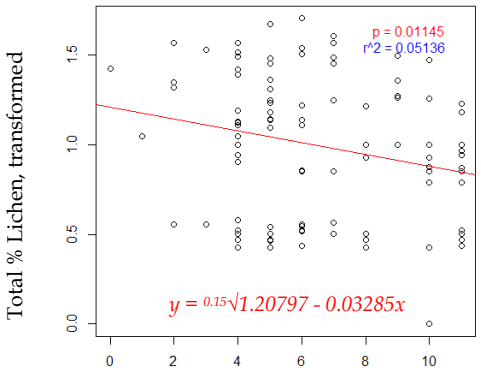
a) Stand Age (years)



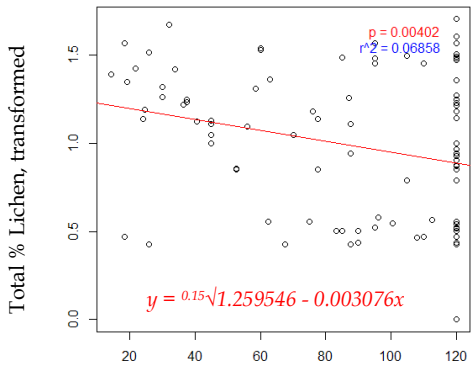
b) Vegetation Cover (%)



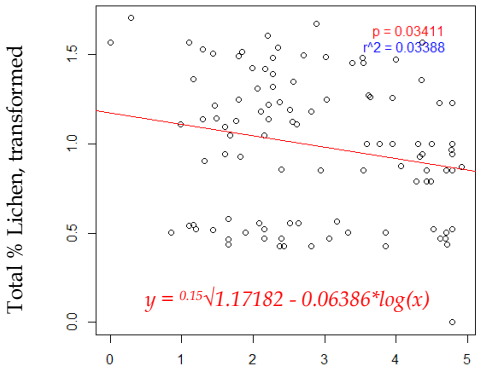
c) Shrub Height (cm), log transformed



d) Moisture Regime (code)



e) Soil Depth (cm)



f) Organic Depth (cm), log transformed

Figure 2.6. Total terrestrial lichen abundance (% cover) in relation to a) Stand Age (years), b) Vegetation Cover (%), c) Shrub Height (cm, log transformed), d) Moisture Regime (code), e) Soil Depth (cm), and f) Organic Depth (cm, log transformed) in 105 conifer-dominated stands. Total lichen abundance data for (b) through (f) were Box-Cox transformed and represent actual % cover data ranging from 0 to 35%. Stands with >100% vegetation cover (b) include those which exceeded 100% due to layering of plants in the ground layer. Moisture regime is represented by moisture regime code as per Table 2.4.

relationship was found with shrub height, but no linear relationships were found with stand age (Figure 2.6), canopy closure, basal area, percent conifer, or shrub cover. R-squared and rho values throughout were relatively small indicating low explanatory strength of continuous variables. With respect to the categorical variables analyzed, mean lichen abundance was significantly higher in stands with <80% canopy closure (5.28 ± 7.01%) than in stands with >80% canopy closure (2.47 ± 6.57%; Figure 2.7). Terrestrial lichen abundance was not significantly different among SFUs (Figure 2.8), but was significantly higher in stands with non-organic, rather than organic texture families (Figure 2.9).

2.3.2.1 Overstory Characteristics

Stand age ranged from 3 to 153 years in conifer-dominated stands. Relatively high terrestrial lichen abundance was observed in some younger (< 50 years) stands, with the highest value (35%) in a stand aged 30 years (Appendix 2a). Lichen abundance ranged from 0 to ~31% in stands with < 80% canopy closure, and from <1 to 35% in stands with ≥ 80% canopy closure (Appendix 2b), but was on average higher in the more open stands (Figure 2.7). In conifer-dominated stands, basal area ranged between less than 1 and approximately 70 m^2/ha, with relatively high lichen abundance (≥15%) found in stands with 10 to 20 m^2/ha (Appendix 2c). Tree height ranged between 3 and 21m in conifer-dominated stands, with relatively high (≥15%) terrestrial lichen abundance observed in stands ranging between 8 and 18m in mean tree height (Appendix 2d). Crown height measurements ranged from 0 to approximately 14 metres in height, with relatively high (≥15%) lichen abundance occurring in stands with crown height ranging between 2 and 8m (Appendix 2e). Among stands with relatively high (≥15%) terrestrial lichen abundance, 8 of 10 were comprised 100% of conifer tree species (Appendix 2f).

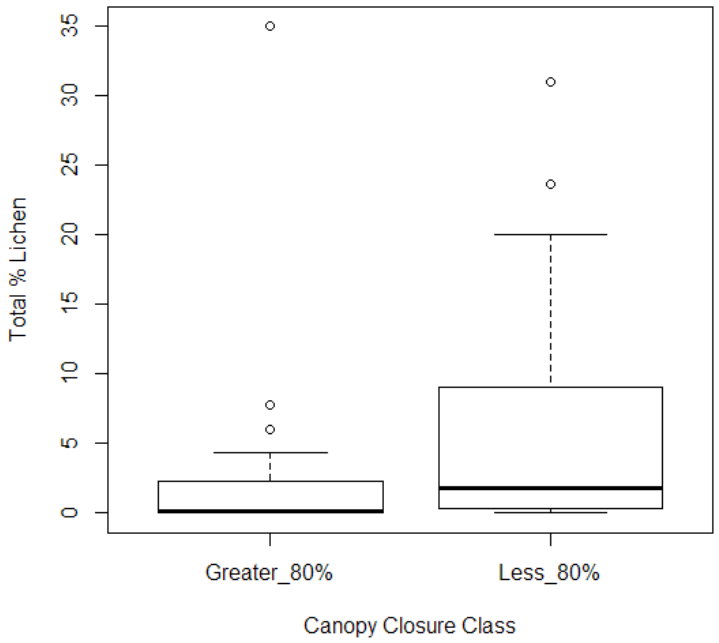


Figure 2.7. Standard boxplots of terrestrial lichen abundance (Total% Lichen) in relation to canopy closure class, in conifer-dominated stands.
Canopy closure classes: Greater than 80%, n = 28; Less than 80%, n = 77.

The greatest terrestrial lichen abundance was observed in one shallow jack pine-dominated (PjSha) stand, with mean lichen abundance of 20.01%. The PjSha standard forest unit (SFU) was omitted from the one-way ANOVA as only one stand belonged to that SFU type. Nine remaining SFUs were represented among the conifer-dominated stands. One-way ANOVA indicated no significant difference in mean terrestrial lichen abundance among SFUs (Figure 2.8). The Kruskal-Wallis test result was also not significant ($p = 0.4321$), indicating no difference in median terrestrial lichen abundance among standard forest units in the stands measured. Mean terrestrial lichen abundance was highest (8.35 ± 11.53%) in jack pine stands on deeper soils (PjDee), while the lowest abundance was observed in lowland spruce-dominated (SbLow) stands (2.66±4.63%) (Figure 2.8a; Appendix 2g).

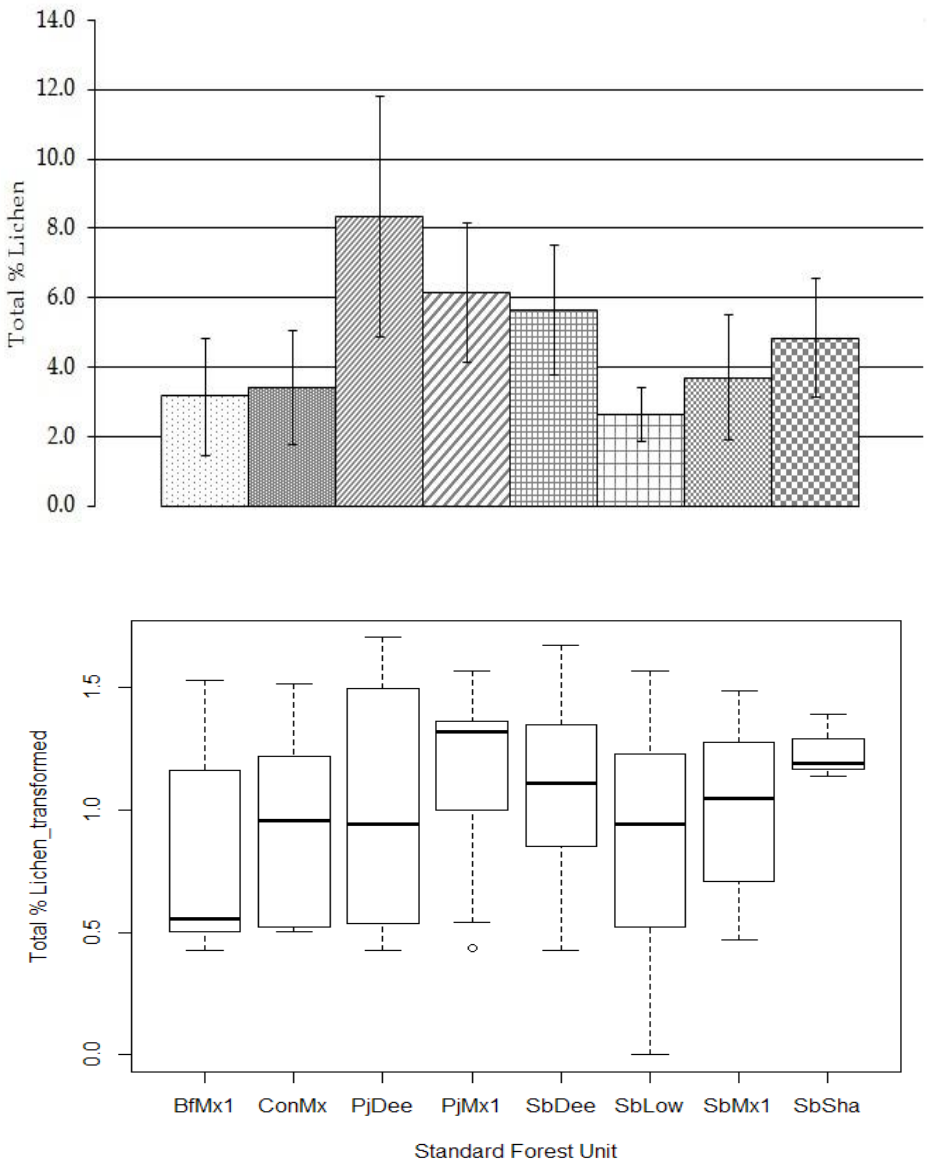


Figure 2.8. a) Mean terrestrial lichen abundance (Total % Lichen) in relation to standard forest unit (SFU) and b) Standard boxplots of terrestrial lichen abundance (Total % Lichen, Box-Cox transformed) in relation to SFU in conifer-dominated stands (n = 105); BfMx1 = Balsam Fir Mixedwood (n = 11), ConMx = Conifer Mixedwood (n = 10), PjDee = Jack Pine on Deeper Soils (n = 11), PjMx1 = Jack Pine Mixedwood (n = 9), SbDee – Black Spruce on Deeper Soils (n = 19), SbLow = Spruce Lowland (n = 34), SbMx1 = Black Spruce Mixedwood (n = 7), SbSha = Black Spruce on Very Shallow Soils (n = 3).

2.3.2.2 Understory Characteristics

Greater abundance of terrestrial lichen was observed in stands with less cover of ground vegetation (Figure 2.6), however lichen cover varied greatly among stands with vegetation cover between 50 and 100% (Appendix 2h). Cover of shrubs and tree foliage between 0.4 and 2m in

height ranged between 2 and 100% in conifer-dominated stands, with relatively high abundances (≥15%) of terrestrial lichen observed in stands with between 16 and 47% shrub cover (Appendix 2i). Relatively high abundances (≥15%) of terrestrial lichen were observed in stands with shrub height between 57 and 565cm (Appendix 2j).

2.3.2.3 Ecosite Characteristics

Lichen abundance was greater in stands with lower moisture regime values, that is, stands with more rapidly draining and drier soils (Appendix 2k). Stand-level moisture regime varied from xeric ("X", moisture regime code "0") to values of 8 (moisture regime "11") in the conifer-dominated stands measured. Soil depth ranged from very shallow to deep in the conifer-dominated stands measured. Stands with more shallow soils generally had higher percent cover of terrestrial lichen than stands with deeper soils (Appendix 2l). Lichen cover was somewhat greater among stands that had lower values for organic depth, although one stand with 20% cover of terrestrial lichen had mean organic depth of 78cm (Appendix 2m).

Of the conifer-dominated stands measured, 34 were classified as belonging to the Coarse Loamy texture family, 34 as Organic, 36 as Sandy, and one stand as Fine Loamy. One Fine Loamy stand was excluded from the ANOVA as it was the only stand of that texture family. The Fine Loamy stand had mean terrestrial lichen abundance of 3.01%. One-way ANOVA indicated differences in mean terrestrial lichen abundance among the Coarse Loamy (4.33 ± 6.79%), Sandy (7.08 ± 8.43%) and Organic (2.07 ± 4.14%) texture families ($p = 0.0259$, $F = 3.789$, $df = 2$; Figure 2.9a; Appendix 2n), with a significant difference in lichen abundance found between the Sandy and Organic texture families (Tukey HSD, $p < 0.05$). The Kruskal-Wallis test indicated that the mean ranks of terrestrial lichen abundance in stands differed among texture family classes ($p = 0.01717$, $\chi^2 = 8.1296$, $df = 2$). A two-sample t-test indicated that terrestrial lichen abundance was significantly greater in non-organic stands than in organic stands ($p = 0.02129$, $t = 2.3524$, $df = 74.618$; Figure 2.9b). Mann Whitney U-test results were also significant ($p = 0.01561$, $W = 1560.5$).

Mean terrestrial lichen abundance in non-organic stands was 5.71 ± 7.75%, and was 2.07 ± 4.14% in organic stands (Appendix 2o).

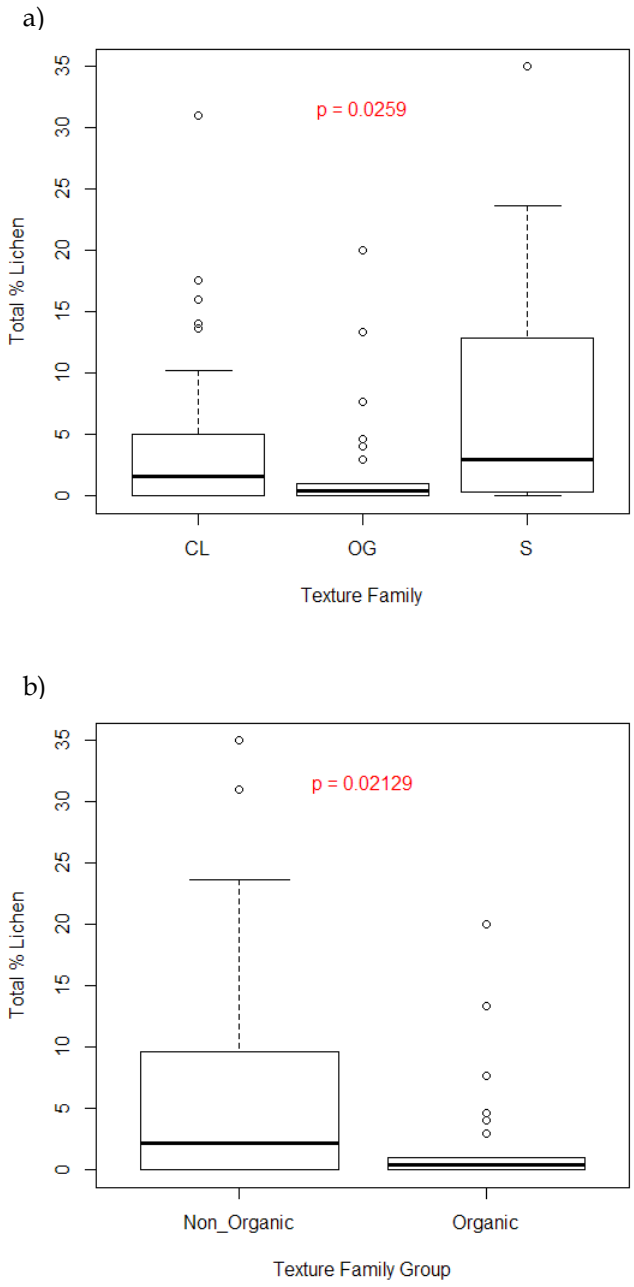


Figure 2.9. Standard boxplots of total terrestrial lichen abundance (% cover, Box-Cox transformed ($y^{0.15}$)) in relation to (a) Texture Family ("CL" = Coarse Loamy, n = 34; "OG" = Organic, n = 34; "S" = Sandy, n = 36) in 104 conifer-dominated stands, and to (b) Texture Family Group ("Non-Organic", n = 71; "Organic", n = 34) in 105 conifer-dominated stands.

2.3.3 Terrestrial Lichen in Non-Organic Conifer-Dominated Stands

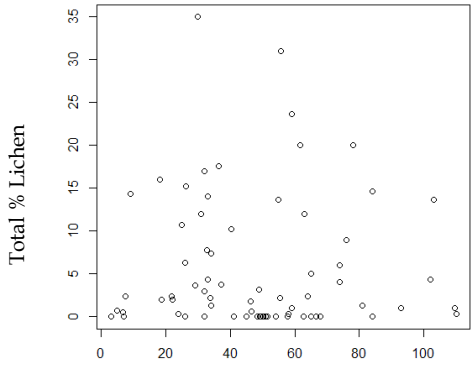
Further statistical analysis was done on the 71 non-organic conifer-dominated stands as these represented areas of higher terrestrial lichen abundance compared to organic conifer-dominated stands. A summary of the results of parametric and non-parametric tests of independent variables is provided in Table 2.8 below.

Table 2.8. Results of parametric and non-parametric tests for continuous and categorical variables in relation to terrestrial lichen abundance in non-organic conifer-dominated stands (n = 71).

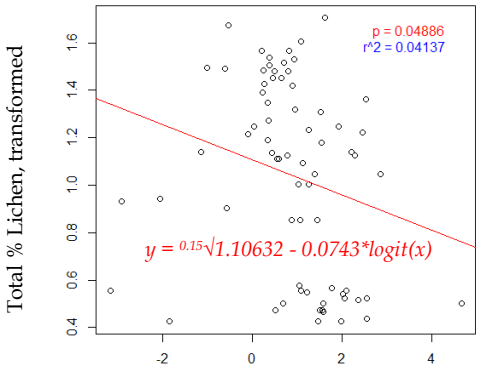
	Parametric		**Non-parametric**	
Independent Variable	Test	Result	Test	Result
Continuous				
Stand Age (years)	SLR*	ns (p = 0.852)	SRC**	ns (p = 0.667)
Canopy Closure (%)[1]	SLR	p = 0.049, r^2 = 0.041, df = 69	SRC	p = 0.001, rho = -0.387
Basal Area (m^2/ha)	SLR	p = 0.065, r^2 = 0.035, df = 69	SRC	p = 0.007, rho = -0.319
Tree Height (m)	SLR	p = 0.019, r^2 = 0.064, df = 69	SRC	p = 0.007, rho = -0.316
Crown Height (m)	SLR	p = 0.001, r^2 = 0.126, df = 69	SRC	p = 0.003, rho = -0.348
Percent Conifer (%)[2]	SLR	p = 0.035, r^2 = 0.049, df = 69	SRC	p = 0.012, rho = 0.297
Ground Vegetation Cover (%)	SLR	ns (p = 0.795)	SRC	ns (p = 0.789)
Shrub Cover (%)	SLR	ns (p = 0.179)	SRC	ns (p = 0.2644)
Shrub Height (cm)[3]	SLR	p = 0.049, r^2 = 0.041, df = 69	SRC	p = 0.043, rho = 0.241
Moisture Regime (code)	SLR	ns (p = 0.470)	SRC	ns (p = 0.482)
Soil Depth (cm)	SLR	p = 0.084, r^2 = 0.029, df = 69	SRC	ns (p = 0.2067)
Organic Depth (cm)[3]	SLR	ns (p = 0.7817)	SRC	ns (p = 0.7474)
Categorical				
Canopy Closure (class)	t-test	p = 0.001, t = -3.427, df = 55.3	Mann-Whitney U	p = 0.0004, W = 281

[1] Logit transformed
[2] Arc sin square-root transformed
[3] Log transformed
* Simple linear regression
**Spearman rank correlation

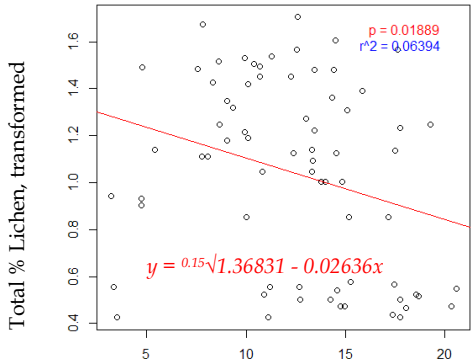
Results of parametric and non-parametric tests were generally consistent (Table 2.8). Statistically significant ($p < 0.05$) negative relationships were found between total lichen abundance (%) and canopy closure, tree height and crown height (Figure 2.10). A weak negative relationship was found between lichen abundance and basal area (Appendix 5a) and soil depth (Appendix 5b), but no correlation was found between lichen abundance and soil depth using



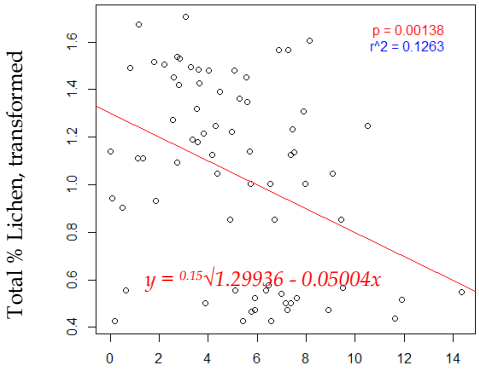
a) Stand Age (years)



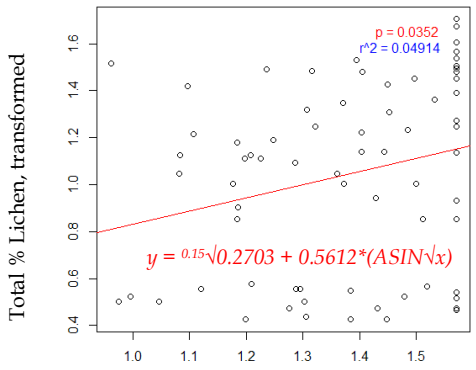
b) Canopy Closure (%), logit transformed



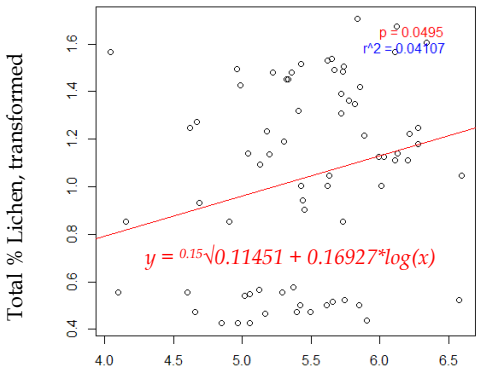
c) Tree Height (m)



d) Crown Height (m)



e) Percent Conifer (%), arc sin square root transformed



f) Shrub Height (cm), log transformed

Figure 2.10. Total terrestrial lichen abundance (% cover) in relation to a) Stand Age (years), b) Canopy Closure (%, logit transformed), c) Tree Height (m), d) Crown Height (m), e) Percent Conifer (%, arc sin square root transformed), and f) Shrub Height (cm, log transformed) in 71 non-organic conifer-dominated stands. Total lichen abundance data for (b) through (f) were Box-Cox transformed and represent actual % cover data ranging from <1 to 35%.

Spearman rank correlation (Table 2.8). Statistically significant positive relationships were found with percent conifer and shrub height (Figure 2.10). No linear relationships were found with stand age, ground vegetation cover, shrub cover, moisture regime, or organic depth. R-squared and rho values throughout were relatively small indicating low explanatory strength of the independent variables. Mean terrestrial lichen abundance was significantly greater in stands with <80% canopy closure than in stands with ≥80% canopy closure (Figure 2.11).

2.3.3.1 Overstory characteristics

Stand age varied from 3 to 110 years among non-organic conifer-dominated stands (Appendix 3a). Mean terrestrial lichen abundance was nearly 3 times higher in stands with < 80% canopy closure (7.33±7.70%) than in stands with > 80% canopy closure (2.71±6.91%; Figure 2.11). Stands with relatively high (> 15%) lichen abundance had mean canopy closure estimates ranging between approximately 26 and 83% (Appendix 3b).

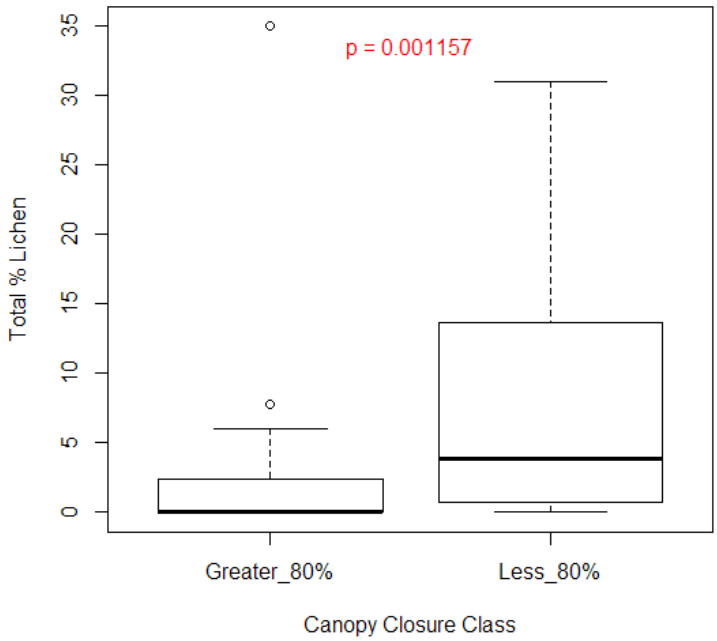


Figure 2.11. Standard boxplots of total terrestrial lichen abundance (% cover) in relation to canopy closure class ("Greater_80%" = stands with ≥ 80% canopy closure n=25, "Less_80%" = stands with <80% canopy closure, n=46) in non-organic conifer-dominated stands.

Relatively high terrestrial lichen abundance (≥ 15%) was found in stands with basal area ranging between 10 and 20 m^2/ha (Appendix 3c) and in stands with mean tree height ranging between approximately 8 and 18 metres (Appendix 3d). The highest (≥15%) observed abundances of terrestrial lichen occurred in stands ranging between 1 to 8 metres in mean crown height (Appendix 3e). Percent conifer ranged from approximately 67 to 100% among non-organic conifer stands. Among the twenty stands that were considered pure conifer (100% conifer tree species), terrestrial lichen abundance varied, with 8 stands having ≥15% and just 5 stands having <1% cover of terrestrial lichen (Appendix 3f).

2.3.3.2 Understory characteristics

Relatively high abundances (≥15%) of terrestrial lichen were observed in stands with vegetation cover ranging between 45 to ≥100% (Appendix 3g), and shrub cover ranging between approximately 16 and 33%. Shrub cover was highly variable (2 to 60%) among stands where terrestrial lichen abundance was low (<1%; Appendix 3h). Shrub height ranged between 56 and 729 cm among non-organic conifer-dominated stands. Mean shrub height was 329 (± 140) cm in stands with relatively high (≥15%) terrestrial lichen abundance, and was 216 (±128) cm in stands with terrestrial lichen present in trace amounts (<1%; Appendix 3i).

2.3.3.3 Ecosite Characteristics

Moisture regime varied among stands and ranged from xeric (moisture regime "X") to very moist (moisture regime "6"), with the highest observed abundance (10.68%) of terrestrial lichen occurring in a xeric stand (Appendix 3j). The lowest observed abundances (1.06±1.36%) of terrestrial lichen were found in moist stands (moisture regime "5"). Among stands with relatively high (≥15%) terrestrial lichen abundance, soil depth classes ranged from shallow (>15 to ≤ 30 cm) to deep (≥120cm). Among the 22 stands characterized as having deep soils, 10 had just trace amounts (<1%), while 4 had relatively high abundances (≥15%) of terrestrial lichen (Appendix 3k). Organic depth ranged from 1 to 52 cm, with relatively high abundances (≥15%) of terrestrial lichen occurring in stands with organic depths of 1 to 18 cm (Appendix 3l).

