ARBOREAL LICHENS IN NATURAL AND MANAGED HIGH ELEVATION SPRUCE-FIR FORESTS OF THE NORTH THOMPSON VALLEY, BRITISH COLUMBIA

by

Douglas Wayne Lewis Bachelor of Natural Resource Science Degree University College of the Cariboo, 1998

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Approval

Name:	Douglas Wayne Lewis	
Degree:	Master of Resource Management	
Title of Research Project:	Arboreal Lichens in Natural and Managed High Elevation Spruce-Fir Forests of the North Thompson Valley, British Columbia	
Project No.:	359	

Examining Committee:

Dr. Kenneth P. Lertzman Senior Supervisor Associate Professor School of Resource and Environmental Management

Dr. Walt Klenner Wildlife Habitat Ecologist BC Ministry of Forests, Research Branch

Date Approved:

_ Cipril 7/2004

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Abstract

Old subalpine spruce (*Picea*)-fir (*Abies*) forests provide abundant arboreal lichen forage for threatened populations of mountain caribou (*Rangifer tarandus caribou*). Clearcut logging has depleted the amount of old forests available to provide foraging habitat in many caribou winter ranges. Partial cutting systems are now used to maintain lichen forage while allowing continued logging, however their long-term efficacy to provide forage is uncertain. Greater understanding of long-term lichen response to changes in structural and micro-environmental conditions in natural forests and under different partial cutting treatments is needed to assess long-term forage availability and management consequences

I used a retrospective approach to compare the abundance and distribution of the prevalent macro-lichens *Alectoria* and *Bryoria* to structural conditions in a range of natural and managed subalpine forests. The abundance and vertical distribution of *Alectoria* increased in older and more structurally complex forests. In partial cuts, *Bryoria* biomass and lower canopy composition increased in response to time since logging and lower residual basal area, while greater *Alectoria* biomass was associated with retention of large trees.

I then used a spatially explicit stand model (TASS) to simulate forest canopy structure and light (climatic) conditions under various partial cutting treatments over a 100-year simulation period. My results suggest *Alectoria* presence will diminish as average light levels exceed 40% Percent Above Canopy Light (PACL). Thus, low removal treatments (<40%) retain conditions in the lower canopy (up to 4 metres above ground) suitable for *Alectoria* while higher removals and larger openings

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create suitable conditions for *Bryoria*. Low removals partial cuts are expected to maintain sufficient forage biomass for caribou while high removal cuts result in an immediate loss of suitable forage conditions. Suitable forage conditions may be replenished in higher removal partial cuts within 20 years if suitable substrate and climatic conditions are present for a sufficient length of time.

Stand-level approaches to managing lichen forage create timber and habitat management concerns at various spatial scales. Thus, no one partial cutting system is best for meeting all management objectives. Managers must acknowledge trade-offs associated with different partial cut treatments and consider their use in the appropriate landscape context.

Dedication

This project is dedicated to my family. My wife Nadia, daughter Jaida and son Samuel. Without your support, love and patience this would not have been possible.

And,

to the memory of Edna Wetheral

1919 - 2003

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Chapter 1- Thesis Introduction

High Elevation Forests, Lichens and Caribou

Old high elevation Engelmann Spruce – Subalpine fir (ESSF) forests (e.g. Lloyd et al. 1991) in the interior wet belt of central and southern British Columbia host some of the largest accumulations of arboreal lichens in the world (Edwards et al. 1960, Goward 1998). Estimates of lichen biomass in these old forests can range as high as 400+ kg/ha (Edwards et al. 1960, Coxson et al. 2003). Most of this biomass is associated with two prevalent hair lichens; Alectoria sarmentosa (Brodo and Hawksworth 1977) and a complex of species of the genera Bryoria and Nodobryoria (Common and Brodo 1995)(hereafter collectively referred to as Bryoria). Alectoria and Bryoria appear to display "old growth dependence", accumulating significant biomass only in old forests that are greater than 150 years of age (Goward 1998). The relationship between old forests and substantial lichen biomass is linked to the distinct structural and climatic properties of old-growth forests including large old trees, multi-layered, structurally complex forest canopies and moderated microclimatic conditions (Lessica et al. 1991, McCune 1993, Esseen et al. 1996).

The distribution of mountain caribou (*Rangifer tarandus caribou*) in British Columbia is closely linked to the abundant arboreal lichen accumulations in high elevation forests of the interior wet belt (Hatter and Kinley 1999, Stevenson et al. 2001). Mountain caribou in central and southeastern British Columbia are a unique ecotype of Woodland caribou (*Rangifer tarandus*) distinguished by their use of mountainous

terrain, arboreal lichen foraging habits, and a distinct bi-annual migration corresponding to annual snowfall (Heard and Vagt 1998). Caribou typically descend to lower elevations in early winter (mid-November to mid-January) to avoid the deep soft snow that begins to accumulate at higher elevations, and utilize mid to high elevation Engelmann spruce – subalpine fir (ESSF) forests and lower elevation Interior Cedar Hemlock (ICH) forests. Mountain caribou return to higher elevations in late winter (mid-January to April) again using high elevation ESSF forests and higher elevation ESSF parkland forests in the late winter when the snow pack has settled and hardened (Edwards and Ritcey 1960, Antifeau 1987, Terry et al. 1996). The late winter migration is believed to be an anti-predator strategy used to escape predators (primarily wolves (*Canus lupus*)) that follow moose (*Alces alces*) and deer (*Odocoileus spp.*) to lower elevation habitats (Bergerud et al.1984, Seip 1992).

Importance of Lichens to Caribou

During the winter stay in high elevation forests, the arboreal lichens *Alectoria* and *Bryoria* provide a critical food source for mountain caribou when other forage is covered by deep snow (Edwards and Ritcey 1960, Antifeau 1987, Rominger and Oldemeyer 1989, Rominger et al. 1996,). Caribou travel with relative efficiency on deep snow to access lichens only available in the lower canopy of standing trees, on blowndown trees and litterfall (Antifeau 1987). Trees with high lichen accumulations are important for caribou winter survival (Terry et al. 1996). As the primary food source available during the winter months,

arboreal lichens are believed to be the main forage for mountain caribou for up to 200+ days of the year (Rominger and Oldemeyer 1990, Rominger et al. 1996, 2000).

The dependence on old high elevation forests for winter forage make caribou vulnerable to habitat loss and change (Stevenson and Hatler 1985, BC MWLAP 2002). Loss of forested habitat from natural and human induced events is one factor that has led to declines in mountain caribou populations through much of the 20th century, resulting in their current status as 'threatened' in Canada (COSEWIC 2002) and 'threatened or endangered' in British Columbia (BC MWLAP 2002). The decline is believed to have started mainly following increased human settlement of interior valleys from the 1930's through 1960's, increasing the rate of habitat loss due to fires and development (Edwards 1954). Change in habitat conditions also prompted an influx of moose throughout the interior in the 1930's, and with them, an increase in predators (mainly wolves) that may have resulted in increased predation (Bergerud and Elliot 1986, Bergerud 1974, Seip 1992). Hunting pressure in this same period has been cited as an additional factor in the decline of some populations (Bergerud 1974). Following bans on caribou hunting in the 1970's, increased timber harvesting in high elevation forests and an influx of backcountry recreationalists have been cited as contributing factors reducing the size of some herds (Simpson 1987, Simpson and Terry 2000, BCMWLAP 2002).

Managing Lichens in Caribou Habitat

Although arboreal lichen forage is currently not believed to be limiting caribou populations in winter habitats (Stevenson 1979, Seip 1992, BC Ministry of WLAP 2002), there is concern that the continued loss of winter habitat due to logging may further threaten mountain caribou populations, highlighting the need to develop alternatives to conventional forest management in caribou winter habitat (Stevenson and Hatler 1985, Stevenson et al. 1994). In the 1990's, forest management guidelines were widely implemented through caribou winter ranges focusing on the use of partial cutting (selection silviculture systems) and lengthened rotation cycles to retain arboreal lichen forage while allowing harvesting to continue (Stevenson et al. 1994, Armleder and Stevenson 1996). More recently, retention silviculture systems (Franklin et al. 1997) have been proposed as an additional or alternative partial cutting treatment in caribou winter habitats (Lewis 2003).

While forest and wildlife managers rely on partial cutting to maintain arboreal lichen forage for mountain caribou, the efficacy of various partial cutting methods at maintaining caribou habitat, particularly arboreal lichen forage, is not well understood. Most selectively harvested forests date back only 10-12 years with some partial cut logging dating back 20-40 years. As a result, only a limited evaluation of the long-term effects of partial cutting on lichen communities has been completed. Furthermore, the trade-offs between managing for lichen forage and other caribou management issues (i.e. road access, interspersion of early seral habitat) has not been adequately addressed.

To ensure adequate forage supply is maintained temporally and spatially within caribou habitat, forest and wildlife managers should understand the dynamics of lichen communities in natural forests and under various partial cutting treatments. Successful long-term protection of caribou populations will require more information to increase our ability to predict and protect future forage supply under continued harvesting. In particular, information is needed to assess arboreal lichen response and recovery following various partial cutting treatments over time and to define specific goals for green tree retention and stand structure objectives following logging. Finally, to integrate forest and caribou habitat management, managers need to assess the implications of managing for lichen forage with other forest and caribou habitat management issues.

Research Objectives

The purpose of this research is two-fold. The first goal is to improve the understanding of arboreal lichen abundance and distribution in forests of various ages, structural conditions and management history. I emphasize describing the relationship between lichen and forest age and structural variables in order to predict lichen abundance and distribution under various natural and managed forest conditions. The second goal of this research is to apply this information in a simulated modeling environment to assess the relative ability of different partial cutting treatments to maintain desirable arboreal lichen forage. The modeling approach will help evaluate the likely benefits and drawbacks of several partial cutting systems at maintaining lichen forage. This

information will better enable forest and wildlife managers to assess trade-offs and weigh the short and long term consequences of harvesting options at maintaining foraging habitat for mountain caribou.

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Chapter 2 - Relationships of Arboreal Lichen to Forest Age and Structure in Natural and Managed High Elevation Engelmann Spruce-Subalpine Fir Forests

Introduction

The diversity, abundance and distribution of forest canopy epiphytes (lichens and bryophytes) are often associated with the age and structure of forests (Yarranton 1972, Rose 1976, Lang et al. 1980, Lessica et al. 1991, McCune 1993, Neitlich 1993). Forest canopy epiphyte functional groups (e.g. alectoroid lichens, cyanolichens, bryophytes; McCune 1993) occupy vertical zones in the forest canopy that appear to correspond to their order of establishment during forest succession and growth (Yarranton 1972, Pike et al. 1977, Lang et al. **1980.** McCune 1993). Epiphytes in the uppermost portion of the canopy of old forests are similar to the dominant epiphyte community in the lower canopy of the youngest forest within a sequence of stand ages. As a result, epiphytes occupying the lower canopy of an old forest may only be present or dominant in old stands (McCune 1993). In addition, many of the epiphyte groups that colonize late in the age sequence (e.g. cyanolichens) also may not attain significant mass until the forest is even older. Hence, the lichen biomass in late successional or old-growth forests often contains several times the lichen mass found in younger forests (Pike et al. 1975, McCune 1993, Sillet and Neitlich 1996). The diversity of the epiphyte community may also increase with forest age (Selva 1994), as the establishment of many epiphytes is limited by dispersal (Sillett et. al. 2000), substrate availability, or environmental conditions (Sillett and Neitlich 1996)

The role of forest age and structure in epiphyte community diversity, distribution and abundance is largely an outcome of epiphyte response to several interacting factors that change with forest age, including canopy microclimate, structure of the canopy, and properties of the bark (Adams and Risser 1971, Yarranton 1972, Rose 1976, Hyvarinen et al. 1992, McCune 1993, Neitlich 1993). As a forest ages, a light and moisture gradient often develops between the upper and lower canopy with the increase in tree height (Yarranton 1972) and the density and distribution of foliage (Van Pelt 1995, Parker 1996, Van Pelt and Franklin 2000). The lower canopy of old forests retains moisture for longer periods while the exposed upper forest canopy typically receives more solar radiation and wind turbulence, resulting in more rapid drying following precipitation (Geiger 1965, Chen et al. 1991, Parker 1996, 1997). Tree branch and bark characteristics also change along the vertical profile of the forest canopy. Young branches in the upper canopy of old forests are mainly foliated with smooth bark resembling branches in the lower canopy of young forests. Older, lower canopy branches are often defoliated, retain moisture longer, and the bark is more scaly, fissured, and acidic (Barkman 1958). Since epiphytes are sensitive to the amount of solar radiation, moisture, and often display substrate specificity, epiphyte establishment and growth is related to the availability of ideal combinations of climatic and substrate conditions positioned within the forest canopy. Thus, old forest canopies provide a multitude of climatic and substrate combinations that may account for the distributional patterns, diversity and appreciable epiphyte biomass that is often found only in older forests (Sillett and Neitlich 1996).

In the high elevation Engelmann spruce – Subalpine fir (ESSF) forests of southern British Columbia, forest age and structure are strong determinants of the abundance and distribution of the dominant macrolichens Alectoria sarmentosa and Bryoria species (Goward 1998, Campbell and Coxson 2001). The distribution of Bryoria is mainly associated with more open, drier conditions found in young or open forest conditions, or in the more exposed upper canopy of old forests (Goward 1998, Campbell and Coxson 2001). In contrast, Alectoria sarmentosa achieves significant accumulations and is distributed mainly in the lower canopy of older forests where it is believed to tolerate prolonged wet conditions associated with reduced wind speed, solar radiation and increased moisture availability (Lessica et al. 1991, McCune 1993, Sillet 1995, Esseen et al. 1996, Esseen & Renhorn 1998). As a result, Alectoria and Bryoria often display a distinct vertical zonation in the canopy of high elevation ESSF forests with Bryoria dominating the upper canopy and *Alectoria* mainly restricted to the middle and lower portion of the forest canopy (Edwards et al. 1960, Goward 1998. Campbell and Coxson 2001, Goward 2004).

A key variable believed to control the distribution of *Alectoria* and *Bryoria* is the influence of forest structure on the frequency and duration of wetting and drying cycles in the forest canopy (Stevenson 1985, Goward 1998, Campbell and Coxson 2001). Goward (1998) proposed that upper canopies of old forests and forests in exposed areas experience increased wind ventilation resulting in rapid moisture evaporation and thus longer and more frequent drying cycles following precipitation events. These conditions provide a more suitable environment for *Bryoria*, which is less tolerant of prolonged wetting. As a result, Goward

(1998) argued that *Bryoria* is limited to defoliated inner portions of branches in less exposed areas, such as the lower canopy of old forests, due to retention of moisture on live foliage, but can accumulate on foliated portions of the branch in exposed conditions. He further suggests significant *Bryoria* accumulations in the lower canopy of old forests occur where the lower canopy is relatively more exposed, such as high elevation ESSF parkland forests where open forest canopy structure does not inhibit wind penetration. Campbell and Coxson (2001) further propose that seasonal differences in moisture retention on branches contribute to the vertical distribution in the forest canopy. They suggest open, more exposed upper canopies of old forests experience longer mid-winter snowmelts favouring *Bryoria* in this season while retention of wet conditions in lower canopies in the summer may favour *Alectoria* growth during this period.

