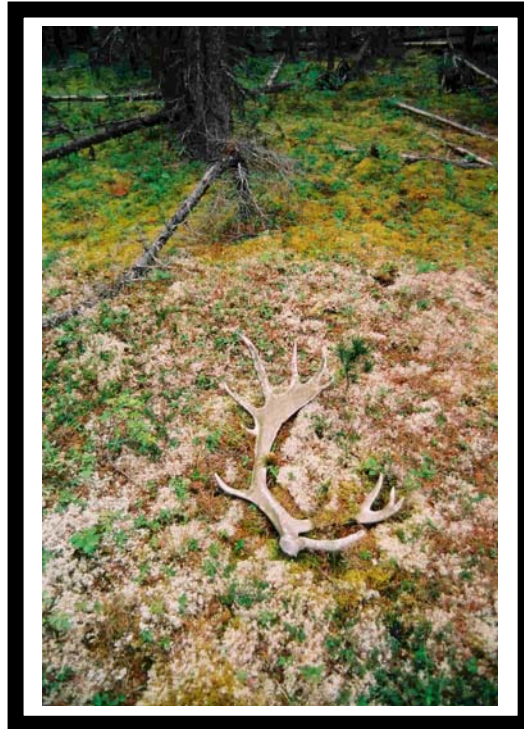


***THE RESPONSE OF CARIBOU TERRESTRIAL FORAGE LICHENS
TO MOUNTAIN PINE BEETLES AND FOREST HARVESTING
IN THE EAST OOTSA AND ENTIAKO AREAS***

ANNUAL REPORT – 2007/08 – YEAR 7



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PREFACE

This report summarizes data collected in 2007 and compares it to data collected from 2001 to 2005. It incorporates information from two adjacent study areas: the East Ootsa area between the Tetachuck Lake and the Chelaslie River; and the Entiako area, which includes Entiako Park.

The focus of our project was to determine the response of caribou terrestrial forage lichens to mountain pine beetles and forest harvesting under various ecological conditions in four biogeoclimatic subzones (SBSmc2, SBSdk, SBPSmc and ESSFmc). We selected sites within sites series in each subzone that supported high lichen cover, but that did not necessarily typify each site series. The data presented in this report are representative of localities that support high lichen cover within these site series/subzones and cannot be used to generalize average conditions within site series or subzones.

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EXECUTIVE SUMMARY

The Tweedsmuir-Entiako caribou (*Rangifer tarandus caribou*) population winters in the Entiako and East Ootsa areas. During winter, caribou select mature lodgepole pine (*Pinus contorta*) forests on poor sites and forage primarily by cratering through the snow to obtain terrestrial lichens. This study was initiated in 2001 to examine the effects of the current mountain pine beetle (*Dendroctonus ponderosae*) epidemic and forest harvesting on caribou terrestrial forage lichens in the East Ootsa and Entiako areas. This year, 2007, marks the seventh year of the study and documents changes over six growing seasons.

In 2001, we established 56 permanent plots in mountain pine beetle attacked stands and 24 permanent plots in clearcuts in 7 biogeoclimatic/site series. In 2004, a wildfire burned 6 of those plots (4 mountain pine beetle and 2 logged). Each plot included 6-12 permanently marked lichen photoplots, coarse woody debris measurements (as an index of obstruction to caribou mobility), basic site information (stand density, tree status, regeneration), and canopy photographs (to measure light availability). Annual growth rates of Cladina, kinnikinnick (*Arctostaphylos uva-ursi*) and red-stemmed feathermoss (*Pleurozium schreberi*) were also measured at three sites. Plots were re-measured in 2003, 2005 and 2007.

By 2007, most attacked trees were in the “grey” phase of the attack and average residual live stem densities ranged from 90 to 329 stems/ha. Overall live stem density and basal area in 2007 were lowest in ecosystems where lodgepole pine was the dominant species. Advance regeneration was highly variable depending on site type and ranged from 200 in the SBSdk/03 to 15,100 stems/ha in the ESSFmc/03.

Over the entire study, lichen abundance on mountain pine beetle affected forested ecosystems declined from 16% in 2001, to 13% in 2003, to 11% in 2005 to 10% in 2007. The rate of decline in lichen cover has diminished or stopped in most site series after 2005. The SBSmc2/01c is an exception as lichen decline in this site series has continued at roughly the same rate throughout the study. The decline in lichens was correlated with increase in abundance of other ground-layer vegetation, especially kinnikinnick. The cover of kinnikinnick increased rapidly from 2001 to 2005 but increases have slowed between 2005 and 2007. Some of the leveling off may have been due to die-back that was observed on some plots. In the SBSmc2/01c, although kinnikinnick abundance leveled off between 2005 and 2007, total ground cover of vegetation continued to increase, primarily due to an increase in twin-flower. In mountain pine beetle affected stands, the ESSFmc/03 differed from other sites series in that there was no change in lichen abundance between 2001 and 2005, but a significant decrease between 2005 and 2007. This may be due to the very low abundance of kinnikinnick in the ESSFmc/03, a greater volume of residual live trees, and a possible delay in the onset of the mountain pine beetle attack. The decline in lichens in the ESSFmc/03 corresponded to a sharp increase in mosses and moderate increases in crowberry (*Empetrum nigrum*) and twin-flower (*Linnaea borealis*). Except in the ESSFmc/03, there were no significant changes in moss abundance between 2001 and 2007.

On logged sites, there was no clear trend in lichen abundance due to high year to year oscillations. These oscillations may have been a byproduct of variation in weather conditions during sampling years. Because lichen colonies often appear larger when wet than dry, lichen abundance may have appeared to be higher during wet years. Overall, lichen abundance in 2007 was higher on logged sites than in mountain pine beetle attacked stands. Kinnikinnick and other vegetation increased in abundance from 2001 to 2007 on logged sites, whereas moss abundance did not differ significantly over time, or by ecosystem.

A wildfire in 2004 consumed all lichens on plots that were fully burned. Twin-flower was the most abundant species on plots following fire. Although we originally expected that kinnikinnick would be fully consumed by fire, some re-sprouting was observed in 2007.

Growth rates for kinnikinnick were an order of magnitude greater than growth rates of *Cladina* or moss, and moss grew at about twice as rapidly as *Cladina*. *Cladina* growth rate was generally constant from 2002 to 2007 and was highest in canopy gaps, followed by underneath a tree canopy and lastly, in clearcuts. Moss growth rate increased both in clearcuts and under a canopy tree after an initial year of slow growth. Change in moss growth rate under a canopy tree was likely due to the shift in growing conditions under a dead canopy tree, which changed to approximate conditions found in a canopy gap, where moss growth rate was higher.

By following transplants over six growing seasons, we observed mosses expanding when transplanted into lichen colonies, while lichens diminished when transplanted into moss colonies.

Coarse woody debris transects show that a limited amount of blowdown is occurring each year but that large-scale blowdown of mountain pine beetle attacked trees has not yet occurred. Currently, the amount of coarse woody debris is generally low on all sites and is not enough to impede animal movements.

Table of Contents

Preface	iii
Acknowledgements	iii
Executive Summary	iv
Introduction	1
Objective	2
Study Area	2
Terrestrial Lichen Ecology	5
Methods	7
Sampling	7
Plot Identification.....	9
Plot Characteristics.....	9
Terrestrial Lichen Photoplots.....	10
Light Availability.....	13
Analysis of 2001 to 2007 trends in ground-layer vegetation.....	13
Transplant Experiment	14
Growth Rates	14
Kinnikinnick Photoplots.....	16
Coarse Woody Debris	16
Results and Discussion.....	18
Stand Structure and Regeneration.....	18
Response of Lichens to Forest Disturbance.....	21
Patterns of Ground-layer Vegetation Change from 2001 to 2007: MPB Forests.....	22
Patterns of Ground-layer Vegetation Change from 2001 to 2007: Clearcuts.....	29
Predictive Models of Lichen Abundance	30
Vegetation Composition Following Fire.....	32
Growth Rates	32
Transplant Experiment	35
Kinnikinnick Photoplots.....	36
Coarse Woody Debris	37
Future Work	43
References	44

List of Maps

Map 1. Location of permanently marked lichen plots in the East Ootsa and Entiako areas.	8
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List of Tables

Table 1. Number of permanent plots established by biogeoclimatic subzone, site series and disturbance type in the East Ootsa and Entiako areas.	9
Table 2. Average density and basal area of trees >7.5 cm dbh for each species for mountain pine beetle plots in the East Ootsa and Entiako areas in 2007.....	19
Table 3. Average density of seedlings (0.1-1.3 m height) and saplings (0.1-7.5 cm dbh) combined on plots in the East Ootsa and Entiako areas, 2007.....	19
Table 4. Multiple regression models for lichen abundance.	31
Table 5. Regeneration and vegetation cover in 2007 for 6 permanent plots in the East Ootsa area that were burned by a wildfire in August 2004.	33

List of Figures

Figure 1. Mountain pine beetle attacked stands in the East Ootsa area on the north side of Tetachuck Lake, 2005.	3
Figure 2. Photoplot with pigtail stakes and labelled tag on the SW corner.	11
Figure 3. Photographing a photoplot.....	12
Figure 4. A transplant of <i>Cladina</i> to a red-stemmed feathermoss colony.	15
Figure 5. Average percent of trees >7.5 cm dbh in each species and mountain pine beetle attack class by biogeoclimatic subzone/site series in the East Ootsa and Entiako areas from 2001 to 2007.	20
Figure 6. Changes in understory vegetation and growth of advance regeneration on plot SBSmc2/01c-C10 from 2001 (top) to 2007 (bottom).	21
Figure 7. Differences in lichen cover by site series between unlogged MPB-affected pine forests and logged clearcuts in (a) 2001 and (b) 2007.....	22
Figure 8. Changes in <i>Cladina</i> lichen abundance following mountain pine beetle, forest harvesting and fire disturbance in the East Ootsa and Entiako areas (2001-2007).	23
Figure 9. Changes in kinnikinnick abundance following mountain pine beetle, forest harvesting, and fire disturbance in the East Ootsa and Entiako areas (2001-2007).	24
Figure 10. Changes in moss abundance following mountain pine beetle, forest harvesting, and fire disturbance in the East Ootsa and Entiako areas (2001-2007).....	25
Figure 11. Changes in abundance of major non-lichen ground-layer species (kinnikinnick + crowberry + twin-flower + moss) following mountain pine beetle, forest harvesting, and fire disturbance in the East Ootsa and Entiako areas (2001-2007).	26
Figure 12. Examples of an increase in kinnikinnick from 2001 to 2007 (left) and an increase in kinnikinnick from 2001 to 2005 and then dieback from 2005 to 2007 (right).	27
Figure 13. Extensive kinnikinnick mortality at plot SBPSmc/02-C03 in the Entiako area, September 2007.	28
Figure 14. Growth of twin-flower on a burned plot in the East Ootsa area, 3 years following fire.	34
Figure 15. Average annual growth rates for red-stemmed feathermoss and <i>Cladina</i> in a gap, under a canopy tree and in a cutblock from 2002 to 2007 on an SBSmc2/01c site in the East Ootsa area.	34
Figure 16. Growth rate of kinnikinnick in a gap, under a canopy tree and in a cutblock from 2002 to 2007 on an SBSmc2/01c site in the East Ootsa area.....	35
Figure 17. Percent cover of red-stemmed feathermoss and caribou forage lichens in transplanted photoplots on an SBSmc2/01c site in the East Ootsa area from 2001 to 2007.	36

Figure 18. Percent cover of kinnikinnick under mountain pine beetle-killed canopy trees on an SBSmc2/01c site in the East Ootsa area from 2002 to 2007.37

Figure 19. Mean volume, mass and pieces of coarse woody debris by biogeoclimatic zone and year in the East Ootsa and Entiako areas, 2001-2007.38

Figure 20. Mean pieces of coarse woody debris on mountain pine beetle plots in each decay class and mobility class by biogeoclimatic zone and year in the East Ootsa and Entiako areas, 2001-2007.39

Figure 21. Mean mobility index of coarse woody debris by year for mountain pine beetle sites in the East Ootsa and Entiako areas, 2001-2007.40

Figure 22. Mean mobility index for mountain pine beetle (MPB) and logged sites by biogeoclimatic zone and year in the East Ootsa and Entiako areas, 2001-2007.41

Figure 23. Mean volume, mass and pieces of coarse woody debris for mountain pine beetle (MPB) and logged plots in 2001 and 2007 in the East Ootsa and Entiako areas.42

INTRODUCTION

The Tweedsmuir-Entiako caribou (*Rangifer tarandus caribou*) population summers in the North Tweedsmuir Park area, moves through the East Ootsa area during spring and fall migration, and winters in the Entiako and East Ootsa areas. During winter, caribou select mature lodgepole pine (*Pinus contorta*) forests on poor sites and forage primarily by cratering through the snow to obtain terrestrial lichens (Cichowski 1993).