A summary of regression results (p-values) described above for conifer-dominated stands, and the subset of data containing non-organic conifer-dominated stands is presented in Table 2.9 below.

Table 2.9. Resulting p-values from simple linear regression and ANOVA (for Texture Family) indicating significance of independent environmental variables in relation to terrestrial lichen abundance in all conifer-dominated stands (n = 105) and conifer non-organic stands (n = 71).

Environmental Variable	Conifer Stands	Conifer Non-organic Stands
	P	*P*
Stand Age (years)	0.781	0.852
Canopy Closure (%)	0.484	0.049*
Basal Area (m^2/ha)	0.862	0.065
Tree Height (m)	0.696	0.019*
Crown Height (m)	0.085	0.001**
Percent Conifer (%)	0.312	0.035*
Ground Vegetation Cover (%)	0.033*	0.795
Shrub Cover (%)	0.186	0.179
Shrub Height (cm)	0.034*	0.050*
Moisture Regime (code)	0.011*	0.47
Soil Depth (cm)	0.004**	0.084
Organic Depth (cm)	0.034*	0.782
Texture Family (class)	0.026*	0.121

Signif. codes: 0.01 '**', 0.05 '*'

2.3.4 *Non-Metric Multi-Dimensional Scaling using Species Abundance Data*

The final NMDS ordination was interpreted in terms of the relative distances among objects in the coordinate frame. Among the 71 non-organic conifer-dominated stands measured, some grouping was evident due to similar abundances of the lichen genera considered (Figure 2.12). Stands with any observed occurrences of *Peltigera* spp. are located in the uppermost portion of the ordination diagram. Stands with abundances of *Cladina* spp. that are relatively higher than observed abundances of *Cladonia* spp. or *Peltigera* spp. are located closest to the lower left-hand side of the ordination diagram. Stands with higher abundance of *Cladonia* spp., but with relatively lower abundances of the other two genera are located nearest the right-hand portion of the ordination diagram.

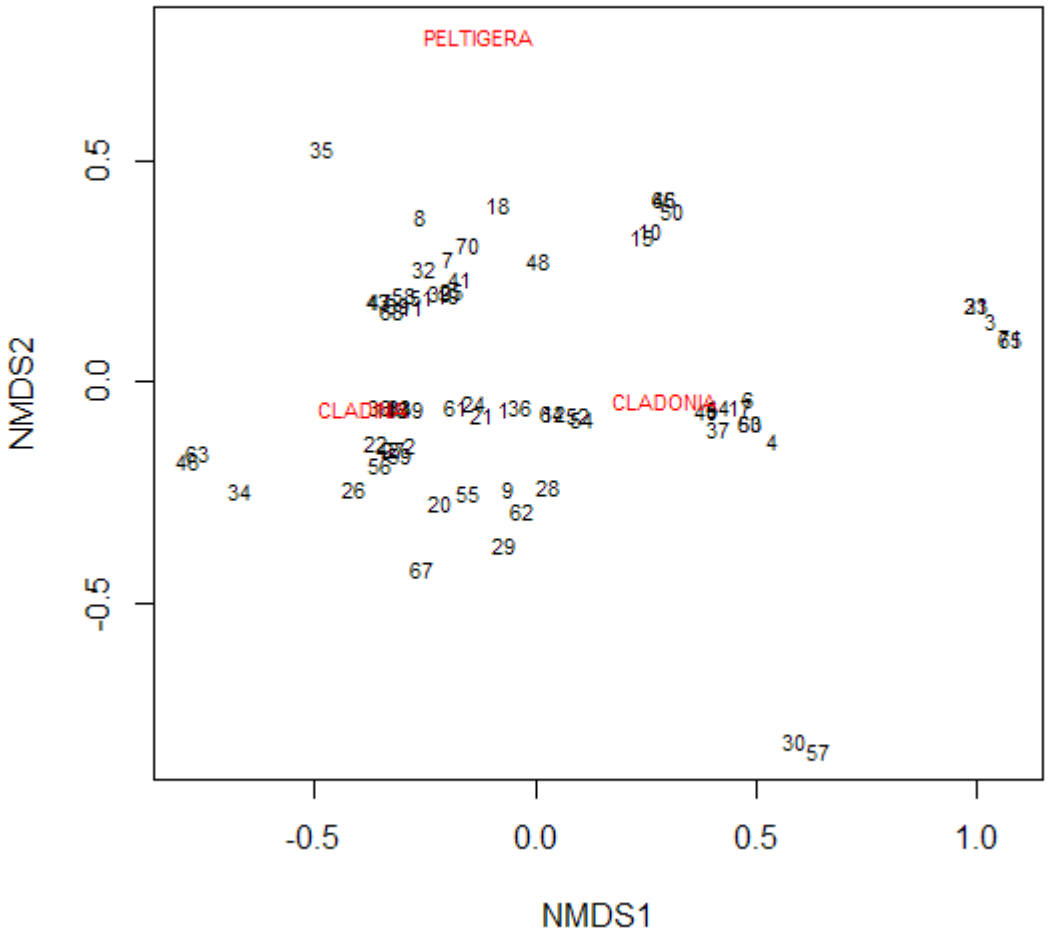


Figure 2.12. Ordination of commonly occurring terrestrial lichen genera (*Cladina* spp., *Cladonia* spp. and *Peltigera* spp.) and stands using non-metric multi-dimensional scaling, on Box-Cox transformed terrestrial lichen abundance data from non-organic conifer-dominated stands.

Four environmental variables were found to be significant (Table 2.10); including the overstory stand characteristics crown height, basal area and percent conifer (envfit permutation tests, $p < 0.05$). Shrub height had weak significance (envfit permutation test, $p < 0.1$) to the ordination. The NMDS ordination shows vectors of significant environmental variables with the arrows indicating direction of increasing gradients (Figure 2.13). The similar relative lengths of the environmental vectors indicate the variables have similar significance to the ordination.

Table 2.10. Significance of environmental variables fit to NMDS ordination.

Environmental Variable	r^2	Pr (>r)
Stand Age (years)	0.036	0.259
Canopy closure (%)	0.039	0.273
Basal area (m^2/ha)	0.091	0.047*
Crown height (m)	0.09	0.042*
Percent Conifer (%)	0.089	0.046*
Ground Vegetation Cover (%)	0.024	0.427
Shrub Cover (%)	0.015	0.615
Shrub Height (cm)	0.079	0.055
Moisture Regime (code)	0.124	0.494
Soil Depth (cm)	0.025	0.436
Organic Depth (cm)	0.0002	0.995
Texture Family (class)	0.031	0.327

Signif. codes: 0.01 '**', 0.05 '*'

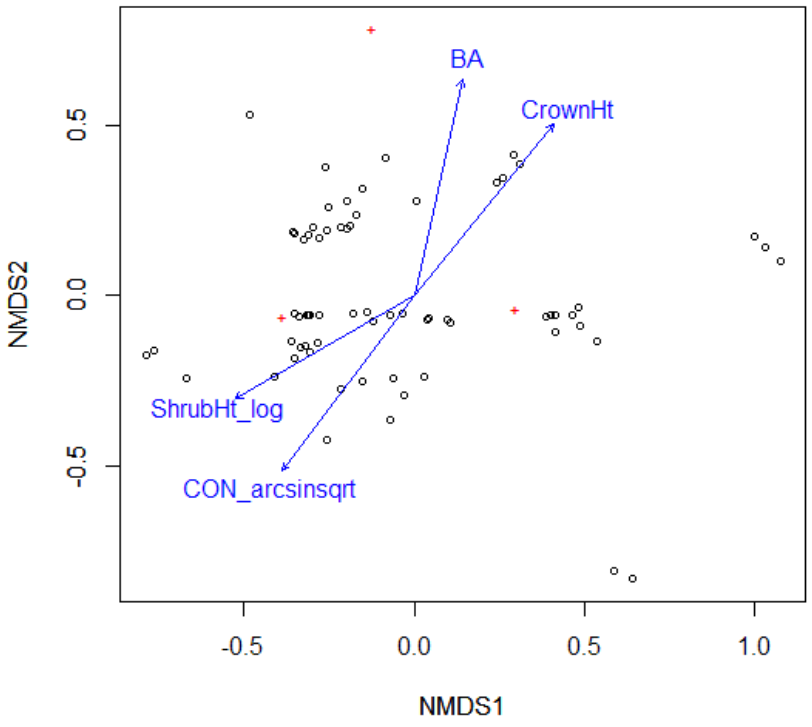


Figure 2.13. Ordination of terrestrial lichen genera and stands in relation to environmental variables with vectors significantly related to the ordination ("BA" – total basal area per ha; "CrownHt" – crown height; "ShrubHt_log" – log-transformed shrub height data; "CON_arcsinsqrt" – arc sin square root-transformed percent conifer data). Open circles represent stands, crosses represent lichen genera. Arrows show direction of increasing gradients; lengths of arrows are proportional to the correlation between the variables and the ordination.

2.3.5 Non-Metric Multi-Dimensional Scaling using Environmental Data

No differentiation of stands was observed in the NMDS ordination (Figure 2.14). Most stands were positioned in the same general area in the ordination diagram, with the exception of a few stands that represented anomalies in terms of their data for one or more of the environmental variables. Stand 12, for example (located near the top left of the diagram) had exceptionally low canopy closure (5%) relative to all other stands, and Stand 65 (located near the bottom left of the diagram), was the absolute youngest (3 years old) of all stands measured. Stand 64 (located at the far left of the diagram) had very low (0.08 m) crown height compared to most other stands. Stand 17 (located near the top right of the diagram) had relatively low shrub cover (~11%) compared to most other stands, while Stand 69 (located near the bottom right of the diagram) had relatively low soil depth (~22cm) compared to other stands. None of the three lichen genera showed any significant correlation to the ordination diagram, indicating no genera-specific preference for any particular stand-level environmental characteristic.

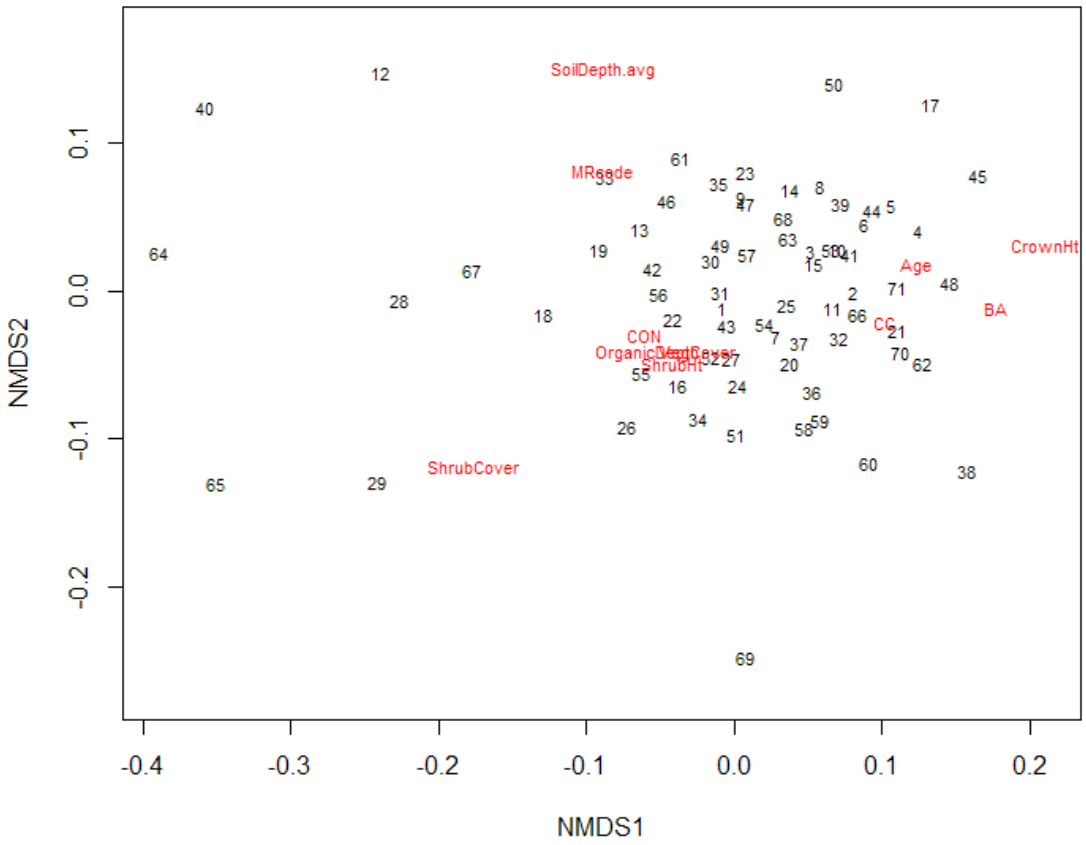


Figure 2.14. Ordination of environmental variables and stands using non-metric multi-dimensional scaling, on un-transformed environmental data from non-organic conifer-dominated stands.

2.3.6 Multiple Linear Regression

The final model included overstory environmental variables stand age, crown height and percent conifer, ecosite variables soil depth and organic depth, and one understory variable, shrub height (Table 2.11). The model accounted for approximately 39% of the variance in terrestrial lichen abundance in the stands sampled (Adjusted $R^2 = 0.3922$, $F_{6,64} = 8.527$, $p = 0.0000008187$).

Table 2.11. Significance and estimated coefficients of environmental variables included in final multiple linear regression model used to predict terrestrial lichen abundance.

Environmental Variable	Regression Coefficient	Pr(> | t |)
Age (years)	0.008	0.001**
Crown Height (m)	-0.092	<0.001***
Percent Conifer (%)	0.641	0.006**
Soil Depth (cm)	-0.002	0.028*
Organic Depth (cm)	-0.217	0.070.
Shrub Height (cm)	0.556	0.001**

Signif. codes: 0.001'***', 0.01 '**', 0.05 '*', 0.1 '.'

2.4 DISCUSSION

Terrestrial lichen abundance was generally low and highly variable (3.23 ± 6.04 % cover) among the forested stands measured in this study, and was influenced by cover type but not disturbance history. Stand-level estimates of lichen cover were negatively skewed with 91 of 158 (57%) stands having less than 1% cover of lichen. Still, lichen cover was higher in conifer-dominated (4.28 ± 6.83%), than in deciduous (0.60 ± 1.51%) or mixedwood stands (0.62 ± 1.01%) (Figure 2.5b). This finding supports the assumption that conifer-dominated stands sustain higher abundances of terrestrial lichen (Lesmerises et al., 2011; Peckham et al., 2009). This association between terrestrial lichen and the presence of conifer tree species is likely more a function of inherent site characteristics, such as dominant soil texture and soil depth, than overstory species composition itself. Deciduous and mixedwood stands generally represent sites with richer soils (Kayahara et al., 2000), where terrestrial lichen is a poor competitor with faster-growing vascular plant species (Harris, 1996).

Though generally higher in terrestrial lichen abundance compared to other stand types, conifer-dominated stands were quite variable in this respect, with many stands exhibiting very low cover estimates of terrestrial lichen. Conifer stands with organic-textured soils had less terrestrial lichen cover than conifer stands with non-organic textured soils such as coarse or fine loams, or sand (Figure 2.9). The organic stands also represented 31 of the 34 spruce lowland (SbLow) stands measured. Spruce lowlands include ecosites such as low treed bogs (B126), organic or mineral poor conifer swamps (B127 or B222), organic or mineral intermediate conifer swamps (B128 or B223), and organic or mineral rich conifer swamps (B129 or B224; ecosite codes as per OMNR, 2009). Terrestrial lichen species such as *C. rangiferina* are capable of growing in these ecosites, but the ground surface of these ecosites is usually dominated by moss (OMNR, 2009). Though a positive relationship was observed between lichen abundance and percent conifer in non-organic stands, it was highly variable, and several pure (100%) conifer stands had very low abundances of terrestrial lichen (Figure 2.10e, Appendix 3f). This suggests that in non-organic conifer-dominated stands, where conifers comprise ≥70% of stand basal area, increases in percent conifer do not necessarily coincide with greater abundances of terrestrial lichen.

No difference in mean terrestrial lichen abundance was found between previously harvested and naturally disturbed stands (Figure 2.4). This finding contrasts those of Coxson and Marsh (2001) who found greater lichen cover in winter-harvested stands than in fire-origin stands, and Dettki and Esseen (1998), who found lichen abundance to be two times higher in natural than in managed stands. The fact that no difference was observed between harvested and natural stands may be explained in part by the relative age class distributions of harvested and natural stands (Figure 2.3), as disturbance history is often confounded with stand age (Johansson, 2008). In general, harvested stands were represented by a higher proportion of younger age classes and natural stands were represented by a higher proportion older age classes (Figure 2.4). Seventy % of harvested stands were < 40 years of age, and 76% of natural stands were > 40 years of age. Although stand age has been reported as an important factor governing lichen abundance

(Boudreault et al., 2002; Hilmo et al., 2011), the relationship between these two variables is not necessarily linear (Johansson, 2008; Hilmo et al., 2009). Younger stands may have lower abundances of terrestrial lichen given the long periods of time required for many species to colonize and grow (Brodo et al., 2001), while terrestrial lichen abundance in older stands may be limited by low light conditions associated with denser canopies (Coxson & Marsh, 2001). Consequently, neither early nor late successional stands may be particularly high in terrestrial lichen abundance. Both the previously harvested and the naturally disturbed stands measured in this study on average represent similar low abundances of terrestrial lichen, albeit for different ecological reasons.

No linear relationship was found between terrestrial lichen abundance and stand age in conifer-dominated stands (Figures 2.6a, 2.10a). This finding is in contrast to that of Arseneault et al. (1997) who found terrestrial lichen biomass to increase with stand age. Their study was conducted in northern boreal forest and forest tundra, where tree height was relatively low (< 8m high) compared with the tree height data observed in this thesis. In the study areas measured for this thesis, occurrences of relatively high lichen cover were observed in stands of both young and old age classes. Two stands under 20 years of age had relatively high abundances (> 10%) of terrestrial lichen. One of these stands was a 9 year old jack pine stand on a deep sandy soil that had very low canopy closure (35%); the other was a conifer mixedwood that also had relatively low canopy closure (67%) and was located on an ecosite characterized by very shallow soils (B012; OMNR, 2009). These observations and the lack of a significant relationship between stand age and lichen abundance suggest that stand age alone is not a determinant of terrestrial lichen abundance. Rather, age, temporal changes in stand structure, and inherent site characteristics all likely influence the abundance of terrestrial lichen on a given site.

Within conifer-dominated stands, no particularly strong relationships were identified between individual stand structural characteristics and terrestrial lichen abundance. Although canopy closure, tree height and crown height all yielded statistically significant regressions

(Figure 2.10), none of the derived models explained more than 12.6% of the variability in terrestrial lichen abundance. These factors, along with basal area (Appendix 5a) were negatively related to terrestrial lichen abundance, consistent with other studies that have found negative relationships between lichen abundance and canopy structural variables that limit the amount of light available at the forest floor (Lesmerises et al., 2011; Waterhouse et al., 2011). For example, Coxson & Marsh (2001) found higher density and basal area to be associated with lower estimates of lichen abundance. Terrestrial lichen abundance was greater in stands with <80% canopy closure, consistent with the findings of others (Racey et al., 1991; Moning et al., 2009). Crown height, or height to lowest live tree branches, had the strongest relationship with terrestrial lichen abundance among all variables measured (Figure 2.10d), and was the only canopy structural variable that had a negative relationship ($p < 0.1$) with lichen cover when organic stands were included in the analysis (Appendix 4). Lower values for crown height are likely associated with greater light penetration within the canopy, with trees grown in more open conditions typically having longer crowns that extend to the ground level (Temesgen et al., 2005). Among the non-organic conifer stands measured in this study, stands with crown heights of ≤1m had mean canopy closure that was relatively low (~16%).

Terrestrial lichen abundance was also found to vary with ecosite characteristics including soil depth, organic depth, moisture regime and soil texture family – inherent factors that are generally not managed intentionally through forest harvest and silviculture operations. The strength of the effects of these characteristics was generally weak, but more apparent with organic stands included in the analysis. Organic stands generally had sparse lichen cover (23 of 34 had lichen cover <1%) and most of them (27 of 34) had soil depths greater than 120 cm. Soil depth may thus have had a negative relationship with terrestrial lichen (Figure 2.6e), simply due to the fact that the low cover values in deep organic sites had a strong influence on the regression. Stands with the deepest soils (> 120 cm deep) exhibited great variability with respect to terrestrial lichen. The stand with the highest cover of lichen (35%) had deep (> 120 cm) soil (Appendix 2l).

Inspection of stand-level data revealed that the shallowest sites, on which terrestrial lichen is generally thought to grow well (Harris, 1996; Brodo et al., 2001) were also associated with relatively low canopy closure and basal area. Organic stands also had greater estimates of organic depth, and included most of the wetter sites. These co-occurring factors likely both contributed to an overall negative effect on lichen abundance in the sample that included organic stands. Low cover of terrestrial lichen in stands with deep organic layers could be a function of poor drainage, or a poor capacity of terrestrial lichen to compete with moss species that dominate the ground layer in such stands. Coarser textured soils (such as sands) are thought to offer better drainage conditions that favour terrestrial lichen (Harris, 1996). Mean lichen abundance tended to be higher in sandy (7.08 ± 8.43%) than in coarse loamy (4.33 ± 6.79%) stands (Appendix 2n), but this difference was not statistically significant.

Understory characteristics including cover of ground and shrub vegetation, and shrub height had either highly variable or no relationships with terrestrial lichen abundance, but likely reflect a combination of understory light and ecosite characteristics. A positive relationship between lichen abundance and shrub height (Figures 2.6c & 2.10f) seemed to contradict the notion that canopy structure, and hence understory light conditions, are important to terrestrial lichen abundance. Most stands (12 of 20) with relatively high (>10%) lichen cover had moderate (100 to 300 cm) estimates of shrub height, and 4 stands with very high lichen cover (>20%) had relatively high values for mean shrub height (342 to 565 cm). These 4 stands were all located on coarser textured soils, had relatively open canopies, and low (16.3 to 30.7%) shrub cover. Greater understory light availability may have contributed to both the increased shrub height and lichen abundance in these stands. Overall, the relationship between lichen cover and shrub height is quite variable ($r^2 = 0.04107$), and removal of the 4 data points representing exceptionally high lichen cover would likely result in a less than significant relationship with shrub height.

Contrary to expectations (Racey et al., 2008, unpublished), terrestrial lichen abundance was not related to shrub cover. Relatively high (> 10%) lichen cover was observed in one SbLow

stand with a combined shrub cover exceeding 100%. Roughly half the shrub cover in this particular stand was comprised of *Ledum groenlandicum*, which only grows up to 1 metre in height (Chambers et al., 1996). Canopy closure in this stand was relatively low (54%), indicating that shrub cover did not greatly reduce available light for terrestrial lichen. This suggests high lichen cover may be observed in stands with high shrub cover, provided the height of shrubs does not seriously impede incoming light, and provided suitable microhabitats are available for terrestrial lichen to become established. The negative relationship between lichen abundance and ground vegetation cover (Figure 2.6b) was highly variable, and was not observed with organic stands removed from the dataset. The ground layer of organic stands is typically dominated by bryophytes (OMNR, 2009), suggesting ecosite factors contributed to the observed relationship. Bryophyte cover is understood to have an inverse relationship with lichen cover (Pharo & Vitt, 2000).

When combined using multiple linear regression, age, crown height, percent conifer, soil depth, organic depth and shrub height were found to account for ~39% of the observed variability in terrestrial lichen abundance in non-organic conifer stands (Table 2.11). Most of the variables included in the final model were consistent with those found significant in previous simple linear regressions. Crown height had a strong negative relationship with lichen abundance and provided the strongest contribution (lowest p-value) to the model, affirming the importance of open understory light conditions to terrestrial lichen abundance. Stand age and organic depth were not found to be significant to lichen in previous analyses of these stands, but did contribute to the model when they were considered in combination with other factors. Stand age had a strong positive relationship with terrestrial lichen abundance when all other independent variables in the model were held constant (Table 2.11). This finding suggests that stand age may be an important predictor of terrestrial lichen abundance provided that stands have suitable understory light conditions (as indicated by variables crown height and shrub height), and possess desirable ecosite characteristics (as indicated by soil and organic depth).

Organic depth had a weak negative relationship with terrestrial lichen abundance when other independent variables in the model were held constant. In a similar fashion, this suggests that organic depth may be important in stands of certain ages that have favourable light conditions and are located on soils that have suitable soil depth (likely shallow) for terrestrial lichen to establish and grow. The multiple regression analysis demonstrates that terrestrial lichen abundance is likely a function of a combination of factors including light availability, soil characteristics and the time required for lichen to grow. That much of the observed variability could not be explained by the model, suggests that other unknown factors not measured in this study may also be important to terrestrial lichen abundance.

Though the highest mean terrestrial lichen abundance was observed in the PjDee (jack pine on deep soils) SFU, ANOVA test results indicated no significant differences among SFUs. The highest observed stand-level estimate of terrestrial lichen cover (~20%) occurred in a single measured shallow jack pine (PjSha) SFU. Limited data from SFUs characterized by shallow soils (e.g. SbSha n = 3), combined with the high variability of terrestrial lichen abundance among most SFUs, may be why standard forest units failed to explain observed variability in terrestrial lichen abundance in the stands measured. Still, SFUs allow forest managers to identify conifer-dominated stands, which supported greater lichen abundance in this study. The SFU designation also allows for identification of stands with lower potential for growth of terrestrial lichen, namely the SbLow stands.

Among non-organic conifer-dominated stands, species ordination using NMDS indicated grouping of stands based on similarities in the abundances of the three most commonly recorded terrestrial lichen genera, *Cladina* spp., *Cladonia* spp. and *Peltigera* spp. (Figure 2.12). It is difficult to conclude whether the distribution reflects any major ecological separation among stands. NMDS ordinations of species abundance data typically use datasets consisting of the entire list of plants recorded in sample plots or stands, as they are commonly used to evaluate total species diversity in relation to various environmental variables or gradients. In this ordination, data for

only 3 genera were used to separate the stands measured. Of these, *Peltigera* spp. were relatively rare, with most stands (48 of 71) having 0% cover. In comparison, most stands had at least some amount of *Cladonia* spp. (66 of 71), usually present in low abundances. Data for *Cladina* spp. seemed to vary the most among stands. Stand-level occurrences of the genera used in this analysis were not exclusive of one another, as all three could occur within the same stand in various abundances. Thus, the observed distances in the ordination space are a reflection of the relative abundances of just three groups of species, two of which seem to represent little overall variation among the measured stands, making it difficult to attribute any pattern in the ordination plot to any considerable ecological differences among stands. Despite this, the fit of environmental variables to the ordination plot suggests that some environmental gradients related to stand structure may be associated with the distribution of some stands in the ordination space. The abundance of *Peltigera* spp., positioned at the top of the ordination plot, may be related to increased basal area and crown height, and may be indicative of a decreasing light gradient (Figure 2.13). *Peltigera* spp. are cyanobacterial lichens that grow best under more shaded and humid habitat conditions (Brodo et al., 2001). The direction of the vector for shrub height corresponded with the general locations of a few stands that had relatively high abundances of *Cladina* spp. and relatively high values for shrub height. For example, stand #63 and stand #46 (located on the right-hand side of the shrub height vector), had 23.67 and 35% cover of *Cladina* spp., and shrub heights of 565.31 and 342.31 cm, respectively. Stand #20 (located on the left-hand side of the shrub height vector) also had relatively tall shrubs (500.22 cm.), but cover of *Cladina* spp. was rather low (2.4%). The apparent significance of the shrub height vector is consistent with the simple linear regression results described previously, but appears to be related to the occurrence of high lichen abundance in just a few stands that also had taller shrubs.

When environmental data were used to differentiate sampled stands, ordination did not reveal any significant groupings (Figure 2.14). This finding implies that environmental data of sampled stands are quite variable, and that for this dataset, values (or ranges of values) for

certain environmental variables do not necessarily correspond with values (or ranges of values) for other environmental variables. Whereas a grouping of stands associated with a significant vector for a particular lichen species would indicate a preference of that species for certain environmental conditions, the lack of any significant groupings or vectors suggests that the occurrence of terrestrial lichen species depends on a complex array of environmental factors, the significance of which may vary from stand to stand.