Partial cutting logging of high elevation ESSF forests can have impacts on the distribution and abundance of *Alectoria* and *Bryoria* by reducing the moderating effects of forest canopy structure on wind and solar penetration into the forest canopy (Stevenson et al. 1994, 2001, Coxson et al. 2003). Lichen loss following logging is believed to increase relative to tree removal with higher removal partial cuts experiencing larger losses due not only to loss of substrate but increased exposure of the remaining canopy (e.g. wind scour; Stevenson 2001). Partial cuts with lower tree removal (i.e. 30% removal) experience fewer lichen losses on the remaining trees as the impact on canopy microclimate is less severe (Stevenson et al. 2001, Coxson et al. 2003). However, following a lag period where lichens have time to respond to the altered climatic conditions, increased exposure due to partial cutting may positively

influence lichen abundance on residual trees. Esseen and Renhorn (1998) noted an increase in *Alectoria* biomass in boreal forests within 30 metres from clearcut edges within 15 years after logging. They believe the increase in solar radiation at this distance provided by the newly formed edge, without other harsh environment effects, benefited *Alectoria* growth. In addition, Rominger et al. (1994), Miller et al. (1999) and Stevenson (2001) noted lower canopy *Bryoria* composition to increase in partial cut forests with higher tree removal (>50% basal area removal) within 10 years after logging. Rominger et al. (1994) noted no difference in lower canopy lichen biomass compared to nearby un-logged forests; it appeared the increase in *Bryoria* mass offset a reduction in *Alectoria* possibly due to wind scouring.

The long-term effects of changes to canopy structure due to natural forest development or partial cutting are not well understood. The goal of my research is to examine the distribution and relative biomass of *Alectoria* and *Bryoria* in high elevation ESSF forests relative to forest age, structure and management history. Since forest canopy structure largely determines forest canopy climate, 1 expect differences in the distribution and abundance of forest canopy lichens to correspond to changes in structure of forests due to forest succession and management interventions. I expect to observe the following relationships between lichen and forests:

1) The largest biomass accumulations and relative composition of *Alectoria sarmentosa* will be associated with forests of greater age and structural complexity that provide an environment more suited to *Alectoria* growth. In contrast, consistent with the hypotheses of Goward

(1998) and Campbell and Coxson (2001), I expect Bryoria to achieve the highest accumulations and relative composition in the lower canopy of younger forests and open forest conditions where increased canopy light and wind ventilation reduce the availability of moisture, favouring Bryoria establishment and growth. I further expect the distribution of Alectoria and Bryoria in the forest canopy to be subject to the same constraints, with Alectoria distributed higher in the forest canopy in older and more structurally complex forests where the lower canopy climate is moderated by greater tree height and greater canopy foliage volume provides conditions more suitable for Alectoria growth. Based on these expectations, I predict the abundance, relative composition and distribution of Alectoria to be greater in the lower forest canopy in older forests and in forests with measures of greater structural complexity, while Bryoria abundance and composition will be greater in younger forests and under more open forest conditions. In this chapter I test those predictions by comparing lichen biomass and composition estimates to measurements of forest age and structural conditions in unmanaged forest stands.

2) In partial cut forests, I expect that with increased tree removal the remnant forest canopy will be exposed to increased wind ventilation and solar radiation resulting in drier conditions, thus increasing the suitability for *Bryoria* establishment and growth. I expect *Bryoria* will compose a greater amount of lower canopy lichen composition in older partial cuts and cuts with lower levels of green tree retention consistent with observations by Rominger et al. (1994) and Stevenson et al. (2001). I also expect *Alectoria* abundance in partially cut forests to be lower

following logging as environmental conditions are less suitable for growth and *Alectoria* dispersal may be limited on small, foliated branches of new growth (Esseen et al. 1996, Sillett et al. 2000). Therefore, I predict the biomass, relative composition and distribution of *Bryoria* to increase in the lower canopy of partial cuts with lower levels of tree retention and greater time since logging, while greater *Alectoria* biomass and composition will be associated with partial cuts with greater tree retention.

Methods

Study Area

The study area was located in the southern interior of British Columbia, south and east of the town of Blue River in the North Thompson River valley (51° 55' 00"/119° 25' 00") (Figure 2-1). The study area falls within the Shuswap Highland Ecosection, distinguished by relatively flat high elevation plateaus, south and west of the more rugged Columbia Mountains. The valley bottoms and sides consist mainly of Interior Cedar Hemlock (ICH) forests changing to Engelmann Spruce-Subalpine Fir (ESSF) forests on the higher elevation plateaus (Lloyd et al. 1991). The sampling area is concentrated exclusively in the ESSFwc2 (wet cold) and ESSFvv (very wet very cold) subzones and variants between approximately 1350 metres to 1750 metres elevation (Lloyd et al. 1991). The ESSF parkland subzones above 1750 metres and ICH forests below 1350 metres bounds the study area.

The position of the study area on the windward side of the Columbia Mountains results in high levels of precipitation. The study area receives upwards of 2000 mm of precipitation annually with most (50-70%) falling as snowfall, resulting in deep snow-packs of 1 to 4 metres (Meidinger and Pojar 1991). The area is relatively cold with average annual temperatures ranging from –2 to 2 degrees Celsius and 0-2 months with temperatures averaging above 10 degrees Celsius (Meidinger and Pojar 1991).

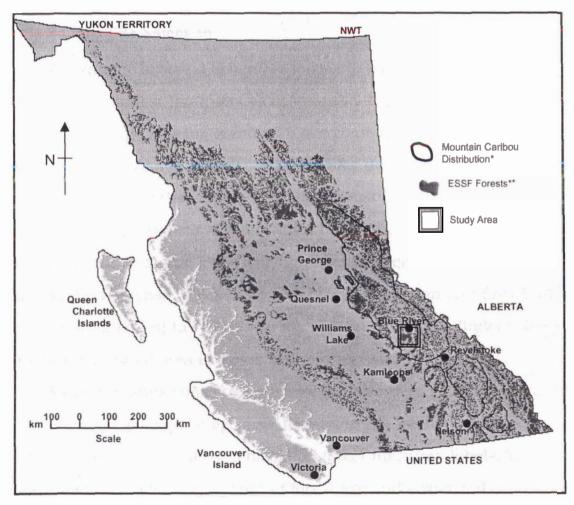


Figure 2-1. Location of the study area relative to the distribution of ESSF forests and mountain caribou in British Columbia.

Large stand-replacing natural disturbance events in these ESSF forests are relatively infrequent with more frequent low intensity insect, pathogen and fire disturbances (BC Ministry of Environment and BC Ministry of Forests 1995). However, large fires early in the 20th century burned in the ICH forests on the steep valley sides and occasionally escaped into the ESSF forests on the plateaus above. These burned areas provided an opportunity to examine the stand structure and lichen composition of early seral stages of ESSF forests.

Sample Site Selection

To examine arboreal lichen responses to forest succession or experimental harvest treatment would require decades if not centuries of direct monitoring of ageing stands. To overcome this problem, I used a retrospective approach, substituting space for time by selecting both unlogged forest stands that reflect a range of forest age and structural conditions and partial cut stands with a range of post-harvest tree retention levels and time since logging. I used a regression design to evaluate the response in lichen abundance, composition and distribution (dependent variables) to changes in stand level conditions (independent variables, e.g. basal area or forest age).

Sampling units consisted of un-logged and partial cut forest stands that were homogeneous in age and density (uncut forests) or logging treatment history (partial cuts) based on forest inventory labels. To ensure that I sampled a full range of forest age and structural conditions, I first identified candidate stands (polygons) using forest cover maps, orthographic and aerial photographs, and silviculture prescription

information. I divided un-logged forest stands into 3 groups based on broad age class categories using forest inventory maps: immature (age class 3-5, 40-100 years old), mature (age class 6-7, 100-140 years), and old (age classes 8-9, >141 years old). I further divided these into three canopy class categories: high (canopy cover class 4+, >40% canopy closure) medium (canopy cover class 3, 30% canopy closure) and low (canopy cover class 0-2, <20% canopy closure). I grouped partial cut stands into 2 categories based on logging history; recent (0-15 years post harvest), and old (15-30+ years post harvest) and classified stands into high (>30% canopy closure), medium (20-30% canopy closure), and low (10% or less crown closure) post-logging forest cover.

I chose candidate stands (polygons) greater than 3 hectares in size, between 1350 and 1750 metres elevation, and less than 50 percent slope on average. I further selected candidate stands from map information that covered a range of aspects and slope positions. I did not attempt to control for the effects of slope position and aspect on lichen conditions. I attempted to ensure similarly aged or disturbed stands were dispersed throughout the study area to ensure effects were not localized. Due to logistical constraints, I subjectively chose stands for proximity to road access so that no stands were greater than 2 km. from a road and most were less than 1 km. Fortunately, an extensive road network provided reasonable access, hence, few forest stands were not selected for this reason.

Stand Structure Sampling

16.5

To assess forest age and structure, I randomly located three 20×20 metre (0.04 hectare) plots within each forest stand, located at least 50

metres from an edge to avoid the influence of adjacent forest stands on lichen condition. I considered an adjacent stand to be distinct if the forest inventory information age was different by more than one age class (20 years or more) or the adjacent forest had been logged. At each plot, I located corners using the four cardinal directions and numbered trees clockwise starting from 360 degrees. Only trees greater than 12cm. diameter at breast height were numbered and measured. I classified plots with greater than 40 trees as half plots and measured only even or odd trees corresponding to the plot number, however, I assessed lichen on all trees within the plot.

I recorded tree species, canopy class and wildlife tree class for each tree. Canopy classes are based on Walmsley et al. (1980) where trees are identified into 4 categories: 1) dominant, 2) co-dominant, 3) intermediate, and 4) suppressed. Wildlife tree class ratings follow the classification described in Lloyd et al. (1991) where trees are broken into the following classes: (1) live healthy, (2) live unhealthy (3) dead, branches and bark attached, (4) dead, loose bark, and (5) dead, no bark. Then, each tree was measured for diameter at breast height (dbh) and total height (metres). To gain simple estimates of canopy structure, I measured height of the base of the full live crown from the ground, and 2 crown radii measurements (at 90 degree angles) to estimate foliage volume and canopy cover (Van Pelt and North 1996, North et al. 1999).

To estimate the age of uncut forest stands, I randomly selected two trees for aging from the co-dominant tree canopy layer. Each tree was bored close to the base (approximately 30 cm from the ground) and labeled by plot and tree number for aging later in the lab. Each core sample was glued to a board and lightly sanded to aid in tree ring aging.

I aged tree core samples with the aid of a microscope when required and used forest inventory map information to provide the time since harvest in partial cut forests.

To provide independent variables that describe the age and structure of forest stands, I calculated one age variable (mean age of the co-dominant tree canopy) and three (3) variables of forest structure for each plot from the tree measurements: 1) stem density (trees/ha), 2) mean basal area per hectare (m^2/ha), and 3) total canopy foliage volume (m^3/ha)(Van pelt and North 1996, North et al. 1999). These were averaged across the three plots to calculate an average for the stand and standardized to per hectare values.

Two stand structure indices were computed from the tree measurements to describe horizontal and vertical forest structure and distribution of foliage volume. The Shannon Structural Diversity Index (SSDI) (Staudhammer and LeMay 2001) was used as a measure of horizontal and vertical structure of a stand. The SSDI is an average of two measures: the Shannon Index for dbh. and the Shannon Index for height. Each measure results in tree heights and diameters arbitrarily grouped into classes. I used ten 5-cm.-diameter classes (12-17,17-22,22-27,27-32,32-37,37-42,42-47,47-52,52-57, 57+ cm.) and seven 5-meter height classes (0-5,5-10,10-15,15-20,20-25,25-30,30+m.). Each measure provides a value based on the natural log of the proportion of total basal area in each dbh or height class, and so is insensitive to tree size. The values from the two measures are averaged to produce the SSDI value. Forest stands with the basal area evenly distributed among a wide range of tree heights and tree diameters will have the largest SSDI index

values. Forests with relatively un-even height and diameter distributions

Second, as a measure of forest canopy foliage distribution, I calculated the Foliage Height Diversity Index (MacArthur and MacArthur 1961, Staudhammer and LeMay 2001). To calculate the Foliage Height Diversity Index (FHDI), I first calculated foliage volume at 1 metre intervals based on the volume of a cone ($\bullet r^2 * 1/3$ crown height) using measurements of total tree height, base of live crown and mean of the two crown radii measurements. Foliage volume (m³) was then separated into seven height classes (0-5,5-10,10-15,15-20,20-25,25-30,30+ metres) to measure to provide an index value based on the proportion of total foliage volume in each height class. Forests with a more even distribution of foliage through the canopy, or the greatest canopy layering, return the highest FHDI value.

Lichen Assessment

The state of the s

Estimating lichen biomass and composition is a difficult and timeconsuming task (Esseen et al. 1996). Hence, I assessed only one functional lichen group (alectoroid lichens) of the four functional groups (cyanolichens, alectoroid lichens, other lichens and bryophytes) described by McCune (1993). I focused only on *Alectoria* and *Bryoria* since another lichen genus, *Usnea*, is present in the sampling area only in small quantities. *Alectoria* and *Bryoria* are the most important to caribou as forage, and alone provided a sufficiently large effort to sample across the sample plots. I needed estimation procedures that quickly and reliably captured relative *Alectoria* and *Bryoria* biomass and composition

mainly in the lower canopy, where lichens are fed on directly by caribou. I also wanted a description of lichen composition throughout the entire tree canopy as it provides further insight into lichen response to forest age and structural conditions and is a potential source of forage for caribou on wind-thrown trees and litterfall.

I used a modification of the lichen classification method developed by Armleder et al (1992) to assess arboreal lichen abundance in the lower 4.5 metres of the tree canopy. I modified this classification system by subdividing their original five abundance classes into nine abundance class categories based on visual estimates of the number of 5-gram clumps in an effort to reduce large differences in biomass estimates between the original five classes (Table 2-1). I further estimated the composition of *Alectoria* and *Bryoria* to the nearest 10% on each tree.

Table 2-1. Modified lichen abundance estimation classes. Shaded boxes indicate the original abundance classes and biomass estimates of Armleder et al. (1992). Non-shaded boxes indicate modified abundance classes added at midpoints between the original classes.

Abundance Class	No. of 5gr. Clumps	Biomass Estimate
1	<1	2.5 grams
1.5	1 - 5	10 grams
2	5 -10	25 grams
2.5	10 - 20	75 grams
··· 3	20 - 40	150 grams
3.5	40 - 60	250 grams
4	60 - 100	450 grams
4.5	100 - 150	600 grams
5	150+	800 grams

To describe the vertical distribution of arboreal lichen in tree canopies of high elevation forests, I used a method described by Goward (2004a), where lichen accumulation in a tree canopy is separated into three layers: A, B and C, along the vertical axis of the tree. The "A" layer is the lower portion of the tree from the ground up where lichens are noticeably absent, mainly because they are unable to survive due to being covered by the winter snow-pack. The "B" layer begins at the lowest point in the tree were lichen begins to significantly accumulate and may be shared by Alectoria and Bryoria. The "C" layer marks the point in the tree where Bryoria is the dominant lichen and maximum Bryoria loading is achieved, forming thick curtains on the branches to the top of the tree. One point on this axis, the "B/C" threshold, where the "B" and "C" layers converge, is notably important as it distinguishes the transition to minimal or absent Alectoria in the upper tree canopy. I recorded the height (to the nearest 0.1 metre) where this Alectoria/Bryoria transition line (B/C threshold) occurred on trees and was noticeably present when viewed from the ground.

From these estimates, I computed five estimates of stand-level lichen biomass and percent composition; total lichen biomass, *Bryoria* biomass, *Alectoria* biomass, percent composition *Alectoria/Bryoria*, and mean height of the *Alectoria/Bryoria* transition (B/C threshold). Lichen biomass estimates for each stand were calculated by assigning individual trees a lichen biomass estimate (grams/tree) based on the lichen abundance class rating (Armleder et al. 1992, Stevenson et al. 1998)(Table 2-1). Individual tree biomass estimates for *Alectoria* and *Bryoria* were calculated by dividing total tree biomass by percent

composition. Individual plot biomass estimates are based on the sum of all trees containing lichen in the plot. I averaged plot biomass, between the three plots for each stand and standardized this estimate to biomass per hectare. Percent composition *Alectoria* and *Bryoria* and height of the *Alectoria/Bryoria* transition are also averaged among the three plots for each stand.