The two main large-scale natural disturbance factors in the area are fire and mountain pine beetles. Fire suppression has been effective in reducing large-scale fires in the Entiako area for the last 40-50 years, resulting in a landscape of primarily older lodgepole pine forests (Cichowski *et al.* 2001). Mature lodgepole pine trees are the preferred host of the mountain pine beetle (*Dendroctonus ponderosae*).

The current mountain pine beetle epidemic was detected in the East Ootsa and North Tweedsmuir Park areas in the early 1990's (Garbutt and Stewart 1991). By the late 1990's, mountain pine beetle numbers reached epidemic levels along Eutsuk and Tetachuck lakes. The area on the south and north side of Tetachuck Lake is an important spring migration staging area and winter range for the Tweedsmuir-Entiako caribou. Low impact "snip and skid" forest harvesting operations were undertaken on the north side of Tetachuck Lake for beetle management purposes; current-attacked trees were removed and efforts were made to protect high value caribou habitat from mechanical disturbance. In some cases, extensive areas were harvested. By 2000, beetle numbers overwhelmed management efforts and beetle management harvesting on the north side of Tetachuck Lake was suspended.

The recent mountain pine beetle outbreak has affected significant areas of mature lodgepole pine caribou winter range in the East Ootsa and Entiako areas and most of the attacked trees have lost their needles and are now in the "grey attack" phase of the epidemic (Figure 1). Prior to this study, there was no information available on the effects of mountain pine beetles on terrestrial forage lichens. A number of studies have documented the effect of fire on terrestrial lichens; however, most of those studies were conducted in boreal forests and their findings may not apply directly to the East Ootsa and Entiako area.

In 2000, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated all woodland caribou in the Southern Mountains National Ecological Area (SMNEA), which includes the Tweedsmuir-Entiako population, as Threatened (Northern Caribou Technical Advisory Committee 2004). That same year, Northern Caribou in all of British Columbia were blue-listed by the BC Conservation Data Centre (CDC). A recovery strategy for Northern Caribou in the SMNEA was recently completed but is awaiting approval (Northern Caribou Technical Advisory Committee 2004). That strategy identified the impact of the extensive mountain pine beetle outbreak on winter forage (terrestrial lichens), on caribou habitat and winter range use, and on population dynamics as one of the greatest threats currently facing Northern Caribou in the SMNEA, and identified research on the effects of mountain pine beetles on Northern Caribou and their habitat as a priority.

Because the Tweedsmuir-Entiako caribou population is the first population to experience the current mountain pine beetle epidemic, information collected on the Tweedsmuir-Entiako population will also benefit other caribou populations where mountain pine beetle will occur.

This study was initiated in 2001 and is the first study to investigate the effects of mountain pine beetles on caribou terrestrial forage lichens. It also assesses the effects of mountain pine beetle management logging on terrestrial lichens. Permanent plots were established in 2001 and revisited in 2003, 2005 and 2007. Although the focus was on disturbances created by mountain pine beetle and forest harvesting, a wildfire burned 6 study plots in 2004, providing some additional information on the initial effects of fire disturbance. This annual report presents results from 2007 and compares this year's results to results from previous years.

OBJECTIVE

The objective of this project is:

- to gain an understanding of how caribou terrestrial forage lichen species respond to mountain pine beetle and forest harvesting disturbances in the East Ootsa and Entiako areas.

Although the focus of this project is on disturbances created by mountain pine beetle and forest harvesting, a wildfire in 2004 has provided an opportunity to also assess disturbance created by fire.

STUDY AREA

The study area is located in west-central B.C., approximately 100 km south of Burns Lake. It includes the portion of the East Ootsa caribou migration and winter range that lies south of the Chelaslie River and north of Tetachuck Lake, and the portion of the Entiako caribou winter range that lies within Entiako Park.

The area is characterized by low-lying, flat or gently rolling terrain on the Nechako Plateau (Holland 1976, Figure 1). The plateau landscape ranges between 850 and 1300 meters, rising gently to 1500 meters in the western part of the East Ootsa area, and rising more rapidly to over 1900 meters in the Fawnie Mountains along the eastern boundary of Entiako Protected Area. Eskers and deep glacio-fluvial deposits are common features of the plateau as the physical landscape is largely a result of glacial movement from southwest to northeast across the area (Holland 1976). Soils are predominantly Brunisolic Gray Luvisols and Dystric Brunisols on morainal and glacio-fluvial deposits (Lewis *et al.* 1986, Clement *et al.* 1987).



Figure 1. Mountain pine beetle attacked stands in the East Ootsa area on the north side of Tetachuck Lake, 2005.

The East Ootsa and Entiako areas fall within 4 main biogeoclimatic subzones and variants:

- the dry cool subzone of the Sub-Boreal Spruce zone (SBSdk);
- the Babine variant of the moist cold Sub-Boreal Spruce subzone (SBSmc2);
- the moist cold subzone of the Sub-Boreal Pine-Spruce zone (SBPSmc); and,
- the moist cold subzone of the Engelmann Spruce-Subalpine Fir zone (ESSFmc).

The SBSdk subzone is located along the lakes of the Nechako Reservoir including Tetachuck Lake, Chelaslie Arm, Euchu Reach, Nataalkuz Lake and Intata Reach. The SBSmc2 occurs upslope of the SBSdk in the East Ootsa area while the SBPSmc is above the SBSdk in the Entiako area. Most of the Entiako area consists of the SBPSmc. The ESSFmc is found at higher elevations above the SBSmc2 in the East Ootsa area and is primarily restricted to the western portion of the study area where the plateau rises towards the Quanchus Mountains in Tweedsmuir Park; however, a small pocket of ESSFmc is also found between Chelaslie Arm and the Tetachuck River. Two additional biogeoclimatic subzones are found in eastern portion of Entiako Park (the Kluskus variant of the SBSmc subzone [SBSmc3] and the moist, very cold subzone of the ESSF [ESSFmv]) but were not sampled as part of this project.

Low elevation forests consist mostly of lodgepole pine or mixed lodgepole pine/white spruce (*Picea glauca*) stands. Spruce stands occur primarily on wetter seepage sites and as bands along lakes and wetlands, and black spruce (*Picea mariana*) is generally restricted to forested wetlands. Deciduous stands of trembling aspen (*Populus tremuloides*) are found mostly in the band of SBSdk along the Nechako Reservoir. Lakes and sedge fens are common and often occur together in mosaics that include fringe forests of spruce. Subalpine fir (*Abies lasiocarpa*) occurs mostly at higher elevations in the ESSF but is also found in the SBSmc2, especially in the understory. Most of the pine and pine/spruce stands that dominate the study area have poorly developed shrub and herb layers. Common understory vascular plant species are soopolallie (*Shepherdia canadensis*), birch-leaved spirea (*Spirea betulifolia*), prickly rose (*Rosa acicularis*), kinnikinnick (*Arctostaphylos uva-ursi*), twin-flower (*Linnaea borealis*), bunchberry (*Cornus canadensis*), and dwarf blueberry (*Vaccinium caespitosum*).

Caribou, moose (*Alces alces*), wolves (*Canis lupus*), grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) are common wildlife species in the study area. Caribou use the area primarily during winter and migration. Entiako Park is the core of the caribou winter range; however, some caribou also use the East Ootsa area during winter (Cichowski and MacLean 2005). Caribou travel through the East Ootsa area during spring and fall migration and the area on the north and south side of Ootsa Lake are important staging areas during spring migration.

Fire and forest insects are the main large-scale natural disturbance factors in the study area. The SBPSmc, SBSmc2 and SBSdk are characterized by somewhat frequent stand destroying fires with mean fire return intervals of 125-175 years, 100-150 years, and 100-150 years respectively (Parminter 1992). The ESSFmc is characterized by infrequent stand destroying fires with a mean fire interval of 200-300 years. Mountain pine beetles are the main forest insects present in the study area; however, spruce beetles (*Dendroctonus rufipennis*) and western balsam bark beetle (*Dryocoetes confusus*) also play an important role in the dynamics of spruce and subalpine fir stands. Mountain pine beetles preferentially attack mature trees; larger trees (>20-25 cm dbh) are especially susceptible (Safranyik and Carroll 2006).

The East Ootsa and Entiako areas lie within the rainshadow of the Coast Mountains and are characterized by a dry, continental climate, with generally cool, short and dry summers, and long, cold and dry winters. Mean monthly temperature averages 13°C in the summer and -14°C in the winter with mean annual precipitation levels of 450 mm in the SBS and the SBPS, and 580 mm in the ESSF (Banner *et al.* 1993). Annual snowfall averages 2 meters for the lower elevation SBS and SBPS, and 2.5 meters for the higher elevation ESSF. Actual snow accumulation is relatively low during winter, especially at lower elevations where snow accumulation rarely exceeds 1 meter in openings.

TERRESTRIAL LICHEN ECOLOGY

Caribou primarily forage on terrestrial forage lichens in the genera *Cladina*, *Cladonia*, *Cetraria*, and *Stereocaulon*. *Cladina* is especially favoured and is represented by four species in the study area: *C. arbuscula*; *C. mitis*; *C. rangiferina*; and *C. stellaris*. This study concentrates on the distributional ecology of *Cladina*; however, the patterns reported apply to most terrestrial forage lichens in the study area.

The distribution and abundance of terrestrial forage lichens in the East Ootsa and Entiako areas is largely determined by interactions among four factors:

- site characteristics (moisture, nutrients, and light);
- disturbance history;
- reproduction and dispersion; and,
- competition with terrestrial plants.

Terrestrial forage lichens, particularly species in the genus *Cladina*, have a broad tolerance for moisture conditions and can be found growing on dry, rapidly draining substrates such as sand, coarse gravel and bedrock, or on (at least temporarily) wet substrates such as *Sphagnum* hummocks. Whether wet or dry, *Cladina* is most abundant on nutrient poor sites where the success of potential competitors is limited (Ahti 1961). Although these lichens are physiologically capable of inhabiting moist, rich sites (and often grow larger on those sites than on drier and poorer ones) they tend to be uncommon on rich sites due to competition from mosses and vascular plants (Ahti 1961). While terrestrial forage lichens are able to withstand desiccation, they also require humidity for transpiration and growth (Ahti and Hepburn 1967). Prolonged humid conditions, such as under the cover of dense forests in most boreal ecosystems, allows red-stemmed feathermoss (*Pleurozium schreberi*) to thrive at the expense of terrestrial lichens. In canopy gaps where terrestrial forage lichens are abundant, humid conditions are interrupted by periods of desiccation, which prevents competitors like mosses from becoming established and allows lichens to flourish.

In many ecosystems, terrestrial forage lichens are dependent on periodic disturbance to maintain their prevalence on the landscape. However, if disturbances are too frequent, for instance constant trampling, lichen cover can be dramatically diminished (Crittenden 2000). Fire is important for maintaining lichen-dominated plant communities on the landscape. Although lichens burn readily, they also re-establish more rapidly than many of their competitors. Undamaged colonies in areas skipped by fire are sources for re-establishment on burned substrates that lack vegetation. Successional studies in boreal forests indicate that terrestrial forage lichens are a part of a dynamic understory community in post-fire landscapes. A generalized post-fire pattern of succession in boreal ecosystems begins with a *Cladonia* dominated understory community, which is replaced by *Cladina* species after 30-80 years (depending on latitude, climate, and site conditions; Ahti 1977), and eventually by feathermoss after 150 years or more (Coxson and Marsh 2001). This pattern is moderated by soil moisture; wetter soils progress to the feathermoss stage more rapidly than drier soils. On very dry soils, sites may not reach the feathermoss stage.

The genus *Cladina* is capable of reproducing by both sexual and asexual spores; however, most species propagate by thallus fragmentation (Ahti and Hepburn 1967). During dry periods, the thallus of *Cladina* species becomes brittle and susceptible to breakage. Broken fragments are then dispersed by wind or by animal vectors. Goward (2000) hypothesized that caribou may be responsible for enlarging established lichen colonies by spreading fragments while cratering. Regardless of the dispersal mechanism, *Cladina* appears to establish most effectively if a nearby source population exists.