Most of the relationships observed in this study were consistent with our expectations in terms of the stand structural conditions considered most suitable for terrestrial lichen. The linear models used however indicated general poor predictive power of the stand structural characteristics measured. This may be partly related to the manner in which stand-level estimates were calculated based on averages of plot-level values for stand structural characteristics. Forest management planning efforts normally depend on the recognition of features that are discernable at the stand-level; however the variability of stand-level data observed in this study suggests that better understanding may be gained through analysis of characteristics at a finer scale. It is therefore recommended that further analysis be carried out on plot-level lichen and environmental data. A more thorough comparison of standard forest units used in planning could also assist in identifying differences in terrestrial lichen, or other features important to woodland caribou habitat, which may be apparent at the stand scale.

3.1 INTRODUCTION

Forest management activities such as harvest and silviculture can manipulate the structure of forest stands, not only for the purpose of timber production but for the creation and maintenance of wildlife habitat (Kuuluvainen & Grenfell, 2012). In recent decades, natural disturbance pattern emulation has become a major tenet of ecosystem based management philosophy (Kuuluvainen & Grenfell, 2012). Forest management strategies aimed at mimicking natural disturbances such as fire are applied under the premise that forest-inhabiting species have evolved with, and have developed resilience to such disturbances. Problems that have emerged due to a history of fire suppression have led to concerns that managed forests do not maintain the same ecological functions as natural forests, and activities such as prescribed burning have often been suggested as part of the solution to this issue (OMNR, 2001). Either prescribed burning or mechanical site preparation have historically been applied following harvest operations in Ontario as ways of increasing mineral soil exposure by clearing slash and competing understory vegetation. The two treatments however, involve fundamentally different processes which may result in differences in stand structure. Such stand structural differences may manifest themselves differently with respect to the response of understory plant communities, including terrestrial lichen.

The purpose of this study is to compare mechanically site prepared stands with stands treated with prescribed burning, in terms of terrestrial lichen abundance. Stand structural characteristics considered important to terrestrial lichen abundance are compared between the treatment groups in order to understand the relative importance of stand structure and treatment effect. The results of this study are used to evaluate the validity of recommendations to use prescribed burning as a silvicultural tool to create or maintain woodland caribou winter habitat in northern Ontario.

3.2 METHODS

3.2.1 Study Area Description

Data were collected from forested stands located within and east (~ 20km) of the Auden study area described in Chapter 2, and within the administrative forest management units of the Lake Nipigon and the Kenogami Forests (Figure 3.1). The study area has a disturbance history that includes fire disturbance and anthropogenic disturbance including forest harvesting and road-building for the purpose of commercial forestry, mining and recreational activities. Recent radio-collar location data indicates some habitat use by woodland caribou of previously harvested stands within this study area (Rodgers, unpublished data). Harvested stands within the area have historically been treated with a variety of silvicultural treatments including either mechanical site preparation or prescribed burning prior to artificial regeneration through planting or aerial seeding.

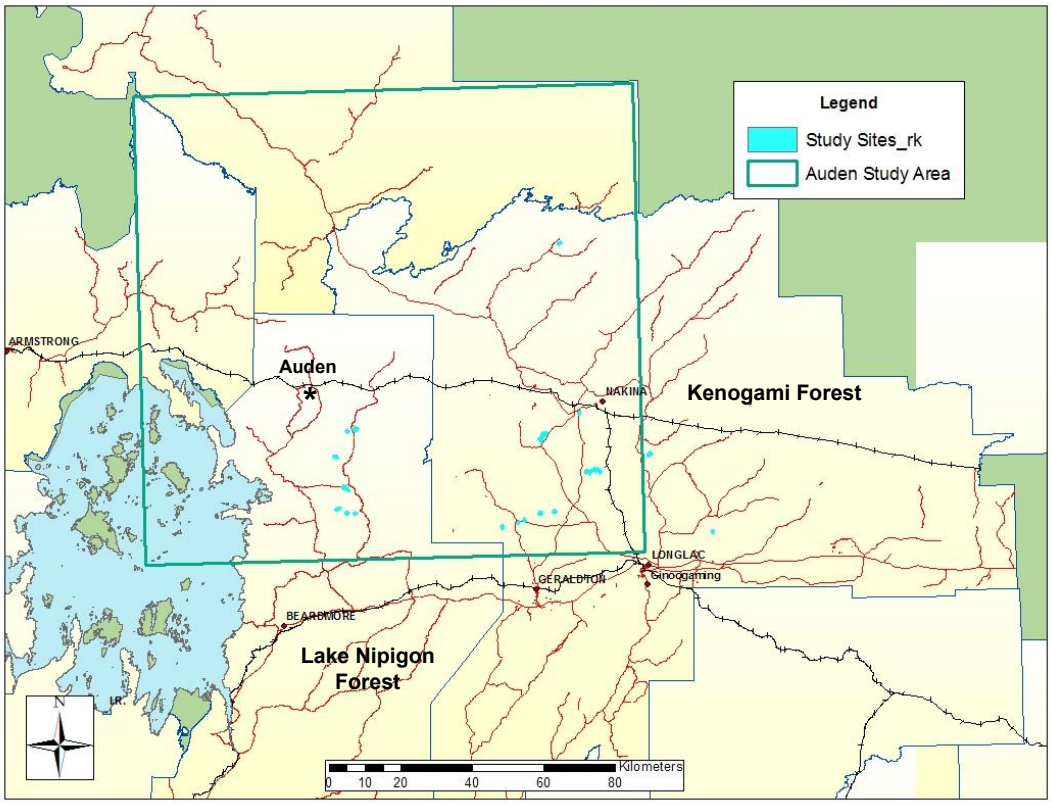


Figure 3.1. Map showing study sites in the Auden study area.

3.2.2 Experimental Design

Historical silviculture data from the Lake Nipigon and Kenogami Forests were used in the selection of candidate stands to be sampled. ArcGIS™ was used to select polygons from available GIS (Geographic Information System) layers containing information on silvicultural treatment history within the study area. Polygons labelled as "Burn" or "Prescribed Burn" within the site preparation (SIP) layer were selected for further consideration as potential candidate sites for the prescribed burn (PB) treatment group. Polygons labelled as "Bracke", "Disc Trencher", "Mechanical", "TTS", "Power Trencher", or "Shear Blade" within the SIP layer were selected for further consideration as candidate sites representing the mechanically site prepared (MSP) treatment group. From each of these selections, polygons that were identified as having been planted after site preparation activities were selected. These polygons were clipped to the 2010 Ontario Forest Resources Inventory (FRI) and a list of candidate stands was created by selecting FRI polygons that were accessible by roads or trails and were conifer-dominated (≥70% conifer according to FRI). Further, stands were selected that had met their respective target standard forest units (SFUs) according to the PLANFU and SFU fields in the FRI, thus the sample represented stands in which silviculture treatments were successful.

The criteria described above limited the selection of accessible candidate PB stands to just twelve planted between 1970 and 1988, since the PB treatment has historically been used less often than other site preparation treatments. Mechanically site-prepared stands planted during this same approximate time period were randomly selected from the list of candidates. Twelve stands from each treatment group were selected for a total sample of 24 stands. Although replication among SFUs was not possible within each treatment group, an attempt was made to select a variety of both spruce and pine-dominated stands, with both shallow and deep soils among those selected for sampling. Based on available FRI and silviculture data, the resulting sampling matrix is representative of a variety of spruce and pine-dominated stands aged approximately 20 to 40 years (Table 3.1).

Table 3.1. Sampling matrix of prescribed burn (PB) treated and mechanically site prepared (MSP) stands representing spruce (Sb) and pine (Pj)-dominated stands aged approximately 20 to 40 years. Standard forest unit (SFU) designations for selected stands based on 2010 Ontario Forest Resources Inventory data.

	Silvicultural Treatment							
	PB				**MSP**			
Stand Type	**Pj-dominated**		**Sb-dominated**		**Pj-dominated**		**Sb-dominated**	
Age	SFU	n	SFU	n	SFU	n	SFU	n
20 - 30	PjDee	2	SbDee	1	PjDee	2	SbDee	2
30 - 40	PjMx1	2	SbDee, SbMx1	5	PjDee, PjSha	4	SbMx1, SbDee	3
40 +			SbMx1, SbSha	2	PjMx1	1		
Total	**12**				**12**			

3.2.3 Sampling Strategy

ArcGIS™ was used to generate a set of randomly located sample points within each stand, positioned at least 50 metres away from each stand boundary and at least 100 metres apart from one another. Sample point location data were uploaded to a handheld GPS unit and a minimum of 3 plots were selected for measurement. The decision regarding which 3 plots should be sampled was made by considering the most efficient way to place a 350 metre-long transect through each stand (Figure 3.2). Sections of the 350m transect were positioned between sample plots to allow the transect to cover as much of the stand as possible, with the assumption that this would capture the greatest variability among sampled features within each stand.

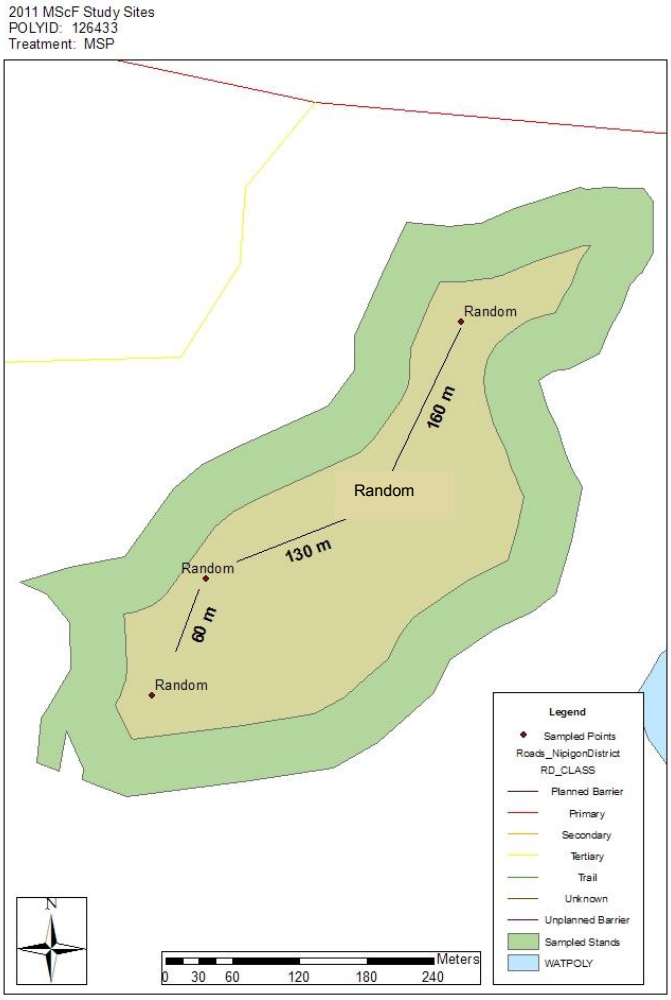


Figure 3.2. Example of stand map showing randomly located sample points and orientation of transect sections comprising the 350m-long belt transect used to measure terrestrial lichen abundance.

3.2.4 Field Data Collection

Terrestrial lichen abundance in each stand was measured by visually estimating percent cover of terrestrial lichen species along a belt transect 1m wide and 350m long (Figure 3.2). Terrestrial lichen species measured included *Cladina rangiferina*, *Cladina stellaris*, *Cladina mitis*, *Cladonia* spp., *Cetraria* spp., *Stereocaulon* spp., and *Peltigera* spp. Percent cover estimates for each species group were recorded for every 10m section of the 350m transect using a cover class

scheme with 1% intervals for species occurring at abundances of less than 5%, and at intervals of five percent for species occurring at abundances of ≥ 5% (i.e. 1, 2, 3, 4, 5, 10, 15…90, 95, 100%). Species occurring in abundances of less than 1% were recorded as "present". Consistency of visual percent cover estimates was achieved by having the same individual estimate all percent cover values.

Tree-level attributes of stand structure were estimated from prism plot data collected in each stand. A complete census of all live and dead trees was conducted using a 2 BAF prism at each of the random sample points. Trees were tallied by species and by 2cm dbh (diameter at breast height) class. In each plot, one tree representative of the average dbh was selected and used to measure tree height, crown height and stand age. Tree height and crown height data were collected using a laser hypsometer (Impulse-200, Lasertech Inc., USA). Tree age was estimated by counting the number of annual rings from increment cores taken at breast height (1.3m).

Understory vegetation was measured in circular fixed-area plots 50 m^2 in size, located at the centre of each random sample point. Vegetation was classified as belonging to the "ground layer" if it measured 40 cm or less in height, or to the "shrub layer" if measured greater than 40 cm and up to 2 metres in height (Rodgers et al., 2008). Ground and shrub vegetation was identified to species; or to genus where field identification to species was not possible. Percent cover of vegetation in each layer was estimated visually using the same percent cover class scheme described above for the terrestrial lichen cover estimates. Trees and shrubs greater than 2 metres in height but having a portion of their live foliage within the 0.4 to 2m height range were included in the shrub percent cover estimates. Mean height of vegetation in the shrub layer was recorded by species to the nearest 0.1 m.

Ecosite characteristics were measured at one randomly located sample point considered to be representative of general stand conditions based on observations of tree species composition and topography. A Dutch auger was used to dig soil cores to determine soil texture and moisture

regime based on substrate condition as described in Ontario's provincial Ecological Land Classification Guide (OMNR, 2009). Substrates were characterized as described in the "Field Guide to Substrates of Ontario" (OMNR, 2010). Diagnostic tests to determine effective soil texture and moisture regime were conducted as per the methods described in Chapter 2. Ecosite was determined by using the dichotomous keys in the field guides, which assign an ecosite code based on the particular combination of dominant soil texture, moisture regime and overstorey tree composition. Soil depth was measured in centimetres and represented the approximate depth to bedrock, with the deepest soils recorded as being ≥120 cm. The organic depth was also recorded in centimetres and represented the measured sum of the depth of the organic horizons.

Canopy closure was measured using a convex spherical densiometer (Forest Densiometers, Model A; Lemmon, 1956). Readings were taken every 20m along the 350m transect, and at the centre point of each fixed area vegetation plot for a minimum total of 21 canopy closure readings taken per stand.

3.2.5 Data Compilation Methods

3.2.5.1 Terrestrial Lichen Data

Stand-level terrestrial lichen abundance was calculated as the mean of all percent cover estimates of terrestrial lichen species recorded at each 10m interval along the 350m belt transect in each stand. Total stand-level terrestrial lichen abundance was calculated by summing the mean percent cover of all terrestrial lichen species measured.

3.2.5.2 Tree Data

Total basal area per hectare (BA/ha) for each stand was calculated by multiplying the combined total number of trees tallied in all plots by the basal area factor 2, and dividing the resulting product by the total number of random plots measured in each stand. Percent conifer of each stand was calculated by dividing the BA/ha of conifer tree species by the total BA/ha in each stand, and multiplying by 100. Percent of spruce and jack pine were each calculated in the same way. Stands were identified as being either spruce (Sb) or jack pine (Pj)-dominated, or as

mixed conifer (Mix) stand types, based on a ≥70% threshold for dominant species. Stand-level tree height, crown height and age were calculated using the mean values of representative trees measured at each plot. Stands were assigned a standard forest unit (SFU) designation based on tree species composition and ecosite using the Northwest Regional Standard Forest Unit definitions (OMNR, 2010, unpublished). The SFU designation characterizes stands in terms of how they are recognized in the FRI and in forest management planning in northwestern Ontario.

3.2.5.3 Understory Vegetation Data

Total ground vegetation cover (%) for each stand was calculated as the mean of ground vegetation cover estimates from the fixed area plots measured at random sample points in each stand. Total shrub cover (%) for each stand was calculated in a similar way. Mean shrub height (cm) was calculated from the height estimates of all shrub and tree species having foliage within the shrub layer, weighted by the proportion each species contributed to total percent shrub cover.

3.2.5.4 Ecosite Data

The texture family corresponding to the effective soil texture in each stand (Table 2.3) was assigned accordingly in order to compare any general differences in soil texture among the treatment groups. Sampled stands were identified as belonging to "Coarse Loamy", "Fine Loamy" or "Sandy" texture families based on descriptions in the Field Guide to Substrates of Ontario (OMNR, 2010).

Moisture regime data were converted to a numeric moisture regime code (Table 2.4) to facilitate analysis. Moisture regime was considered a ranked variable, with low values representing drier conditions, and high values representing wetter conditions.

Soil depth was considered a continuous variable, with a maximum value of 120cm. This represents the minimum soil depth of the deepest soil depth class (Table 2.5) used to characterize ecosites in the field (OMNR, 2010). Organic depth (cm) was also considered a continuous variable.

3.2.5.5 Canopy Closure Data

Canopy closure readings taken at each fixed-area vegetation plot and at the regular stations along the 350m transect were used to calculate a mean value for each stand.

3.2.6 Statistical Analysis

All analyses were completed using the statistical computing software R, version 2.15.1 (R Development Core Team, 2012). The base package in R was used to compare terrestrial lichen abundance (% cover) between the two treatment groups representing the prescribed burned (PB) and the mechanically site-prepared (MSP) stands. The two groups were also compared in terms of environmental characteristics represented by independent variables. The independent variables compared between treatment groups were canopy closure (%), stand age (years), tree height (m), crown height (m), basal area per hectare (m^2/ha), percent conifer (%), percent pine (%), percent spruce (%), moisture regime, soil depth (cm), organic depth (cm), ground vegetation cover (%), shrub cover (%) and shrub height (cm).

All continuous variables were tested for normality using the Shapiro-Wilk's normality test (Appendix 1c). This procedure was done for the sample of all stands (n = 24), as well as for the samples representing each treatment group (n = 12, each). Variables that did not satisfy assumptions of normality were transformed to achieve normality where possible. These transformations maximized the p-value obtained in the Shapiro-Wilk normality test and appeared normal on visual inspection. The distribution of total lichen abundance data was most normal using a logit transformation (Figure 3.3) for the sample of 24 stands. A Box-Cox ($y^{0.15}$) transformation of these data also produced a normal distribution (Shapiro-Wilk's, $p > 0.05$). The Box-Cox transformed lichen data was used for regression analyses, to be consistent with the approach used in Chapter 2 data analysis. Untransformed, Box-Cox-transformed and logit-transformed lichen data were used in 3 separate t-tests to compare PB and MSP stands, as the samples for each of these treatments could be normalized using either Box-Cox or logit transformations. For all other analyses, percent conifer data were arc sin square-root transformed

to achieve normality. Log transformations were used for organic depth and shrub cover data, though organic depth data did not meet assumptions of normality. Data for canopy closure and soil depth did not improve with transformations, and were analysed using original units. All original data for the remaining independent variables (stand age, basal area, tree height, crown height ground vegetation cover and shrub height) met assumptions of normality.

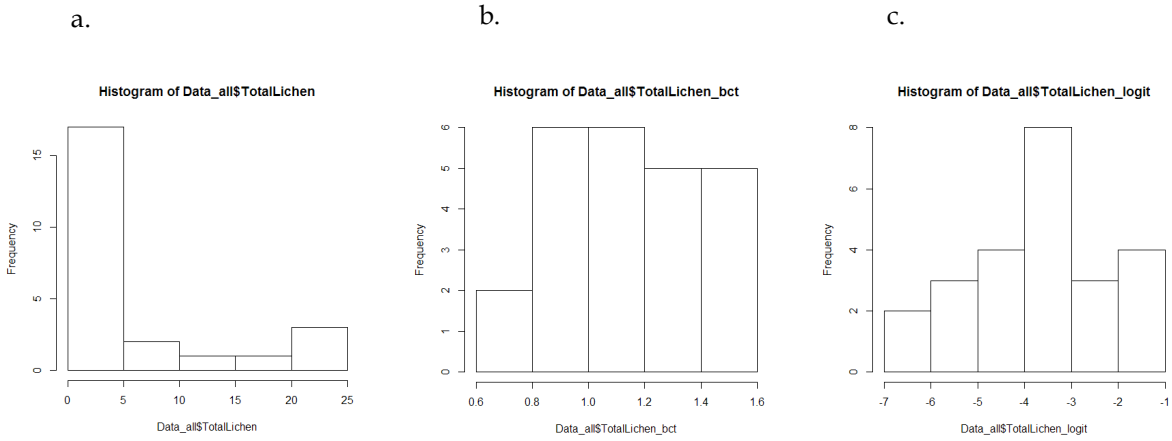


Figure 3.3. Frequency distributions of original, untransformed (a), Box-Cox ($y^{0.15)}$ transformed (b), and logit transformed (c) terrestrial lichen abundance data for all 24 stands.

Stands were summarized by treatment group (PB or MSP) and by stand type (Sb or Pj-dominated or Mix, Table 3.2) to determine whether a 2 x 3 (Treatment x Stand Type) factorial ANOVA was appropriate. Due to insufficient replication among groups a factorial ANOVA was not used to analyze data; instead Welch's two sample t-tests were used to compare PB and MSP stands in terms of terrestrial lichen abundance and the continuous environmental variables measured. The variable moisture regime was also analyzed using a t-test although it violated normality assumptions as a ranked categorical variable. For all variables with data that did not meet normality assumptions, the non-parametric Mann-Whitney U-test was also used to compare treatment groups. A one-way ANOVA was used to compare terrestrial lichen abundance among the 3 stand types, with the Tukey HSD (Honestly Significant Difference) test used to find which sample means were significantly different from one another. Descriptive statistics were used to

do a qualitative comparison of PB and MSP stands in terms of the categorical variables measured – texture family and moisture regime. Frequency distributions of the levels of each categorical variable were compared between PB and MSP stands.

Table 3.2. Number of stands sampled by silvicultural treatment and stand type.

	Silvicultural Treatment	
Stand Type	**PB**	**MSP**
Sb-dominated	9	1
Pj-dominated	2	7
Mix	1	4

Independent environmental variables were analyzed individually in relation to terrestrial lichen abundance among all 24 stands measured. Continuous variables were analyzed using simple linear regression. For variables with data that did not meet assumptions of normality, the non-parametric Spearman rank correlation test was used in addition to regression to determine whether significant relationships existed with terrestrial lichen abundance. Moisture regime was also analyzed using simple linear regression since the alpha/numeric moisture regime coding system used represented a gradient ranging from dry to wet ecosite conditions. Texture family was analyzed as a categorical variable in relation to terrestrial lichen abundance using Welch's two sample t-test. Among the stands measured, only one stand was classified as belonging to the "Fine Loamy" texture family, 15 stands were classified as "Coarse Loamy" and 8 stands were classified as "Sandy". The fine loamy stand was omitted from the texture family analysis due to insufficient sample size. The remaining stands were analyzed using both the t-test and the non-parametric Mann-Whitney U-test to determine whether terrestrial lichen abundance differed significantly between coarse loamy and sandy textured stands. Results for all tests were considered significant at a 0.05 significance level.

3.3 RESULTS

3.3.1 Terrestrial Lichen Abundance by Silvicultural Treatment and Stand Type

Mean terrestrial lichen abundance was 5.66 ± 6.97% among all 24 stands measured. Prescribed burn stands had mean terrestrial lichen abundance of 8.95 ± 8.45%, while stands treated with mechanical site preparation had 2.37 ± 2.03% cover of terrestrial lichen (Figure 3.4). Welch's two sample t-test indicated a potential weak significant difference in terrestrial lichen abundance between PB and MSP stands, depending on the transformation of the data. T-tests conducted using untransformed, logit transformed, and Box-Cox transformed terrestrial lichen abundance data, produced varying results. T-test results using untransformed data indicated a significant difference ($p = 0.027$) between PB and MSP stands. No significant difference was observed using logit transformed data ($p = 0.143$), or Box-Cox transformed terrestrial lichen data ($p = 0.096$). The Mann-Whitney U test indicated a potential difference in terrestrial lichen abundance between the two treatment groups ($p = 0.089$).

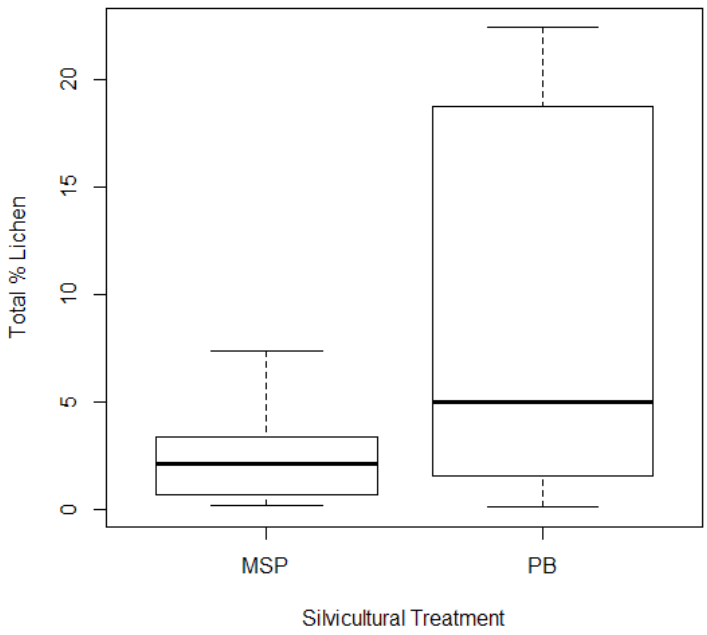


Figure 3.4. Standard boxplots of terrestrial lichen abundance (% cover) in stands treated with mechanical site preparation (MSP, n=12) and prescribed burning (PB, n=12).

Stand type had a significant influence on terrestrial lichen abundance ($p = 0.026$). Mean terrestrial lichen abundance was significantly greater in Sb-dominated (10.44 ± 8.42%) than in Pj-dominated (1.73 ± 1.45%) and mixed conifer (3.18 ± 2.17%) stands (Figure 3.5).

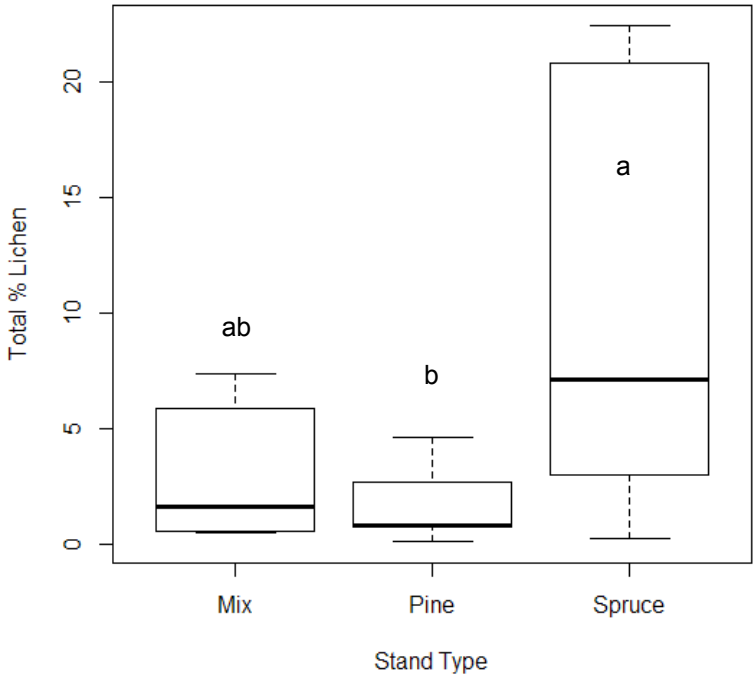


Figure 3.5. Mean terrestrial lichen abundance (% cover) in mixed conifer (Mix, n=5), Pj-dominated (Pine, n=9), and Sb-dominated (Spruce, n=10) stand types. Different letters indicate significant differences between stand types according to post-hoc comparison using the Tukey HSD test.

3.3.2 Stand-Level Silvicultural Treatment Comparison

No significant differences were observed between the prescribed burn (PB) and mechanically site prepared (MSP) stands studied for most of the environmental variables measured (Table 3.3). The two treatment groups were of relatively the same age and both represented stands that were composed almost entirely of conifer tree species. PB stands had slightly lower mean basal area than MSP stands, but this difference was not significant. Mean soil and organic depth, shrub cover and shrub height varied greatly among all stands and did not differ significantly between treatment groups.