To verify the lichen assessment protocol, I periodically returned to selected sample plot locations within two weeks following the original assessment to re-assess lichen composition, abundance and the location of the *Alectoria/Bryoria* transition. At each plot, lower canopy biomass and composition estimates were re-assessed for each tree and remeasured the height of the *Alectoria/Bryoria* transition on all trees where the transition was originally recorded. This procedure was used to evaluate and maintain the consistency of lichen estimates between forest types.

Data Analysis

I located and sampled191 plots in 63 different forest stands including 37 natural un-logged forests and 26 partial cut forests over a three month period in the summer of 2001. I eliminated one partial cut forest from the analysis, as it was later found to be very near the lower elevation limit of the study area and consisted largely of *Thuja plicata* (western red cedar) and *Tsuga heterophylla* (western hemlock), unlike other stands measured in the study area.

I used multiple regression and non-linear regression models in the JMP 4.03 platform (SAS Institute 2000) to examine relationships between lichen conditions and stand structure. Prior to the analysis, I reviewed

the distributions of all independent and dependent variables to check for normality. Only estimates of lichen biomass displayed non-normal distributions, as lichen biomass estimates are count data and generally have a poisson distribution (Campbell and Coxson 2001). To improve the normality of these lichen biomass estimates, I used a natural log transformation and added one lichen gram (y = Log (y+1) to each mean stand biomass estimate to avoid taking the logarithm of zero (Campbell and Coxson 2001).

To avoid problems with multi-collinearity in the regression analyses, independent variables were reviewed to identify correlations that would confound the results. In partial cut forests, the Shannon Structural Diversity Index and stand basal area were correlated ($r^2=0.59$,P<0.0001), as were stand basal area and mean stand foliage volume ($r^2=0.92$,P<0.0001). In un-logged forests, stand basal area was correlated with Shannon Structural Diversity Index ($r^2 = 0.51$,P<0.0001) and Foliage Height Diversity Index ($r^2 = 0.66$, P<0.0001). SSDI and FHDI were also correlated in uncut forests ($r^2 = 0.82$, P<0.0001). In the regression analyses I did not use correlated variables to avoid over-fitting model results.

Results and Discussion

Consistency of Lichen Estimates

I re-assessed estimates of biomass, lower canopy lichen composition and height of the *Alectoria/Bryoria* transition on 328 trees in 16 plots during the course of the sampling (Table 2-2). Re-sampled

were the same as the original scores on 280 trees (85.4%) and within one lichen abundance class on the remaining 48 (14.6%)trees. At individual plots, the lowest consistent estimation was 73% (6 of 22 trees estimated differently) and the highest was 100% (11 of 11 trees estimated consistent). I estimated percent composition of *Alectoria/Bryoria* on the same 328 trees, and I obtained the same result on 170 trees (52%), 123 trees (37.5%) differed by 10%, 33 trees (10%) differed by 20%, and 2 (0.5%) trees by 30%.

Table 2-2. Consistency of lichen biomass, composition and height of the *Alectoria/Bryoria* transition estimations between original and re-assessment plots. Parentheses (*) indicate one standard error about the mean for height estimates.

Biomass Estimates			Alectoria/Bryoria Transition Estimates			
Stand Type	Plot #	Consistent Re- Estimates (%)	Original Ht mean (*)	Check Ht mean (*)	No. Trees	Avg. Height Dif. Mean(Min-Max)
Partial	1	20/23 (87%)	14.4(1.5)	15.6(0.9)	3	1.16m (0.6-2.0)
Partial	4	1/10 (90%)	8.5	7.8	1	0.7m (0.7-0.7)
Partial	6	9/12 (75%)	14.5(0.7)	14.7(0.8)	5	0.5m (0.1-0.7)
Partial	9	3/4 (75%)	10.7	11.0	1	0.3m (0.3-0.3)
Partial	10	3/3 (100%)	1	/	0	1
Partial	11	11/11 (100%)	8.3	7.5	2	0.9m (0.8-1.0)
Uncut	12	22/28 (79%)	12.4(0.8)	12.6(0.9)	8	1m (0.5-1.9)
Uncut	13	15/17 (88%)	12.6(1.1)	13.5(1.3)	8	1.4m (0.4-2.4)
Uncut	14	21/27 (78%)	13.3(2.0)	13.6(1.8)	8	0.7m (0.1-1.4)
Uncut	39	42/45 (93%)	9.3(1.4)	10.0(1.0)	14	1.2m (0.1-2.3)
Uncut	41	37/42 (88%)	12.8(0.9)	12.8(1.5)	6	1.1m (0-3.3)
Uncut	55	24/29 (83%)	13.3(0.7)	12.1(1.3)	5	1.24m (0.2-3.4)
Uncut	81	32/35 (91%)	8.3(1.0)	8.6(1.0)	16	0.6m (0-1.3)
Uncut	91	16/22 (73%)	16.8(2.8)	16.2(1.3)	6	1.43m (0-4.9)
Partial	120	6/7 (86%)	14.2	14.0	1	0.2m (0.2-0.2)
Partial	135	10/13 (77%)	10.1(2.2)	8.5(2.2)	4	1.6m (0.1-2.1)

Overall, *Alectoria/Bryoria* composition on almost 90% (293 of 328) of all trees was re-estimated within 10% or less of the original composition estimates. The largest differences in *Alectoria/Bryoria* composition estimates occurred mainly on trees with low lichen abundance classes (less than class 3) where small, dispersed thalli often made estimating lichen composition difficult.

The mean difference in height of the *Alectoria/Bryoria* transition between original and check plots was less than1.0 metre at 8 of the 15 plots (no transition zone observed at one plot) with the remaining 6 plots having a mean difference less than 1.5 metres (Table 2-2). Large differences in *Alectoria/Bryoria* transition height estimates on individual trees (>1.5 metres) occurred in some plots in uncut forests (plots 41, 55, and 91). In all cases the large discrepancies between original and check estimates were associated with tall, dominant Engelmann spruce (*Picea engelmannii*). On these trees, I often observed a broad transition zone between *Alectoria* and *Bryoria* high in the canopy (>15 metres) that made consistent measurements difficult, particularly when observed from different locations on the ground. Otherwise, variability in the *Alectoria/Bryoria* transition zone between trees at plots was relatively small.

Alectoria and Bryoria in Un-logged Forests

Alectoria biomass in the lower canopy (<4.5 metres) displayed the only clear relationship to forest age or canopy structure in un-logged forests. I fitted a logistic growth model (r^2 adj.=0.62, MSE = 0.465) to explain the increase in *Alectoria* biomass in the lower canopy with age of

the co-dominant tree canopy (Figure 2-2A). Lower canopy *Alectoria* biomass increased rapidly in forests less than 100 years and reached its maximum abundance as age of the co-dominant canopy reached ages greater than 125 years old. This maximum *Alectoria* abundance in forests at approximately 100 years of age coincides with results from Arsenault et al. (1997) that show *Alectoria* to accumulate biomass on branches up to 90 year after establishment, after which the rate of accumulation declines. The increase in *Alectoria* biomass with forest age is also consistent with other research where the highest *Alectoria* biomass accumulations are associated with old forests (e.g. > 100 years old; Lessica et al. 1991, Esseen et al. 1996).

The increase in lower canopy *Alectoria* biomass with forest age may be largely attributed to changes in structural conditions associated with older forest stands. The Foliage Height Diversity Index (FHDI) proved to be the structural variable most significantly related to lower canopy *Alectoria* biomass (Figure 2-2B). *Alectoria* biomass increased with higher FHDI values ($r^2=0.51$, P=<0.001). However, age also played a role as lower canopy *Alectoria* biomass achieved greater accumulations in older forests with higher FHDI values ($r^2=0.66$, P=<0.001). *Alectoria* biomass was also higher in older forests with greater stand basal area ($r^2 = 0.61$, P=0.0001).

In contrast, *Bryoria* achieved high biomass accumulations in the lower canopy stratum (<4.5 metres) of intermediate aged forests (70-100 years old). With the exception of young forests (<50 years old), which contained low lichen biomass, high *Bryoria* biomass estimates in the lower canopy of some intermediate aged stands (50-100 years) resulted in high total lichen biomass estimates (40-80 kg/ha) for some stands.

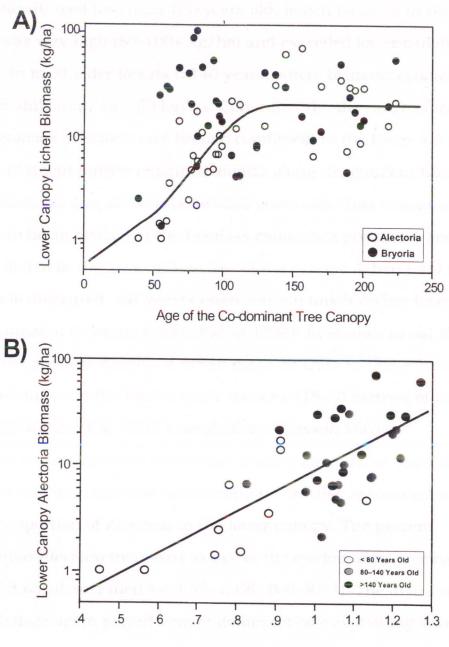
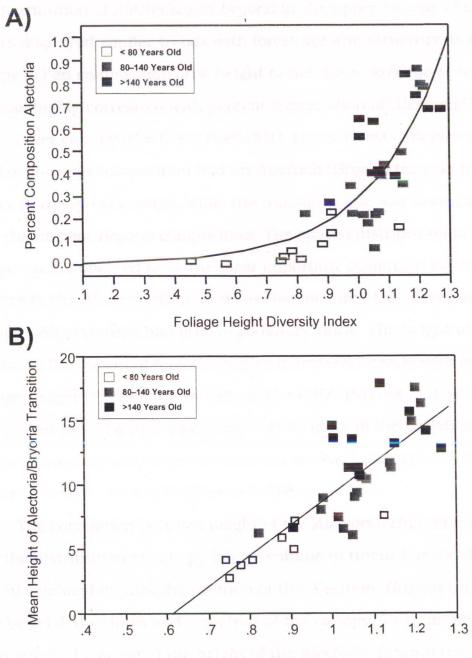




Figure 2-2.Comparison of lower canopy lichen estimates with age of the codominant canopy (A) and the relationship of lower canopy *Alectoria* biomass with Foliage Height Diversity Index (FHDI) values and forest age (B) in un-logged ESSF forest stands. (A) shows lower canopy *Alectoria* biomass increasing in older forests (In (*Alectoria*) = $3.05/1+72.7*e^{(-0.56*age)}$, r² = 0.64, MSE = 0.46) while (B) illustrates the linear increase of *Alectoria* biomass with higher FHDI values (In (*Alectoria*) = -2.123+4.327x FHDI, r² = 0.51, MSE = 0.596). In two stands aged less than 100 years old, lichen biomass in the lower canopy was very high (80-100+ kg/ha) and exceeded lower canopy biomass in most older forests (>140 years) where biomass estimates ranged mainly from 45 – 90 kg/ha. Consequently, the range of total lichen biomass (*Alectoria* and *Bryoria* combined) in the lower 4.5 metre stratum of uncut forests remained similar along the gradient from intermediate aged to old forests (50-200 years old). This conclusion appears to be an artifact of the biomass estimation procedure accounting for only lichen in the lower 4.5 metres of the canopy. When total tree biomass is measured, old forests (Selva 1994). In studies in old ESSF forests, the greatest density of lichen mass on trees in these forests is often distributed in the mid to lower sections (15-20 metres) of the tree canopy (Edwards et al 1960, Campbell and Coxson 2001).

The same structural conditions of older forests that appear to allow for higher *Alectoria* biomass accumulations are also associated with a greater proportion of *Alectoria* in the lower canopy. The percent composition *Alectoria* increased as age of the co-dominant tree canopy and stand basal area increased (r^2 = 0.66, *P*<0.0001). The distribution of canopy foliage again played a more dominant role explaining lower canopy *Alectoria/Bryoria* composition than stand basal area or even forest age. Percent composition of *Alectoria* increased exponentially with increasing FHDI values (r^2 = 0.67, *P*<0.0001) (Figure 2-3A) and with greater age of the co-dominant canopy and increased FHDI values (r^2 = 0.74, *P*<0.0001).



Foliage Height Diversity Index

Figure 2-3. Relationship of lower canopy *Alectoria/Bryoria* composition (A) and height of the *Alectoria/Bryoria* transition line (B) to forest age and distribution of canopy foliage (FHDI index). Lower canopy *Alectoria* composition (A) increased exponentially with higher FHDI values (%*Alectoria* = 0.0046 x EXP (4.14 x FHDI), $r^2adj = 0.63$). Height above ground of the *Alectoria/Bryoria* transition line increased in un-logged forests with higher FHDI values (Height of A/B transition = -14.942 + 24.22 x FHDI, $r^2 = 0.67$, *P*<0.0001).

The distribution of Alectoria and Bryoria in the upper canopy of uncut forests displayed similar trends with forest age and structure as lower canopy lichen composition. The height of the Alectoria/Bryoria transition line was highly correlated with percent composition of Alectoria/Bryoria in the lower canopy ($r^2 = 0.81$, *P*=<0.001). Lower forest canopies with greater Alectoria composition had an Alectoria/Bryoria transition line higher in the forest canopy, while the transition line was lowest in forests with the highest Bryoria composition. The spatial distribution of the foliage again appeared to be the most important structural variable relating to the Alectoria/Bryoria transition as stand basal area and total canopy foliage volume had little explanatory value. The height of the transition line in uncut forest canopies increased linearly with greater Foliage Height Diversity Index values ($r^2 = 0.67$, P<0.0001). Forest age also played less of a role explaining slightly more of the variation in height of the Alectoria/Bryoria transition increase with greater FHDI values ($r^2 = 0.77$, P< 0.0001)(Figure 2-3B).

V

The correlation between height of the *Alectoria/Bryoria* transition and the distribution of canopy foliage volume in uncut forests (described by FHDI values) implies the position of the *Alectoria/Bryoria* transition may be related to form and structure of the canopy. To examine this relationship, I compared the height of the *Alectoria/Bryoria* transition line with the distribution of foliage volume above the forest floor (Figure 2-4). Most sampled forests displayed a 'bottom-heavy" distribution of canopy foliage with a sudden sharp decline in foliage volume in the mid to upper canopy. Older forests (>140 years) often contained a greater amount of foliage volume evenly distributed in the lower portion of the canopy below the point where canopy foliage volume rapidly declines

compared to intermediate and younger aged forests (<100 years) (Figure 2-4). I expected the transition to *Bryoria* in the upper canopy to be associated with this decline in forest canopy foliage volume as the upper forest canopy is exposed to greater solar radiation and moisture evaporation. In fact, the position of the *Alectoria/Bryoria* transition line in old forests was associated with this point of rapid decline in foliage volume in the upper canopy (Figure 2-4). The location of the *Alectoria/Bryoria* transition line in young forests also appeared to be correlated with the rapid decline in foliage volume, but the position of the transition relative to a sudden shift in canopy foliage density was less apparent (Figure 2-4).

The significance of canopy foliage distribution as the variable most influencing *Alectoria* biomass, lower lichen canopy composition, and height of the *Alectoria/Bryoria* transition may largely be due to the forest structure characteristic of many high elevation ESSF forests. Old high elevation ESSF forests typically portray a relatively open stand structure with many small canopy gaps and clumpy distribution of tree stems given the nature of disturbance events and patch dynamics (Veblen 1986, Antos and Parrish 2002). In addition, trees in these forests have relatively thin crown profiles compared to tree crowns of other forests (Antos and Parrish 2002) that could allow solar radiation and wind to penetrate deep into the lower canopy. However, many old high elevation forests contain a significant sub-canopy of suppressed shade tolerant stems (Varga and Klinka 2001) resulting in a "bottom-heavy" distribution of foliage (Parker 1997) such as 1 observed.