Lichens compete poorly with vascular plants and mosses, in part because of their slow growth rates. Vascular plants and mosses grow much more rapidly and are able to overgrow adjacent lichen colonies (Ahti and Hepburn 1967). *Cladina*, however, is able to out-compete many other lichen genera, including the closely related genus *Cladonia*, especially those that are shorter in stature. The main competitors of terrestrial forage lichens in the study area are:

- kinnikinnick;
- red-stemmed feathermoss;
- crowberry (*Empetrum nigrum*); and,
- twin-flower.

However, other plant species also play a role in restricting the distribution of terrestrial lichens.

Kinnikinnick is a low-growing (less than 10 cm tall in the study area) evergreen dwarf shrub that grows by sending a radial series of horizontal shoots from a central axis. Kinnikinnick is adapted to dry habitats and is intolerant of persistent humidity; it is most commonly found growing on subxeric sites such as south facing slopes, eskers, or outwash plains.

Red-stemmed feathermoss is the most abundant ground cover in the study area and grows well in humid habitats often dominating submesic to subhygric sites, primarily over till landforms, which account for much of the landscape. On mesic sites, red-stemmed feathermoss can comprise close to 100 % cover and can be up to 15 cm thick earning the nickname ‘smother moss’. It grows slowly, approximately 1.5 cm/yr in boreal ecosystems (Ahti 1961), which is still more than twice as fast as most terrestrial lichens. Red-stemmed feathermoss is unable to tolerate dry moisture conditions, although on drier sites, it will inhabit humid microsites, such as beneath the cover of a low bush. Although red-stemmed feathermoss is a prominent component of fire-driven boreal ecosystems, it is not a common post-fire species. Large areas in recently burned ecosystems are relatively dry, owing to the loss of moisture-retaining litter, and provide little in the way of suitable habitat for this moisture-dependent species. Instead, red-stemmed feathermoss is dominant in late successional plant communities where it tends to out-compete species like terrestrial forage lichens that are able to establish earlier.

Crowberry is a low growing (usually less than 25 cm tall in the study area) evergreen shrub that bears numerous short, ascending branches. This shrub is tolerant of cold, nutrient poor soils and it can occur under a broad range of moisture conditions. The distribution and germination of crowberry seeds may be related to the location of animal droppings; however,

the main mechanism for propagation is vegetative layering (Bell and Tallis 1958). Crowberry is most common in subalpine habitats where it can form a near-continuous cover.

Twin-flower is another fast-growing understory species in the study area. While reasonably common, the distribution of this species is patchy and it rarely accounts for more than 5 to 10 percent cover in any one site.

In the East Ootsa and Entiako areas, caribou terrestrial forage lichens are most abundant in the following ecosystems:

- SBSmc2/01c (submesic);
- SBSmc2/02 (subxeric);
- SBSdk/03 (subxeric);
- ESSFmc/03(subxeric);
- SBPSmc/02 (subxeric); and,
- SBPSmc/01b (submesic).

In the SBPSmc, mesic phase sites (01a) with open canopies also support a modest cover of terrestrial caribou forage lichens.

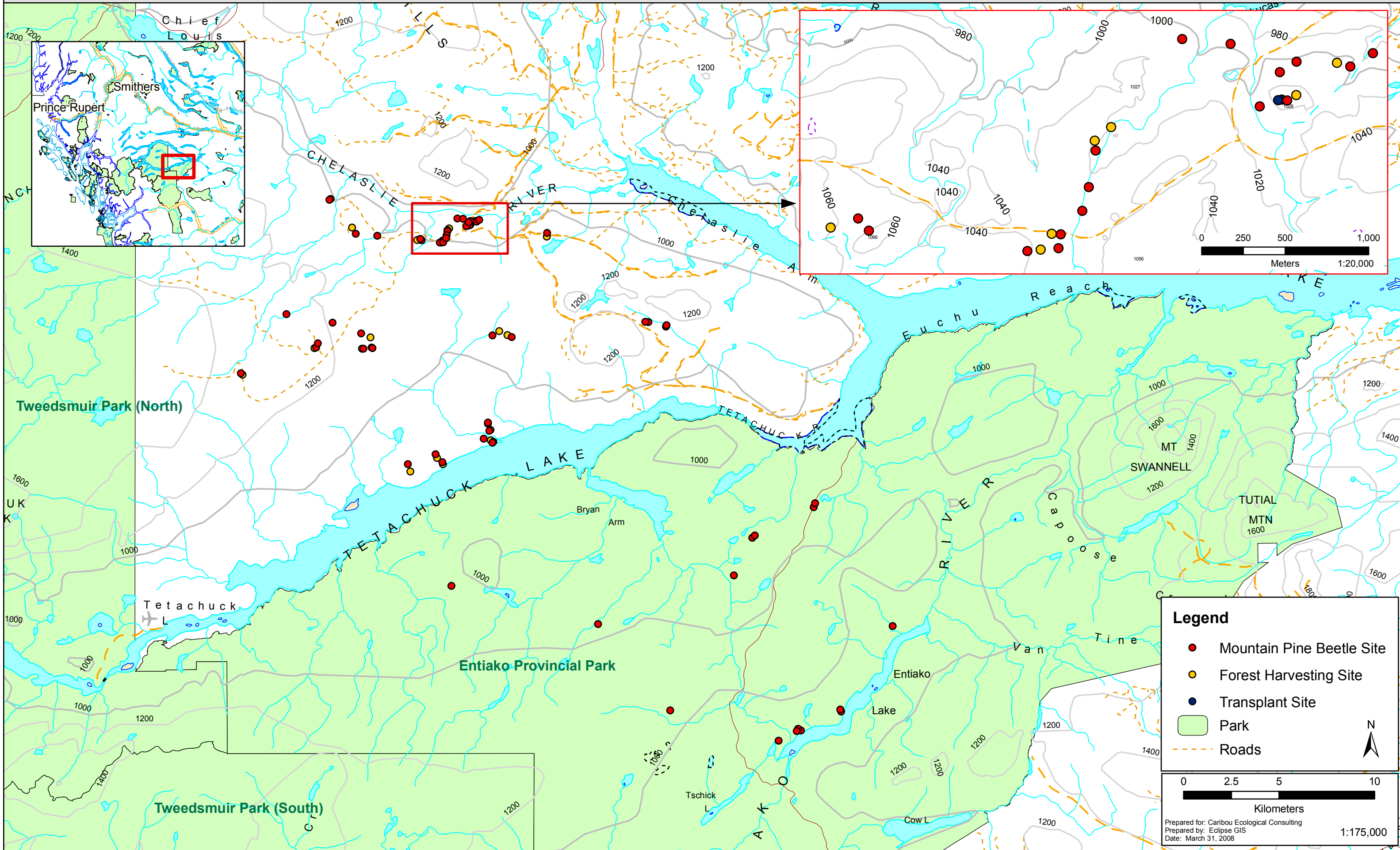
METHODS

SAMPLING

We initiated this project in 2001 as a long-term study monitoring the response of terrestrial forage lichens to epidemic mountain pine beetle numbers and forest harvesting. The effect of mountain pine beetles was considered to be a gradual loss of canopy trees, while the effect of forest harvesting was considered to be a rapid loss of canopy trees. Permanent sample plots were established in 2001 and were re-sampled in 2003, 2005 and 2007. In 2002, we collected additional information at permanent plots in the East Ootsa area including canopy openness using a fish-eye camera, we refined the coarse woody debris data collection methods, and we established growth rate monitoring sites for terrestrial lichen, red-stemmed feathermoss and kinnikinnick at three SBSmc2/01c sites. This year, 2007, marks the seventh year of the study and documents changes over six growing seasons.

In 2001, we established 5 to 14 long-term permanent plots for each biogeoclimatic subzone/site series and disturbance type (Map 1, Table 1). Terrestrial lichen response to forest harvesting and mountain pine beetles depends on competition from other plants and on site type, and may vary between biogeoclimatic subzones due to varying overall site conditions. Therefore, we treated each site series within each biogeoclimatic zone as a separate site. All mountain pine beetle plots were established in mixed red and green attacked stands. Originally, half of the mountain pine beetle plots in the East Ootsa area were intended for forest harvesting; however, none of the sites were harvested. We also established plots on already harvested sites; sampling occurred one or two years after harvesting so we were not able to directly compare conditions prior to harvesting to following harvesting. To avoid confounding effects of canopy loss and mechanical disturbance to terrestrial forage lichens due to forest harvesting, we only sampled in

Map 1. Location of permanently marked lichen plots in the East Ootsa and Entiako areas.



- Legend**
- Mountain Pine Beetle Site
 - Forest Harvesting Site
 - Transplant Site
 - Park
 - - - Roads

0 2.5 5 10
Kilometers

Prepared for: Caribou Ecological Consulting
Prepared by: Eclipse GIS
Date: March 31, 2008

1:175,000

cutblocks that were harvested during the winter (when the snowpack prevents the disturbance of the forest floor) and/or where harvested sites appeared to be “machine-free” zones. We do not have any control sites that lack a disturbance type because all mature pine stands in the study area were affected by the mountain pine beetle epidemic. In addition, a wildfire in August 2004 burned six of our permanent plots in the East Ootsa area, providing us with some information on the effects of fire.

Table 1. Number of permanent plots established by biogeoclimatic subzone, site series and disturbance type in the East Ootsa and Entiako areas.

Study area	Biogeoclimatic subzone	Biogeoclimatic site series	Disturbance type	
			Forest Harvesting	Mountain Pine Beetles
East Ootsa	ESSFmc	Subxeric (03)	5 ¹	10
	SBSmc2	Submesic (01c)	7 (1) ²	14 (1)
		Subxeric (02)	5 (1)	10 (3)
	SBSdk	Subxeric (03)	7	7
Entiako	SBPSmc	Subxeric (02)	-	5
		Submesic (01b)	-	5
		Mesic (01a)	-	5

¹ One plot was disctrenched following establishment and was removed from the study since it could no longer be re-established accurately

² The number in parentheses indicates the number of the total number of sites that were burned in 2004

We focused our efforts on submesic sites in the SBSmc2 biogeoclimatic subzone and subxeric sites in the SBSmc2, SBSdk and ESSFmc subzones in the East Ootsa area. In the SBPSmc in the Entiako area, we sampled subxeric, submesic and mesic sites. In total, we sampled 65 sites in the East Ootsa Area and 15 in the Entiako.

PLOT IDENTIFICATION

In 2001, a 7.98 meter diameter circular plot (200 m²) was permanently established at each site. Plot centres were marked using a labeled stainless steel pigtail pin. Permanent stakes were pushed down flush to the ground in mountain pine beetle plots to minimize disturbance to stakes during potential future harvesting treatments. We established a guide tree for each plot and recorded the distance and bearing from the guide tree to the centre pin as a precaution in the event that the plot centre pin was disturbed. Guide trees were usually small (usually less than 5 m) understory spruce and were marked by three pieces of flagging and orange marker paint around the bole about 1.3 m above the ground.

PLOT CHARACTERISTICS

In 2001, we recorded basic location and site information including GPS coordinates, elevation, slope, and aspect, and estimated vegetation cover for shrubs, herbs, bryophytes and

lichens for each plot. For stand characteristics, we visually estimated canopy closure, and measured dbh and age of the largest lodgepole pine tree on the site. On sites where most large pine trees had been killed by mountain pine beetles, a representative live tree was selected adjacent to the plot since ages were difficult to determine for beetle-killed trees at some sites. Percent cover of each vegetation species was re-estimated for each plot in 2007.

In 2001 and 2003, each conifer tree within the plot was counted, identified to species, classified as alive or dead, and classified into the following size classes:

- > 12.5 cm dbh;
- 7.5 – 12.49 cm dbh;
- > 1.3 meters in height to 7.49 cm dbh; and,
- <1.3 meters in height.

In addition, lodgepole pine trees were classified into the following categories:

- alive;
- mountain pine beetle – green attack;
- mountain pine beetle – faded (yellow/orange) attack;
- mountain pine beetle – red attack;
- mountain pine beetle – red/grey attack;
- mountain pine beetle – grey; and,
- dead (not due to mountain pine beetle attack).

In 2005, in addition to counting each tree >1.3 meters in height within the 400 m² permanent plot and classifying them into size and status classes as above, we tagged all trees >7.5 cm dbh individually with a number and measured their dbh. In 2007, we re-tagged trees with aluminum tags and spray painted the circumference of each tree at the height of the tag with blue paint to aid in identifying the tree once it falls.

In 2005 and 2007, trees <1.3 meters in height were counted and classified by species into the following size classes on a 3.99 m radius plot radiating from plot centre of the permanent plot:

- <10 cm in height;
- 10-30 cm in height; and,
- 30-130 cm in height.