The two treatment groups differed with respect to overstory attributes (Table 3.3). There was a non-significant trend toward lower canopy closure in PB stands than in MSP stands (p = 0.095, Appendix 7a). Tree height was also slightly lower in PB stands than in MSP stands (p = 0.075, Appendix 7b). Mean crown height in PB stands was 1.51m lower than in MSP stands (p = 0.033, Figure 3.6). In terms of dominant species, PB stands tended to be dominated by black spruce (Figure 3.7, p = 0.0007), while jack pine generally dominated MSP stands (Figure 3.8, p = 0.019).

Table 3.3. Comparison of mean values for environmental variables in prescribed burn (PB) and mechanically site prepared (MSP) stands, and results of Welch's t-tests (and Mann-Whitney U-tests for non-normal variables). Moisture regime represented by the range of values found in each treatment.

			Results	
Independent Variable	**PB**	**MSP**	**T-test**	**Mann-Whitney U test**
Canopy Closure (%)	76.4 ± 12.4	84.1 ± 7.5	p = 0.096, t = 1.76, df = 18	p = 0.0827, W = 102.5
Stand Age (years)	27.4 ± 4.9	28.3 ± 5.6	ns (p = 0.687)	
Tree Height (m)	10.57 ± 1.76	12.34 ± 2.58	p = 0.075, t = 1.88, df = 19	
Crown Height (m)	3.18 ± 1.37	4.69 ± 1.71	0.0331*	
Basal area (m^2/ha)	22.53 ± 7.16	24.83 ± 5.20	ns (p = 0.398)	
Percent Conifer[1]	93.0 ± 7.1	91.2 ± 9.6	ns (p = 0.828)	ns (p = 0.862)
Percent Pine[1]	20.6 ± 35.6	57.1 ± 31.8	p = 0.029*, t = 2.35, df = 21	p = 0.066, W = 104
Percent Spruce[1]	71.9 ± 34.8	21.2 ± 23.1	p = 0.003**, t = -3.45, df = 18	p = 0.007**, W = 25
Moisture Regime	"xeric" to "5"	"0" to "4"	ns (p = 0.364)	ns (p = 0.393
Soil Depth (cm)	96.4 ± 34.2	84.0 ± 42.0	ns (p = 0.454)	ns(p = 0.711)
Organic Depth (cm)[2]	4.5 ± 5.1	3 ± 1.7	ns (p = 0.642)	ns (p = 0.765)
Veg Cover (%)	56.8 ± 28.5	53.5 ± 22.7	ns (p = 0.764)	
Shrub Cover (%)[2]	33.6 ± 23.2	26.9 ± 15.6	ns (p = 0.557)	
Shrub Height (cm)	414.6 ± 207.9	367.9 ± 171.2	ns (p = 0.571)	

[1]Arc sin square root transformed
[2]Log transformed

Signif. codes: 0.01 '**', 0.05 '*', 0.1 '.'

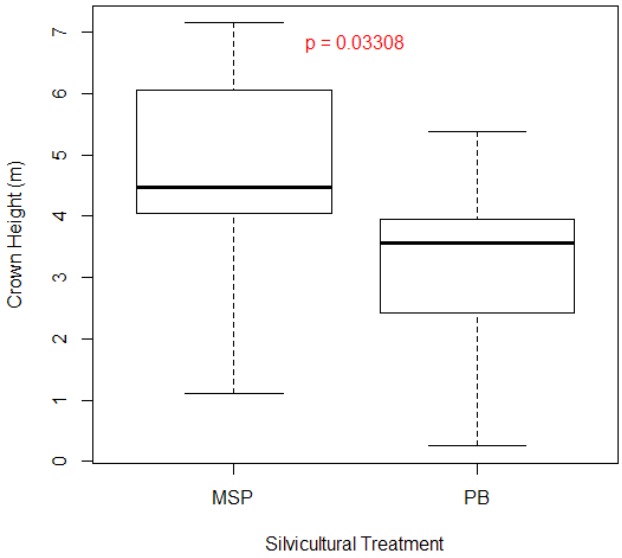


Figure 3.6. Standard boxplots showing crown height (m) is significantly lower ($p < 0.05$) in prescribed burn (PB, n = 12) than in mechanically site prepared (MSP, n = 12) stands.

a. b.

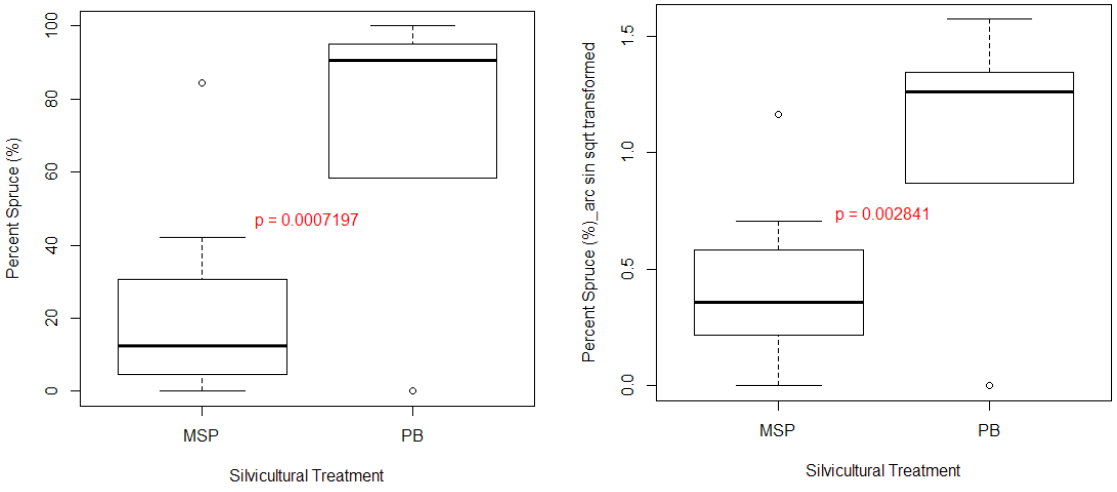


Figure 3.7. Standard boxplots showing percent spruce (%) is significantly higher in prescribed burn (PB, n = 12) than in mechanically site prepared (MSP, n = 12) stands. T-tests were conducted using both untransformed (a) and arc sin square root transformed (b) percent spruce data.

a. b.

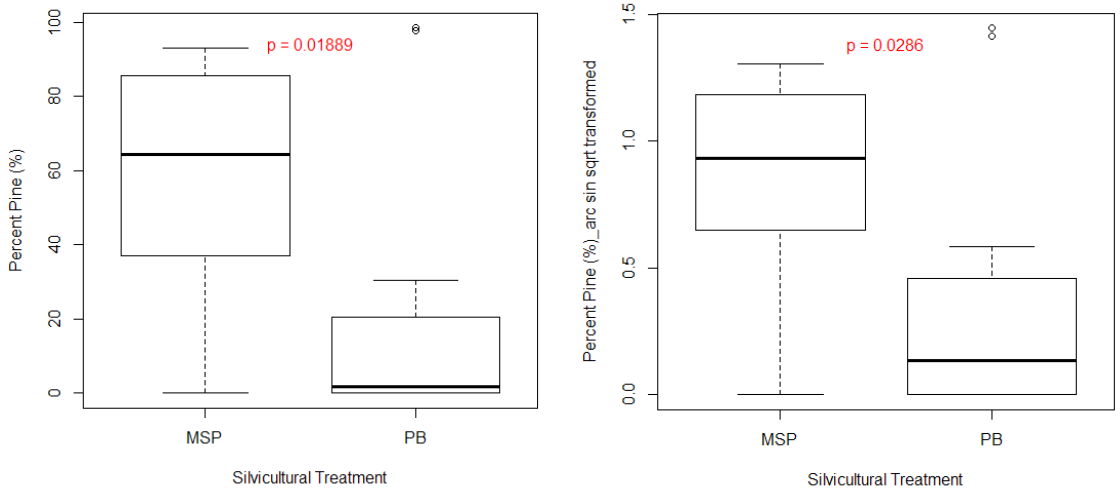


Figure 3.8. Standard boxplots showing percent pine (%) is significantly higher in mechanically site prepared (MSP, n = 12) than in prescribed burn (PB, n = 12) stands. T-tests were conducted using both untransformed (a) and arc sin square root transformed (b) percent pine data.

The treatment groups were similar in terms of the distribution of texture families they represented (Figure 3.9). Eight of the 12 PB stands (~66%) and 7 of the 12 MSP stands (~58%) were of coarse loamy texture. Four stands of each treatment group were of sandy texture. One stand of fine loamy texture was represented among the MSP treatment group.

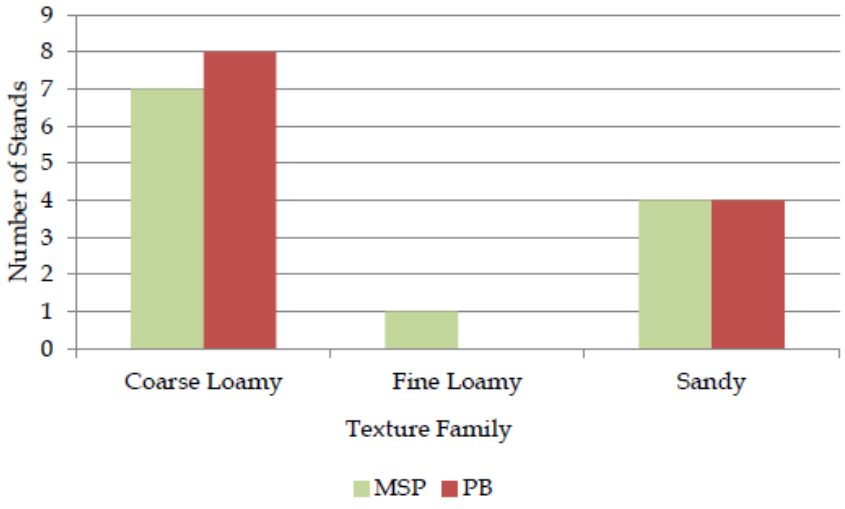


Figure 3.9. Distribution of texture families represented by prescribed burn (PB, n = 12) and mechanically site prepared (MSP, n = 12) stands.

Each treatment group represented a range of moisture conditions (Figure 3.10). PB stands represented a slightly broader range of moisture conditions than MSP stands, with one stand characterized as having a "xeric" moisture regime and one stand with a moisture regime of "5". The majority of all stands measured (~71%) had moderately dry ("0") to fresh ("2") moisture conditions, with half of all MSP stands measured having a moisture regime of "1".

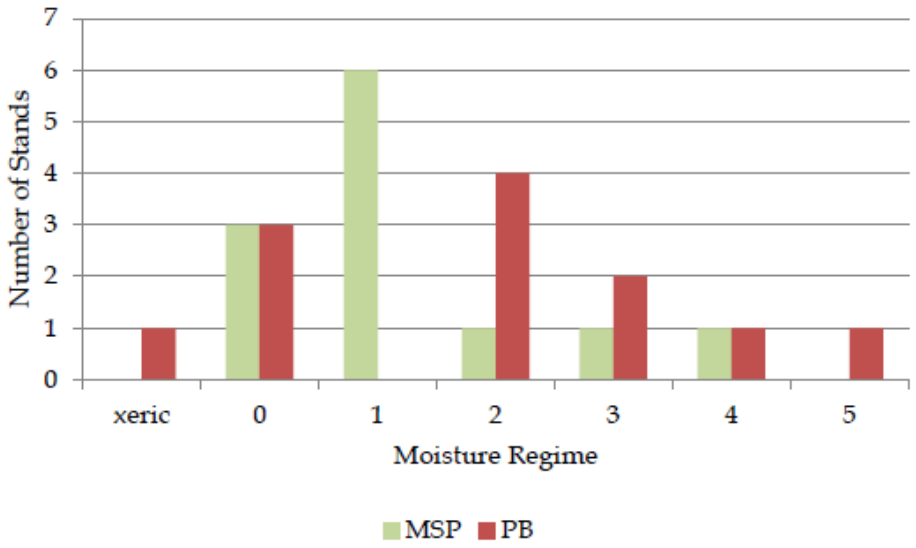


Figure 3.10. Distribution of moisture regime classes represented by prescribed burn (PB, n = 12) and mechanically site prepared (MSP, n = 12) stands.

3.3.3 Terrestrial Lichen Abundance in Relation to Stand Structure

Results of the simple linear regressions and Spearman rank correlations used to evaluate the significance of the independent variables among all 24 stands are presented in Table 3.4 below.

Table 3.4. Resulting p-values from simple linear regression of measured environmental variables on terrestrial lichen abundance. Spearman rank correlation results displayed for non-normal variables.

	Results	
Independent Variable	**Simple Linear Regression**	**Spearman Rank Correlation**
Canopy Closure (%)	p = 0.0002***, r^2 = 0.457, df = 22	p = 0.003**, rho = -0.579
Stand Age (years)	ns (p = 0.231)	
Tree Height (m)	p = 0.074, r^2 = 0.099, df = 22	
Crown Height (m)	p = 0.023*, r^2 = 0.178, df = 22	
Basal area (m^2/ha)	p = 0.022*, r^2 = 0.182, df = 2	
Percent Conifer (%)[1]	p = 0.069, r^2 = 0.104, df = 2	p = 0.056, rho = -0.395
Percent Pine (%)[1]	p = 0.023*, r^2 = 0.179, df = 22	p = 0.033*, rho = -0.438
Percent Spruce (%)[1]	p =0.020*, r^2 = 0.186, df = 22	p = 0.027*, rho = 0.450
Moisture Regime (code)	ns (p = 0.627)	ns (p =0.513)
Soil Depth (cm)	ns (p =0.225)	ns (p =0.588)
Organic Depth (cm)[2]	ns (p =0.243)	ns (p =0.161)
Ground Vegetation Cover (%)	p = 0.065, r^2 = 0.108, df = 2	
Shrub Cover (%)[2]	ns (p =0.301)	
Shrub Height (cm)	p = 0.011*, r^2 = 0.226, df = 22	

[1] Arc sin square root transformed Signif. codes: 0.001'***',0.01 '**', 0.05 '*', 0.1 '.'
[2] Log transformed

Canopy closure had a strong negative relationship with terrestrial lichen abundance (regression, p = 0.0002), with higher lichen abundance observed in more open stands with lower mean values for canopy closure (Figure 3.11). A strong negative relationship was observed between terrestrial lichen abundance and crown height (p = 0.023) with stands of lower mean crown height having higher abundances of terrestrial lichen (Figure 3.12). Terrestrial lichen abundance had a significant negative relationship with basal area per hectare (p = 0.022); with higher abundances observed in stands with relatively lower basal area (Figure 3.13). Both regression and the Spearman rank correlation showed weak significant relationships (p = 0.069 and p = 0.056, respectively) between terrestrial lichen abundance and percent conifer, with less lichen observed in stands with higher percentages of conifer tree species (Appendix 7d). Percent pine and percent spruce showed opposite linear relationships with terrestrial lichen abundance, using either simple linear regression or Spearman rank correlation. Terrestrial lichen abundance decreased with increasing percent pine (Figure 3.14), and increased with increasing percent

spruce (Figure 3.15). A weak relationship was found with ground vegetation cover (p = 0.065), with higher estimates of terrestrial lichen abundance being associated with higher estimates of vegetation cover (Appendix 7e). Shrub height also had a significant positive relationship (p = 0.011) relationship with terrestrial lichen (Figure 3.16).

Terrestrial lichen abundance did not have linear relationships with stand age, moisture regime, soil depth, organic depth or shrub cover (Table 3.4), and there was no significant difference between coarse loamy and sandy textured stands in terms of terrestrial lichen abundance (Appendix 7f) based on either the t-test or the Mann-Whitney U test.

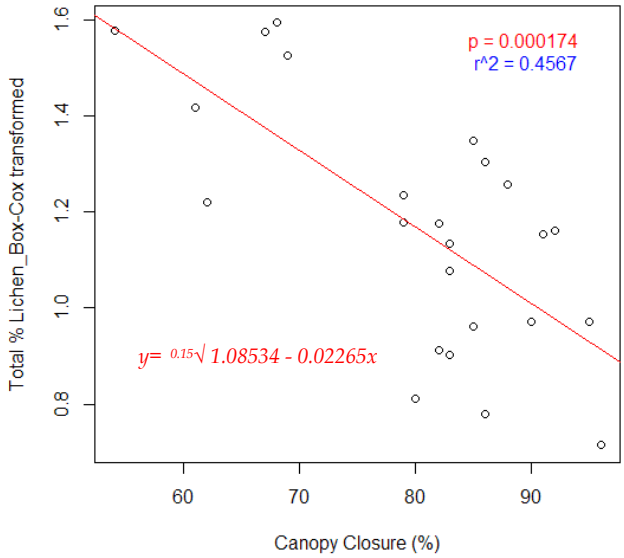


Figure 3.11. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to canopy closure (%) in prescribed burn and mechanically site prepared stands (n = 24).

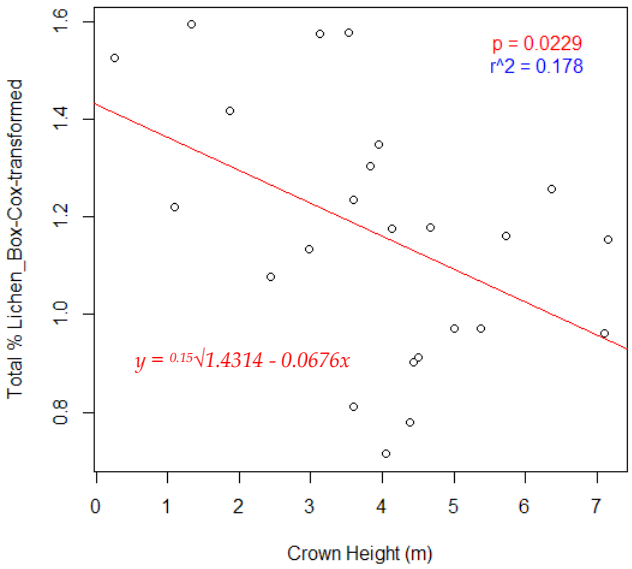


Figure 3.12. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to crown height (m) in prescribed burn and mechanically site prepared stands (n = 24).

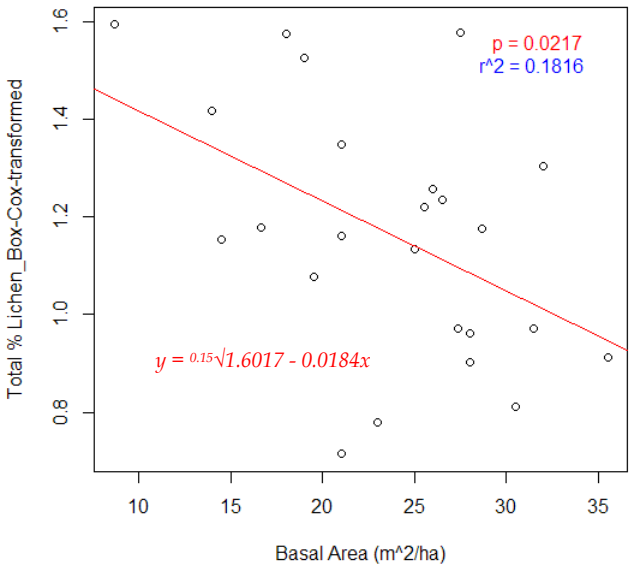


Figure 3.13. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to basal area (m^2/ha) in prescribed burn and mechanically site prepared stands (n = 24).

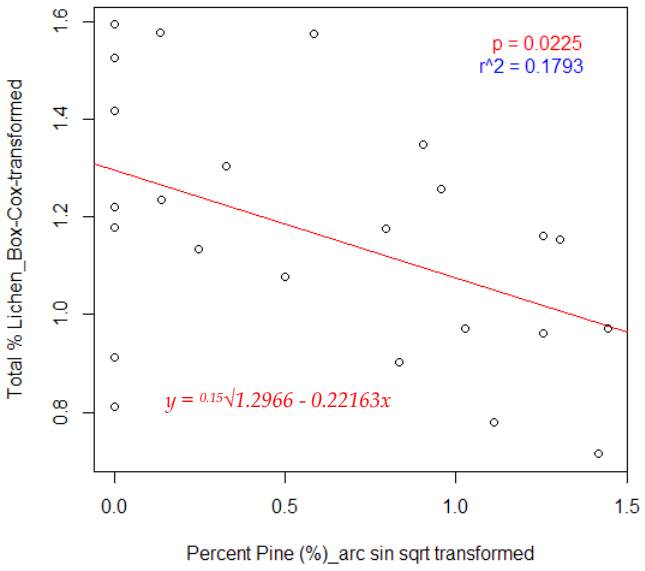


Figure 3.14. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to percent pine (%, arc sin square-root transformed) in prescribed burn and mechanically site prepared stands (n = 24).

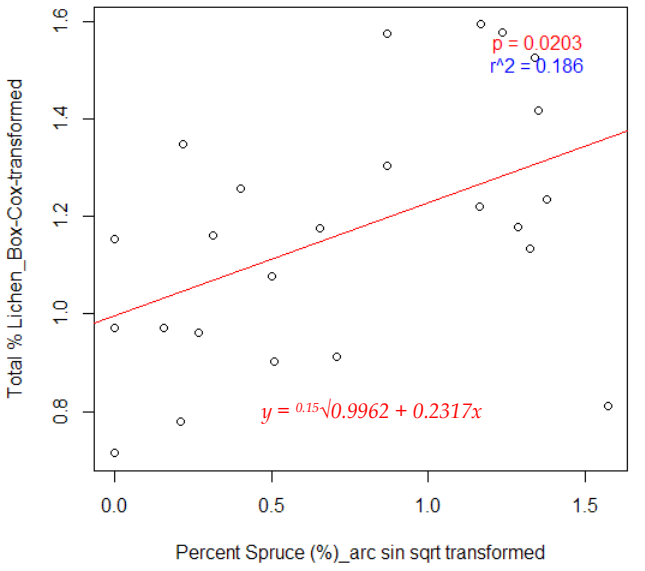


Figure 3.15. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to percent spruce (%, arc sin square-root transformed) in prescribed burn and mechanically site prepared stands (n = 24).

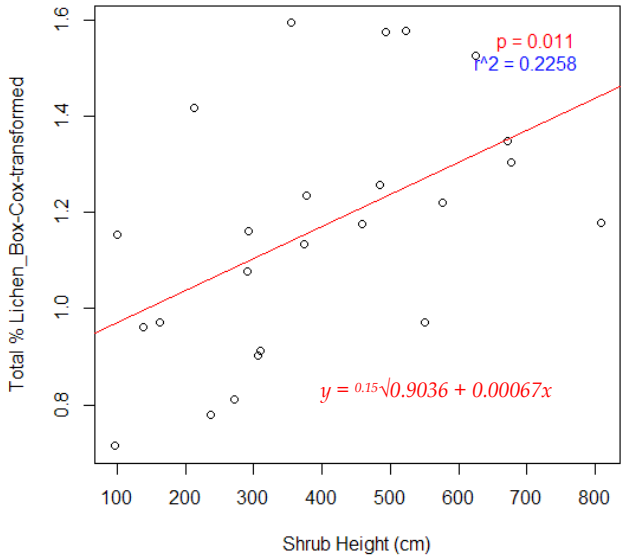


Figure 3.16. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to shrub height (cm) in prescribed burn and mechanically site prepared stands (n = 24).

3.4 DISCUSSION

Though mean terrestrial lichen abundance was higher in prescribed burn (PB) stands (8.95 ± 8.45%) than in mechanically site prepared stands (2.37 ± 2.03%) (Figure 3.4), the statistical tests used to assess the significance of this difference were not conclusive. Stand-level estimates of terrestrial lichen abundance were highly variable; with mean lichen cover equal to 5.66 ± 6.97% among all 24 stands measured. Terrestrial lichen abundance data were negatively skewed with 8 of the 24 stands measured (33%) having less than 1% cover of terrestrial lichen. The effect of treatment could be confounded by potential effects of stand type. Nine of the 12 prescribed burn stands were spruce-dominated, while 7 of the 12 mechanically site prepared stands were dominated by jack pine (Table 3.2). Thus, it is possible that the difference observed in terrestrial lichen abundance between PB and MSP treatments is as much a function of structural characteristics associated with stand type as a response to silvicultural treatments.

Prescribed burn (PB) and mechanically site prepared (MSP) stands were similar in terms of age, understory and ecosite characteristics (Table 3.3), but different in terms of overstory canopy structure and composition. PB stands had a higher proportion of spruce trees, while jack pine tended to dominate MSP stands (Figures 3.7 & 3.8). PB stands had a non-significant trend toward lower mean canopy closure than MSP stands, and lower values for both tree height and crown height (Table 3.3). The trend toward higher terrestrial lichen abundance PB stands may thus be related to improved understory light conditions associated with more open canopies in these stands. This finding is consistent with studies that have found similar relationships between terrestrial lichen abundance and open canopy structure (Moning et al., 2009; Humphrey et al., 2002).

Spruce-dominated stands had higher lichen cover than pine-dominated or mixed conifer stands (Figure 3.5), though as described above, this effect may have been confounded with silvicultural treatment. In all, 9 of the 10 spruce dominated stands were also prescribed burned. Differences observed in the field of canopy structure among stand types indicated that canopies of the 20 to 40-year old jack pine stands were relatively dense compared to similar-aged stands dominated by spruce. Spruce stands had an average basal area of 21.1 m^2/ha while pine stands had an average basal area of 24.6 m^2/ha. Individual spruce trees tend to be more conical and narrower than pine (Thorpe et al., 2010), which may contribute to greater light availability and hence a better growing environment for terrestrial lichen. Higher terrestrial lichen abundance in spruce-dominated stands (Figure 3.15) may therefore reflect better light conditions in the understory. Jack pine stands in Ontario tend to be denser than spruce-dominated stands and often require thinning treatments 10 to 15 years after establishment (OMNR, 1997). Mean tree height of jack pine stands is also generally taller than that of similar-aged black spruce stands, with maximum stem heights of these tree species reaching 30 and 25 metres, respectively (OMNR, 1997). Thus, species specific differences in stand density and tree height may influence understory light conditions, and hence photosynthetic capacity and growth of terrestrial lichen.

The strongest relationship observed in this study was the negative relationship between canopy closure and lichen cover (Figure 3.11). This finding is similar to the results of the previous Chapter, and consistent with findings of other studies that have found light to be of major importance to terrestrial lichen (Coxson & Marsh, 2001; Lesmerises et al., 2011). Though canopy closure did not differ between silvicultural treatments, it was significantly lower in spruce-dominated stands (70.2 ± 9.3%) compared to pine-dominated (89.4 ± 4.3%) or mixed conifer (84.0 ± 1.7%) stands. Thus, regardless of silvicultural treatment, terrestrial lichen abundance was greater where more light was able to reach the forest floor. Crown height had a negative relationship with terrestrial lichen abundance (Figure 3.12), which was expected as higher crowns are associated with closed canopies that allow less light penetration to the forest floor. The more open spruce-dominated stands tended to have shorter trees (10.15 ± 2.14m) than pine-dominated (12.75 ± 2.26m) or mixed conifer (11.74 ± 1.47m) stands. Spruce-dominated stands also had lower crown height (2.60 ± 1.32m) than pine-dominated (5.48 ± 1.13m) or mixed conifer (3.83 ± 0.75m) stands. A strong negative relationship was observed between basal area per hectare and terrestrial lichen abundance (Figure 3.13), consistent with the findings of other studies that have observed lichen cover to decrease with increased estimates of basal area (e.g. Coxson & Marsh, 2001). These results highlight the importance of light for the growth and the development of terrestrial lichen, and the potential negative effect of managing for dense canopies in conifer plantations.

That understory characteristics were not significantly different between treatments suggests the effects of site preparation methods either have no effect on the subsequent understory community, or that these effects are not apparent 20 to 40 years after their application. PB treatments, which consume some portion of organic matter, were expected to be more successful than MSP treatments in reducing the abundance of the understory plants thought to compete with terrestrial lichen. Ground and shrub vegetation cover were not significantly different between treatments, however (Table 3.3). Site preparation method also failed to

contribute to any enduring differences in humus layer reduction, as indicated by variable organic depth estimates in both PB and MSP stands (Table 3.3). In the 24 stands measured, it appears PB treatments were no more effective than MSP treatments in promoting understory and ecosite characteristics important to lichen growth. Observable treatment effects may exist, though at (shorter) temporal scales not accounted for in this study.