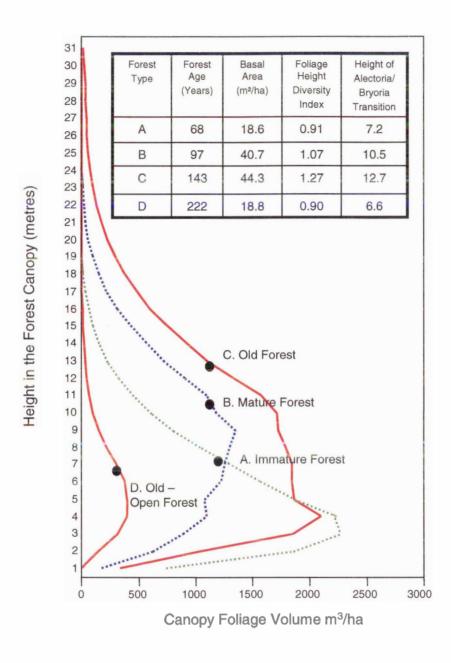


Figure 2-4. Comparison of the mean height of the *Alectoria/Bryoria* transition to the distribution of foliage through the forest canopy in different aged uncut ESSF forest stands. Dots represent the location of the *Alectoria/Bryoria* transition in each stand relative to the distribution of foliage.

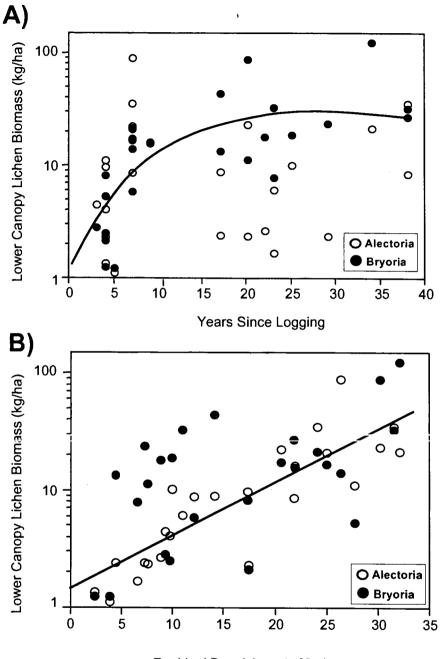
This multi-layering of canopy foliage, especially typical of older forests, results in a dramatically different three dimensional distribution of canopy foliage (Stewart 1986, Spies and Franklin 1989) and under-story light conditions than even aged forests with similar foliage volume concentrated in one layer (Van Pelt 1995, Van Pelt and Franklin 2000). Coupled with the height of some tall trees and relatively low sun angle in the sky typical of forests in northern latitudes, these conditions may prevent a great deal of solar radiation from reaching the forest understory (Van Pelt and Franklin 2000).

The influence of canopy foliage on light transmittance may produce a gradient in light conditions or 'lumicline" (Parker 1997) along the vertical axis of the forest canopy. The heavy concentration of foliage in the lower part of the canopy produces a lower canopy zone of dim-light giving way rapidly to mixed and variable light conditions in the upper canopy, then very open light conditions at the very top of the canopy (Parker 1997). Wind speed and turbulent airflows are further moderated by an increase in canopy foliage density in the lower canopy (Geiger 1965). Presumably, this multi-layered canopy structure found in many older ESSF forests limits solar radiation and wind evaporation, allowing moisture and humidity to persist, providing conditions that allow Alectoria to prevail in the lower canopy. Moderated wind speeds may further allow Alectoria thalli to grow to greater length and achieve greater biomass accumulation than in more open forests. Under such conditions Alectoria should continue to colonize the upper canopy until held in check by unfavorable environmental conditions as the upper canopy foliage thins and exposure increases (Campbell and Coxson 2001). The important influence of canopy structure on lichen distribution is

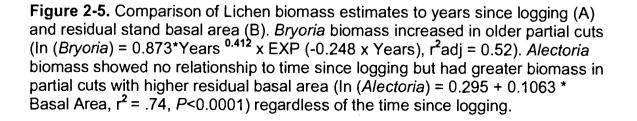
particularly illustrated in one old, open forest stand (>200 years old, 18.8 m²/ha) where visibly lower foliage volume and canopy layering most likely had less influence on canopy climate (Figure 2-4, Stand "D"). As a result, in this old forest stand lower canopy *Bryoria* composition was very high (>80%) and the height of the *Alectoria/Bryoria* transition was quite low (<7 metres). Old, open sub-alpine parkland stands at higher elevations where *Bryoria* dominate the canopy profile (Antifeau 1987, Goward 1998) corroborates the conclusion that canopy-mediated environmental conditions often dictate the relative distribution of *Alectoria* and *Bryoria*. These observations suggest the influence of canopy foliage density and spatial distribution on canopy microclimate plays a large role on lichen distribution patterns when lichen succession (dispersal and colonization) may not be limiting such as in old forests.

Alectoria and Bryoria in Partial Cut Forests

In partial cut forests, strong relationships existed between lichen estimates and time since logging and remnant forest structure. Partial cut forests showed a dramatic increase in lower canopy *Bryoria* biomass after logging, with as much as a ten-fold increase in biomass in forests with similar residual structure in as little as 15-20 years (Figure 2-5A). *Bryoria* biomass appeared to accumulate quickly after logging, for about the first 20 years, however, the rate of increase in *Bryoria* biomass appeared to decline in partial cuts older than 15 years (r^2 = 0.54, *P*<0.001) reaching maximum biomass levels within 25-30 years.



Residual Basal Area (m²/ha)



The rapid increase in *Bryoria* mass is consistent with Arsenault et al. (1997) who noted that growth rates of *Bryoria* on new branches declined after 30 years. Some species of *Bryoria* may actually act as 'pioneers' that colonize quickly and accumulate rapidly on new growth.

The increase in *Bryoria* biomass in partial cuts may be largely due to the retention of large green trees after logging. Green tree retention has been shown to play a critical role in retaining lichen mass and species diversity in managed forests (Neitlich and McCune 1997, Peck and McCune 1997, Sillet et al. 2000). Bryoria biomass accumulations were greatest in partial cuts with higher residual stand basal area, though the rate of biomass accumulation was slowest in partial cuts with higher basal area retention $(r^2 = 0.90, P < 0.0001)$. However, partial cuts with very low green tree retention ($<10m^{2}/ha$), while apparently creating a micro-environment suitable for Bryoria establishment, result in few large retained trees with significant lower canopy biomass and many small trees incapable of high lichen accumulations. As a result, while the rate of Bryoria biomass accumulation appeared to be greatest in these stands, biomass levels after even 20 years were still relatively low (<10 kg/ha). In contrast, some older partial cut forests with higher basal area retention (10-20m²/ha) showed very high *Bryoria* biomass accumulation. Often, total stand biomass in the lower canopy of older partial cuts exceeded that of older natural forests, while stem density was much lower. Since Bryoria does not appear to be limited by dispersal (Goward, 2004b) the availability of suitable substrate provided by larger older trees allows for significant Bryoria accumulations that typically would not be found on smaller, younger trees in immature forests or even-aged artificially regenerated forests (Esseen et al, 1996). The only limitation to

Bryoria growth may be thalli tensile strength (Goward, 1998), limiting thalli length as *Bryoria* often obtain thick curtains on lower branches of large trees in partial cuts within 15 years following harvest.

Unlike Bryoria, Alectoria biomass in partial cut forests displayed a strong correlation only to remnant forest structure and not time since logging. Alectoria biomass increased linearly with greater residual stand basal area ($r^2=0.74$, P<0.0001) and Shannon Structural Diversity Index $(r^2 = 0.63, P < 0.0001)$ regardless of the time since the stand was logged (Figure 2-5B), suggesting retention of large trees is important to allow Alectoria biomass to persist in the post harvest tree canopy. Recent partial cuts with heavier removals ($<10m^2$ /ha retained) contained little Alectoria biomass immediately following logging. In addition, old partial cuts with low retention levels and few large trees also showed little Alectoria biomass. Thus, low retention levels may exclude Alectoria from parts of the forest canopy with no large remnant trees for long periods given Alectoria may be limited by dispersal (i.e. Sillett et al. 2000). The increase in lower canopy *Bryoria* biomass in many of the partial cut forests after logging resulted in high percent composition of lower canopy Bryoria. Lower forest canopy Bryoria composition increased steadily with vears since logging ($r^2 = 0.64$, *P*<0.0001) from compositions similar to pre-harvest un-logged forests (<50%) reaching a peak (>80%) within 20 years (Figure 2-6A). The oldest partial cuts (>30 years old) showed a slight decline in the relative composition of *Bryoria*, primarily in partial cuts with higher basal area $(>20m^2/ha)$. Differences in lower canopy Bryoria composition in partial cuts was similarly related to residual forest structure.

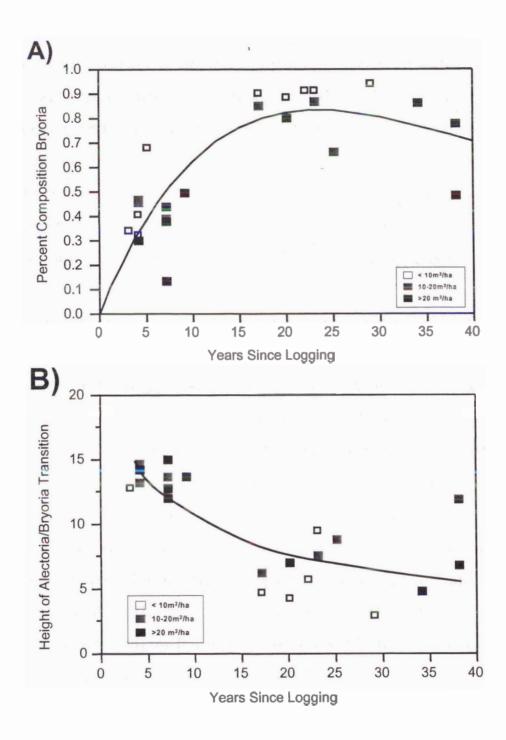


Figure 2-6. The lower canopy of older partial cuts showed increased *Bryoria* composition (A) due to accumulation of *Bryoria* mass (%*Bryoria* = 0.096 x Years 0.999 x EXP (-0.042 x Years, $r^2adj = 0.64$). The height of the *AlectorialBryoria* transition zone (B) also descended lower in the tree canopy in older partial cuts (height of A/B transition = 19.11 + -3.73 x Log (Years), $r^2adj = 0.72$)).

Using multiple regression, I applied a quadratic polynomial to represent the non-linear increase of *Bryoria* composition over time with residual stand basal area (Figure 2-6A). *Bryoria* composition increased with time since logging and in partial cut forests with lower stand basal area ($r^2 =$ 0.80, *P*<0.0001).

As Bryoria composition increased in the lower canopy of partial cut forests in the years following logging, the height of the Alectoria/Bryoria transition line also descended lower in the forest canopy. As with unlogged forests, percent composition of lower canopy Bryoria was correlated to the height of the Alectoria/Bryoria transition ($r^2 = 0.85$, *P*=<0.001). Recent partial cuts displayed lower canopy *Bryoria* composition and transition similar to that of un-logged forests while Bryoria composition reached as much as 85% and the Alectoria/Bryoria transition line descended as low as 5-7 metres in partial cuts within 20 years after logging. The height of the Alectoria/Bryoria transition in partial cuts was also related to remnant basal area and the Shannon Structural Diversity Index (SSDI). The height of the Alectoria/Bryoria transition descended in the tree canopy in older partial cuts and in partial cut stands with lower remnant basal area ($r^2 = 0.80$, P<0.0001; Figure 2-6B) or fewer large trees (low Shannon Structural Diversity Index values; r2= 0.80, *P*<0.0001).

Unlike natural forests, the distribution of canopy foliage did not play a strong role in partial cut forests as the position of the *Alectoria/Bryoria* transition line. In forests which were partial cut in the last 10 years the *Alectoria/Bryoria* transition was not correlated with a shift in the distribution of canopy foliage as it was in uncut forests (Figure 2-7).

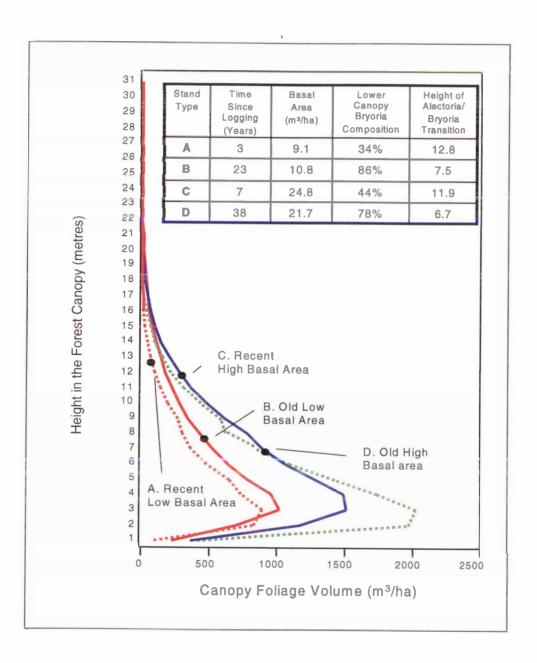


Figure 2-7. Comparison of the mean height of the *Alectoria*/*Bryoria* transition to the distribution of foliage through the forest canopy in partial cut ESSF forest stands.

Rather, the Alectoria/Bryoria transition line maintained a position in the canopy similar to pre-harvest conditions (old uncut forests) at approximately 12-15 metres above ground. However, within 20 years after logging the position of the transition line appeared to descend to a similar position above ground associated with the abrupt transition in upper canopy foliage volume as in uncut forests (Figure 2-7). Old partial cut forests with similar post harvest basal area and canopy foliage distribution as recent partial cuts separated only by time displayed a lower position of the Alectoria/Bryoria transition.

The combined effect of time after logging and the structure of the residual tree canopy on lichen community abundance and distribution in partial cut forests has not been well acknowledged in the literature. Too often, studies are limited to reporting immediate post-logging losses in lichen biomass to summarize the effects of partial cutting treatments, when in fact lichens are relatively slow to respond to changing environmental variables (Sillet and Neitlich 1996). For changes in the lichen community to be observed lichen require time to respond to altered canopy conditions, so may show a delayed response to partial cutting treatments. Even in the short time period captured in this retrospective study, dramatic shifts in *Alectoria* and *Bryoria* abundance, and distribution are evident. As a result, I identify three transitional periods in the post-logging dynamics of *Alectoria* and *Bryoria* biomass and distribution. These represent a conceptual model for *Alectoria* and *Bryoria* response to partial cutting in high elevation ESSF forests.

1) Lichen Loss - The initial and most obvious shift, typically observed in post-logging assessments, is the loss in arboreal lichen abundance immediately (within the first 1-3 years) following logging.

Lichen loss is directly related to the reduction in mature lichen-bearing trees (Stevenson et al. 1994, Esseen et al. 1996). Smaller disturbances in the canopy, such as low basal area, individual tree removal may result in little change in overall canopy biomass and a brief period when losses occur. Indeed, few losses of lichens on residual stems in high retention harvests have been reported in post-harvest assessments (Stevenson et al. 2001, Stevenson and Coxson 2003). However, low green tree retention levels will result in large initial losses in biomass from the immediate loss of large lichen bearing trees. Losses in low green tree retention partial cuts may continue for many years due to wind scouring, desiccation or photoinhibition in remaining lichens (Esseen et al. 1996, Esseen and Renhorn 1998).