Each tree was further classified as acceptable or unacceptable in terms of vigour.

TERRESTRIAL LICHEN PHOTOPLOTS

At each permanent plot, we established 6 to 12 photoplots based on the abundance of lichens. Generally, fewer photoplots were established on plots with lower lichen abundance and more plots were established on plots with greater lichen abundance, with an average of 10 photoplots per site. In total, 771 photoplots were established. For each photoplot, a 75 cm x 75 cm frame was placed around a lichen colony with its sides aligned in the cardinal directions. The frame defined the boundary of the photoplot and provided a scale reference for analysis. The position of the frame was permanently marked with two stainless steel

pigtail stakes (marked with flagging tape) in the southwest and northeast corners (Figure 2). Each southwest pigtail was labeled with an aluminium tag that contained the site and photoplot numbers. For each photoplot, we recorded the distance and bearing from the plot centre (of the 7.98 m radius plot) to the southwest corner pigtail stake of the photoplot.



Figure 2. Photoplot with pigtail stakes and labelled tag on the SW corner.

A 35 mm camera with a 28 mm lens was mounted on a tripod and boom and positioned approximately 1.2 m directly over the frame (Figure 3). A small erasable board with the subzone, site series, site number, photoplot number and date written on it was placed on the west edge of the frame within the field of view. The camera was consistently aligned so that north was at the top of the viewfinder. If the photoplot was situated beneath a tree, the influence of the tree's canopy and the state of that tree (live; green attack; red attack) was recorded. Photoplots were photographed and analyzed in 2001, 2003, 2005 and 2007.

In 2001, 2003 and 2005, photographs were taken using 200 ASA film and scanned to high resolution digital jpeg files to be used for image analysis. In 2007, a digital camera was used instead of a film camera. We analyzed lichen colony percent cover within each frame using the software program Gap Light Analyzer (GLA; Canham 1988). We were unable to analyze terrestrial forage lichens to the level of species because the software could not differentiate lichens to the species level, nor could it detect differences among vascular plant species. To capture changes in lichen competitors, we visually estimated the cover of the dominant species (including lichens) from printed photographs of each photoplot.



Figure 3. Photographing a photoplot.

A visual estimate of terrestrial lichen cover and the cover of the dominant competitors (kinnikinnick, feathermoss, crowberry and twin-flower) was also recorded for each photoplot for the years 2001 and 2005 by examining printed photographs of the photoplots. One observer determined all visual estimates.

We used a stepwise approach to develop multiple regression models of *Cladina* lichen and kinnikinnick percent cover as a function of environmental, tree canopy, and ground vegetation characteristics in 2001, across all-years (2001, 2003 and 2005), and to predict the change in lichen and kinnikinnick percent cover between 2001 and 2005. The lichen cover values were digitally derived, whereas the kinnikinnick cover values were visually estimated from photographs.

LIGHT AVAILABILITY

We predicted that canopy tree mortality would result in changing light conditions in the understory, especially once the dead canopy trees defoliated and eventually fell to the ground, and that the changing light environment will influence the distribution of lichens. We used fisheye photographs of the canopy to quantify the change in light availability in beetle-killed stands and in harvested sites (Canham 1988). A canopy photograph was taken at each 7.98 m radius permanent plot centre using a fisheye lens on a 35 mm camera with 400 ASA film. The camera was mounted on a tripod 1.2 m above the ground over the plot centre pin and oriented so that the top of the camera was pointed north. Initial photographs were taken in 2002 (except the SBPSmc sites), and then again in 2003 and 2005. In 2007, canopy photographs were taken with a digital camera. The software program Gap Light Analyzer version 2 (GLA; Canham 1988) was used to determine the percent transmission of light through the canopy.

ANALYSIS OF 2001 TO 2007 TRENDS IN GROUND-LAYER VEGETATION

We used ANOVA to compare 2001 and 2007 lichen cover on unlogged forest and logged clearcuts in the ESSFmc, SBSdk and SBSmc2. The SBPS forest sites and burned SBSmc sites were not included in this analysis. We pooled the photoplot data for each site and transformed the lichen % cover data with a log transformation to improve normality and homogeneity of variances. Orthogonal contrasts were used to compare the four forested treatment means and the four clearcut treatment means.

Repeated measures ANOVA was used to compare site level changes in abundance of lichen, kinnikinnick, moss and all major non-lichen ground layer species (% kinnikinnick + % crowberry + % twin-flower + % moss) across ecosystems for 2001, 2003, 2005 and 2007. For this analysis the unlogged forest sites and the logged clearcuts were analysed separately so that the SBPSmc forest sites could be included in the analysis. Burned sites were excluded. With repeated measures, a significant linear time trend indicates that the variable of interest either increased or decreased over the time period, a significant quadratic trend allows us to conclude that the variable either accelerated or decelerated (leveled off) during the time period, and a significant cubic trend indicates that the variable oscillated over the time period. The percentage of variance explained by each of these trends indicates their relative importance.

Because the repeated measures analysis indicated that the lichen cover was stabilizing in some ecosystems but not in others, we used t-tests to compare the annual rate of change in lichen abundance between 2001 and 2005 to the annual rate of change between 2005 and 2007 using the formula $\Delta L_{rate} = ([L(5) - L(1)]/4 - [L(7) - L(5)]/2)$, where $L(x)$ = % lichen cover in year x . We tested the null hypothesis that $\Delta L_{rate} = 0$ separately for each ecosystem. No linearizing transformations were needed for ΔL_{rate} .

Stepwise linear regression was used to develop predictive models at the photoplot scale for 2007 lichen abundance and changes in lichen cover between 2001 and 2007 and between

2005 and 2007. 2007 lichen cover was first transformed using a square root transformation. Changes in lichen cover were normally distributed and did not require transformation.

Digital % cover estimates were used for all lichen models whereas visual % cover data were used for all other plant species.. The significance value was set at 0.05 for site-level ANOVA and t-tests, and at 0.01 for entrance into photoplot-level regression models. SYSTAT version 11 software (SYSTAT Software Inc. 2004) was used for all analyses.

TRANSPLANT EXPERIMENT

In addition to monitoring lichens in photoplots, we transplanted terrestrial forage lichens into red-stemmed feathermoss colonies, and red-stemmed feathermoss into lichen colonies to document competitive interactions over time and to observe the replacement of lichens by feathermosses.

We established five replicates of lichen/moss transplants at a single SBSmc2/01c site that supported large colonies of both terrestrial forage lichens and red-stemmed feathermoss. The transplant site was situated on a glacio-fluvial bench with well-drained soils and a relatively open lodgepole pine canopy (15% closure) with about an initial 35% mortality due to mountain pine beetles. Transplants were removed from single species colonies using a 19.5 cm diameter cylinder and were placed into a hole of the same dimension surrounded by either the competing species or by the original transplanted species (Figure 4). Each replicate included the following:

- a lichen transplant to a lichen colony;
- a lichen transplant to a red-stemmed feathermoss colony;
- a red-stemmed feathermoss transplant to a lichen colony; and,
- a red-stemmed feathermoss transplant to a red-stemmed feathermoss colony.

We conducted 20 transplants in total with four transplants per replicate and five replicates. Transplants were removed and re-placed into their parent colony to test if there was a transplanting effect.

Each transplant was photographed within a 50 cm x 50 cm frame, which was used as a reference for scale. Stainless steel pigtail pins were used to mark the centre of each transplanted colony to facilitate the re-establishment of photo-centres in future years. Photographs were analyzed for percent cover using the image analysis Gap Light Analyzer version 2 software. Transplants were photographed in 2002, 2003, 2005 and 2007.

GROWTH RATES

To gain a better understanding of competition between terrestrial forage lichens and vascular plants, we initiated a monitoring project to determine the growth rates of *Cladina*, red-stemmed feathermoss, and kinnikinnick in harvested areas, under the tree canopy and in canopy gaps.



Figure 4. A transplant of *Cladina* to a red-stemmed feathermoss colony.

In 2002 we selected three sites within the SBSmc2 submesic (01c) site series to conduct the growth rate experiment. At each site we tagged 5 red-stemmed feathermoss and 5 *Cladina* stems, as well as 5 kinnikinnick shoots under three microsite conditions: a canopy gap; under a canopy tree (red-attacked in 2002); and, in a harvested area. In total, 15 shoots were tagged for each species in each microsite type. Each moss and lichen was marked 10 mm from the tip with a black nylon thread and individually numbered with flagging tape attached to the free end of the thread. Growth was determined by measuring the length from the thread to the tip of the longest shoot and subtracting 10 mm. In a few instances, tagged mosses and lichens were broken, lost, or had died, and new plants were tagged. For kinnikinnick, we marked 5 of the longest shoots at each microsite (under the canopy, in a gap and in a cutblock). Each shoot was measured from the branch-tip to the last bud-scar to quantify only the present year's growth. In subsequent years we continued to choose the longest shoot of each plant; however, several plants died over the span of the study and were not replaced with new plants.

Growth was re-measured in 2003 and 2005. The annual growth of *Cladina* and red-stemmed feathermoss between 2002 and 2003 was simply the length from the thread to the tip minus 10 mm. Average annual growth for 2004 and 2005 was calculated using the following formula:

$$\frac{(\text{Shoot Length 2005}) - (\text{Shoot Length 2003})}{2}$$

A similar formula was used to calculate average annual growth rate for 2006 and 2007.

KINNIKINNICK PHOTOPLOTS

During our field studies in the submesic forests of the East Ootsa and Entiako areas, we noticed that kinnikinnick was primarily distributed beneath the cover of canopy trees and was sparse or absent from the surrounding forest floor matrix. We hypothesized that kinnikinnick is restricted to the rain-shadow of trees in the submesic SBSmc2 forests because it is intolerant of prolonged wet soils. This may be a function of the edaphic limitations of kinnikinnick's associated mycorrhizal fungi (i.e. a sensitivity to soil moisture).

In Year 2 (2002) we established 5 photoplots on a morainal till, submesic (SBSmc2-01c) site where kinnikinnick was confined to growing under the rainshadow of the canopy trees. Kinnikinnick was growing well on these dry microsites, forming more than 50% cover in each photoplot. Each photoplot was situated beneath a lodgepole pine tree killed by mountain pine beetles. We established these photoplots to monitor the fate of kinnikinnick colonies living in submesic sites beneath dying canopy trees, and to better understand the factors influencing the distribution of kinnikinnick in the study area. Photoplots were photographed in 2002, 2003, 2005 and 2007. Canopy photographs were taken in 2003, 2005 and 2007 above each photoplot to document canopy openness and to determine if changes in kinnikinnick cover was linked to changes in canopy openness.

COARSE WOODY DEBRIS

We measured coarse woody debris to document potential obstructions to caribou movement (mobility) on each site. Coarse and fine woody debris measurements were adapted from Trowbridge *et al.* (1986) and from the Field Manual for Describing Terrestrial Ecosystems (B.C. Ministry of Environment, Lands and Parks and B.C. Ministry of Forests 1998). In 2001, bearings for two transects 30 meters in length, originating at plot centre, were selected randomly from a list of random bearings. The bearing for the second transect was located at least 80° from the first bearing to avoid encountering the same pieces on the second transect. Occasionally, on sites of limited size, several random bearings had to be tested to determine whether a transect still represented the site along its full length. On some sites, transects were terminated at distances less than 30 meters and in 2 cases, only one transect was established. For each transect, the number of pieces were recorded for the following diameter classes and transect distances:

- 0-0.5 cm diameter from 0-5 meters;
- 0.6-1.0 cm diameter from 0-10 meters;
- 1.1-3.0 cm diameter from 0-15 meters;
- 3.1-5.0 cm diameter from 0-20 meters;
- 5.1-7.0 cm diameter from 0-25 meters; and,
- >7.0 cm for all 30 meters.

For all coarse woody debris pieces >7.0 cm in diameter, we measured the diameter using calipers and recorded decay class, length class, and mobility class. We also recorded distance from plot centre in 2002 (East Ootsa plots only), 2003, 2005 and 2007.

Decay classes included:

- 1: log hard; bark, branches, and twigs <3cm still present;
- 2: log hard to partly decaying; bark and some branches still present;
- 3: log hard to partly decaying and round; trace of bark still present;
- 4: all of log on ground and sinking; bark absent;
- 5: all of log on ground and partly sunken; oval; and,
- 5+: all of log mostly sunken; overgrown by moss; part of forest floor.