Shrub height had a significant positive relationship with terrestrial lichen abundance (Figure 3.16), consistent with the findings reported in the previous chapter. Higher estimates of shrub height likely correspond with greater understory light penetration. Inspection of stand-level data revealed that stands with higher shrub height had lower average estimates of canopy closure. The nature of the shrub height measurement also warrants consideration given that the shrub layer included any tree foliage occurring between 0.4 and 2m in height. Mean shrub height was therefore higher when tree foliage was included in the calculation. The presence of tree foliage within the shrub layer implies lower estimates of crown height, which are understood to indicate greater understory light penetration (Temesgen et al., 2005).

The findings of this study suggest that forest management activities can provide stand conditions to benefit terrestrial lichen communities. The relatively low values for terrestrial lichen abundance observed across both treatments, however, make it unclear whether the increased cost/risk associated with prescribed burning can be justified. Harvest and silvicultural treatments that improve understory light availability could provide environments conducive to terrestrial lichen establishment and growth. Prescribed burning treatments applied with the objective of reducing post-harvest organic debris could potentially improve light conditions for terrestrial lichen, while mechanical site preparation could be of benefit by reducing the soil humus layer, freeing space for lichen to become established. Further research to examine the functional responses of terrestrial lichen to specific silvicultural treatments is recommended.

4.1 SUMMARY

Terrestrial lichen is an important habitat feature that is highly variable in terms of its abundance in forested stands of northern Ontario. In order to manage for woodland caribou winter habitat, measurable stand level characteristics associated with terrestrial lichen need to be identified. These characteristics must be considered in terms of whether they can or cannot be altered by forest management activities, and must also be considered within the broader context of the landscape matrix in which caribou select habitat.

Stand structural characteristics that correlate best with terrestrial lichen abundance appear to include those that can be managed strategically through harvest and silvicultural decisions. Understory light conditions that are important for the photosynthesis and growth of terrestrial lichen communities can be manipulated by controlling certain aspects of overstory stand structure. Canopy closure and basal area, both found to have significant influences on terrestrial lichen abundance, can be regulated at the stand initiation stage by planting lower densities of tree seedlings, or may be maintained during later successional stages through activities such as thinning or partial harvest. Stand age, which appears to play a role in stands with suitable light conditions, can also be managed by extending the rotation age in managed stands to allow a longer period of time for various lichen species to colonize and grow. Stand level heterogeneity may be a further consideration when managing stands for terrestrial lichen. Retention of older trees during harvest operations, and maintaining some level of tree species diversity are ways that forest management can benefit terrestrial lichen communities.

Many stand characteristics of importance to terrestrial lichen are outside the control of forest management, but are nonetheless worthy of consideration as they represent factors that limit the extent to which forest managers can enhance woodland caribou winter habitat. Cover type has considerable influence in determining the potential for stands to grow abundant

communities of terrestrial lichen. Conifer-dominated cover types are most likely to supply higher lichen cover than deciduous or mixedwood cover types. Poorly drained stands with organic texture however, provide less suitable conditions for terrestrial lichen, and may present fewer opportunities for woodland caribou habitat improvement in this respect. Ecosite attributes such as soil texture and richness govern characteristics including cover of competing understory vegetation – an aspect of forest stands that may or may not be ecologically (or economically) feasible to manage.

Distinction between the inherent and the manageable aspects of forest stands provides a basis for coarse and fine-filter approaches to woodland caribou habitat management. Stands with the most potential to grow abundant communities of terrestrial lichen may be identified at the landscape level by large-scale features such as dominant cover type or proportion of exposed bedrock. These stands likely have great potential to grow terrestrial lichen with or without intervention and hence, may be of lower priority for forest management efforts. Stands with inherently low potential for growing terrestrial lichen may similarly be identified within the landscape, and also be assigned lower priority in terms of management efforts. Those stands lying within the range of this spectrum however, could represent opportunities for stand-level caribou habitat management.

Natural forest disturbance often provides a template for coarse-filter approaches to habitat management. In this study, differences in disturbance history did not reflect major differences in terrestrial lichen abundance, suggesting that natural and previously harvested stands provide equal potential as caribou winter habitat. It is well understood however, that woodland caribou are highly sensitive to landscape-level disturbance regimes. Caribou re-occupation of previously harvested stands depends not only on the provision of sustainable food resources at the stand level, but on the availability of habitat features existing at broader spatial scales. Silvicultural treatments aimed at mimicking natural disturbance should be applied with this taken into consideration.

Effects of forest management on terrestrial lichen are not well understood and warrant further research efforts. In mature stands, experimental harvest treatments can be applied to test effects of overstory tree removal on terrestrial lichen abundance. The manipulation of understory light conditions through variable retention harvests can be examined to better understand what constitutes optimal light environments for terrestrial lichen growth. This information can then be used to establish appropriate density targets for stands in which there is potential to enhance supplies of terrestrial lichen.

The succession of terrestrial lichen species post-disturbance is also worthy of further investigation. Temporal changes in terrestrial lichen species composition following disturbance have implications on the quality of woodland caribou winter habitat, as caribou to demonstrate preference for certain lichen species over others. Preferred species such as *C. stellaris* are most abundant in older successional stages (Morneau & Payette, 1989), suggesting habitat management strategies need to acknowledge changing forest dynamics. Also less understood are the functional responses of terrestrial lichen to the various types of disturbance. Harvest and fire disturbances involve fundamentally different processes that likely impact succession of terrestrial lichen species. A greater understanding of both natural and anthropogenic disturbance effects could serve to either validate or nullify theories of natural disturbance pattern emulation.

This study indicates there is potential for forest management to have a positive influence on terrestrial lichen, and by extension, woodland caribou winter habitat. Forest management strategies aimed at sustaining woodland caribou winter habitat must consider ways to maintain or enhance the forest conditions that promote abundant communities of terrestrial lichen. Management limitations at varying temporal and spatial scales should also be considered in the development of such strategies in order to prioritize efforts to improve current and future woodland caribou winter habitat.

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Appendix 1a. Results of Shapiro-Wilk's normality tests for conifer-dominated stands (n = 105; Chapter 2) indicating assumptions of normality were not met for most variables. Original tree height and log-transformed shrub height data met assumptions of normality at the desired significance level of $p < 0.05$.

Independent Variable	Shapiro-Wilks p-value
Total Lichen (%)[1]	0.00005072
Canopy Closure (%)[2]	0.0002029
Stand Age (years)	0.0109
Tree Height (m)	0.1634
Crown Height (m)	0.0008736
Basal Area (m^2/ha)	0.005066
Percent Conifer (%)[2]	3.77E-10
Moisture Regime (code)	4.35E-06
Soil Depth (cm)	9.45E-11
Organic Depth (cm)[3]	0.0001823
Ground Vegetation Cover (%)	0.00012
Shrub Cover (%)	0.04914
Shrub Height (cm)[3]	0.8347

[1] Box-Cox transformed
[2] Arc sin square root transformed
[3] Log transformed

Appendix 1b. Results of Shapiro-Wilk's normality tests for non-organic conifer-dominated stands (n = 71; Chapter 2) indicating assumptions of normality were met for stand age, tree height, crown height, basal area, organic depth and shrub height.

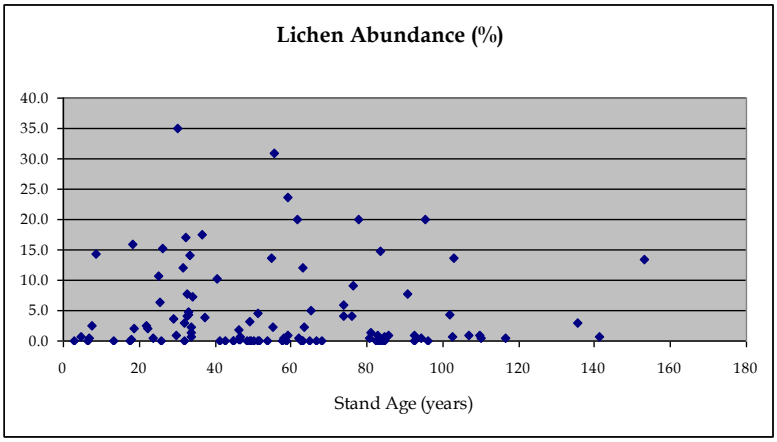
Independent Variable	Shapiro-Wilks p-value
Total Lichen (%)[1]	0.00007491
Canopy Closure (%)[2]	0.001669
Stand Age (years)	0.1231
Tree Height (m)	0.1984
Crown Height (m)	0.2167
Basal Area (m^2/ha)	0.08313
Percent Conifer (%)[3]	0.00005042
Moisture Regime (code)	0.01655
Soil Depth (cm)	4.66E-06
Organic Depth (cm)[4]	0.6572
Ground Vegetation Cover (%)	0.04378
Shrub Cover (%)	0.03773
Shrub Height (cm)[4]	0.3952

[1] Box-Cox transformed
[2] Logit transformed
[3] Arc sin square root transformed
[4] Log transformed

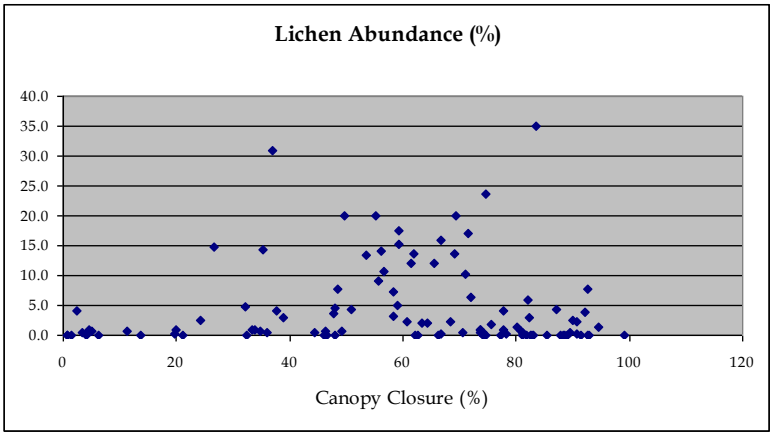
Appendix 1c. Results of Shapiro-Wilk's normality tests for Chapter 3 data (n = 24) indicating assumptions of normality were met for most variables with the exception of canopy closure, percent pine, percent spruce, soil depth and organic depth.

Independent Variable	Shapiro-Wilks p-value
Total Lichen Cover (%)[1]	0.5537
Total Lichen Cover (%)[2]	0.4645
Canopy Closure (%)	0.04913
Stand Age (years)	0.5155
Tree Height (m)	0.9026
Crown Height (m)	0.8037
Basal Area (m^2/ha)	0.8516
Percent Conifer (%)[3]	0.2738
Percent Pine (%)[3]	0.004746
Percent Spruce (%)[3]	0.03554
Soil Depth (cm)	0.000079
Organic Depth (cm)[4]	0.0108
Ground Vegetation Cover (%)	0.1366
Shrub Cover (%)[4]	0.3161
Shrub Height (cm)	0.6008

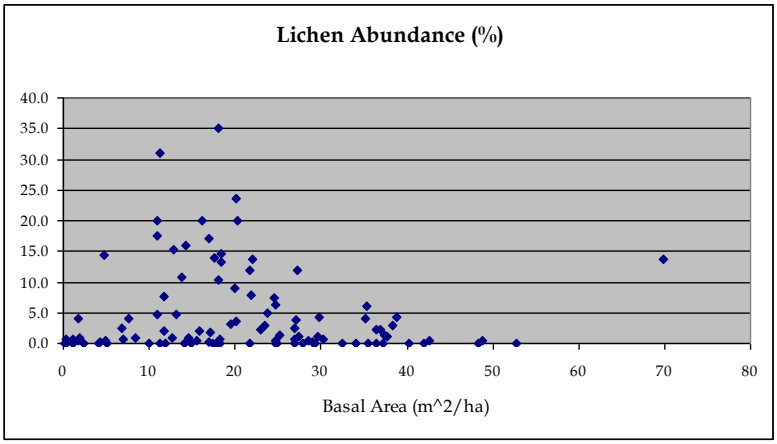
[1]Logit transformed
[2]Box-Cox transformed
[3]Arc sin square root transformed
[4]Log transformed



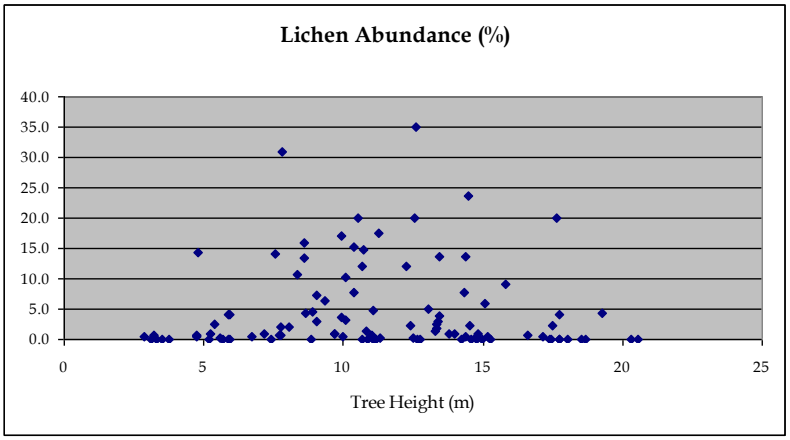
Appendix 2a. Total terrestrial lichen abundance (% cover) in relation to stand age (years) among conifer-dominated stands (n = 105).



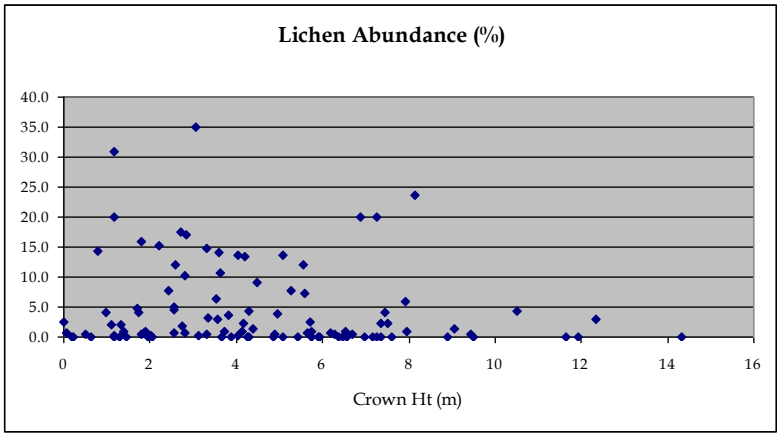
Appendix 2b. Total terrestrial lichen abundance (% cover) in relation to canopy closure (%) among conifer-dominated stands (n = 105).



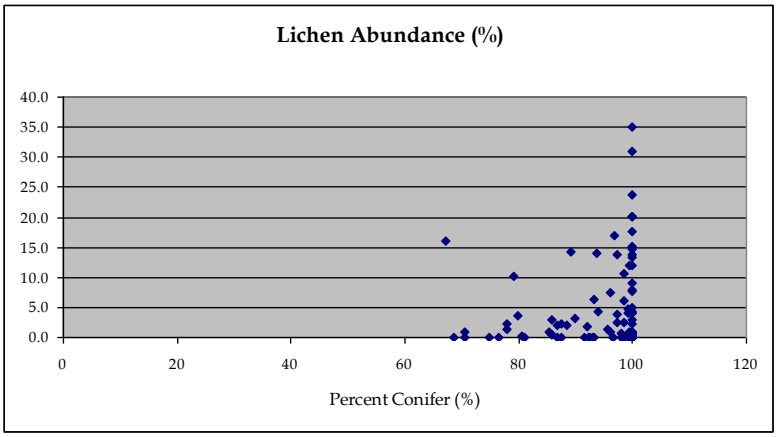
Appendix 2c. Total terrestrial lichen abundance (% cover) in relation to basal area (m^2/ha) among conifer-dominated stands (n = 105).



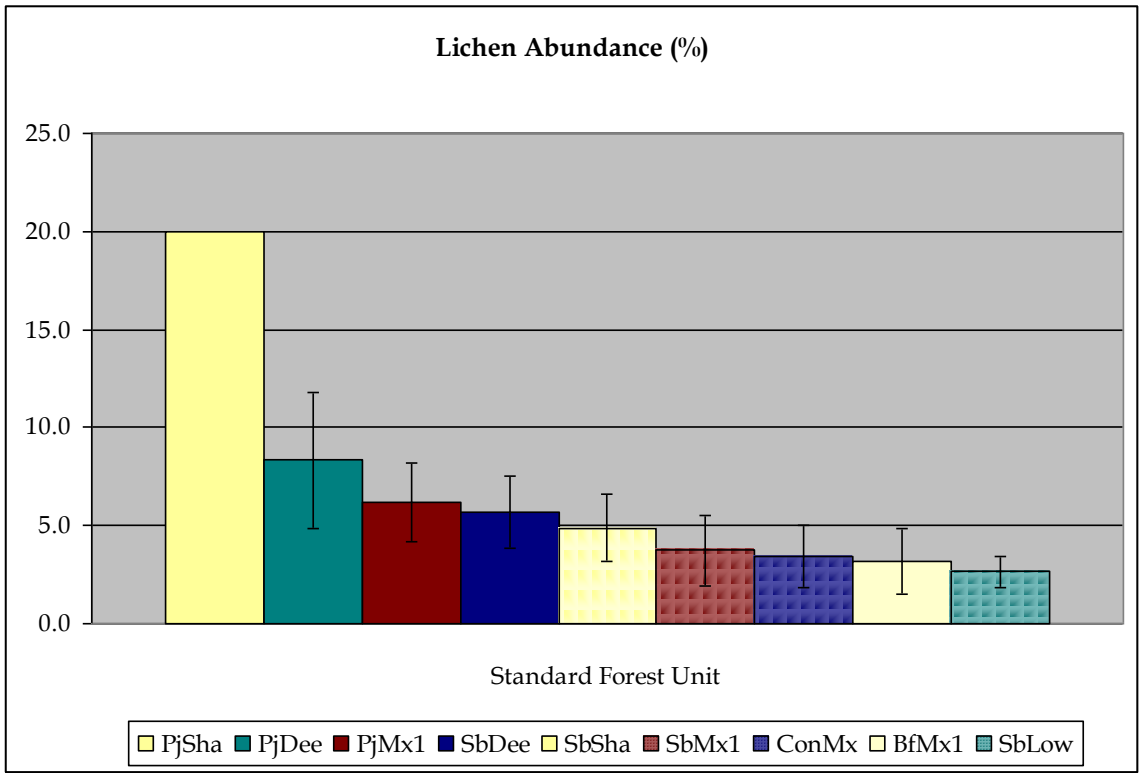
Appendix 2d. Total terrestrial lichen abundance (% cover) in relation to tree height (m) among conifer-dominated stands (n = 105).



Appendix 2e. Total terrestrial lichen abundance (% cover) in relation to crown height (m) among conifer-dominated stands (n = 105).

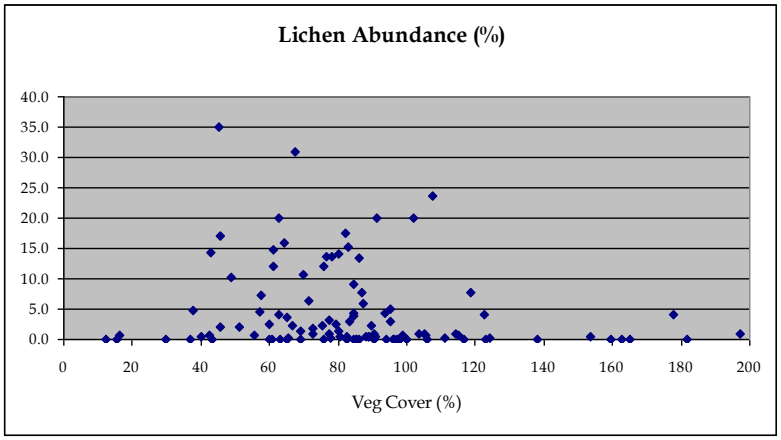


Appendix 2f. Total terrestrial lichen abundance (% cover) in relation to percent conifer (%) among conifer-dominated stands (n = 105).

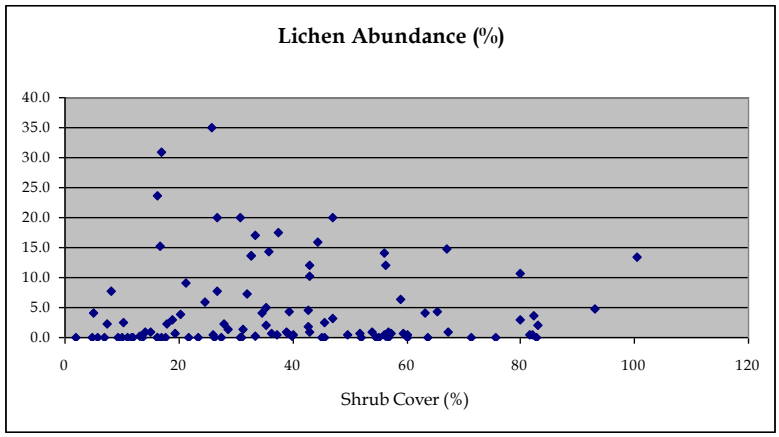


Standard Forest Unit	n	Mean % Lichen	Std Error
BfMx1	11	3.1645	1.6790
ConMx	10	3.4285	1.6297
PjDee	11	8.3515	3.4753
PjMx1	9	6.1743	2.0279
PjSha	1	20.0067	-
SbDee	19	5.6699	1.8511
SbLow	34	2.6584	0.7938
SbMx1	7	3.7296	1.7843
SbSha	3	4.8722	1.6984

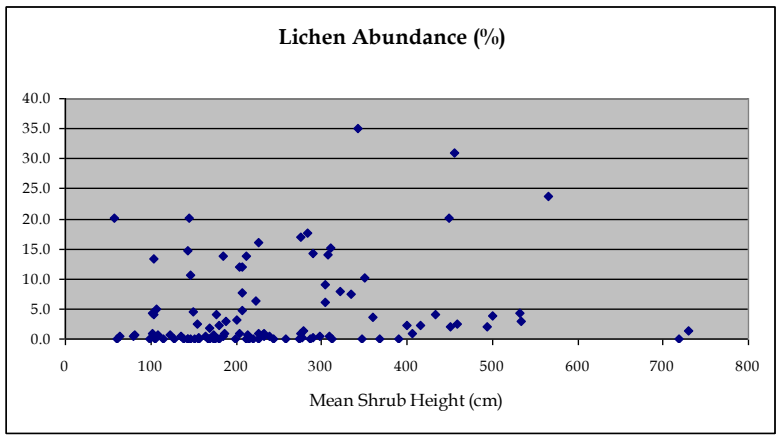
Appendix 2g. Total terrestrial lichen abundance (% cover) in relation to Standard Forest Unit (SFU) among conifer-dominated stands (n = 105).



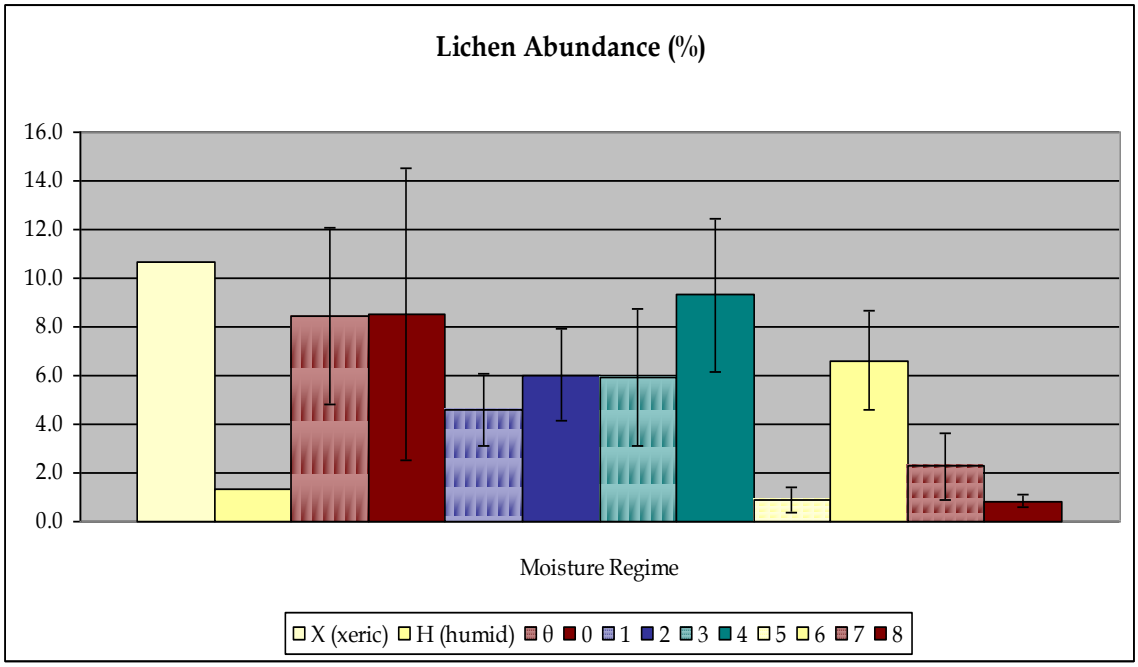
Appendix 2h. Total terrestrial lichen abundance (% cover) in relation to ground vegetation cover (%) among conifer-dominated stands (n = 105).



Appendix 2i. Total terrestrial lichen abundance (% cover) in relation to shrub cover (%) among conifer-dominated stands (n = 105).

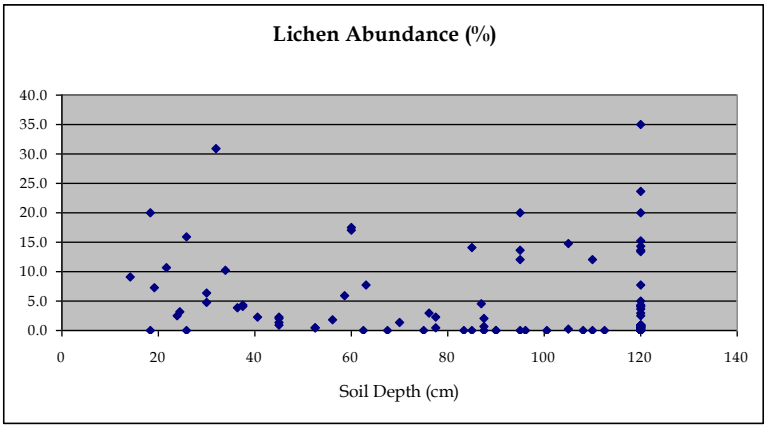


Appendix 2j. Total terrestrial lichen abundance (% cover) in relation to mean shrub height (cm) among conifer-dominated stands (n = 105).