2) Colonization and Biomass Accumulation - This stage can be characterized by a relatively rapid colonization and accumulation of *Bryoria* in the partial cut stand. The magnitude and duration of the *Bryoria* response is dictated by the level of tree removal (Stage 1). Low levels of tree retention will see greater *Bryoria* colonization on remnant trees as environmental conditions favor *Bryoria* establishment and quick accumulation rates account for significant increases in biomass within relatively short periods (i.e.15 – 20 years post-logging). Such dramatic changes are clearly illustrated in my data, where partial cuts with high levels of removal logged 15-30 years ago show marked increase in *Bryoria* biomass, greater *Bryoria* composition and lowering of the *Alectoria/Bryoria* transition line. Older partial cuts exhibit a higher proportion of *Bryoria* (>80%) and significant accumulations of up to 85-125 kg/ha in the lower canopy compared to estimates of 0.2 – 1.25 kg/ha of *Bryoria* in recent (<5 years), low retention partial cuts (<10m²

basal area/ha remaining). In these low retention partial cuts the height of the *Alectoria/Bryoria* transition dropped as low as 5 metres. Rominger et al. (1994) presented similar findings, noting no difference in lichen biomass in partial cuts 10 years after harvest compared to uncut forests, but the composition of *Bryoria* increased, possibly offsetting a loss of *Alectoria* following harvest.

The duration of this period where *Bryoria* begins to dominate the lower canopy lichen community and biomass may last decades until the forest canopy regenerates and lower canopy conditions again favor *Alectoria* growth. Alternatively, partial cuts with a high retention level may see very little *Bryoria* accumulate in the lower canopy as the minor change in climatic conditions are not suitable for *Bryoria* establishment. *Bryoria* presence in this transition period may also last a short time, as pre-logging structural conditions may be quickly recovered within the largely intact forest stand of low removal partial cuts.

3) Recovery - This stage is characterized by the recovery of an *Alectoria* dominated lower canopy as partial cut forests grow back and lower canopy conditions begin to resemble that of older natural forests. The timing of this transition is largely dependent on the level of removal (Stage 1) and the duration of Stage 2. These factors determine the level of growth in retained stems and regeneration success following logging that will drive recovery of the forest canopy. Evidence of this recovery period is illustrated by the linear increase in *Alectoria* biomass with increased stand basal area regardless of the time the stand was logged. One old partial cut stand (38 years old) displayed strong tree growth in residual trees and basal area recovery (currently estimated > $30m^2/ha$) since logging, considering the high level of removal most likely implemented at

time of logging (estimated 10m²/ha or less retained basal area). This older partial cut forest also displayed the highest *Alectoria* composition of any partial cut stand with the height of the *Alectoria/Bryoria* transition line at almost 12 metres above ground. These results suggest tree growth at this site may be starting to alter the lower canopy environment to favour *Alectoria* establishment and growth.

Despite the typical association of Alectoria as an old-growth species, some evidence suggests Alectoria may persist in partial cuts and even continue to grow and colonize on new growth following harvest. Esseen and Renhorn (1998) observed that Alectoria abundance recovered within 30 metres from clearcut edges within 15 years after logging, even surpassing initial estimated abundance following an initial short-term loss. This suggests that Alectoria may respond to an increase in solar radiation due to removal of the tree canopy. Such a response by an "oldgrowth associated lichen" is not unheard of. Sillett et al. (2000) found the cyanolichens Lobaria oregana and Lobaria pulmonaria survived and grew relatively well in open and stable habitats, and that the habitats and substrates of old growth forests do not appear to be essential for establishment and accumulation in a forest canopy. Rather, these lichens were limited by a source of propagules, leading these researchers to believe dispersal was most limiting. In most of the partial cuts I sampled, Alectoria appeared to persist in many of the larger trees retained after logging, thus these trees may be an important source of propagules for Alectoria establishment as the partial cut forest canopy grows and recovers.

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Chapter 3 - Using a Stand Simulation Model to Estimate Arboreal Lichen Response to Partial Cutting Treatments in High Elevation Engelmann Spruce-Subalpine Fir Forests.

Introduction

Clearcut logging in the interior of British Columbia through the 1970's to early 1990's has prompted concern about the depletion of mountain caribou winter habitat (Stevenson and Hatler 1985, Stevenson et al. 1994). The primary concern has been the loss of mature lichenbearing trees in old mid-high elevation Interior Cedar Hemlock (ICH) and Engelmann spruce-Subalpine fir (ESSF) forests that provide lichen forage for caribou during the winter (Stevenson and Hatler 1985, Stevenson et al. 1994, 2001). Replacement of old forests with even-aged, managed forests on short rotation cycles potentially compounds the direct losses of lichens through logging by reducing the amount of time that mature forest conditions exist, thus inhibiting the dispersal of lichen propagules, altering microclimatic conditions and substrate availability for lichen colonization and growth (Esseen et al. 1996). Consequently, the continued loss of old forest conditions may limit the ability of future managed landscapes to provide adequate forage lichens to sustain caribou populations threatened by other factors (i.e. predation, disturbance; BC Ministry of WLAP 2002).

To maintain arboreal lichen forage while allowing continued logging in caribou winter ranges, two selection silviculture systems, Single Tree Selection (STS) and Group Selection (GS) have been implemented by forest managers since the early 1990's (Stevenson et al. 1994). Both STS and GS silviculture systems are designed for one-third (33%) volume removal at each entry on a three-pass logging system over

a 240-year rotation with 80 years between logging entries (Stevenson et al. 1994). The STS system removes individual trees from across the diameter distribution or by imposing a minimum diameter cutting limit while the Group Selection system removes trees in small patches, generally from 0.1 to 1.0 hectares with an average size of 0.5 hectares. Both systems were designed to retain at least two-thirds of the harvest area in mature (> 80 years old) and old (>140 years) forest as either continual forest cover or in retained patches throughout the harvest rotation. Therefore, low removal systems are expected to maintain sufficient lichen biomass for caribou foraging immediately following logging (Stevenson et al. 1994, Armleder and Stevenson 1996).

The long-term efficacy of these low removal selection silviculture systems to effectively maintain caribou lichen forage remains largely untested as their use dates back to only the last 10-12 years. While low removal silviculture systems may provide a short-term solution to loss of caribou foraging habitat, their use may create indirect habitat and timber management issues that are not immediately evident, including:

1) The continual use of a low removal, multiple entry logging pass approach, without a significant reduction in the rate of cut, may lead to the proliferation of road networks and landscape fragmentation (Crow and Gustafson 1997). Extensive road networks may account for greater disturbance to caribou through increased human access to high elevation caribou habitats (Stevenson and Hatler 1985, Simpson and Terry 2000). In addition, the accelerated rate of landscape fragmentation and the interspersion of early seral habitat (particularly patch cutting at large scales) may increase predation on caribou as alternative prey (e.g.

moose *Alces alces*) becomes more numerous and widely dispersed through high elevation caribou ranges (Seip 1992, BC Ministry of WLAP).

2) Successful regeneration of planted seedlings in silviculture system trials in these high elevation forests has been shown to decrease in low removal treatments such as in single tree selection and patch cuts with small openings (e.g. 0.1 ha openings; Newsome et al. 2000) where residual canopy cover intercepts light penetration and prevents warming of the soil (Lajzerowicz et al. 2004). In addition, some selectively cut blocks have experienced significant regeneration failure due to frost damage and defoliation from spruce budworm ingress from the upper canopy (Bieber, 2002).

3) Loss of large upper canopy trees from insect mortality may result in periods when low removal partial cuts are unable to act as a future lichen forage source (Coxson et al. 2003) or to provide subsequent logging entries. Periodic intense attacks of western balsam bark beetle (*Dryocoetes confusus* Swaine) or spruce bark beetle (*Dendroctonus rufipenis* (Kby.)) are common in these forests and may kill a large component of overstory spruce and fir (e.g. Parish et al. 1999) that contain a disproportionately greater amount of lichen biomass in a stand (Campbell and Coxson 2001, Coxson et al. 2003) and a larger proportion of standing timber volume (Lewis, 2003). Thus, loss of a component of large trees to a higher severity insect attack may result in a period of time where a stand is dominated by small releasing advanced regeneration with low timber volume and low available lichen biomass.

In response to these management concerns, Retention silviculture systems have recently been proposed for use in caribou winter habitats (Bieber 2002, Lewis 2003, Kamloops LRMP 2004). The proposed

Retention silviculture system will use higher basal area removal (60-80% basal area removal) on a single logging entry with a short rotation period (100-120 years). The short-term focus of the Retention system is on timber management objectives, primarily greater up-front wood utilization on the site and increased regeneration success. This focus on timber objectives is expected to result in an immediate loss of a substantial amount of large, mature lichen-bearing trees and loss of usable foraging conditions for caribou immediately following logging.

The long-term habitat objective of a high basal area removal Retention system is to create climatic conditions in the lower canopy of the partial cut stand suitable for Bryoria establishment and retain enough tree substrate for biomass accumulation. This objective will essentially "descend" the level of maximum Bryoria accumulation, often found in the upper canopy of old forests where suitable climate and branch substrate exist (Campbell and Coxson, 2001), to a position in the lower canopy for caribou to forage on standing trees, approximating forage conditions available in more open or exposed natural forest stands or edge environments. Examples of some older low basal area partial cuts (< 20 m²/ha retained) show remarkably high lower canopy Bryoria biomass accumulations within as little as 10-20 years after logging (e.g. Rominger et al. 1994, Lewis 2001, 2004). In many cases, lower canopy biomass totals for a stand are equal to or can exceed that of old forests that contain a lower density of large trees (Antifeau 1987, Miller et al. 1999, Lewis 2004).

The rationale supporting the use of Retention silviculture systems is the apparent preference for *Bryoria* as forage displayed by caribou (Rominger et al. 1996). Caribou winter migration patterns associated

with snow condition and depth suggest this preference may be a physiological adaptation to habitats with greater *Bryoria* lichen availability such as open ESSF Parkland forests and natural edge environments. Recent recorded observations support this rationale as high intensity caribou foraging behavior has been observed on *Bryoria* biomass accumulations in older high removal partial cut forests, along old edges and larger residual trees in cut blocks (Lewis 2004, unpublished data)

For abundant lower canopy *Bryoria* accumulations to develop requires a combination of three factors; a climatic environment that favors *Bryoria* growth, older tree branch substrate, and time to establish and grow (Lewis 2004). The combination of these three factors must be present simultaneously and remain present for a sufficient time span to provide suitable *Bryoria* biomass accumulations for caribou foraging. Given that lichen grow slowly and time is required to observe a response, information is needed to estimate the partial cutting treatments that provide the ideal combinations of these factors to provide suitable *Bryoria* accumulations for caribou foraging.

The goal of this study was to use a stand model to simulate conditions of high elevation ESSF forests to explore the long-term effects of various partial cutting treatments on the suitability of the lower canopy environment (from 1-4 metres above ground) for lichen. My first objective was to identify the canopy light environment associated with the distribution of the main forage lichens *Alectoria sarmentosa* and *Bryoria*. My second objective was to explore the suitability of the lower canopy light environment for *Alectoria* and *Bryoria* under a range of partial cutting scenarios over a simulation period of 100 years. I

conclude by discussing the strategy of arboreal lichen forage management with other management implications (i.e. regeneration success) that result from various partial cutting systems.

Methods

Stand Model Description

I used the TASS model (Tree And Stand Simulator; Mitchell 1975) to simulate ESSF forest conditions. TASS is a spatially explicit, individual tree, distance dependent, growth and yield model that simulates tree growth and interactions in three-dimensional space (Mitchell 1975, Mitchell and Cameron 1985, Cameron 2004). TASS simulations are generally started from bare ground conditions such as those created by a stand initiating disturbance (i.e. wildfire or logging) or based on conditions of existing stands where spatial coordinates of stems are defined. TASS simulates the crowns and stems of trees from functions derived from detailed measurements of individual trees. Tree mortality occurs as neighboring competitors overtop trees or crown size becomes too small relative to tree size. Mortality rates and overall stand statistics are calibrated to conform to the yields of re-measured plots, with particular emphasis on spacing and thinning trials (Cameron 2004). The user can further modify tree growth and mortality as external environmental factors (site quality, age, disease, insects) are introduced to the stand simulations. In addition, the model can also respond to a range of silviculture treatments introduced by the user (Mitchell 1975).

TASS provides detailed predictions of stem and crown attributes as well as summaries of stand statistics.

Model Calibration for ESSF stands

Cameron (2004) outlined methods to calibrate the TASS model to approximate growing conditions in high elevation ESSF forests for an analysis of stand structure and habitat conditions. He describes the procedure as a meta calibration of the model since little information exists for individual tree conditions from permanent sample plots in ESSF forests. Thus, tree growth and yield coefficients were not available for either Engelmann spruce (*Picea engelmannii*) or subalpine fir (*Abies lasiocarpa*) in the operational version of the model, TASS II. However, inventory data suggest that relative tree size and density relationships for Engelmann spruce and subalpine fir is similar, and that basic yield relationships for both are similar to white spruce (*Picea glauca*), although growth is slower. Thus, Cameron (2004) based yield relationships for both Engelmann spruce and subalpine fir on growth and yield coefficients of white spruce from permanent sample plots from BC, Alberta and Ontario (Mitchell and Cameron 1985).

To more adequately represent tree canopy architecture within ESSF forest stands, Cameron (2004) modified crown dimensions for white spruce to portray the more narrow dimensions of Engelmann spruce and subalpine fir in ESSF forests. Crown profile coefficients for Engelmann spruce and subalpine fir were approximated from 70mm air photos. Crown widths derived from these coefficients were then verified

based on crown width as a function of crown height from various ESSF forest data sets.

Since TASS was originally developed to model growth and yield of second-growth coastal Douglas-fir forests, regeneration issues specific to ESSF forests required special considerations in the model. To maintain the "clumpy" tree distribution typical of ESSF forests, Cameron (2004) allocated patches of ground as unavailable for seedling occupation to account for micro-sites unsuitable or limiting to tree growth including; rock, open water, excessively wet, or cold micro-sites. Thus, he created an 'eligible grid' for the stand from which trees could germinate. The locations of the eligible grid from which trees can germinate are based on the spatial coordinates from a different ESSF research site at Adams Lake (Figure 3-1) from Antos and Parish (2002). The eligible grid results in approximately 40% of the area of the stand unavailable for seedling germination.

Simulation of Baseline Stand Conditions

I used a simulated stand developed by Cameron (2004) to act as a "baseline condition" for the partial cutting scenarios. He used TASS to generate forest structural conditions of an old ESSF forest based on spatial coordinates and tree mensuration information from an ESSF research site near Sicamous. British Columbia (Parish et al. 1999). He constructed a simulated "stand" of 125 x 125 metres as the basic unit to which each partial cutting treatment was applied. The simulated stand was intended to approximate a 150-year old ESSF single cohort stand initiated from a stand-replacing disturbance.

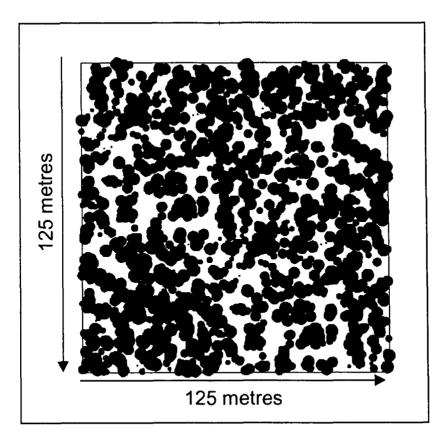


Figure 3-1. An aerial view of the spatial pattern of trees from four 50x 50 metre plots from the Antos and Parrish (2002) ESSF research site merged into one 125 x 125 metre plot. Tree information and spatial coordinates from this stand were used to derive the 'eligible grid' for tree regeneration in the TASS generated 'control' stand.