Length classes included:

- 1: <2 meters;
- 2: 2-5 meters;
- 3: 5-10 meters; and,
- 4: >10 meters.

Mobility classes included:

- 0: top side of log <10 cm above ground; log mostly part of forest floor;
- 1: top side of log 10-40 cm above ground; log mostly branch free;
- 2: top side of log or branches 40-100 cm above ground; scattered branches;
- 3: top side of log or branches 40-100 cm above ground; dense branches, or top side of log >100 cm above ground (log mostly branch free); and,
- 4: top side of log or branches >100 cm above ground; dense branches with branches reaching down to the ground if log is raised off the ground.

Mobility classes were determined for the condition of the log at the point of intersection with the transect. A mobility index was calculated for each log as the length class multiplied by the mobility class.

$$\text{Mobility index (MI)} = \text{Length class} \times \text{Mobility class}$$

The mobility index provides the relative contribution of each log to mobility obstructions on the plot. The mobility index for the plot was calculated as the sum of mobility indices for all logs on the plot.

Volume, mass, and density (pieces/ha) of coarse woody debris were calculated using the Coarse Woody Debris Assessment module of the CWD/Fuel Calculator Version 1.0a (B.C. Ministry of Forests 1997). The Coarse Woody Debris Assessment required piece lengths so the midpoints of the first 3 length classes were used (Class 1 [0-2 m]: 1 m; Class 2 [2-5 m]: 3.5 m; and, Class 3 [5-10 m]: 7.5 m). For Class 4 (> 10 m), an average tree height of 15 m was estimated and used.

In 2003, we re-measured coarse woody debris on all plots and fine woody debris only on mountain pine beetle plots. In 2005, we re-measured coarse and fine woody debris only on mountain pine beetle plots. Coarse and fine woody debris on harvested plots were re-measured only on the two harvested plots that were burned. In 2007, we re-measured coarse and fine woody debris on all plots.

RESULTS AND DISCUSSION

All plots were re-visited in 2007 during two field sessions:

- August 27 – September 4; and,
- September 18-23.

The results reported here describe patterns that occur on sites with high lichen cover and do not necessarily typify the average conditions found on each site series. Although we recognize that choosing sites with high lichen cover is subjective, we feel that these sites can be used to characterize the greatest lichen potential in selected site series of each subzone, and that the patterns observed here provide insight into what may be happening at the landscape level.

STAND STRUCTURE AND REGENERATION

Prior to mountain pine beetle attack, the dominant canopy tree species on all site series was lodgepole pine (Table 2). Most of the lodgepole pine trees > 7.5 cm dbh on each site series were attacked by mountain pine beetles in 2001. By 2005, additional trees were attacked and the majority of attacked trees were in the “grey attack” phase (Figure 5). In 2007, some additional mortality was also observed and average pine mortality (based on stems/ha) ranged from 78% on SBSdk/03 sites to 96% on SBPSmc/01a sites. By 2007, live trees averaged between 90 and 329 stems/ha with subalpine fir contributing to stand structure on ESSFmc/03 and SBSmc2/01c plots and spruce contributing to stand structure on all plots (Table 2).

Overall, live stem density and basal area were lowest in the Entiako area and on SBSmc2/02 sites where lodgepole pine is the dominant species (Table 2). The SBSdk/03 and ESSFmc/03 contained the highest average densities of live trees > 7.5 cm dbh, and the ESSFmc/03 contained the highest basal area of live trees (Table 2).

Advance regeneration was highly variable within and between biogeoclimatic subzones/site series (Table 3). Average understory density on mountain pine beetle plots was highest on ESSFmc/03 plots and lowest on SBPSmc and SBSdk/03 plots. Regeneration on harvested plots, including planted trees, was similar to regeneration on mountain pine beetle plots. Lodgepole pine was the dominant understory tree species on all mountain pine beetle plots except for ESSFmc/03 plots where subalpine fir was dominant and lodgepole pine was the second most prevalent (Table 3). Subalpine fir was a minor component of the understory on SBSmc2/01c, SBSmc2/02 and SBPSmc/01b plots. Spruce was present on all mountain pine beetle plots and was most prevalent on SBSmc2/01c plots. Trembling aspen was a significant component of the understory on SBSdk/03 plots. Considerable growth of advance regeneration was observed on many plots (Figure 6).

Table 2. Average density and basal area of trees >7.5 cm dbh for each species for mountain pine beetle plots in the East Ootsa and Entiako areas in 2007.						
MPB Attack Plots	Average density (stems/ha)					Total Live
	N ¹	Fir	Spruce	Pine Not Attacked	Pine MPB Attacked	
<i>EAST OOTSA</i>						
ESSFmc/03	10	95	145	75	425	315
SBSmc2/01c	13	42	146	46	558	235
SBSmc2/02	7	0	43	93	586	136
SBSdk/03	7	0	50	279	986	329
<i>ENTIAKO</i>						
SBPSmc/01a	5	0	60	30	680	90
SBPSmc/01b	5	0	60	130	940	190
SBPSmc/02	5	0	10	70	750	80
Average basal area (m³/ha)						
<i>EAST OOTSA</i>						
ESSFmc/03	10	1.3	2.7	1.5	25.7	5.5
SBSmc2/01c	13	0.5	1.9	0.9	30.4	3.3
SBSmc2/02	7	0	0.5	1.6	25.9	2.1
SBSdk/03	7	0	0.5	3.1	22.9	3.6
<i>ENTIAKO</i>						
SBPSmc/01a	5	0	1.1	0.2	25.0	1.3
SBPSmc/01b	5	0	0.8	1.5	27.1	2.3
SBPSmc/02	5	0	0.05	0.7	20.6	0.8

Table 3. Average density of seedlings (0.1-1.3 m height) and saplings (0.1-7.5 cm dbh) combined on plots in the East Ootsa and Entiako areas, 2007.							
Plots	N ²	Regeneration (Stems/ha ¹)					Range
		Pine	Spruce	Fir	Aspen	Total	
<i>MOUNTAIN PINE BEETLE PLOTS</i>							
ESSFmc/03	10	1030	350	3450	5	4835	250-15100
SBSmc2/01c	13	1785	704	238	19	2746	350-7300
SBSmc2/02	7	2564	364	321	0	3250	200-8250
SBSdk/03	7	771	214	0	193	1179	250-3300
SBPSmc/01a	5	1930	430	0	20	2380	1900-3450
SBPSmc/01b	5	930	50	40	40	1060	500-2050
SBPSmc/02	5	1160	10	0	10	1170	600-2500
<i>HARVESTED PLOTS³</i>							
ESSFmc/03	4	4138	163	475	0	4775	900-7050
SBSmc2/01c	6	2542	283	8	0	2833	1250-6500
SBSmc2/02	4	1913	150	850	0	2913	1850-4800
SBSdk/03	7	1429	0	0	0	1429	200-4250

¹ all saplings in plot (7.98 m radius) counted; seedlings counted in a 3.99 m radius subplot; includes only "acceptable" trees

² N = number of permanent plots

³ Harvested plots include planted trees on some sites

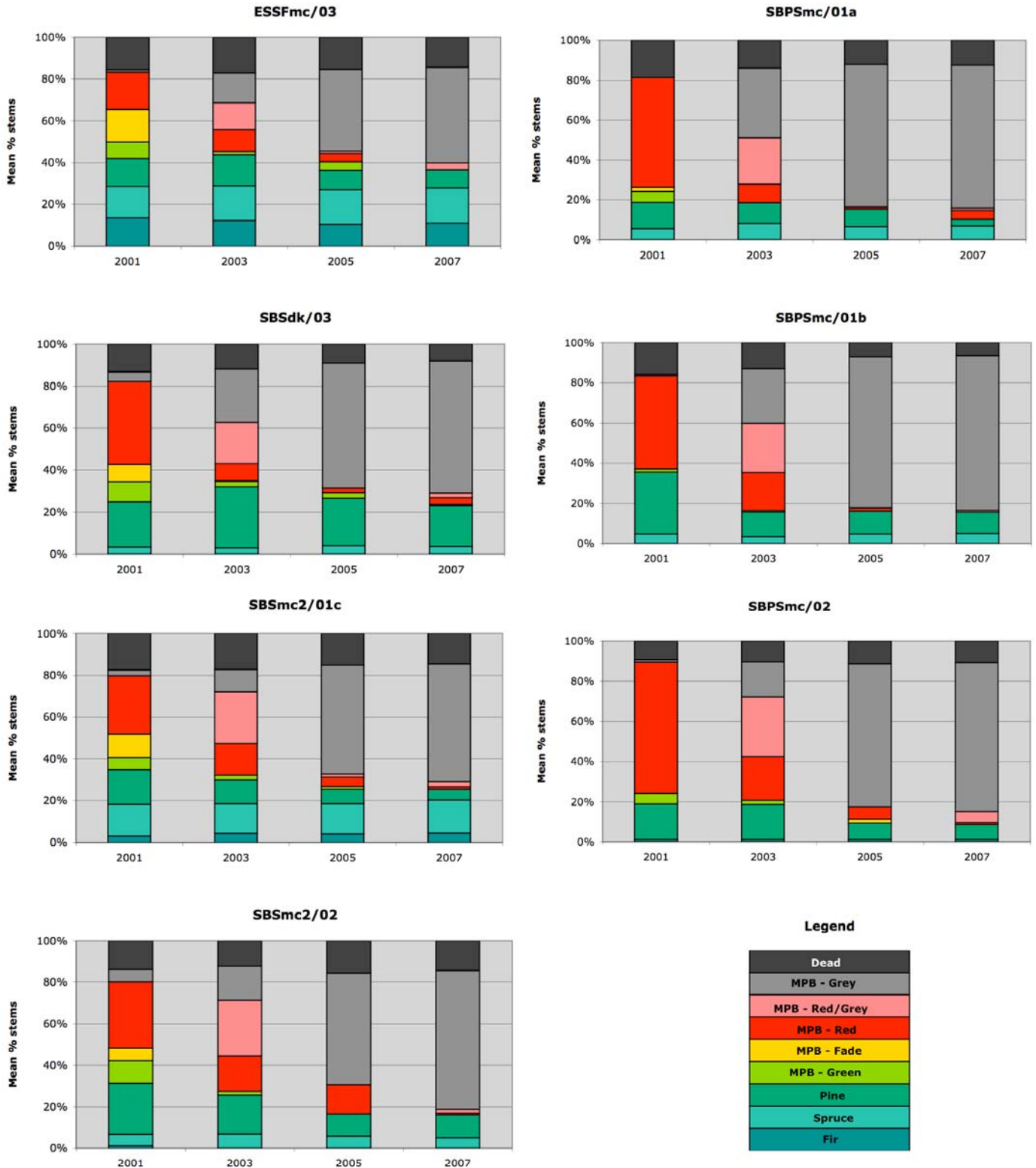


Figure 5. Average percent of trees >7.5 cm dbh in each species and mountain pine beetle attack class by biogeoclimatic subzone/site series in the East Ootsa and Entiako areas from 2001 to 2007.



Figure 6. Changes in understory vegetation and growth of advance regeneration on plot SBSmc2/01c-C10 from 2001 (top) to 2007 (bottom).

RESPONSE OF LICHENS TO FOREST DISTURBANCE

In 2001, *Cladina* lichen cover on photoplots averaged 16 % cover across all ecosystems and there was no difference in lichen abundance between unlogged forest sites affected by MPB and nearby clearcut-logged sites (Figure 7a, $p=0.42$). The SBSmc2/02 photoplots had significantly higher lichen cover both in the MPB affected forest and on clearcuts (21% on average) than the other three subzones/site series (14 % on average; $p=0.001$ for contrast). In 2004, a wildfire in the East Ootsa area burned through several SBSmc2/01c and SBSmc2/02 forested and clearcut plots. These sites have begun to recover some of their vascular plant

cover by 2007, but lichen and moss cover remain near zero percent (see lower panels in Figures 8-10). The burned plots are not included in the ANOVA results that follow.

By 2007, lichen cover had increased to 23% overall on clearcut sites, but decreased to 10% overall on forest sites affected by MPB (Figure 7b). This difference was highly significant ($p < 0.001$). In 2007, the SBSmc2/02 and the ESSFmc/03 had significantly more lichen cover than the SBSdk/03 and the SBSmc1/01c ($p = 0.001$ for between-group contrast; $p \geq 0.60$ for within-group contrasts). Surprisingly, although lichens were responding quite differently in MPB affected forests than in clearcuts, the relative abundance by subzone/site series was the same in the MPB affected forest as it was in clearcuts ($p = 0.84$ for ecosystem \times disturbance interaction). The difference between lichen abundance in MPB affected forests and in clearcuts is further discussed in the section “Patterns of Ground-layer Vegetation Change from 2001 to 2007: Clearcuts”.