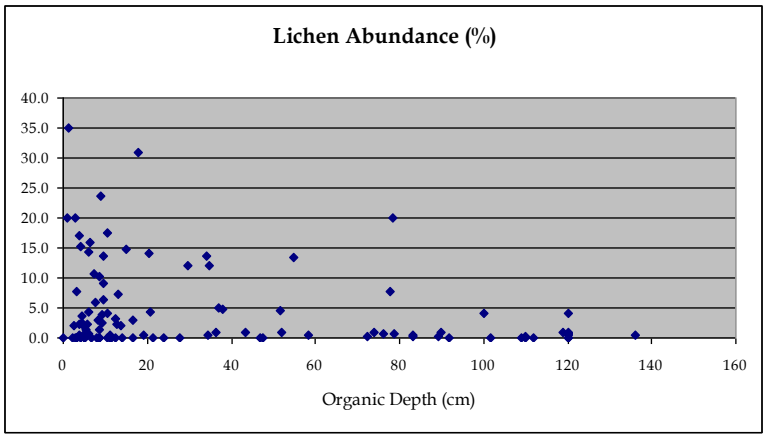


Moisture Regime	n	Mean % Lichen	Std Error
X (xeric)	1	10.6800	-
H (humid)	1	1.3500	-
θ	4	8.4300	3.6251
0	2	8.5167	6.0081
1	18	4.6040	1.4646
2	17	6.0137	1.8798
3	13	5.9028	2.8133
4	8	9.3028	3.1314
5	6	0.8889	0.5331
6	5	6.6100	2.0377
7	9	2.2807	1.3790
8	21	0.8293	0.2661

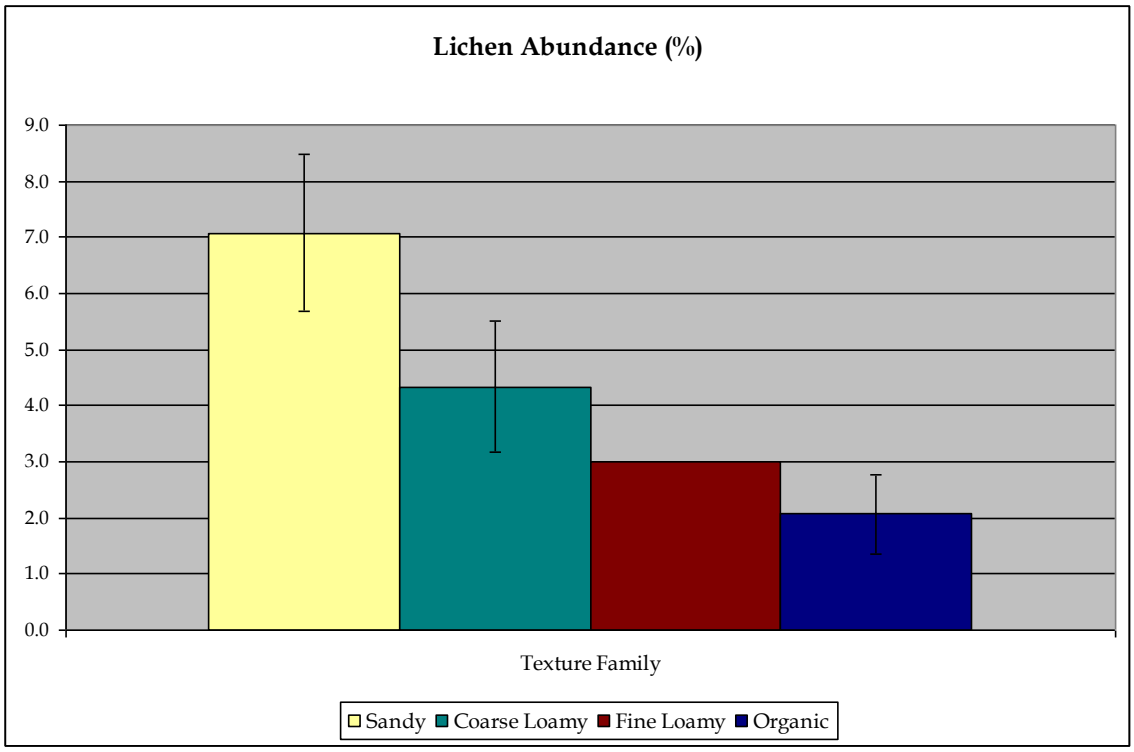
Appendix 2k. Total terrestrial lichen abundance (% cover) in relation to moisture regime (code) among conifer-dominated stands (n = 105).



Appendix 2l. Total terrestrial lichen abundance (% cover) in relation to soil depth (cm) among conifer-dominated stands (n = 105).

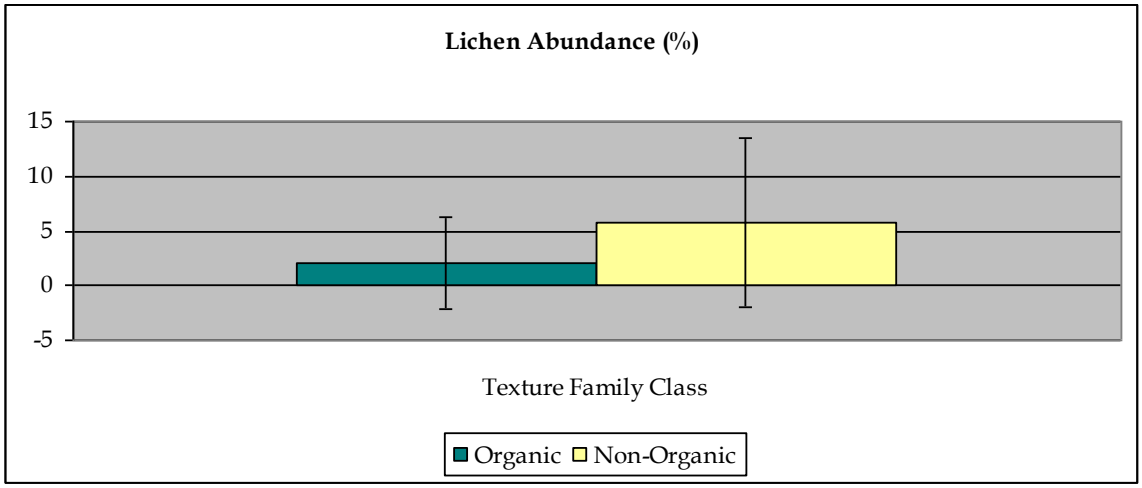


Appendix 2m. Total terrestrial lichen abundance (% cover) in relation to organic depth (cm) among conifer-dominated stands (n = 105).

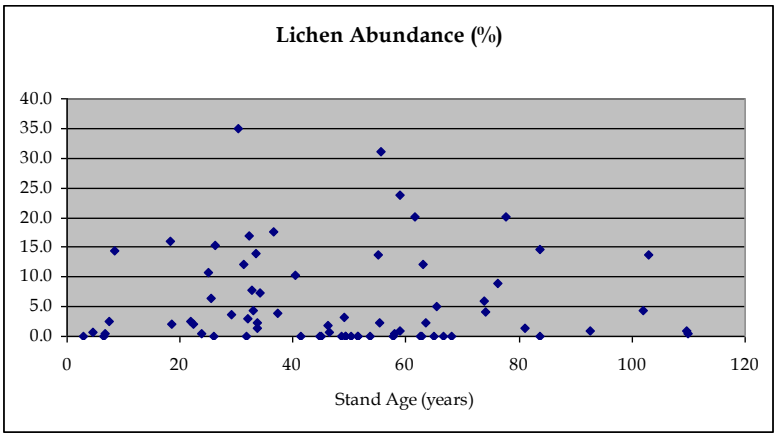


Texture	n	Mean % Lichen	Std Error
Coarse Loamy	34	4.3300	1.1653
Fine Loamy	1	3.0080	-
Organic	34	2.0678	0.7095
Sandy	36	7.0789	1.4051

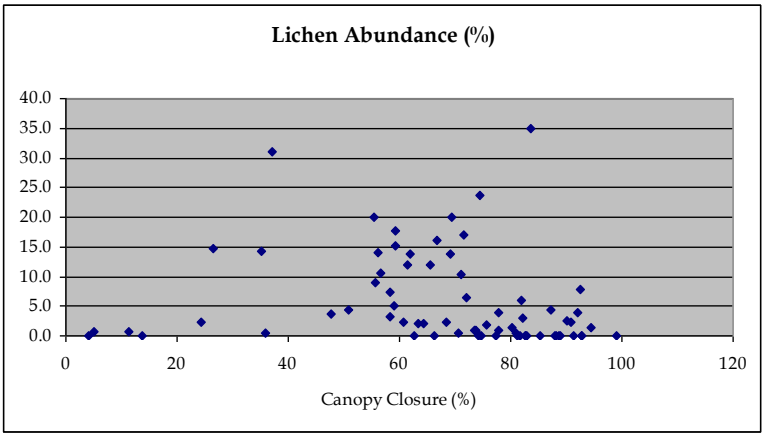
Appendix 2n. Total terrestrial lichen abundance (% cover) in relation to texture family (class) among conifer-dominated stands (n = 105).



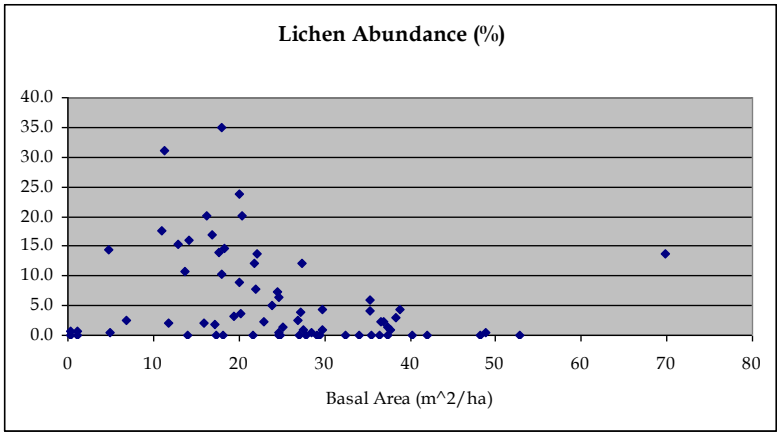
Appendix 2o. Total terrestrial lichen abundance (% cover) in relation to texture family (class) among conifer-dominated stands (Organic, n = 34; Non-Organic = 71).



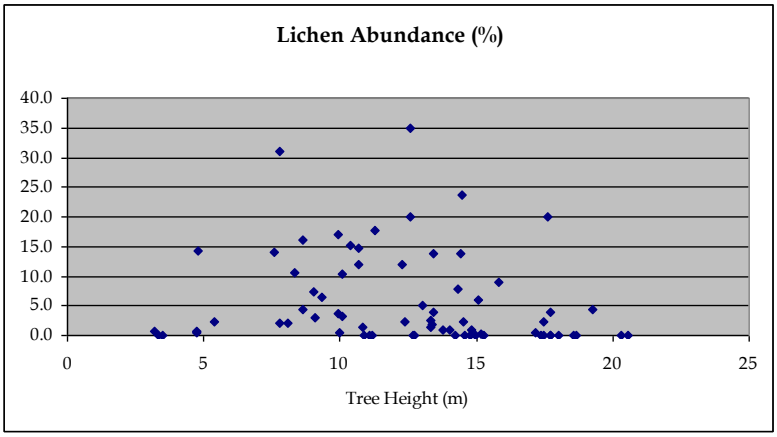
Appendix 3a. Total terrestrial lichen abundance (% cover) in relation to stand age (years) among non-organic conifer-dominated stands (n = 71).



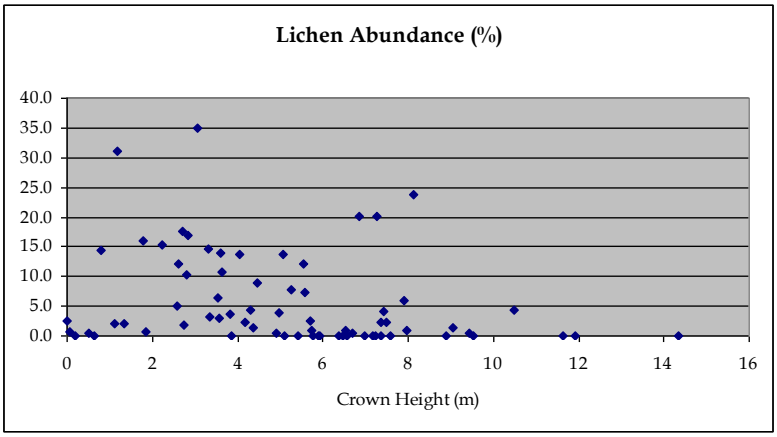
Appendix 3b. Total terrestrial lichen abundance (% cover) in relation to canopy closure (%) among non-organic conifer-dominated stands (n = 71).



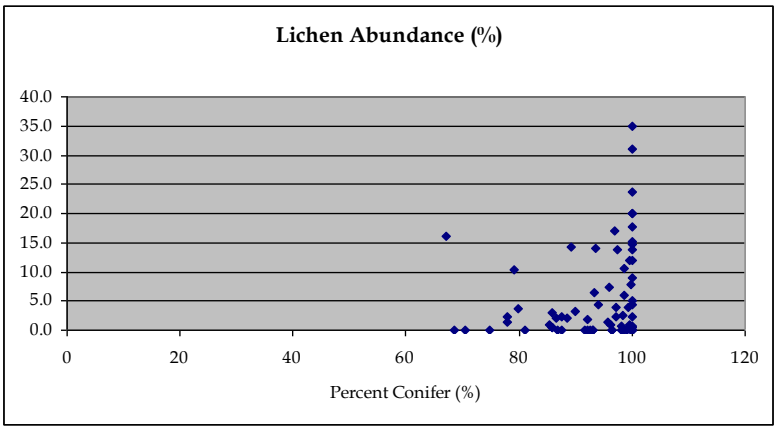
Appendix 3c. Total terrestrial lichen abundance (% cover) in relation to basal area (m^2/ha) among non-organic conifer-dominated stands (n = 71).



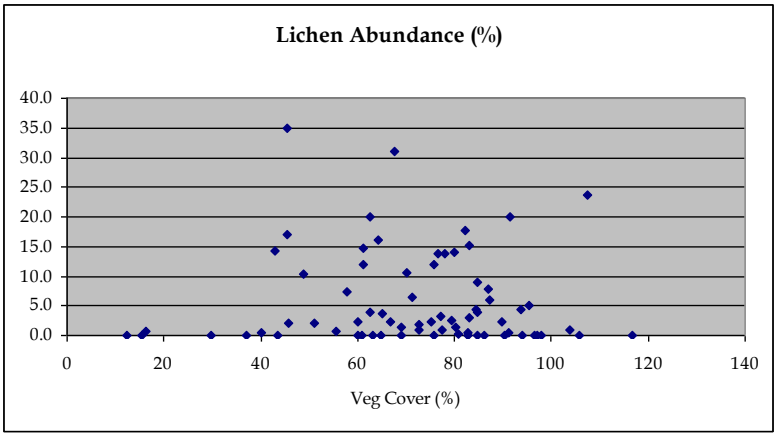
Appendix 3d. Total terrestrial lichen abundance (% cover) in relation to tree height (m) among non-organic conifer-dominated stands (n = 71).



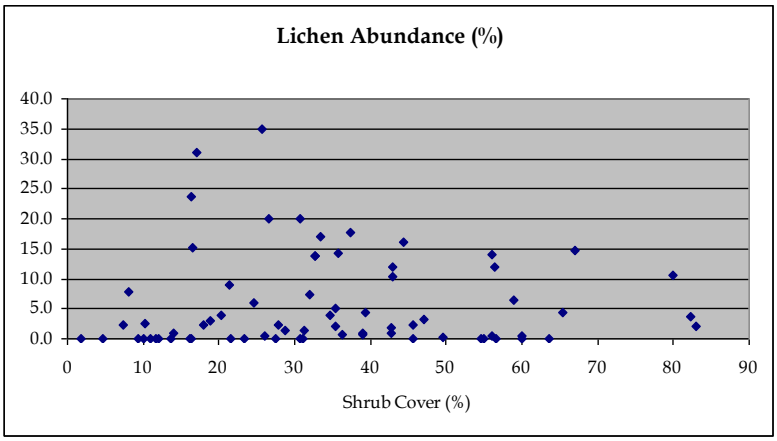
Appendix 3e. Total terrestrial lichen abundance (% cover) in relation to crown height (m) among non-organic conifer-dominated stands (n = 71).



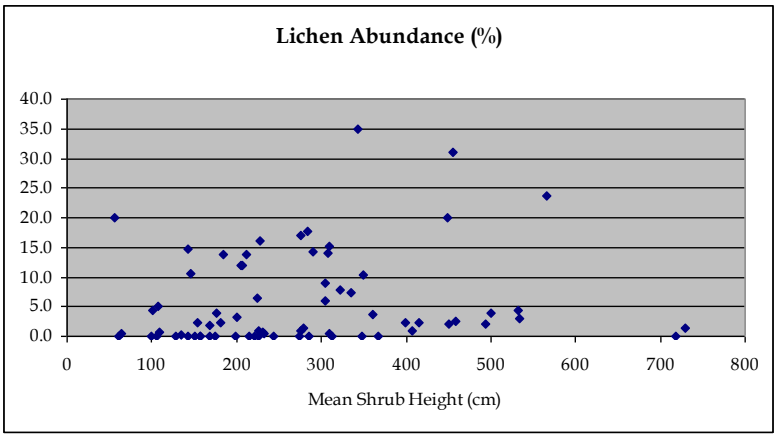
Appendix 3f. Total terrestrial lichen abundance (% cover) in relation to percent conifer (%) among non-organic conifer-dominated stands (n = 71).



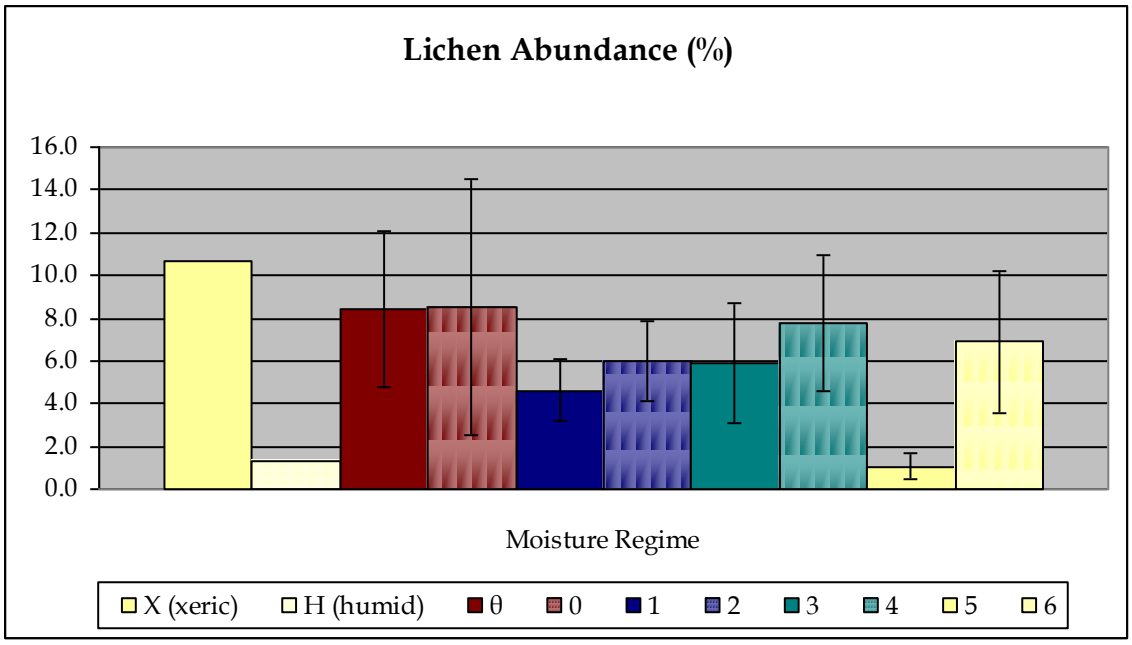
Appendix 3g. Total terrestrial lichen abundance (% cover) in relation to ground vegetation cover (%) among non-organic conifer-dominated stands (n = 71).



Appendix 3h. Total terrestrial lichen abundance (% cover) in relation to shrub cover (%) among non-organic conifer-dominated stands (n = 71).

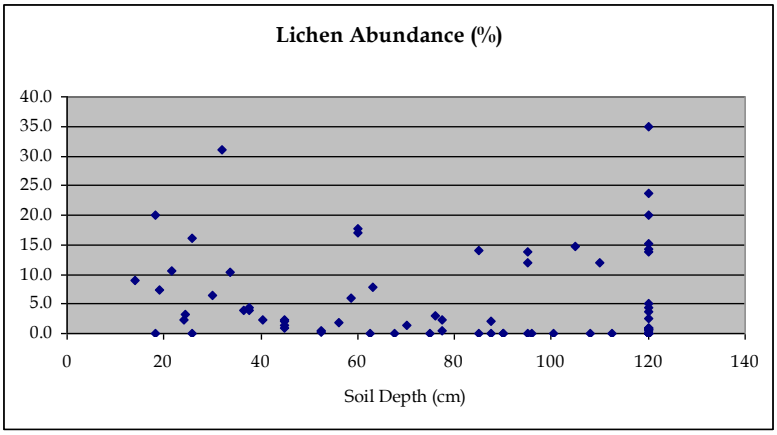


Appendix 3i. Total terrestrial lichen abundance (% cover) in relation to mean shrub height (cm) among non-organic conifer-dominated stands (n = 71).

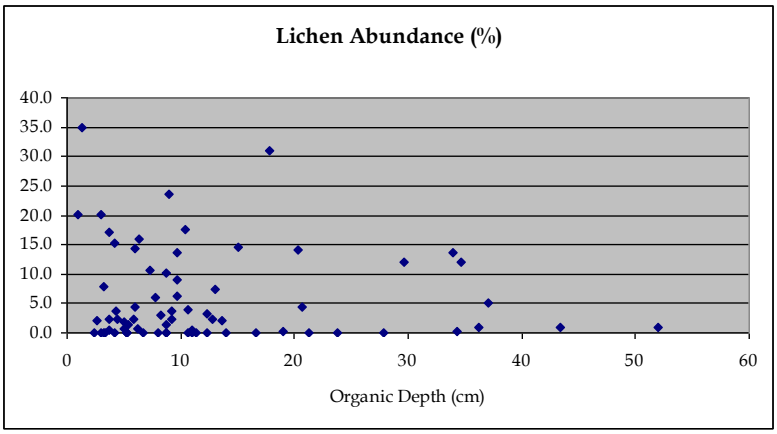


Moisture Regime	n	Mean % Lichen	Std Err
X (xeric)	1	10.6800	-
H (humid)	1	1.3500	-
θ	4	8.4300	3.6251
0	2	8.5167	6.0081
1	18	4.6040	1.4646
2	17	6.0137	1.8798
3	13	5.9028	2.8133
4	7	7.7742	3.1838
5	5	1.0647	0.6101
6	3	6.9000	3.3116

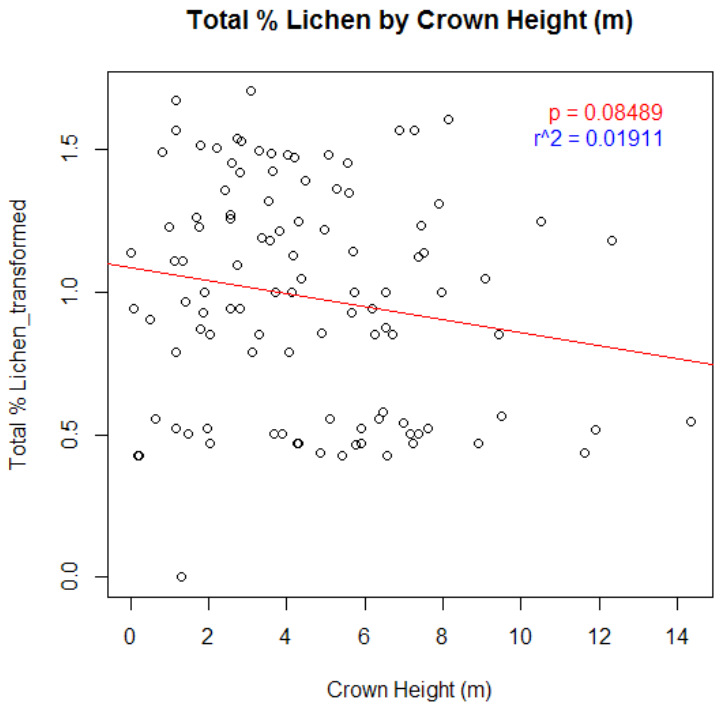
Appendix 3j. Total terrestrial lichen abundance (% cover) in relation to moisture regime (code) among non-organic conifer-dominated stands (n = 71).



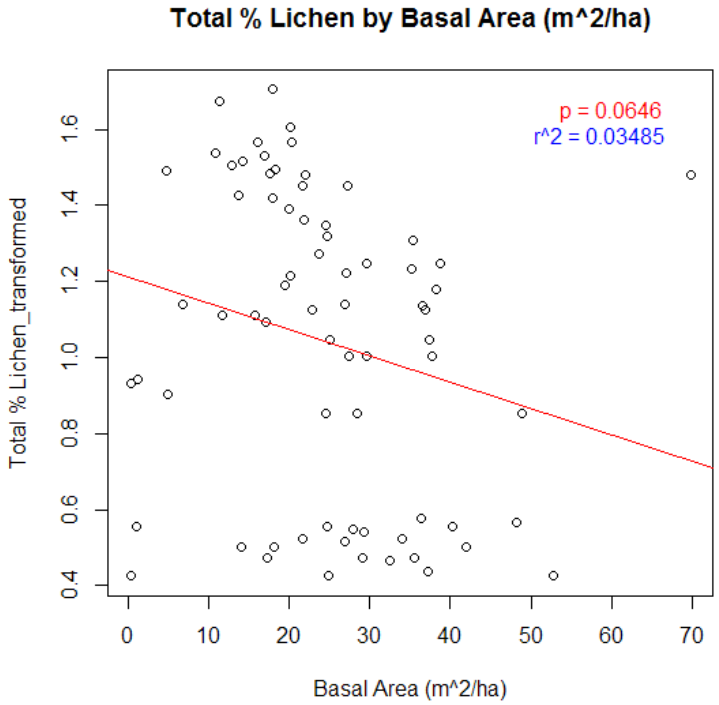
Appendix 3k. Total terrestrial lichen abundance (% cover) in relation to soil depth (cm) among non-organic conifer-dominated stands (n = 71).



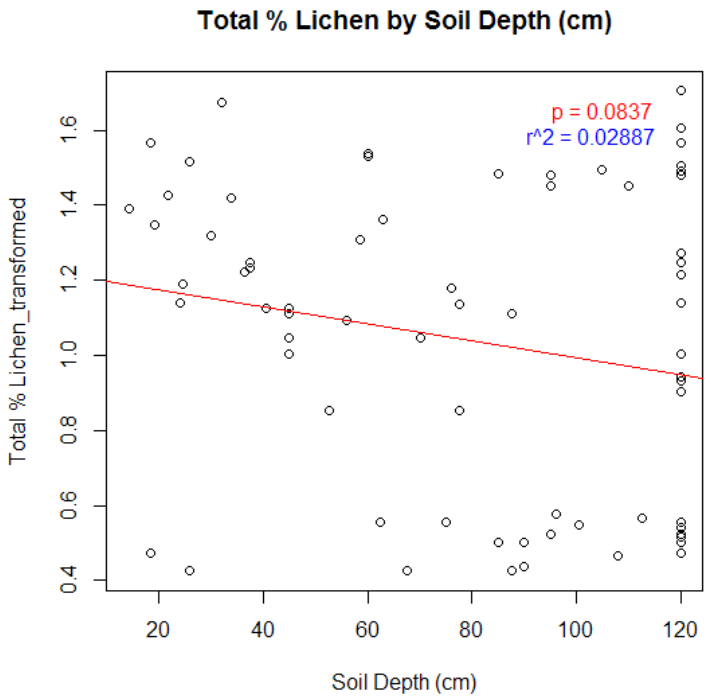
Appendix 3l. Total terrestrial lichen abundance (% cover) in relation to organic depth (cm) among non-organic conifer-dominated stands (n = 71).



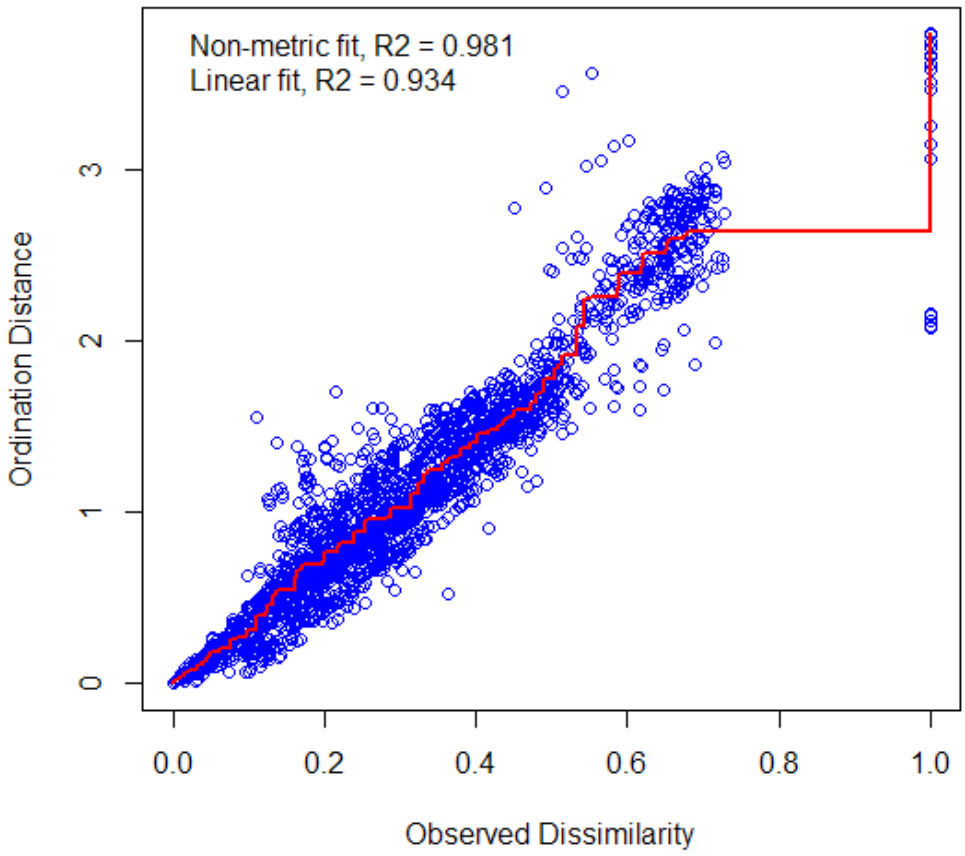
Appendix 4. Total terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to crown height (m) in 105 conifer-dominated stands ($y = {}^{0.15}\sqrt{1.08534 - 0.02265x}$).