The stand was constructed from bare ground conditions by introducing an initial cohort of 2000 trees per hectare over a 10-year period onto the eligible grid of tree locations. Regeneration is introduced at a ratio of 80/20 subalpine fir to Engelmann spruce ratio to maintain the species composition of these forests. Since mortality of individual stems in TASS results strictly from overtopping and shading from larger overstory crowns (Mitchell 1975), successful regeneration under the canopy of large trees is limited. Such limitations to tree growth under a tree canopy is somewhat unrealistic in ESSF forests that often have a contingent of very shade tolerant subalpine fir advanced regeneration that can survive and grow in very low light conditions next to larger trees (Knapp and Smith 1982). To improve the potential for germinates to survive, recurring regeneration were introduced after 50 years to represent the release of advanced regeneration. The recurring regeneration was germinated at700 randomly located potential eligible tree location "clusters" per hectare where a new tree was germinated in each "cluster" every decade.

For the analysis I needed to assign lichen condition estimates to the baseline condition stand. Since the tree information used to derive the TASS forest stand was outside the North Thompson study area, I verified that starting forest conditions were consistent with similar measured old forest stands in that study area. Stand summary information from the Parrish et al. (1999) Sicamous ESSF research site show forest conditions fall within a similar range of conditions of at least four older sample forest stands from the North Thompson study area (Table 3-1). **Table 3-1.** Comparison of forest age, structure and lichen estimates between the ESSF research site (Parish et al. 1999) used to derive the TASS generated baseline stand and four sampled un-logged forests from Lewis (2004). Lichen composition estimates are only for the lower 4.5 metres of the forest canopy.

Stand Information	P et al. (1999)	Stand #5	Stand #20	Stand #25	Stand #31
Forest Age	150	143*	193*	155*	169*
Basal Area (m²/ha)	34.4	44.3	40.8	42.6	44.1
Mean Tree Height (metres) ¹	1	19.5	16.4	16.2	17.1
Mean Tree Diameter (metres) ¹	1	28.8	27.4	23.9	28.9
Stems/hectare ¹	442	600	583	817	517
Foliage height Diversity Index	1.19	1.27	1.05	1.15	1.19
Lichen Estimates					
Alectoria mass (kg/ha)	1	61.6	27.2	70.6	29.5
Bryoria Mass (kg/ha)	1	29.2	16.3	14.5	10.3
Percent composition Alectoria	65%	68%	63%	83%	74%
	(57-73%)				, •
Height of Alectoria/Bryoria	`14.2 <i>´</i>	12.7 (1.3)	13.5 (1.1)	13.1 (1.1)	15.6
Transition	(1.1)	. ,	. ,	、	(1.1)

(*) Indicates forests where ages are derived from mean values from six co-dominant trees aged in each stand, while the age of the Parish stand is based on the approximated time since the last major disturbance (Cameron 2003). (¹) Mean tree height and diameter values and stems/ha are for trees greater than 12cm. diameter in the Lewis (2004) stands while values for the Parish et al. (1999) stand are for live trees greater than 17.5 cm Dbh only. Values in parentheses indicate standard deviations.

Partial Cutting Simulations

I used a factorial design to simulate a range of partial cutting scenarios that encompass existing guidelines for selection silviculture systems and proposed retention silviculture systems in caribou habitat. The factorial design includes four treatment types including one single tree selection, and three group selection with 25, 50 and 100 metre opening sizes at 20, 40 60 and 80 percent removal levels (Figure 3-2). The removals reduced the stand basal area of 44.9 m²/ha of the TASS baseline condition to 35.9, 27.9,18.0 and 9.0 m²/ha for the 20,40, 60 and 80% removal respectively. Each of the sixteen combinations of removal and treatment were separately applied to the baseline condition stand. As a result, only one (N=1) example of each treatment and removal option exists. Each option was simulated for 100 years to approximate the lower rotation period limit for clearcut or low retention systems and allows for a brief insight into forest conditions prior to the second-logging pass (after 80 years) in selection silviculture treatments.

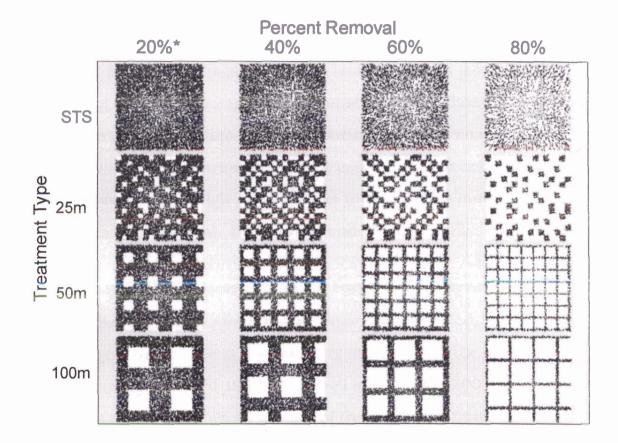


Figure 3-2. Post harvest conditions illustrating the factorial design used in the 16 simulated partial cut harvest treatments. Treatments include Single Tree Selection (STS) and three opening sizes of 25, 50 and 100 metres and 4 removal levels of 20, 40, 60 and 80% basal area removal.

Following the simulated partial cutting of the baseline condition, a pulse of regeneration was added to simulate planting of trees and natural regeneration. All germinate locations were chosen from the 'eligible grid' and the density and species composition altered according to treatment. An 80/20 subalpine fir to Engelmann spruce ratio was used in small openings less than 0.05 ha, a 70/30 ratio in openings of 0.051 to 0.2 ha and a 60/40 ratio in opening sizes greater than 0.20 ha in size. To simplify the model runs, no extrinsic mortality agents (i.e. insect attack or disease) were introduced into the simulations to influence forest structure so all tree mortality occurs only as a result of over-topping and shading out from larger trees. Given this lack of external tree mortality, few standing dead trees (snags) are available in the baseline stand at 150 years or carried forward into the model partial cutting scenarios. This effect simplifies the scenarios, however it is somewhat unrealistic as snags often comprise a high percentage of total stems in many older ESSF forests (Parrish et al. 1999, Antos and Parrish 2002).

Estimating Lichen Response to the Forest Canopy Environment

The distribution of *Alectoria* and *Bryoria* in high elevation ESSF forests suggest these lichens respond very differently to the openness of the forest canopy (Goward 1998, Campbell and Coxson 2001, Lewis 2004). I use the position above ground of the transition from predominantly *Alectoria* in the lower canopy of old forests to nearly complete *Bryoria* dominance in the upper canopy (*Alectoria/Bryoria* transition zone; Lewis 2004 (Chapter 2)) as a measuring point in the canopy to distinguish the tolerance of each lichen genera to climatic conditions. Thus, I assume the climatic conditions above the *Alectoria/Bryoria* transition point are largely unsuitable for *Alectoria* growth based on the premise that dispersal into the upper canopy is not limiting the distribution of *Alectoria* in old forests (i.e. Sillett et al. 2000).

I use forest canopy light in this study as a surrogate for canopy climatic conditions. Solar radiation is an important climatic variable influencing lichen survival and growth (Rhoades 1996). Sunlight can affect lichen thallus hydration by influencing the frequency and duration of wetting and drying cycles in the forest canopy (Rhoades 1996, Campbell and Coxson 2001). Light is by no means the only environmental factor influencing lichen thallus hydration since wind ventilation, temperature and relative humidity also moderate climate in forest canopies (Parker 1996). However, sunlight can be correlated with these other climatic variables in the canopy such as wind, moisture, humidity and temperature that respond to openness of the forest canopy (Geiger, 1965).

To assess sunlight entering the forest canopy, I used a spatially explicit light model tRAYci (Brunner 1998) incorporated in the latest version of the TASS model. The light model tRAYci provides an index of photosynthetically active radiation (PAR), based on solar geometry and estimates of canopy light transmittance, over an entire growing season. The index provides values of proportion of above canopy light (PACL), which range from 0% in total darkness to 100% in the center of a large clearcut or above the forest canopy (Brunner 1998,).

I used the tRAYci light model to place a three-dimensional light sensor array through the TASS simulated 125 x 125 metre baseline condition stand. The three-dimensional sensor array consisted of a twodimensional light grid located at 1-metre intervals throughout the forest canopy in the bottom 16 metres of the canopy starting from 0.5 metres above ground to 16.5 metres above ground, and then every 4 metres from 16.5 to 32 metres above ground. Each two-dimensional light grid is

composed of individual light sensors on a 1.0 x 1.0 metre grid requiring 15,625 light sensors to cover the 125 x 125 metre area of the simulated stand. The light sensor array remains fixed once a partial cut treatment is applied to the baseline stand to allow direct comparisons of pre- and post-logging light conditions. I used the entire light sensor array in the baseline condition old forest to compare light in the canopy against the estimated vertical distribution of *Alectoria* and *Bryoria*. However, in the partial cut treatments, I tracked light conditions at the 2.5 metre height interval that acts as a midpoint between 1 and 4 metres above ground where lichens are available to caribou as forage on standing trees in the winter. I used the 12.5 metre height interval to assess upper canopy light influence on the lower canopy. I assessed the light environment at 20-year intervals over the 100-year simulation period to examine changes in light conditions with tree regeneration and mortality.

Results

Lichen Distribution in Relation to Forest Canopy Structure and Light Environment

Values of Percent Above Canopy Light (PACL) along the vertical axis of the TASS simulated baseline condition stand show a clear gradient in light values associated with the distribution of canopy foliage (Figure 3-3).

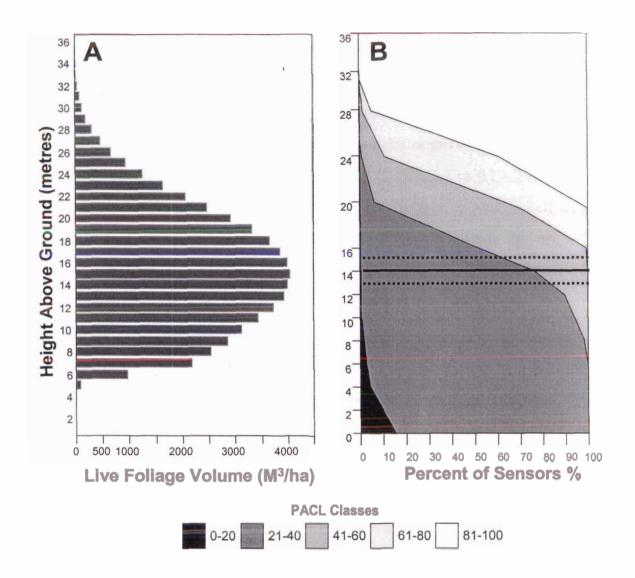


Figure 3-3. The distribution of live canopy foliage (m³/ha) at 1 metre height intervals above ground (A) and the percent of light sensors in each percent above canopy light (PACL) class at 2 and 4 metre height intervals above ground (B) in the TASS generated baseline stand. The lines in (B) show the estimated height of the *Alectoria/Bryoria* transition point (middle solid line) with 95% Confidence intervals (outside dashed lines).

In the lower 10 metres of the canopy, over 90% of average growing season light levels are between 20-40% PACL with a mean PACL of 25% at 2 metres increasing to 31% at 10 metres above ground. At 12-20 metres above ground an abrupt transition in light occurs where light values increase from a mean of 33% PACL at 12 metres to 41% PACL at 16 metres and 54% at 20 metres. This increase in light is associated with an abrupt decline in upper canopy foliage. At 12 to 20 metres above ground the light range shifts from 90% of sensors below 40% PACL at 12 metres to more than 50% of sensors over 40% PACL at 16 metres. Upwards of 24 metres in the canopy, light levels remain high given the sparse canopy conditions, with 90% of all light sensors reporting greater than 60% PACL, corresponding with the few tree crowns in this zone.

The estimated distribution and lower canopy composition of *Alectoria* and *Bryoria* for the TASS simulated starting condition forest closely correspond to the canopy light gradient. Average lower canopy light conditions (less than 4 metres above ground) of mainly less than 30% PACL are associated with high estimated *Alectoria* composition (65% (SE = 57-73%). The estimated height of the *Alectoria/Bryoria* transition at14.2 metres (95% Confidence Interval =13.1 – 15.3 metres) above ground occurs at approximately the same position above ground as the rapid change in average canopy light levels begins at 12 to 20 metres in the canopy (Figure 3-3). At 16 metres above ground where *Bryoria* dominates the lichen composition and *Alectoria* would be almost completely absent, PACL values increase rapidly from an average of 41% PACL with an increase beyond 25% of all light sensors values in the 40-60% PACL range > At 16 metres above ground the proportion of light values above 60% PACL also begin to increase rapidly. Thus, average

light conditions of greater than 40% PACL with 25% or more of sensors reporting values in the 40-60% PACL range and the inclusion of light values in the 60% PACL class appear to limit the distribution of *Alectoria*. A high percentage (90%) of all light below 40% PACL and average light levels predominantly below 35% PACL are required for *Alectoria* to remain the dominant lichen species in the canopy. In contrast, *Bryoria* appears to tolerate a broader range of light conditions as *Bryoria* is present in the canopy from the lowest light conditions in the lower canopy of the baseline stand right up to the highest light levels at the top of the canopy. However, once light levels report an average of 40% PACL, and a proportion of light levels reach values of 61-80% PACL, *Bryoria* is the dominant lichen genera in the canopy.

Change in Light Environment due to Harvest Treatment and Level of Removal

The light environment measured in the lower canopy (2.5 metres) varied largely with both removal and partial cutting treatment (Figure 3-4). Average lower canopy light increased with higher basal area removal. In STS forests for example, lower canopy light (at 2.5 metres above ground) increased from an mean of 26% PACL and more than 90% of sensors between 21-40% PACL in the baseline (control) stand to a mean of 40% PACL, with 50% of the sensors between 21-40% PACL in the 40% removal STS. In the 80% removal STS stand 95% of light sensors reported light values greater than 60% PACL and an average of 67% PACL. Partial cuts with small opening sizes, such as 25 x 25 meters openings, showed a similar increase in the range of lower canopy light conditions as the STS stands.

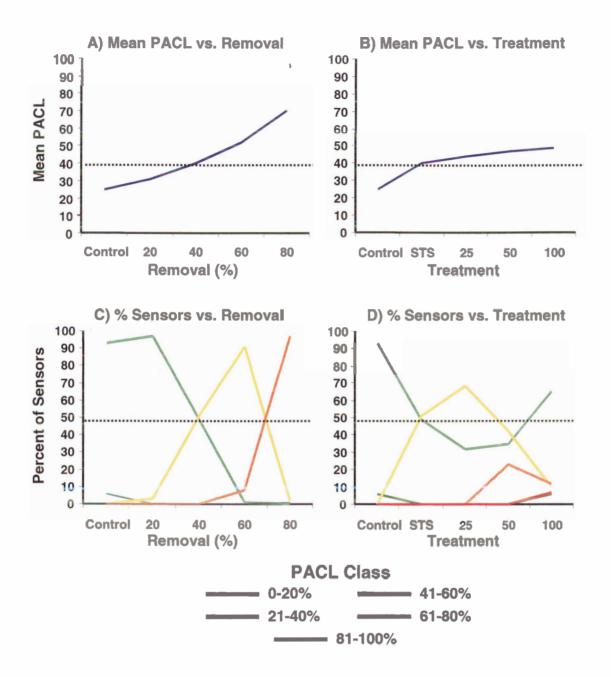


Figure 3-4. A comparison of the canopy light environment (PACL) at 2.5 metres above ground due to basal area removal and treatment immediately following logging. Figure 3-4 shows the change in mean PACL in the STS stands with increasing basal area removal (A) and in the different treatments (B) at a constant removal of 40%. The dashed line in both figures shows the mean PACL value associated with the upper light tolerance for *Alectoria*. The percent of sensors for each PACL class also changed due to basal area removal (C) and treatment (D). The dashed line in both figures 50% of sensors. "Control" refers to the TASS baseline stand; 'STS' to the single tree selection stand, and '25', '50' and '100' refer to opening sizes.