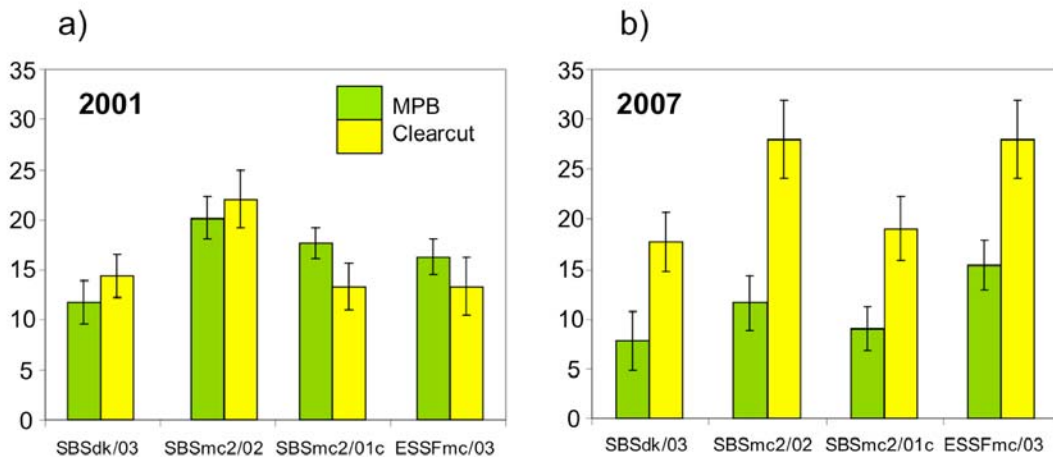


Figure 7. Differences in lichen cover by site series between unlogged MPB-affected pine forests and logged clearcuts in (a) 2001 and (b) 2007. Error bars are + 1 S.E.

PATTERNS OF GROUND-LAYER VEGETATION CHANGE FROM 2001 TO 2007: MPB FORESTS

Over the entire study, including SBPSmc sites, lichen abundance on MPB affected forested ecosystems declined from 16% in 2001, to 13% in 2003, to 11% in 2005 to 10% in 2007 (Figure 8a). Although there was a highly significant decline in lichen abundance over this time period (linear trend = 89% of explained variability, $p < 0.001$), the rate of decline leveled off significantly after 2005 (quadratic trend = 11% of explained variability, $p < 0.001$). Among ecosystems, however, the shape of the trend was inconsistent (Figure 8a; $p < 0.001$ for ecosystem \times time interaction). Most notably, the ESSFmc/03 differed from other site series in that there was no change in lichen abundance between 2001 and 2005, but a significant ($p = 0.03$) decrease in lichen abundance between 2005 and 2007. In the SBSmc2/01c, lichen

decline continued at the same rate as from 2001 to 2005 ($p=0.11$). In all of the other subzones/site series, the rate of lichen decline leveled off significantly from 2005 to 2007 ($p<0.05$).

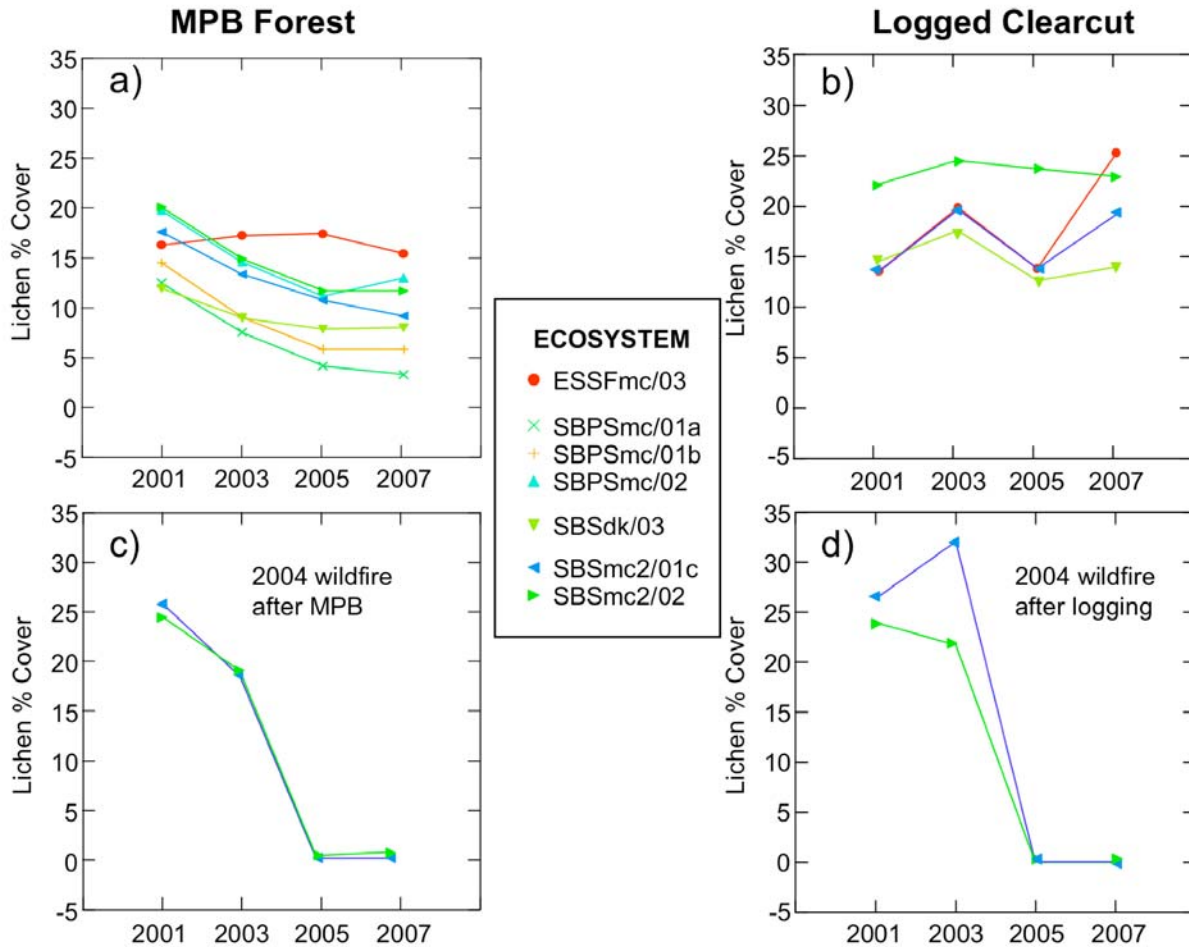


Figure 8. Changes in *Cladina* lichen abundance following mountain pine beetle, forest harvesting and fire disturbance in the East Ootsa and Entiako areas (2001-2007).

The behaviour of competing ground-layer vegetation species, particularly kinnikinnick, helps to understand the lichen results. The anomalous ESSFmc/03 sites had less than 2% kinnikinnick cover and there was no change in kinnikinnick abundance between 2001 and 2007 (Figure 9a). All other subzones/site series averaged 20-40% kinnikinnick cover in 2001 and experienced a doubling of kinnikinnick cover (to 30 – 60+ %) by 2007 (linear trend = 93% of explained variance, $p<0.001$). On average, the rate of increase in kinnikinnick cover leveled off slightly between 2005-2007 (quadratic trend = 7 % of explained variation, $p<0.001$), but no leveling off was evident on SBSdk/03 and SBSPmc/02 sites.

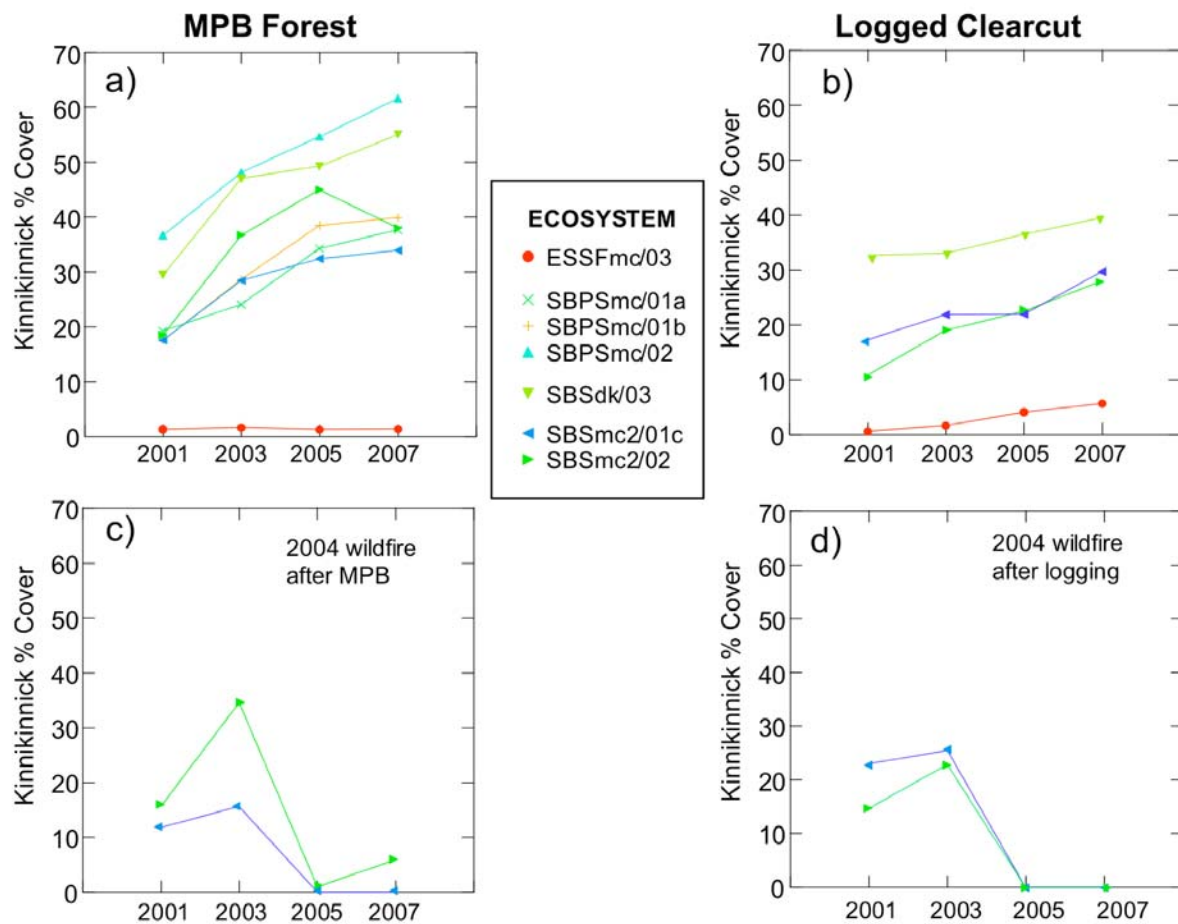


Figure 9. Changes in kinnikinnick abundance following mountain pine beetle, forest harvesting, and fire disturbance in the East Ootsa and Entiako areas (2001-2007).

A number of factors may be contributing to the different pattern of lichen abundance in the ESSF. The mosses and crowberry that grow at higher elevations in the ESSF are less aggressive and slower growing plants than kinnikinnick, and are less able to take advantage of increasing resource availability after mountain pine beetle attack. Also, the ESSFmc/03 has the highest basal area of live trees (see Table 2). These live trees may be absorbing a greater proportion of the additional resources freed up by the dead MPB trees, than live trees in other ecosystems. Also, green and faded attack made up a greater proportion of attacked trees in the ESSF in 2001 than in other ecosystems, suggesting that the stage of the MPB epidemic may have been slightly behind the stage of attack in other ecosystems, resulting in a delay in the decrease in lichen abundance.

Ground-layer species other than kinnikinnick were also correlated with patterns of lichen decline. In the ESSFmc, a sharp increase in mosses, and moderate increases in crowberry and twin-flower from 2005 to 2007 (Figures 10a, 11a) matched the decline in lichen cover during the same time period (Figure 8a). In the SBSmc2/01c, where kinnikinnick growth began to level off in 2005 (Figure 9a), total ground layer vegetation continued to increase in a linear fashion (Figure 11a) that corresponded well with the linear decline in lichen on this site series (Fig 8a). This increase was mainly due to twin-flower.