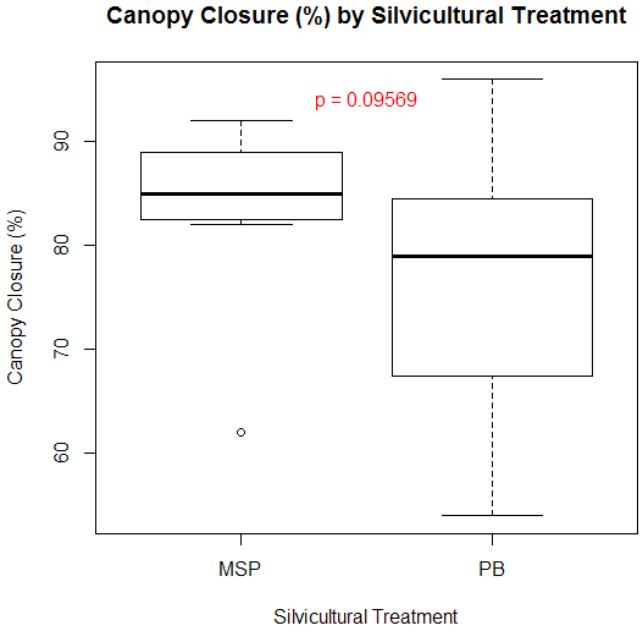
Appendix 5a. Total terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to basal area (m^2/ha) of trees in 71 non-organic conifer-dominated stands ($y = {}^{0.15}\sqrt{1.211125 - 0.006913x}$).



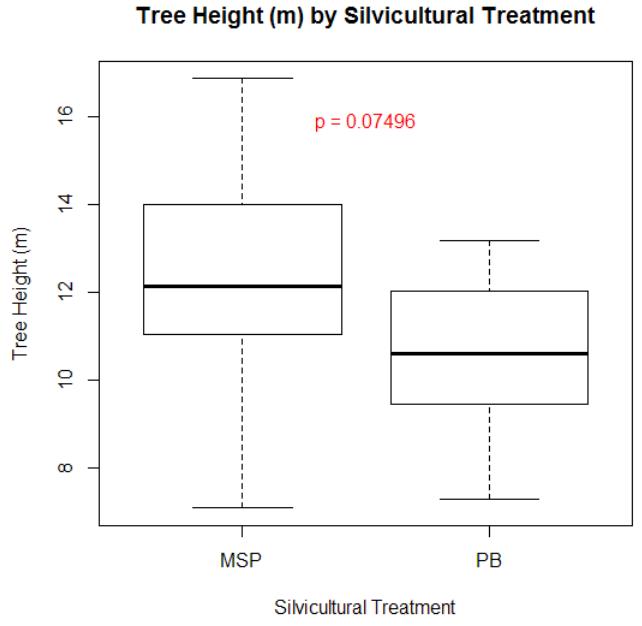
Appendix 5b. Total terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to soil depth (cm) in 71 non-organic conifer-dominated stands ($y = \sqrt[0.15]{1.219926 - 0.002266x}$).



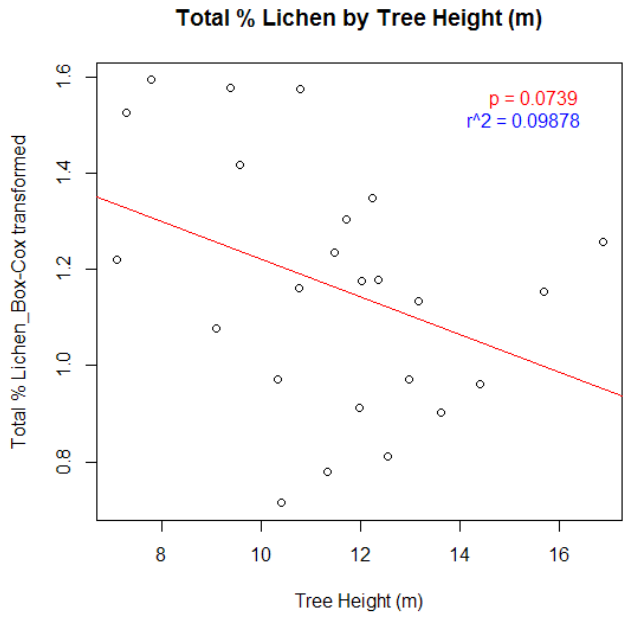
Appendix 6. Shepard plot showing the relationship between inter-site distances and dissimilarities using the terrestrial lichen abundance dataset for non-organic conifer-dominated stands (n = 71).



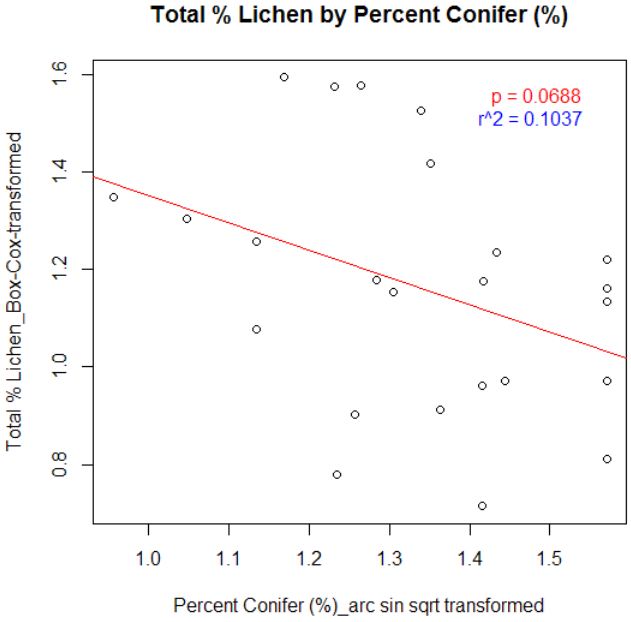
Appendix 7a. Standard boxplot showing canopy closure (%) is higher ($p < 0.1$) in mechanically site prepared (MSP, n = 12) than in prescribed burn (PB, n = 12) stands.



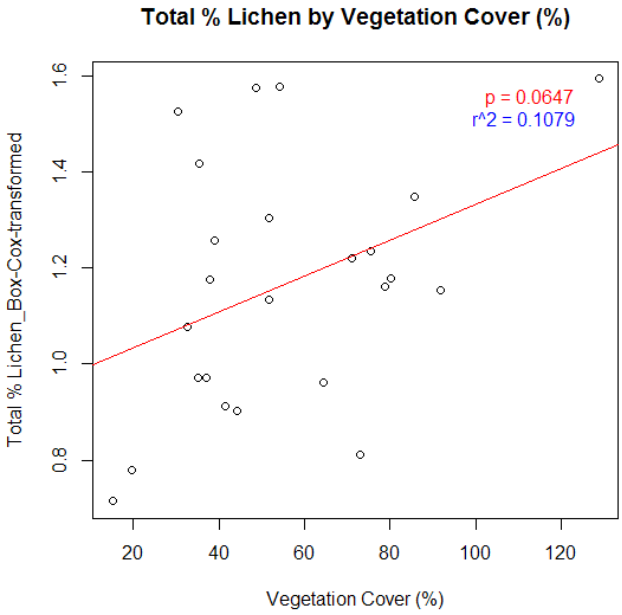
Appendix 7b. Standard boxplot showing tree height (m) is higher ($p < 0.1$) in mechanically site prepared (MSP, n = 12) than in prescribed burn (PB, n = 12) stands.



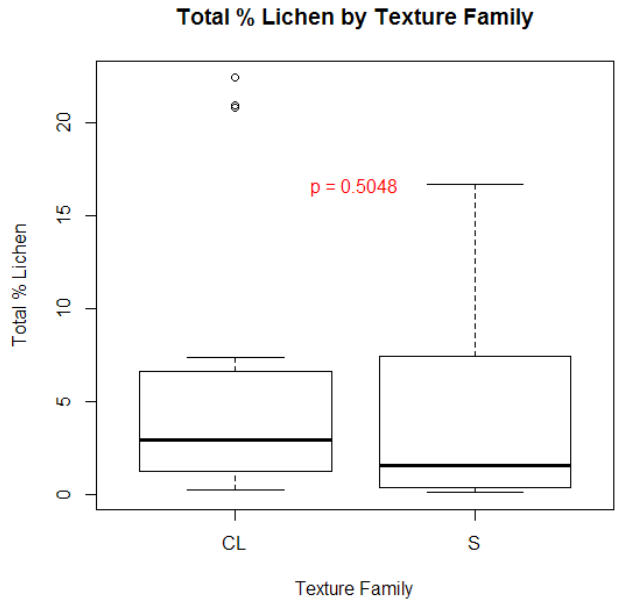
Appendix 7c. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to tree height (m) in prescribed burn and mechanically site prepared stands (n = 24) ($y = {}^{0.15}\sqrt{1.6159 - 0.03934x}$).



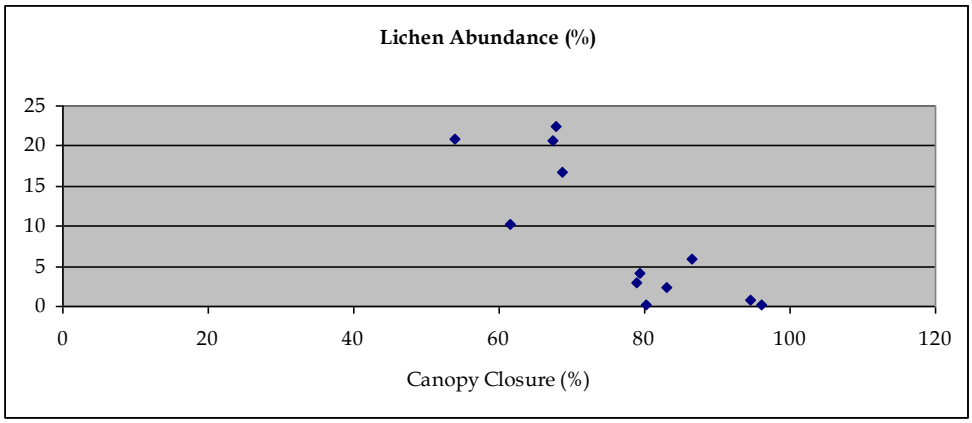
Appendix 7d. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to percent conifer (%) in prescribed burn and mechanically site prepared stands (n = 24) ($y = {}^{0.15}\sqrt{1.9126 - 0.5598x}$).



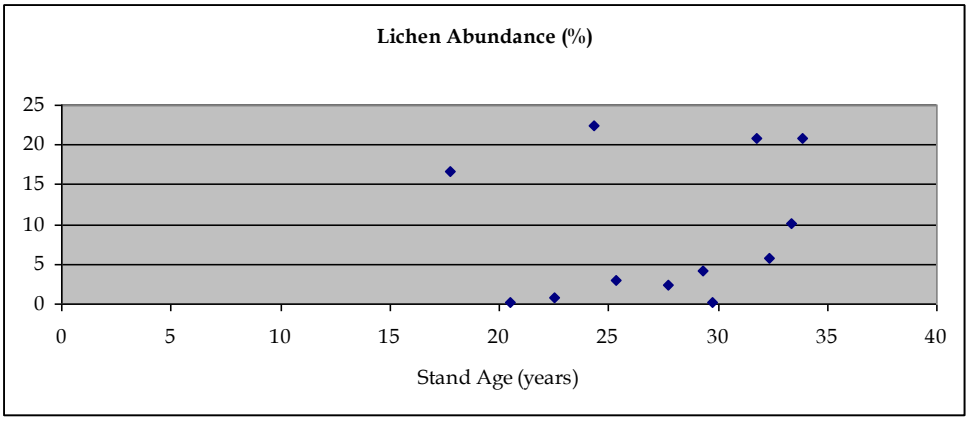
Appendix 7e. Terrestrial lichen abundance (% cover, Box-Cox transformed) in relation to ground vegetation cover (%) in prescribed burn and mechanically site prepared stands (n = 24) ($y = {}^{0.15}\sqrt{0.959} + 0.0037x$).



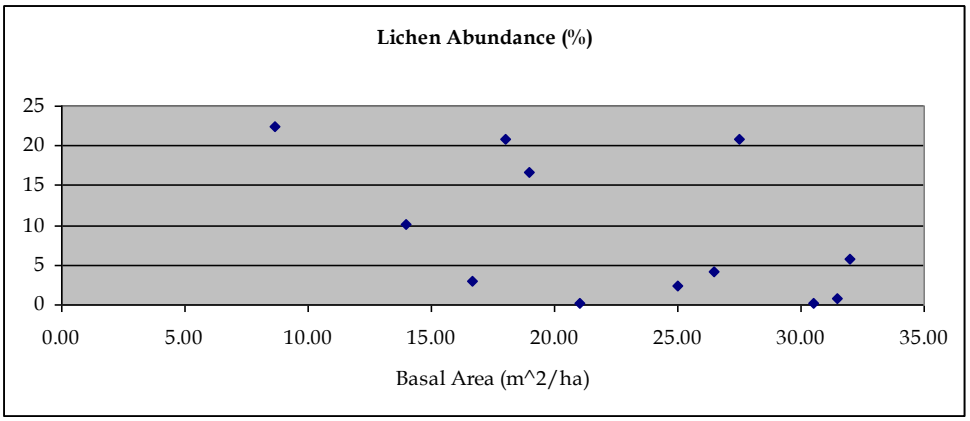
Appendix 7f. Standard boxplot showing terrestrial lichen abundance (% cover) is not significantly different between coarse loamy (CL, n = 15)) and sandy (S, n = 8) textured stands, in the prescribed burn and mechanically site prepared stands (n = 24).



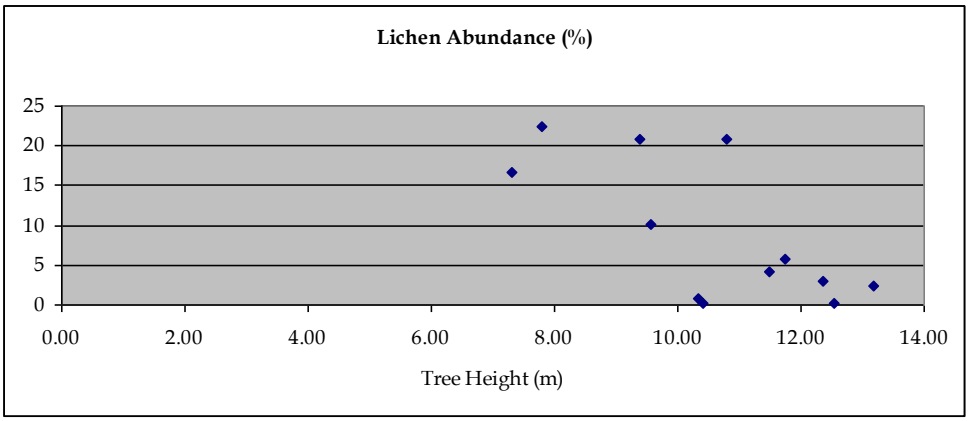
Appendix 8a. Total terrestrial lichen abundance (% cover) in relation to canopy closure (%) among prescribed burned stands (n = 12).



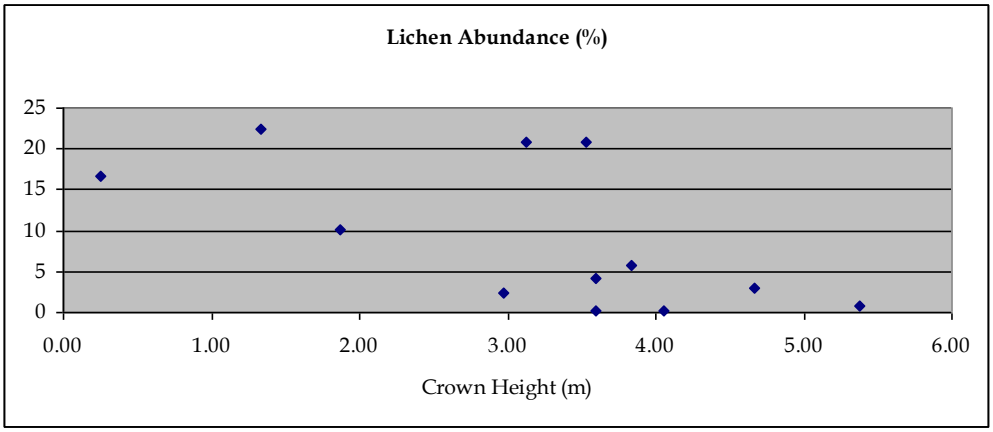
Appendix 8b. Total terrestrial lichen abundance (% cover) in relation to stand age (years) among prescribed burned stands (n = 12).



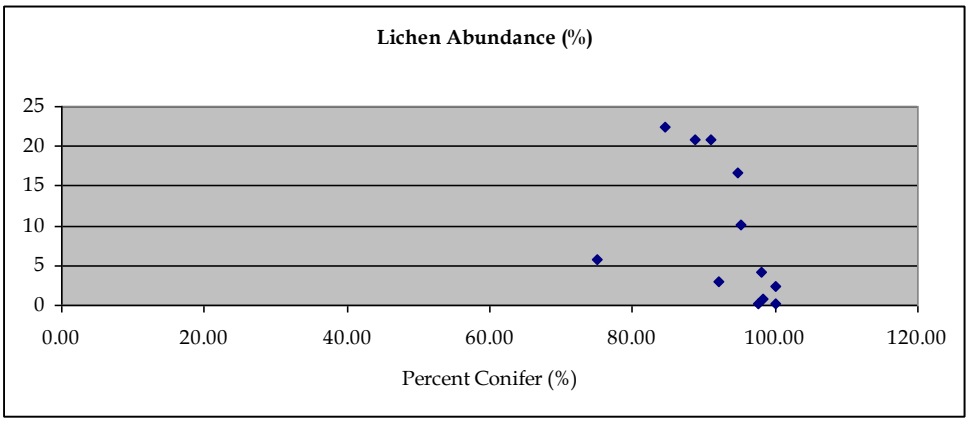
Appendix 8c. Total terrestrial lichen abundance (% cover) in relation to basal area (m^2/ha) among prescribed burned stands (n = 12).



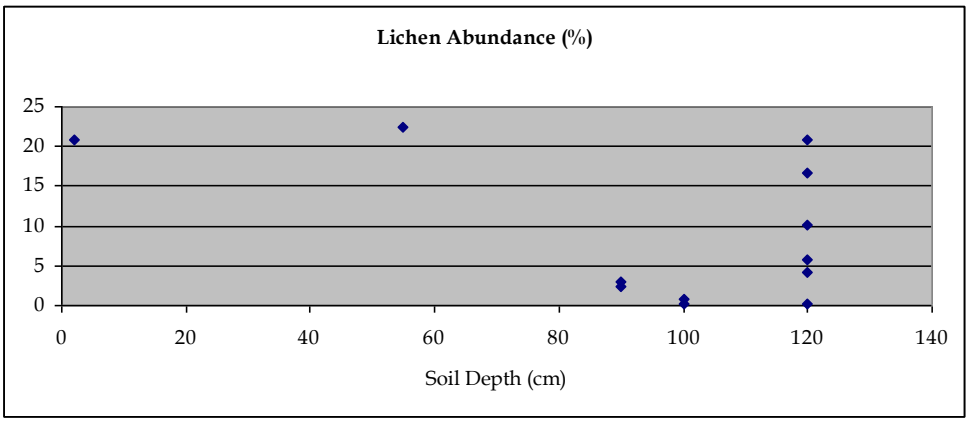
Appendix 8d. Total terrestrial lichen abundance (% cover) in relation to tree height (m) among prescribed burned stands (n = 12).



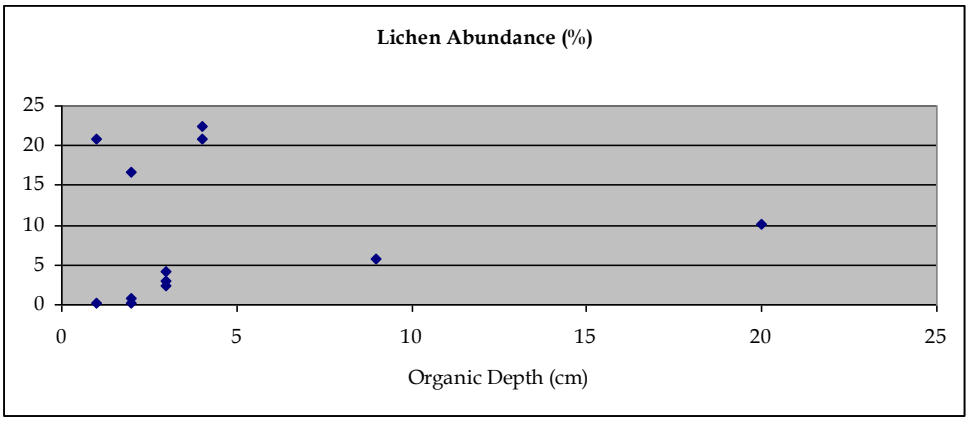
Appendix 8e. Total terrestrial lichen abundance (% cover) in relation to crown height (m) among prescribed burned stands (n = 12).



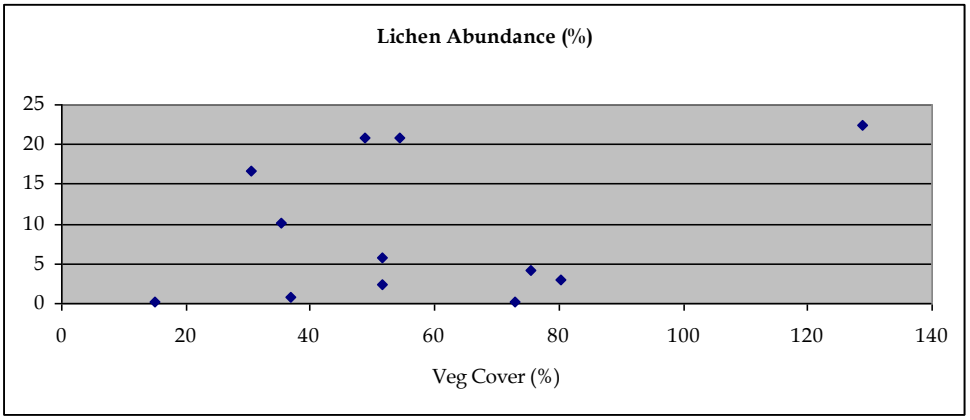
Appendix 8f. Total terrestrial lichen abundance (% cover) in relation to percent conifer (%) among prescribed burned stands (n = 12).



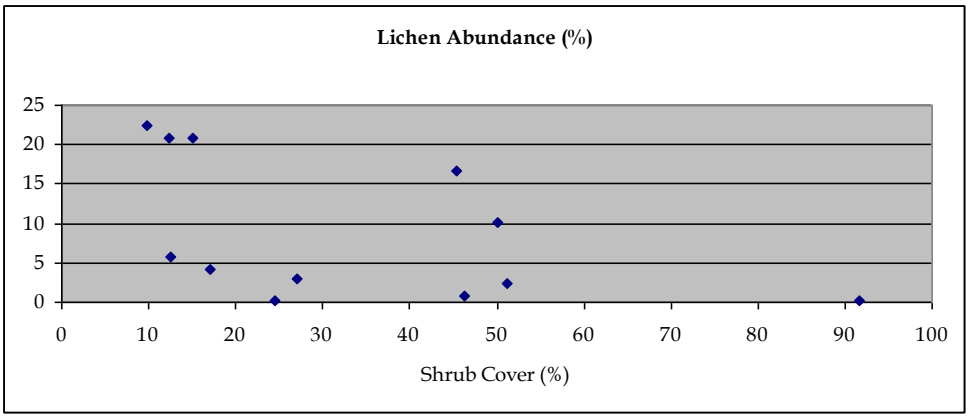
Appendix 8g. Total terrestrial lichen abundance (% cover) in relation to soil depth (cm) among prescribed burned stands (n = 12).



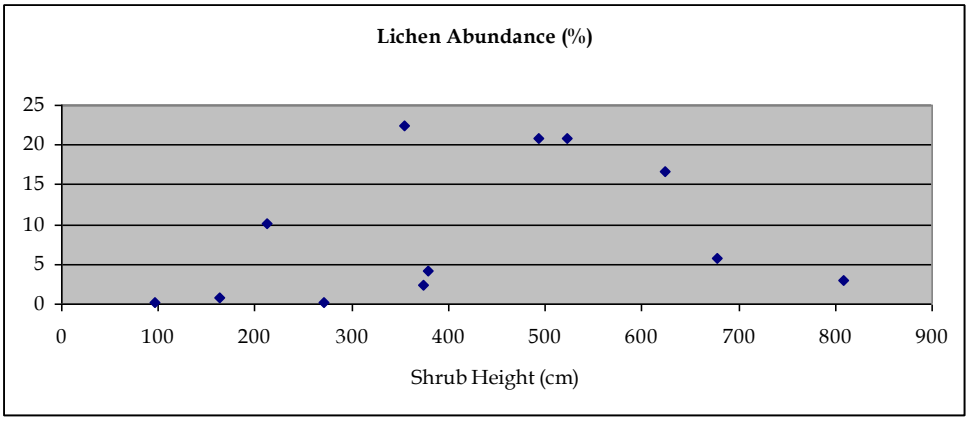
Appendix 8h. Total terrestrial lichen abundance (% cover) in relation to organic depth (cm) among prescribed burned stands (n = 12).



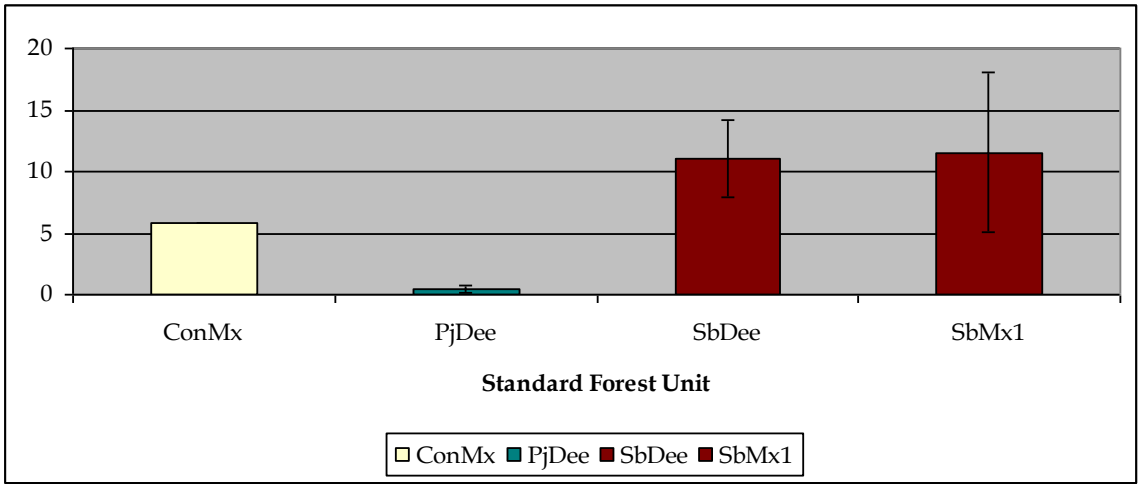
Appendix 8i. Total terrestrial lichen abundance (% cover) in relation to ground vegetation cover (%) among prescribed burned stands (n = 12).