However, at lower levels of removal (i.e. 40% removal) the larger opening sizes (50 x 50 and 100 x 100 metre openings) resulted in the middle of the openings achieving higher light conditions of > 60% PACL while retained patches maintain low light values similar to the uncut stand. As a result, while mean light values increase slightly, larger opening sizes provide a greater range of light values compared to singletree selection and 25 x 25 metre openings. The large range of light values that characterize treatments with larger openings is lost at higher levels of removal (i.e. >60 % removal) as the residual forest between openings is diminished.

Given the distribution of *Alectoria* to relatively lower light conditions, the TASS simulated partial cuts suggest that high basal area removal partial cuts (60-80% removal; or less than 20 m^2 /ha residual basal area) will result in a range of lower canopy light conditions more suited to Bryoria establishment and growth. Low removal partial cuts (40% basal area removal or less; residual basal area of > 27 m²/ha) appear to maintain lower canopy light conditions suitable to retain Alectoria as the dominant lower canopy lichen. The 40% removal treatments appeared to create light lower canopy conditions slightly above the maximum where Alectoria will remain the dominant lower canopy lichen with an average of over 40% PACL maintained at 2.5 metres above ground (Figure 3-4). However, in the treatments with larger openings, light conditions in the retained patches would remain largely similar to pre-logging levels of generally less than 40% PACL while the higher light conditions are associated strictly with the openings. Thus, in the retained patches, little change to the lower canopy lichen composition is expected to that of the un-logged forest and Alectoria

should remain the dominant lower canopy lichen even though average light values exceed the average 40% PACL value.

Change in Canopy Light Environment Through Time

Combinations of partial cutting treatment and removal level had variable influence on the lower canopy light environment over time. Low harvest removals (i.e. 20-40% removal) resulted in the smallest changes in the lower canopy light environment over the 100-year simulation period. The 20% removal resulted in almost no change in range of light conditions over the 100-year period compared to the un-logged stand. The STS 40% removal had a slightly greater impact on light conditions with a mean PACL 40% and a larger proportion of sensors reporting PACL values in the 41-60% range, however, within 40 years after logging light conditions at 2.5 metres in partial cuts returned to pre-logging levels (Figure 3-5). Partial cutting treatments with high removals (60-80%) removal) resulted in a much greater increase in lower canopy light. Even so, lower canopy light conditions returned to pre-logging levels in under 60 years (Figure 3-4). The high basal area removals appeared to invoke a greater regeneration response than in the lower basal area removal treatments resulting in the lower canopy light environment becoming quickly shaded. Similar to the STS stands, larger opening sizes resulted in higher average PACL values immediately after logging but did not maintain these light conditions for a longer period of time. Regardless of the opening size, pre-logging light conditions returned to the lower canopy in 60 years after logging.

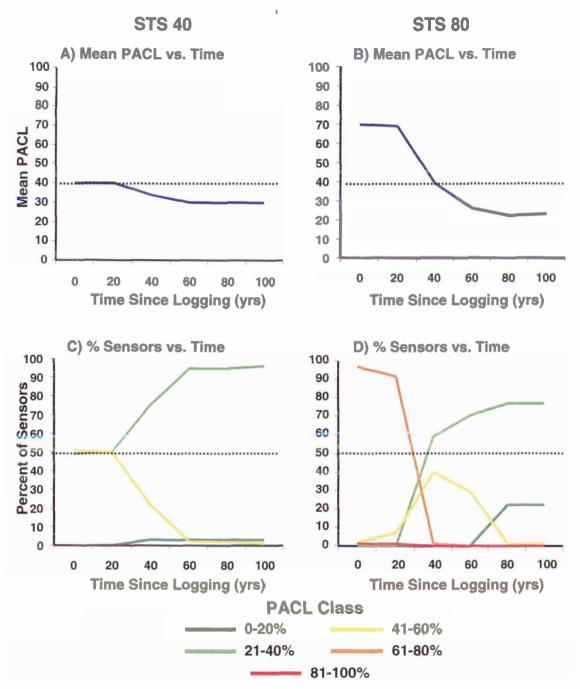


Figure 3-5. Mean PACL and percent of sensors in each PACL class at 2.5 metres above ground at 40% and 80% removal in the STS stands. Mean PACL is shown for the 40% (A) and 80% (B) STS stands. The dashed line in both figures shows the mean PACL value associated with the upper light tolerance for *Alectoria*. The percent of sensors (%) in each PACL class is shown for the 40% (C) and 80% (D) STS stands. The dashed line in both figures indicates 50% of sensors.

Light conditions at 12. 5 metres above ground return to pre-logging levels at roughly the same time for both high and low removal partial cuts at 80-100 years. The main difference between high and low removal partial cuts are light levels at this height. Low removal cuts provide light conditions that remain just above the upper limit for *Alectoria* growth (i.e. 40% mean PACL, light values of greater than 60% PACL) and favor *Bryoria* growth for up to 100 years after logging. However, light values at this height are generally lower than the STS 80% stand that maintain a high proportion high light conditions of greater than 60% for up to 80 years. These results suggest that very high light conditions at 12.5 metres created by high basal area removals are likely to maintain openness conditions suitable for *Bryoria* lower in the canopy for up to 80 years after logging.

Spatial Variability in Forest Structure and Light Environment

Partial cutting treatments results in very different spatial patterns of light in the lower canopy. The entire range of light conditions is distributed evenly in the stand in the STS treatments at all levels of removal (Figure 3-7). As a result, most residual trees are exposed to a similar range of light conditions and would experience a similar canopy environment throughout the treatment area.



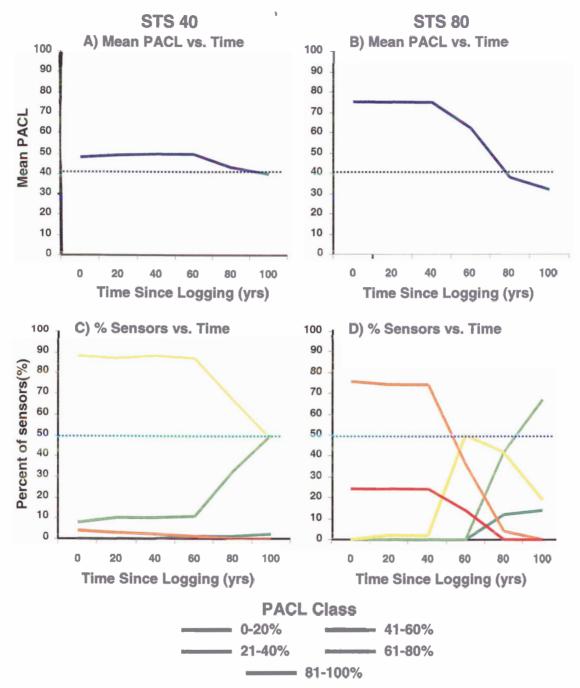


Figure 3-6. Mean PACL and percent of sensors in each PACL class at 12.5 metres above ground at 40% and 80% removal in the STS stands. Mean PACL is shown for the 40% (A) and 80% (B) STS stands. The dashed line in both figures shows the mean PACL value associated with the upper light tolerance for *Alectoria*. The percent of sensors (%) in each PACL class is shown for the 40% (C) and 80% (D) STS stands. The dashed line in both figures indicates 50% of sensors.

As the size of openings increases, light conditions become more variable across the treatment area, with high light conditions associated with openings and lower light values are associated with patches of residual forest. Treatments with large leave areas between openings, such as in lower removal harvests (less than 40%), appear to retain pre-logging light values within the remnant tree patches. As a result, the high light conditions in larger openings are associated with little to no residual tree substrate found within the openings and with a small amount of older timber along the north edge of the openings (Figure 3-6). However, as the removal level increases, this effect diminishes, as residual patches between openings become smaller and influence the light values in the residual patches.

Discussion

Distribution of Alectoria and Bryoria Relative to Forest Canopy Light

The light gradient through the canopy of the TASS generated old forest showed distinct "zones" of light relative to the distribution of foliage above the ground. This light gradient shows a similar trend as light gradients from vertical transects of old-growth Douglas-fir forests in the Pacific Northwest (e.g. Parker 1997). Noteworthy is the presence of a "light transition" zone where an abrupt transition in light conditions occurs (Parker 1997). This light transition zone may be particularly important to the distribution of canopy epiphytes in these forests (McCune et al. 1997).

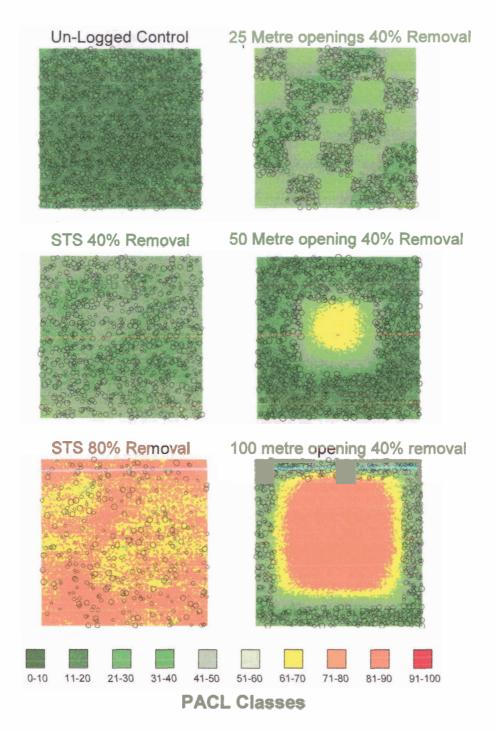


Figure 3-7. The spatial pattern of light (PACL) classes at 2.5 metres in the canopy relative to residual forest structure (represented by black circles) under different treatment types and removal levels. Images on the left show the change in lower canopy light from the "control" TASS baseline stand to the 80% removal STS stand. Images on the right illustrate the change in light with larger opening sizes at a constant level of tree removal of 40%.

McCune et al. (1997) noted the vertical distribution of canopy epiphytes to correspond with this "light transition" zone, in particular, the upper limit in the distribution of the "old-growth associated" cyanolichens *Lobaria* occurred at the base of this light transition zone.

In Chapter 2, I observed the Alectoria/Bryoria transition to correspond to an abrupt decline in canopy foliage in measured forests. I hypothesize this position is also associated with a distinct change in the climatic gradient in the stand. The estimated height of the vertical distribution of Alectoria and Bryoria for the baseline TASS stand correlated well to the light gradient. The TASS stand light gradient showed a "light transition" zone to occur at approximately 12-20 metres above ground. In the model, the estimated limit in the distribution of Alectoria in to the upper canopy occurred at the same position as the base of the light transition zone at 14-16 metres above ground. These model results lend support to my findings in Chapter 2 relating the height of the Alectoria/Bryoria transition to the abrupt transition in canopy foliage and the climatic gradient. In additions these findings support hypothesis by both Goward (1998) and Campbell and Coxson (2001) that the distribution of *Bryoria* in the upper canopy is responding to drying effects due climatic gradients associated with forest age and structure. (e.g. McCune 1993, Goward 1998).

The relative absence of *Alectoria* with the higher range of light conditions (greater than 40% mean PACL and sensors above-60% PACL) at 16 metres above ground does not preclude *Alectoria* growth from these light conditions. *Alectoria* has been shown to maintain a presence in the lower canopy of high basal area removal partial cuts (e.g. Rominger et al. 1994, Lewis 2004). These exposed partial cut conditions could contain

similar average light conditions in the lower canopy as the 80% STS removal (i.e. 61-80% PACL). However, the presence of *Alectoria* under these high light conditions may be attributed to the fact that *Alectoria* thalli are already established in the canopy prior to logging. Alectoria may be more successful in these open conditions when it does not have to colonize the stand and compete for substrate with a more active 'colonizer' such as *Bryoria* that disperses relatively well (Goward 2004) and accumulates mass quickly (Arsenault et al. 1997). Their persistence may also be due to their ability to positively respond to the increased exposure (e.g. Esseen and Renhorn 1998, Sillett et al. 2000) or may be attributed to sheltered micro-environments provided in more protected, shaded canopies of larger remnant trees that appear important to maintain *Alectoria* mass following logging (Sillett and Goslin 1999, Lewis 2004).

In contrast, *Bryoria* displayed a greater distribution across the entire range of light conditions in the canopy, from relatively low light conditions in the lower 4 metres of the canopy to the highest light conditions in the uppermost portion of the canopy. The presence of *Bryoria* across a large range of light conditions may be due to the mixture of many *Bryoria* species found in the canopy. Goward (2003, pers. comm.) suggests a vertical zonation of individual *Bryoria* species exists within the *Bryoria* species mix in these forests. This stratification within the *Bryoria* species mix may explain the greater tolerance to varied light conditions expressed by the distribution of *Bryoria*.

Expected Long-Term Lichen Response to Partial Cutting Treatments

Low removal (20% and 40%) partial cuts had the least impact on lower canopy light environment and are expected to result in the least impact to lichen community composition. The low removal partial cuts saw a relative increase to 30-45% PACL compared to an average of 25% PACL in the baseline stand. These light conditions should maintain Alectoria as the dominant lower canopy lichen. Most post-logging monitoring of lichen communities in partial cutting treatments have only been observed for less than 10 years (e.g. Pinkerton Mountain; Coxson et al. 2003, Lucille Mountain; Jull and Stevenson 2001) so it may be too early to observe a change in lower canopy lichen composition. However, these studies show lower canopy Alectoria and Bryoria composition responds in a similar way as lower canopy light conditions in the TASS generated partial cuts. At the Lucille Mountain trial, light levels in a 49% removal single tree selection trial increased to about 43% of above canopy light (Sagar et al. 2001) and the number of trees with high Alectoria mass (> 50% Alectoria) declined relative to the uncut control stand after 8 years (Stevenson 2001). At Pinkerton Mountain, Coxson et al. (2003) noted no real change in canopy climate and lichen thallus hydration in low removal (30%)partial cuts with a residual basal area of $23-27 \text{ m}^2$ /ha. As a result, the composition of Alectoria appeared to remain similar to pre-logging conditions two years after logging.

The only expected impact to lichen distribution in low removal partial cuts may be along the edges of large openings (i.e. greater than 50 x 50 metres (0.25 hectares). Coxson et al. (2003) measured higher light values and decreased thalli hydration on north edges of openings in a 33% basal are removal group selection stand with 1.0 hectare sized

openings, and concluded that an increase in *Bryoria* in the canopy might be expected under such conditions. In the TASS partial cut treatments, larger opening such as the 100 x 100 metre (1.0 hectare) openings created higher light values and had a distinct band of high light values on the north edge of openings that would favour *Bryoria* colonization and growth at the edge of residual patches. The increased exposure at these edges may result in the distribution of *Bryoria* descending lower in the canopy as increased light conditions will prevail at 12.5 metres in the canopy for upwards of 80 years until regenerating trees in the openings can effectively intercept light.

In measured low removal partial cut forests in the North Thompson (Lewis 2004; Chapter 2) ranging from 3 to 12 years after logging, lichen composition was variable but generally above 50% *Alectoria* composition in the lower canopy and the height of the *Alectoria/Bryoria* transition zone remained similar to uncut forests at 12- 15 metres above ground. However, in high removal partial cuts canopy conditions favored *Bryoria* growth. Thus, *Bryoria* composition of greater than 70% was found in most high removal partial cuts within 20 years after logging. In addition, these partial cuts showed a downward displacement of *Bryoria* distribution as the light gradient increased all the way down through the canopy. In most high removal partial cuts older than 15 years, the height of the *Alectoria/Bryoria* transition descended to 6-10 metres above ground.