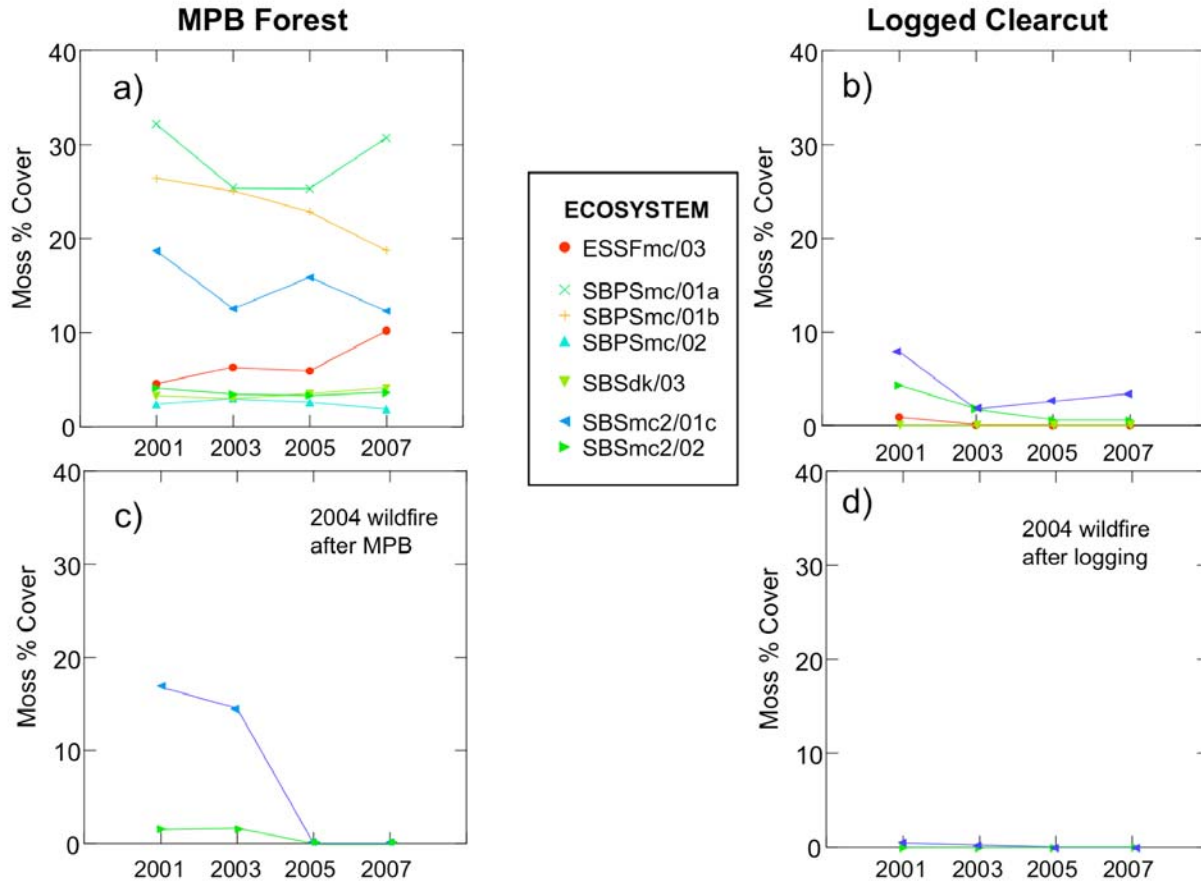


Figure 10. Changes in moss abundance following mountain pine beetle, forest harvesting, and fire disturbance in the East Ootsa and Entiako areas (2001-2007).

Except in the ESSFmc, there were no significant changes in moss abundance in MPB-affected forests between 2001 and 2007 (Figure 10a, $p=0.12$). In the SBS and SBPS, lichen declines were more closely correlated with increases in vascular species than with changes in the abundance of mosses.

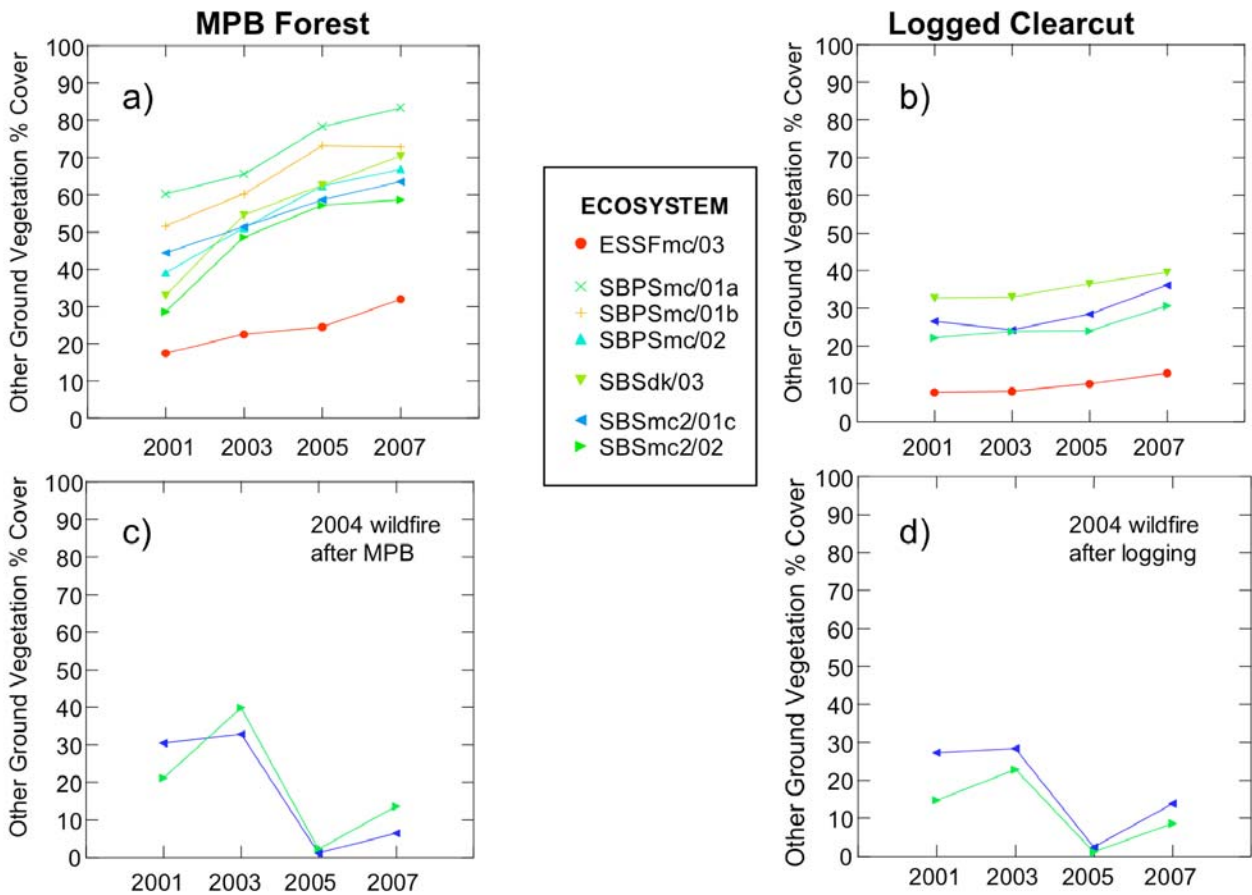


Figure 11. Changes in abundance of major non-lichen ground-layer species (kinnikinnick + crowberry + twin-flower + moss) following mountain pine beetle, forest harvesting, and fire disturbance in the East Ootsa and Entiako areas (2001-2007).

Throughout the study area kinnikinnick abundance showed an overall pattern of increasing in abundance then leveling off, although the timing of the peak of kinnikinnick abundance was different on different plots and photoplots (and, as mentioned, the ESSFmc/03 demonstrated an exception to this pattern). Figure 12 shows changes in forest floor vegetation for two photoplots. The photoplot on the left shows a steady increase in kinnikinnick abundance from 2001 to 2007, whereas the photoplot on the right shows an increase in kinnikinnick abundance from 2001 to 2005, then a decrease or die-back of kinnikinnick between 2005 and 2007. On some plots, die-back was quite extensive (Figure 13), but mostly it was localized in small patches.

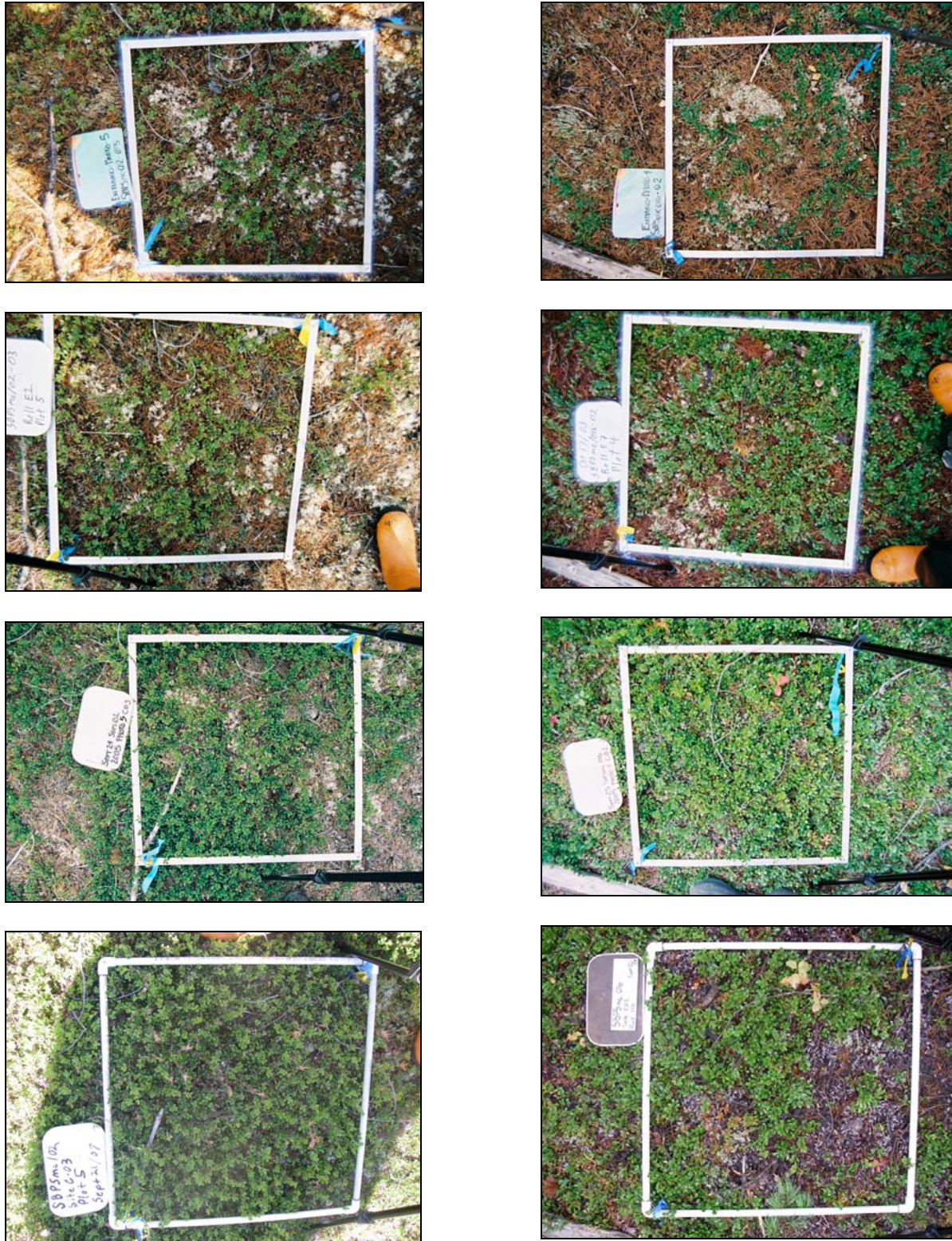


Figure 12. Examples of an increase in kinnikinnick from 2001 to 2007 (left) and an increase in kinnikinnick from 2001 to 2005 and then dieback from 2005 to 2007 (right). Photos are from 2001 to 2007 from top to bottom.



Figure 13. Extensive kinnikinnick mortality at plot SBPSmc/02-C03 in the Entiako area, September 2007.