Appendix 8j. Total terrestrial lichen abundance (% cover) in relation to shrub cover (%) among prescribed burned stands (n = 12).

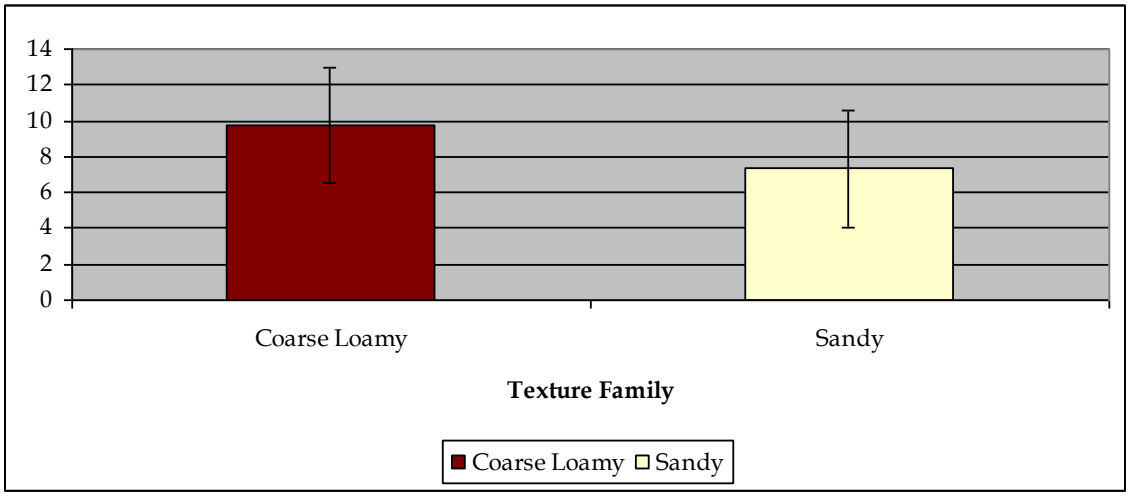


Appendix 8k. Total terrestrial lichen abundance (% cover) in relation to shrub height (cm) among prescribed burned stands (n = 12).



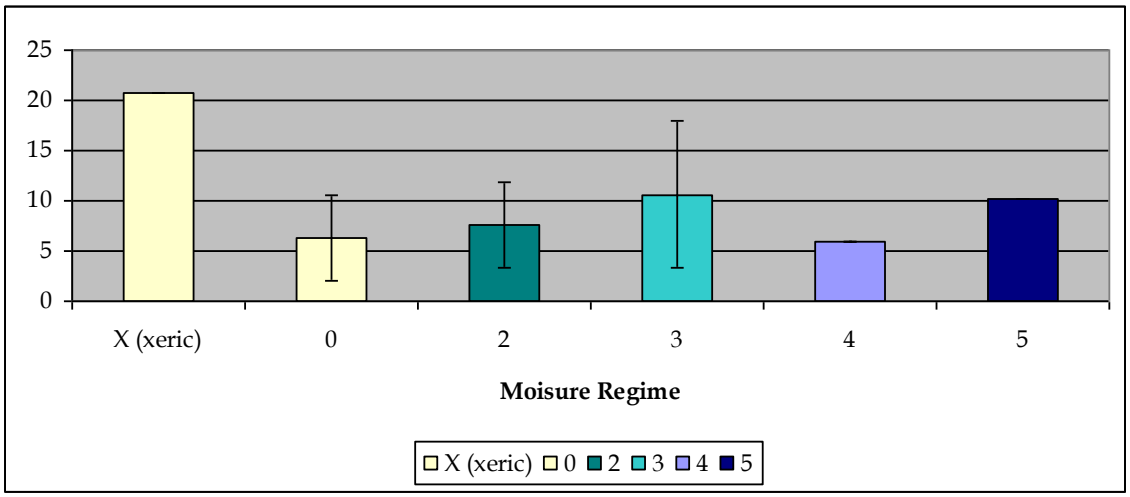
Standard Forest Unit	Mean % Lichen	Std Dev	n	Std Error
ConMx	5.85	0.00	1	0.0000
PjDee	0.47	0.36	2	0.2553
SbDee	11.08	8.35	7	3.1577
SbMx1	11.54	9.22	2	6.5211

Appendix 8l. Total terrestrial lichen abundance (% cover) in relation to standard forest unit (SFU) among prescribed burned stands (n = 12).



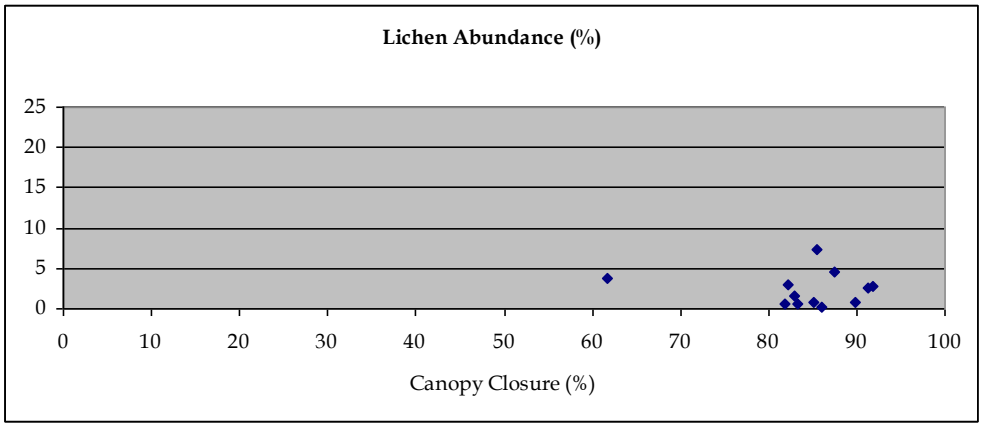
Texture Family	Mean % Lichen	Std Dev	n	Std Error
Coarse Loamy	9.76	9.14	8	3.2320
Sandy	7.33	6.58	4	3.2912

Appendix 8m. Total terrestrial lichen abundance (% cover) in relation to texture family (class) among prescribed burned stands (n = 12).

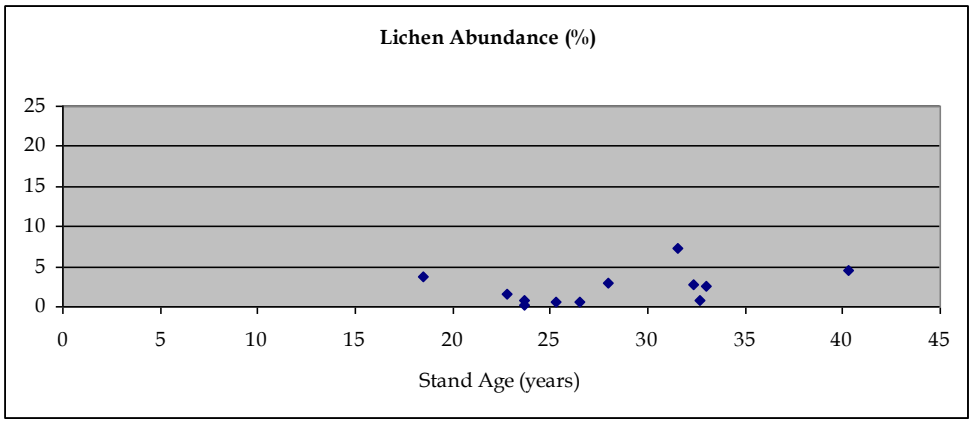


Moisture Regime	Mean % Lichen	Std Dev	n	Std Error
X (xeric)	20.76	0.00	1	0.0000
0	6.37	7.35	3	4.2462
2	7.57	8.63	4	4.3155
3	10.59	10.34	2	7.3091
4	5.85	0.00	1	0.0000
5	10.21	0.00	1	0.0000

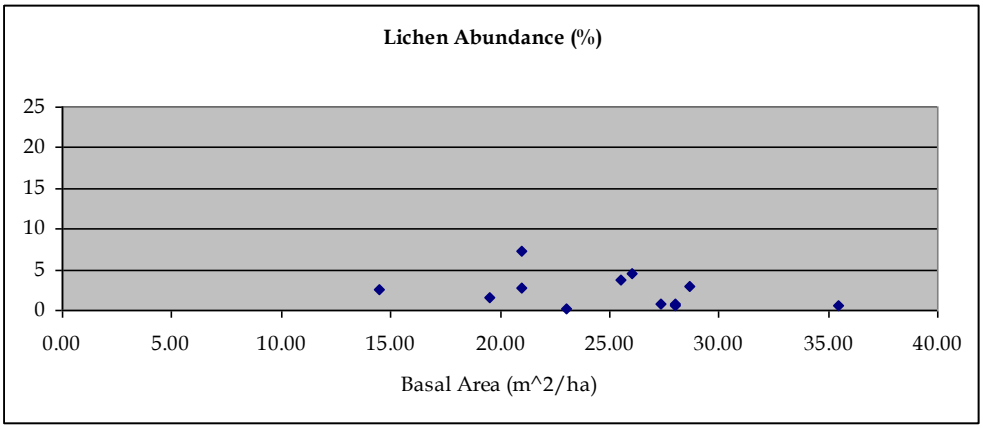
Appendix 8n. Total terrestrial lichen abundance (% cover) in relation to moisture regime (code) among prescribed burned stands (n = 12).



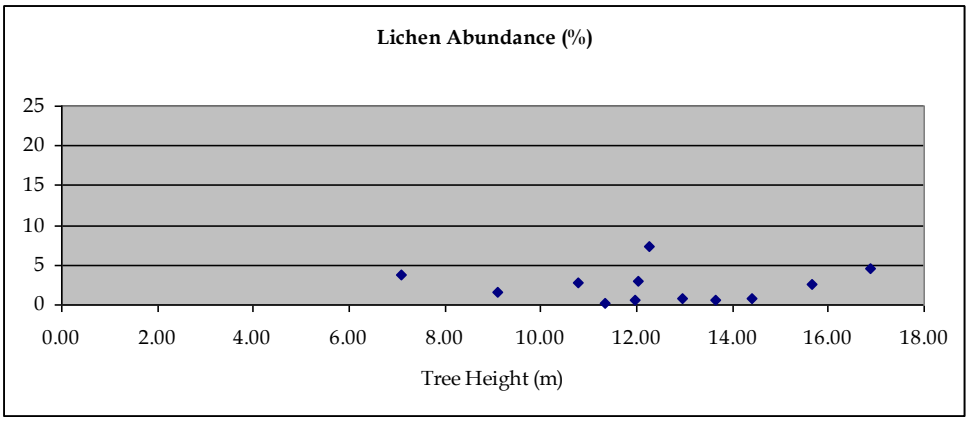
Appendix 9a. Total terrestrial lichen abundance (% cover) in relation to canopy closure (%) among mechanically site prepared stands (n = 12).



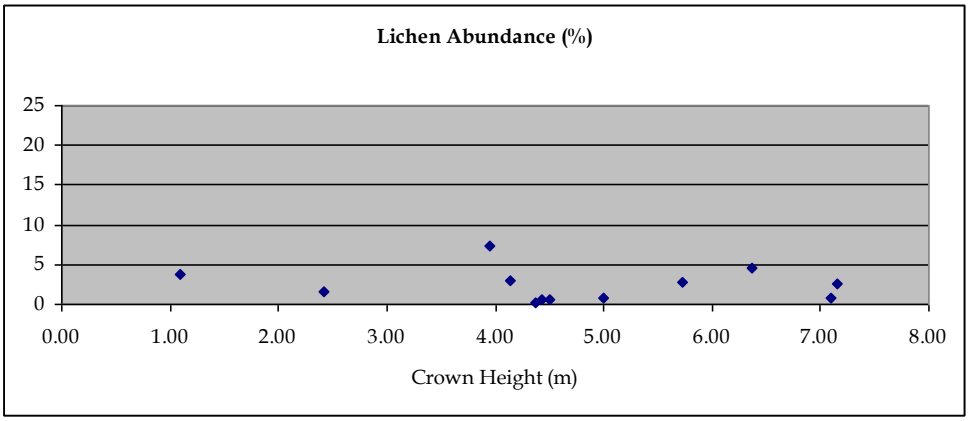
Appendix 9b. Total terrestrial lichen abundance (% cover) in relation to stand age (years) among mechanically site prepared stands (n = 12).



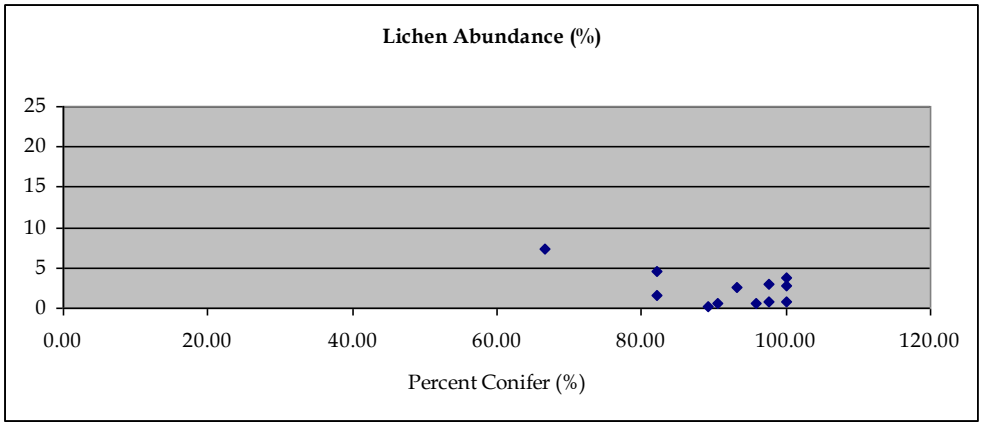
Appendix 9c. Total terrestrial lichen abundance (% cover) in relation to basal area (m^2/ha) among mechanically site prepared stands (n = 12).



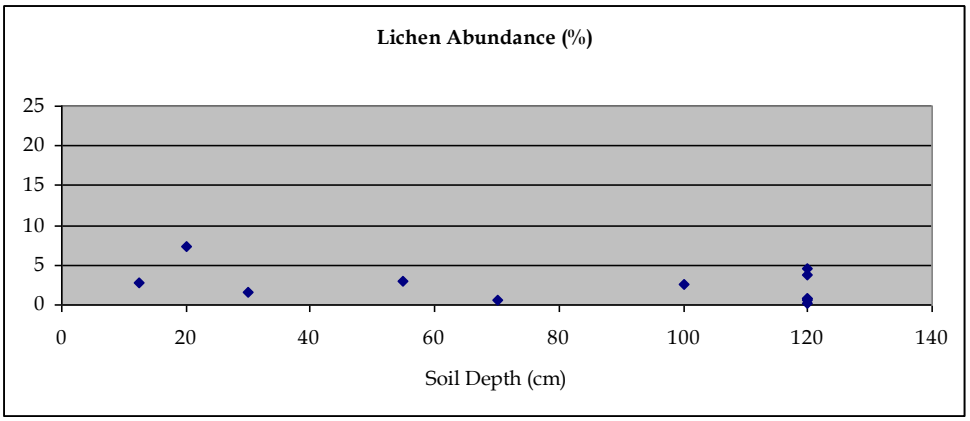
Appendix 9d. Total terrestrial lichen abundance (% cover) in relation to tree height (m) among mechanically site prepared stands (n = 12).



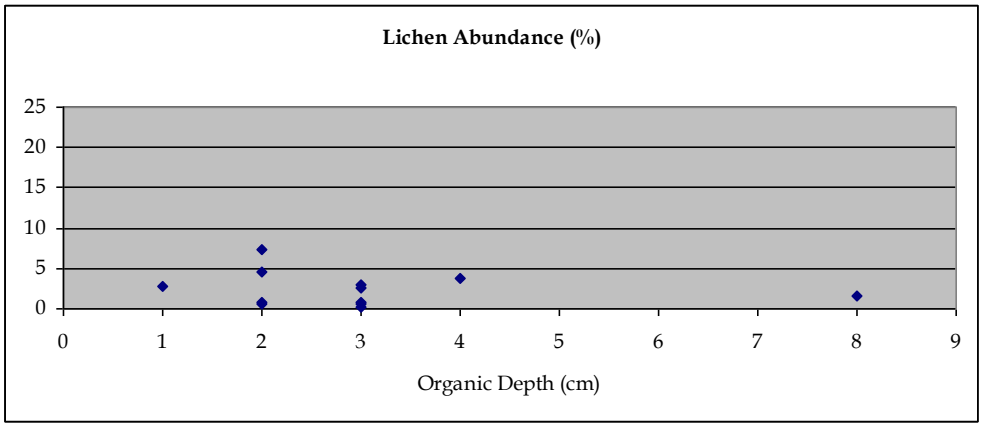
Appendix 9e. Total terrestrial lichen abundance (% cover) in relation to crown height (m) among mechanically site prepared stands (n = 12).



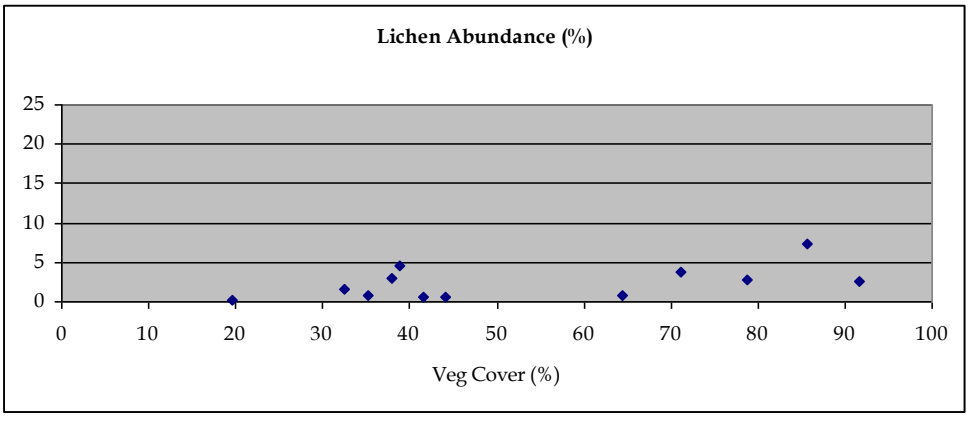
Appendix 9f. Total terrestrial lichen abundance (% cover) in relation to percent conifer (%) among mechanically site prepared stands (n = 12).



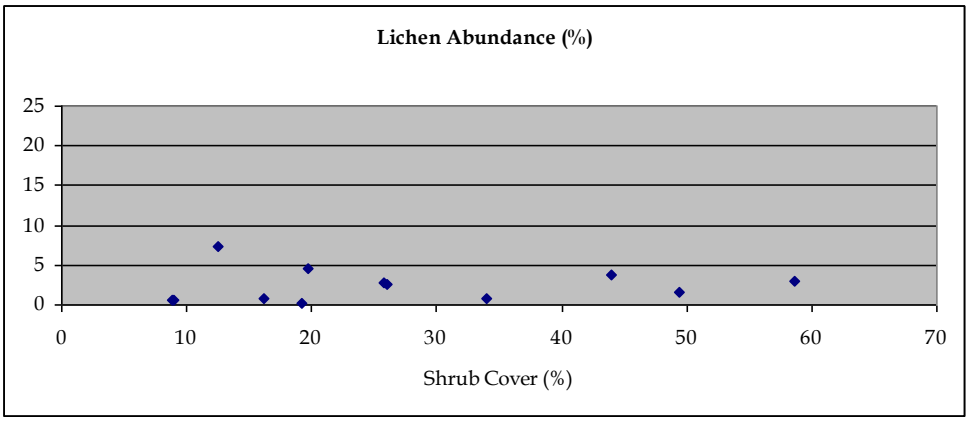
Appendix 9g. Total terrestrial lichen abundance (% cover) in relation to soil depth (cm) among mechanically site prepared stands (n = 12).



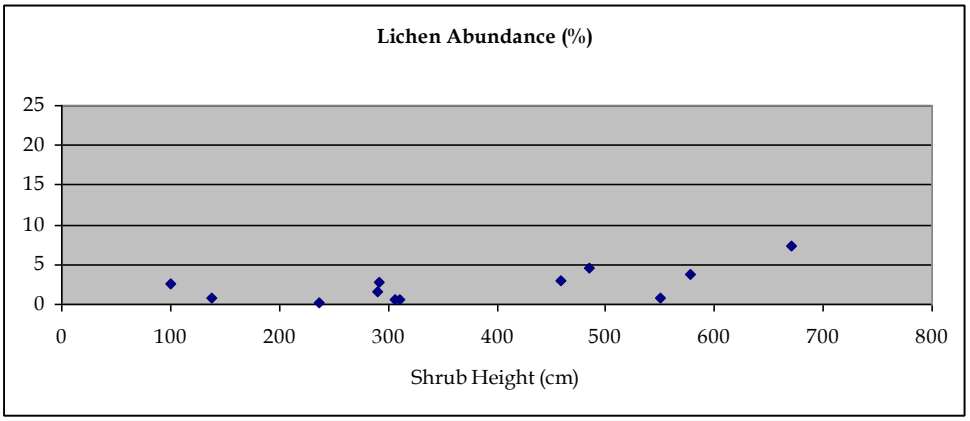
Appendix 9h. Total terrestrial lichen abundance (% cover) in relation to organic depth (cm) among mechanically site prepared stands (n = 12).



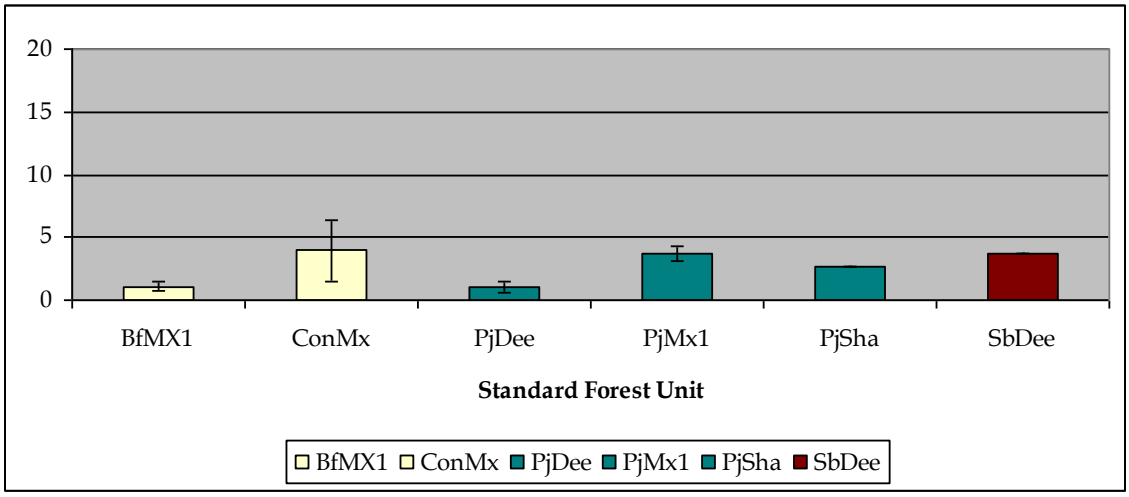
Appendix 9i. Total terrestrial lichen abundance (% cover) in relation to ground vegetation cover (%) among mechanically site prepared stands (n = 12).



Appendix 9j. Total terrestrial lichen abundance (% cover) in relation to shrub cover (%) among mechanically site prepared stands (n = 12).

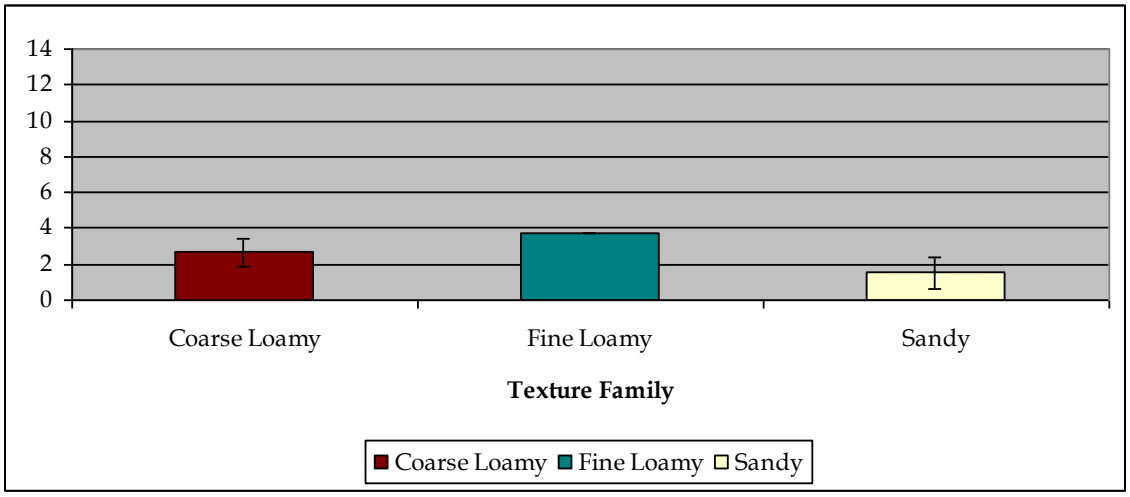


Appendix 9k. Total terrestrial lichen abundance (% cover) in relation to shrub height (cm) among mechanically site prepared stands (n = 12).



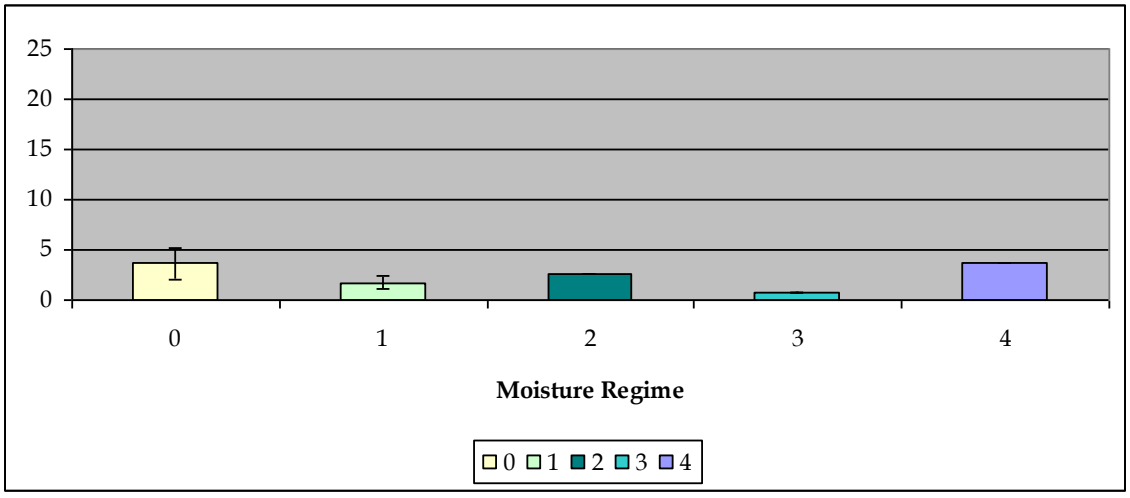
Standard Forest Unit	Mean % Lichen	Std Dev	n	Std Error
BfMx1	1.09	0.55	2	0.3873
ConMx	3.93	3.43	2	2.4233
PjDee	1.10	0.90	4	0.4504
PjMx1	3.77	0.83	2	0.5872
PjSha	2.71	0.00	1	0.0000
SbDee	3.75	0.00	1	0.0000

Appendix 9l. Total terrestrial lichen abundance (% cover) in relation to standard forest unit (SFU) among mechanically site prepared stands (n = 12).



Texture Family	Mean % Lichen	Std Dev	n	Std Error
Coarse Loamy	2.65	2.11	7	0.7981
Fine Loamy	3.75	0.00	1	0.0000
Sandy	1.53	1.79	4	0.8927

Appendix 9m. Total terrestrial lichen abundance (% cover) in relation to texture family (class) among mechanically site prepared stands (n = 12).



Moisture Regime	Mean % Lichen	Std Dev	n	Std Error
0	3.61	2.76	3	1.5955
1	1.74	1.58	6	0.6448
2	2.60	0.00	1	0.0000
3	0.83	0.00	1	0.0000
4	3.75	0.00	1	0.0000

Appendix 9n. Total terrestrial lichen abundance (% cover) in relation to moisture regime (code) among mechanically site prepared stands (n = 12).