The primary mechanism lichen biomass is lost in partial cuts is loss of mature lichen bearing trees as the immediate loss in available lichen forage biomass after logging is roughly proportional to the level of timber removal (Stevenson et al. 2001). Estimates of post-logging lichen

biomass in low removal forests from the North Thompson (Lewis 2004; Chapter 2) support this claim. At four low removal partial cuts (33% basal area removal - Single Tree Selection (STS) stands) within the North Thompson study area, average post-logging lower canopy biomass levels were approximately 63% of un-logged mature forests that would have contained similar pre-logging forest structure to these partial cuts. STS forests with post-logging basal area estimates of $20.5 - 24.9 \text{ m}^2$ /ha (22.8 m²/ha average) had lower canopy lichen biomass levels of 31-56 kg/ha (average 41 kg/ha) compared to biomass levels of 40-91 kg/ha (average 65 kg/ha) in uncut forests containing basal area estimates of 40.8 - 44.1m²/ha (average 42.9 m²/ha).

Future lichen biomass loadings in low removal partial cuts may be the most uncertain to forecast. A positive lichen biomass response in low removal partial cuts may occur as lichen growth is stimulated by the slight increase in solar radiation while the environment remains relatively stable (Coxson et al. 2003). Esseen et al. (1996) noted an increase in *Alectoria* mass 30 metres from the edge compared to the immediate edge of large clearcuts within 15 years after logging. They attributed this change to increased solar radiation resulting in increased lichen growth while the negative influences of edge exposure were diminished further in the forest. Stevenson and Coxson (2003) also noted that growth rates remained high for both *Alectoria* and *Bryoria* in partial cut stands. However, Coxson et al. (2003) suggest that after the second pass, the post-logging forest will have a smaller proportion of large trees than after the first pass due to the second logging entry in a stand. Since large trees contain a disproportionately greater amount of lichen biomass

than small trees, the expected result may be a significant decrease in lichen biomass in the stand.

High basal area removal partial cuts are likely to have an immediate loss of lichen beyond the proportion of timber removal as a greater amount of lichen on residual trees is lost to wind or to excessive post-logging wind-throw (Stevenson et al. 2001). In the North Thompson area, three recently logged (3-7 years after logging) high removal partial cuts with post-logging basal area estimates of 3.7, 9.6 and 11.9 m²/ha (average 8.4 m²/ha, or less than 20% residual basal area of the same previously mentioned un-logged stands with an average of 42.9 m²/ha) contained lower canopy lichen biomass estimates of 2.3, 6.5 and 14.2 kg/ha respectively, or an average of 7.6 kg/ha (less than 12% of the lower canopy lichen biomass of un-logged forests with similar pre-logging conditions). In addition, none of the trees in any of these partial cuts contained a lower canopy lichen class greater than lichen class 2, and remnant lichen thalli were observed to be significantly smaller than on similarly sized trees in un-logged forests (Lewis 2004; Chapter 2).

In high removal partial cuts lichen biomass loadings can be expected to increase with time since logging. In the North Thompson study area, seven older partial cuts ranging in ages from 17-29 years post-logging and basal area estimates of $6.4 - 14.0 \text{ m}^2/\text{ha}$ (average 9.2 m²/ha) contained lower canopy lichen estimates of 13.3 - 52.1 kg/ha(average 28.2 kg/ha, or 43% of the un-logged stands). Many trees had lower canopy lichen classes greater than Lichen class 3, and in most cases *Bryoria* composed more than 80% of the lichen composition. Older partial cuts with higher post-logging basal area estimates ($15 \text{ m}^2/\text{ha}$ or more) often contained substantially higher lower canopy biomass

estimates that ranged as high as 85 – 125 kg/ha and were composed of greater than 90% *Bryoria*, often exceeding lower canopy biomass of the old un-logged stands while at a lower density of trees.

Retention of large trees will play a large role in the amount of Bryoria biomass accumulated after logging in high removal partial cuts. Most live branches greater than 20 years old on older trees contain an inner defoliated zone that is essential for Bryoria establishment (Goward 1998). This may be the reason Rominger et al. (1994) noted live branches in partial cut forests contain more lichen per branch (mainly Bryoria spp.) than in un-logged forest 10 years after logging. The older residual trees left in the partial cuts they sampled probably had low live branches with a significant defoliated zone capable of supporting Bryoria accumulation. In these old partial cuts, retaining residual stems in a more dispersed pattern may also result in greater amount of substrate with suitable climatic conditions for Bryoria establishment and growth. In contrast, the use of larger openings results in large areas with suitable climatic conditions for Bryoria growth but is occupied by young growth or regenerating trees unsuitable for Bryoria establishment. Thus, the spatial pattern of retained trees is important.

Retained green trees have been shown to play a major role in post logging lichen community persistence and re-establishment (Neitlich and McCune 1997, Peck and McCune 1997, Sillett and Goslin 1999, Sillett et al. 2000). Drever and Lertzman (2003), noted forest structure retained in partial cuts had an influence in micro-scale light conditions at the forest floor. Thus, small clumps of trees and large retained patches can provide some low light conditions in high removal partial cuts and creating a greater range of light variability. These patches of trees and low light

conditions may provide refuge for "old-growth" associated lichens such as *Alectoria* and will provide valuable sources of dispersal into the managed forest (Sillett and Goslin 1999).

Consequences of Partial Cutting on Management of Landscapes

Large-scale use of partial cutting systems to manage for lichen will ultimately affect the management of landscapes. Assuming a constant annual cut, the use of low removal partial cuts can encroach upon undisturbed forest areas at a greater rate than under a management regime utilizing high removal systems (Crow and Gustafson 1997). Thus, the outcome of extensive use of low removal partial cuts may be larger road networks and faster rate of dispersion of early seral habitats on the landscape (Mladenoff et al. 1993, Spies et al. 1994). Increased road networks and landscape fragmentation are potential concerns to managing current threats (i.e. backcountry access and predation) on caribou (BC Ministry of WLAP 2002).

Used in a proper spatial and temporal landscape context, the use of high basal area removal partial cuts may provide greater flexibility and control in the management of human access and in spatial and temporal management of habitats. Aggregating low retention harvests may allow larger areas of forest interior to be maintained for longer periods (Gustafson and Crow 1994, 1996, Von Sacken 1998). Such protective measures may be particularly useful in already highly fragmented landscapes where further dispersion of cutblocks may increase habitat fragmentation, isolate habitats and lower habitat connectivity (Crow and Gustafson 1997). In addition, high removal partial cuts focused in

already highly disturbed areas may allow managers to spatially and temporally manage large portions of the landscape to manage recovery of suitable forested habitat or spatially separate early seral habitats that attract other ungulates away from high use caribou areas.

Timber Management Objectives

From a timber management perspective, high removal partial cuts offer a better opportunity to meet timber objectives. High removal partial cuts utilize a greater amount of tree volume on the site, potentially decreasing logging costs (Mitchell 1996). Single logging entries also allow greater use of temporary roads and minimize extensive road networks for frequent access (Crow and Gustafson 1997). Both these factors can potentially minimize road construction and maintenance costs (Bieber, 2002). High removal partial cuts may also provide for better survival and growth of planted regeneration (Newsome et al. 2000) or release of advanced regeneration (Messier et al. 1999) as more solar radiation reaches the forest floor and can warm the soil (Lajzerowicz et al. 2004). Soil warming may offer better survival of favored commercial tree species such as spruce that are less tolerant of shade (Messier et al. 2000).

Maintaining Biological Diversity

In most circumstances, wildlife and plant response to tree removal and retention in partial cuts results is variable and individualistic (Hansen et al. 1995, Franklin et al. 1997). A relative decrease in plant and wildlife species compared to the pre-logging species community may be expected (Hansen et al. 1995, Lloyd et al. 1996, Beese and Bryant 1999). The MASS (Montane Alternative Silviculture System) trial on

coastal British Columbia (Beese and Bryant 1999) noted a decrease in plant cover, especially species associated with moist conditions (e.g. bryophytes) as the level of tree removal increased. Many wildlife species associated with the pre-logging species composition remain in partial cuts after logging such as small mammal populations (Klenner and Sullivan 2003) or songbird communities (Dickinson and Leupin 1996) but numbers and densities are often reduced (Dickinson and Leupin 1996). Younger stands with tree retention can retain species generally associated with old-growth forests, as has been seen for 'old-growth associated' canopy epiphytes (e.g. Sillett and Goslin 1999, Sillett et al. 2000), northern spotted owl (e.g. North 1993) and small mammal populations (e.g. Carey and Johnson 1995) on remnant trees in young Douglas-fir stand in the Pacific Northwest (Franklin et al. 1997). Other species such as marten alter their use of partial cuts stands by responding positively to edges (Huggard 1999).

Plant diversity and species richness may increase in partial cuts (Beese and Bryant 1999). In many cases this is due to an influx of herbaceous 'colonizers' that are often also associated with openings or clearcuts (Beese and Bryant 1999). Therein lies the main limitation of high basal area partial cuts to mountain caribou management. Greater solar radiation at the forest floor as a result of higher tree removal can produce an increased shrub and herb response after logging (Beese and Bryant 1999) making these conditions attractive to ungulates such as Moose (*Alces alces*) and Deer (*Odocoileus spp.*)(Franzmann and Schwartz 1998). These conditions may increase the abundance of ungulates in high elevation caribou habitats that may otherwise have been unsuitable

habitat and may lead to an increase in the number and proximity of predators (e.g. wolf and cougar) (BC Ministry of WLAP 2002).

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Chapter 4 – General Conclusions

Introduction

Arboreal lichens in old high elevation forests play a critical role as winter forage for mountain caribou in British Columbia. As the decline of mountain caribou populations became apparent, the need to alter forest management to maintain lichen forage became a management priority (Stevenson and Hatler 1985, Stevenson et al. 1994). Lichens are currently not believed to be limiting to caribou in their winter habitats, as the decline of mountain caribou populations is now largely believed to be a result of increased predation (Seip 1992,) and possibly disturbance due to increased human backcountry access (Simpson and Terry 2000). However, understanding the long-term response of lichens to natural forest development and forest management is important to ensure the availability of lichen forage over time.

Maintaining suitable lichen forage for caribou will be important if the current decline of populations can be slowed or reversed through management interventions (i.e. predator control)(BC Ministry of WLAP, 2002). In addition, stand-level partial cutting systems used to maintain lichen for caribou indirectly influence the proximate factors causing caribou decline (i.e. increased predation through creation of early seral habitat for other ungulates; Wittmer 2004). Thus, more information is required to assess the long-term implications of various partial cutting treatments not only on availability of lichen forage but also their consequences to landscape habitat management.

Objectives

My objective in this study was to increase our understanding of forest age, structural and management conditions that affect available lichen forage for caribou. I chose a retrospective approach to collect data on lichens in real forests and a simulated modeling approach that would allow some long-term insight into future lichen conditions in natural forests and under various partial cutting treatments. This approach allowed me not only to explore the long-term response of lichens to partial cutting but to also examine the potential benefits and drawbacks of different partial cutting options.

Findings

Lichen Relationships to Forest Age and Structure in Natural Forests My research suggests the complex, multi-layered forest canopies typical of many old ESSF forests may be a primary factor leading to the significant accumulations of arboreal lichens. The microenvironment experienced by forest canopy epiphytes is influenced by the spatial arrangement of branches, foliage and organisms that modify the canopy environment (Rhoades 1996). Consequently, gradients in light, temperature, wind turbulence and humidity within the forest canopy can vary largely depending on forest structural conditions (Geiger 1965, Chen et al. 1991, Van Pelt and Franklin 2000,Parker 1997). The multi-layered structure characteristic of older ESSF forests is an important feature that contributes to the gradient in canopy climatic conditions. The subcanopy provides a stable lower canopy environment suitable for

significant *Alectoria* lichen accumulation. In contrast, the upper canopy of the same forest would have a markedly different exposure to wind and sunlight exposing lichen to a much more ventilated environment than the lower canopy, creating conditions favorable to *Bryoria*. Consequently, old forests provide suitable conditions for high accumulations of both *Alectoria* and *Bryoria* and the distinct vertical stratification of these lichens in the upper canopy that is characteristic of many old ESSF forests. My results support hypothesis by Goward (1998) and Campbell and Coxson (2001) regarding the distribution of canopy lichens in ESSF forests and lend further support to the "similar gradient hypothesis" of McCune (1993) regarding the distribution of canopy epiphytes relative to forest age and structure.

Lichen Response to Partial Cutting

Lichen abundance and distribution will respond over time to changes in forest canopy structural and environmental gradients associated with the level and pattern of tree removal in partially cut forests. I propose a conceptual model of lichen response to partial cutting in high elevation ESSF forests where the intensity and duration of the lichen community response to a partial cut will be proportional to the level of disturbance. Partial cuts with a basal area removal less than 40%, or retained basal area of 25 m²/ha or greater will have the least impact on lichen composition and biomass and appear to maintain conditions that favour *Alectoria* as the dominant lower canopy lichen. High basal area removals of 60% removal or more create and maintain lower canopy light conditions suitable for *Bryoria* growth for at least 60-80 years following logging. Basal area removals in excess of 80%, or less

than $10m^2$ /ha retained basal area create conditions suitable for *Bryoria* growth but may not retain enough old tree substrate to allow significant lower canopy lichen accumulations.

Retention of large green trees in the post-logging forest appears to be important for accumulation of post-logging *Bryoria* biomass as it provides suitable substrate for colonization and growth. Partial cuts with residual trees dispersed or in small clumps have more old tree substrate associated with suitable light conditions for *Bryoria*. Large retained green trees are also important to maintain *Alectoria* presence in the forest canopy. These trees may be critical to allow *Alectoria* to re-colonize and re-establish in the managed forest as *Alectoria* establishment and growth on residual and regenerating trees may be limited less by the change in climate as by dispersal ability.

Implications to Management of Mountain Caribou Habitat

Existing mountain caribou guidelines that recommend the practice of low basal area removal (30% basal area removal, residual basal area of greater than 25 m²/ha) may be sufficient to maintain short-term lichen biomass for continued caribou use immediately after logging (Coxson et al 2003, Stevenson et al. 2001, Stevenson and Coxson 2003). Comparisons of pre- and post-logging lichen biomass suggest retention of stand level lichen biomass and biomass on individual trees may provide adequate foraging opportunities for caribou in post logging forests (Coxson et al. 2003, Stevenson 2001).

Alternatives to the use of low removal selection silviculture systems, such as high removal "retention" silviculture systems offer the

possibility to provide long-term forage for caribou. Since *Bryoria* appears to be the preferred lichen forage for caribou, then low retention silviculture systems may be a worthwhile option to create stand conditions that increase *Bryoria* biomass in the lower canopy where it is accessible to caribou. Primarily, this partial cutting option may prove worthwhile in early winter habitats where caribou are forced to lower elevations due to snow and *Bryoria* forage is typically less available (unless on recently wind-thrown trees) compared to more open parklandlike higher elevation late winter habitats. The lag period before suitable forage conditions return in low retention partial cuts may further offer flexibility to plan long-term recovery of landscape habitat conditions by timing new cutting in highly fragmented areas to coincide with the recovery of suitable conditions in other early seral habitats (i.e. regenerating clearcuts).

In summary, both low and high basal area removal partial cuts appear to have the ability to provide adequate levels of forage biomass for caribou over time. The only difference will be in the timing that suitable forage conditions occur, as low removal cuts appear to be able to maintain sufficient foraging biomass immediately after logging while many high removal partial cuts may have a period of at least 15-20 years before suitable foraging biomass on standing trees has accumulated. Thus, these options have short and long-term trade-offs between timber and habitat management objectives. Forest and wildlife managers should acknowledge that any stand-level management strategy to manage for forage lichens would have different benefits and drawbacks at various spatial and temporal scales. Managers should acknowledge the consequences of their stand-level management strategies within the

broader context of landscape-level habitat management and to use such strategies where they deem appropriate given the potential future consequences.

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