The precise cause of the dramatic increase in kinnikinnick cover is not known, but is likely due to the increased availability in resources (light, nutrients and water) corresponding to the death of the canopy caused by MPB. It is more challenging to explain why kinnikinnick appears to be dying-back in some of the photoplots. There are at least three possible explanations: 1) the rapid spread of a pathogen such as a fungus; 2) a life history that includes basal mortality; and, 3) the exhaustion of extra short-term resources relating to the canopy death and absence of continued needle litter. Although a pathogen may be the cause of the observed kinnikinnick die-back, we do not have data to support this hypothesis. Over the course of the study we have observed basal mortality in kinnikinnick stems that continued to regenerate from living branch-tips, and yet many colonies persist without obvious signs of basal senescence and death. Several observations support the third hypothesis and suggest that continual nutrient inputs (needle litter) may be important for the growth of kinnikinnick on edaphically poor sites. For example, kinnikinnick often forms circular colonies (skirts) in the high needle litter deposition zone beneath live lodgepole pine trees. The rapid expansion of kinnikinnick in the study area following mountain pine beetle attack corresponds to both the increased availability of resources and the massive needle deposition by canopy trees killed by MPB. It is possible that the needle-pulse combined with the increase in available nutrients have allowed kinnikinnick to expand beyond its ‘skirt’ at the base of trees, into

areas normally too poor in nutrients to support kinnikinnick. Now that needle deposition throughout the study area is slowing down, and in some areas has completed stopped, the extra nutrient pulse that may have allowed kinnikinnick to establish in marginal habitats is no longer available, resulting in a slowing of kinnikinnick growth or even die-back. In many instances, dead kinnikinnick plants reveal the remnants of lichen colonies that were buried in foliage, allowing opportunities for lichen recovery. In several photoplots, substrates exposed by dead kinnikinnick have been colonized by twin-flower.

Most importantly, the ecosystem shift to kinnikinnick does not appear to be a lock-step mechanism; kinnikinnick die-back, regardless of the cause, assures that on many sites the shift to kinnikinnick may be at least partially reversible. In general, however, there are few foreseeable scenarios that would cause a significant increase in the abundance terrestrial forage lichens following MPB attack. Kinnikinnick die-back may cause the loss of lichen abundance to slow or plateau, but it will probably not cause an increase in lichen cover at the landscape level. Large-scale fire disturbance may create habitats suitable for the reproduction and growth of lichens at the landscape level, but vegetation recovery after fire has become complicated by climate change and it is increasingly difficult to predict the plant communities of the future.

PATTERNS OF GROUND-LAYER VEGETATION CHANGE FROM 2001 TO 2007: CLEARCUTS

The four-year trends in lichen abundance on clearcuts (Figure 8a) indicate that the pattern of lichen development is more complex than is suggested by the 2001 to 2007 comparison shown in Figure 7. Lichen cover averaged 15% in 2001, rose to 20% in 2003, then dropped back to 15% in 2005 and increased to 22% in 2007. Across the four site series, there was a highly significant upward trend over the 6-year monitoring period (linear trend = 44% of explained variance, $p=0.003$), but year-to-year oscillations were even more significant (cubic trend = 55% of explained variance, $p<0.001$). Due to the high variability, there were no significant differences among ecosystems ($p=0.21$) and no significant differences in time trends by ecosystem ($p=0.26$).

By comparison, trends in kinnikinnick (Figure 9b), moss (Figure 10b) and all non-lichen ground layer vegetation (Figure 11b) were more straightforward. Kinnikinnick and all vegetation had parallel linear increases (83-99% of explained variation, $p \leq 0.01$) across all four site series (ecosystem x time interaction: $p=0.15$ for kinnikinnick, $p=0.97$ for all vegetation). Moss cover on clearcuts averaged 1.5 % and did not differ significantly by ecosystem ($p=0.24$, by time period ($p=0.08$) or over time among ecosystems ($p=0.58$).

With a boundary layer smaller than found in forests, clearcuts are exposed to greater temperature and moisture extremes. Clearcuts can be hotter, colder, wetter and drier than adjacent forests, even MPB affected forests, and this broad variation in site conditions may help explain the variation in the lichen abundances recorded in cutblocks. Lichen colonies often appear larger when wet than when dry. The 2003 and 2007 sampling seasons coincided with rain events, while in 2001 and 2005, the prevailing weather conditions were somewhat

drier. This effect was not observed in MPB affected forests, likely due to the presence of standing dead and live trees that moderated the effects of the dry conditions in 2001 and 2005.

PREDICTIVE MODELS OF LICHEN ABUNDANCE

Eight variables together explained 66% of the total variability in percent cover of lichens on photoplots in 2007 ($n = 728$, $p < 0.001$, Table 4a). The burned plots, which had virtually no lichen cover, accounted for 26% of total variance. With these plots taken into consideration, the abundance of all other ground vegetation (kinnikinnick, mosses, twin-flower and crowberry) was the single best predictor of lichen abundance, accounting for 32% of total variance. Interestingly, non-lichen cover in 2005 was a better predictor of 2007 lichen cover, than non-lichen cover in 2007; however, twin-flower cover in 2007 provided an extra 2% of explanatory power, presumably because it was negatively correlated with changes in lichen abundance in the ESSFmc/03 and SBSmc1/01c. Blowdown on photoplots and higher MPB basal area both had a minor additional negative effect on lichen abundance. ESSF sites, higher elevations and subxeric site conditions all had minor positive effect on lichen abundance. Logged vs. forested sites were differentiated indirectly in this model by means of the % non-lichen vegetation and the MPB basal area variables, both of which were significantly lower on clearcuts than in forests.

The regression model for changes in lichen abundance between 2001 and 2007 had a total of 11 variables that together explained 63% of the total variance ($n = 728$, $p < 0.001$, Table 4b). In this model, a negative correlation indicates a larger decline in lichen cover. Burning and % cover (plus 2001 to 2005 change in cover) of non-lichen vegetation once again explained the lion's share of the variability (80% of explained variation) and both were strongly associated with declines in lichen abundance. The more MPB mortality, the greater the decrease in lichen cover (6% explanatory power over-and-above the increase in competing vegetation). Once the effect of MPB mortality was taken into account, shading of photoplots by blowdown, live, or dead standing trees, had a negative effect on lichen cover, whereas greater light conditions had a positive effect. The unidentified and aspen snags appear to be mainly a spurious correlation linked to single sites with abnormally rapid rates of kinnikinnick growth.

The final regression model (Table 4c) examines changes in lichen abundance between 2005 and 2007. Our interest here is to determine whether abiotic or stand factors can shed some light on the leveling-off phenomenon observed on most forest sites after 2005 and the anomalous behaviour of the ESSFmc sites. This model had much less predictive power than the two previous models, with 10 variables explaining only 34% of total variation. Most of the difference is due to the fact that burned sites (which accounted for 26-27% of the variability in Models 1 and 2) had essentially no change in lichen cover between 2005 and 2007. In this model, differentiating between logged sites (which tended to increase in lichen cover after 2005) and forested sites (which tended to decrease in lichen cover), accounted for 19% of total variation. Northerly sites experienced a greater decline in lichen abundance after 2005 than southerly sites (1.2 % explanatory power). Competing vegetation had only

Table 4. Multiple regression models for lichen abundance.					
Response Variable	Explanatory Variables				
	Variable	Correlation¹	p-value	% variance explained	
				Extra fit(r²)	Total fit (R²)
a) 2007 lichen percent cover (square root transformed) n = 728	Burned = 1 Unburned = 0	-0.43	< 0.001	--	26.1
	% all non-lichen veg 2005	-0.40	< 0.001	32.1	58.2
	% Twin-flower 2007	-0.22	< 0.001	2.0	60.2
	Blowdown = 1 no blowdown = 0	-0.08	< 0.001	2.2	62.4
	ESSF = 1 other zones = 0	0.23	< 0.001	1.1	63.5
	Elevation (m)	0.20	< 0.001	1.1	64.6
	Subxeric = 1 Submesic = 0	0.19	< 0.001	0.9	65.5
	BA MPB 2005 ²	-0.18	0.001	0.6	66.1
	Equation: $Y^{1/2} = 2.25 - 5.41(\text{burned}) - 0.039(\text{Veg05}) - 0.018(\text{Twin07}) - 1.26(\text{Blwdn}) - 1.5(\text{ESSF}) + 0.003(\text{elev.}) + 0.45(\text{Subxeric}) - 0.014(\text{BAMPB05})$				
b) Change in lichen percent cover (2001-2007) (untransformed) n = 728	Burned	-0.47	< 0.001	--	27.5
	% all non-lichen veg 2007	-0.26	< 0.001	19.9	47.4
	BA MPB 2005 ²	-0.22	< 0.001	6.4	53.8
	Blowdown	-0.09	< 0.001	2.0	55.8
	% change non-lichen veg 2001-05	-0.17	< 0.001	2.3	58.1
	BA unidentified snags	-0.21	< 0.001	1.2	59.3
	BA aspen snags	-0.17	< 0.001	0.9	60.2
	Canopy ³	-0.21	0.003	0.5	60.7
	Light trans % 2003	0.39	< 0.001	0.8	61.5
	Standing BA	-0.26	0.001	0.8	62.3
	% change Crowberry 2001-05	-0.12	< 0.002	0.6	62.9
Equation: $Y = -35(\text{burned}) - 0.099(\text{Veg07} + \text{Veg01-05}) - 0.44(\text{BAMPB05}) - 9.1(\text{Blowdn}) - 29(\text{BAASnag}) - 1.8(\text{BAUSnag}) + 0.73(\text{Canopy}) + 0.16(\text{Light Trans \%}) + 0.38(\text{standing BA}) - 0.14(\text{Crowberry 01-05})$					
c) Change in lichen percent cover 2005- 2007 (untransformed) n = 728	Logged	0.41	< 0.001	--	19.2
	BA unidentified snags	0.24	< 0.001	3.8	23.0
	BA blowdown 2005	-0.18	< 0.001	2.0	25.0
	BA dead fir 2007	-0.10	0.004	1.3	26.3
	Latitude	-0.04	< 0.001	1.2	27.5
	% all non-lichen veg 2007	-0.26	< 0.001	1.5	29.0
	Regen sph ⁴ 2007	-0.14	0.002	1.1	30.1
	Light interception % 2007	0.32	< 0.001	1.3	31.3
	Light trans % 2005	0.38	0.015	1.4	32.7
	% kinnikinnick 2003	0.01	< 0.001	1.3	34.0
Equation: $Y = 530 - 4.5(\text{logged}) + 1.4(\text{BA unid. snag}) - 1.8(\text{BA blowdown} + \text{BA dead Fir}) - 9.9(\text{lat.}) - 0.05(\text{Veg07}) - 0.001(\text{Regen sph}) - 0.09(\% \text{ Light interception}) + 0.07(\% \text{ Light trans 05}) + 0.03(\text{Kinn 03})$					

¹ Raw correlations, not adjusted for factors previously added to the model.

² Basal area (BA) of lodgepole pine trees per hectare (m²/ha) killed by mountain pine beetle

³ Canopy tree immediately above photoplot (status in 2001): 0 = open, clearcut, 1 = no tree, forest; 1 = old snag; 2 = gray attack; 3 = red attack; 4 = faded green attack; 5 = green attack; 6 = live pine 7 = live spruce or subalpine fir

⁴ sph = stems per hectare

2.8% explanatory power in this model, which suggests that the surge in competing vegetation after MPB mortality has now run its course. Of particular interest is the fact that changes in light transmission or interception between 2005 and 2007 had a significant effect on changes in lichen abundance, suggesting that the increased light levels associated with the later stages of MPB mortality may now be beginning to create more favorable conditions for lichen recovery. The unidentified snags, dead fir and regeneration are again believed to be spurious correlations related to a few anomalous sites, but may also reflect differences in shading on lichen response.

VEGETATION COMPOSITION FOLLOWING FIRE

In August 2004, a wildfire burned several hundred hectares on the south side of the Blanchet Main Road, just south of the Chelaslie River. In the process, 4 of our mountain pine beetle plots and 2 of our logged plots were burned. Table 5 summarizes regeneration and vegetation cover on those plots, 3 years following the fire.

New pine and spruce seedlings have started to establish on burned plots. On 4 of the 6 plots, pine >10 cm were recorded. Pine was the most abundant species on all plots; spruce was present only on the partially burned plot. Regeneration was generally more abundant on burned MPB plots than on burned logged plots.

The dominant vegetation species on fully burned sites were *Linnaea borealis* (twin-flower), *Vaccinium caespitosum*, *Vaccinium membranaceum*, *Shepherdia canadensis*, *Carex* sp., *Epilobium angustifolium* and *Cornus canadensis*. Although kinnikinnick was largely absent from burned plots in 2005, some resprouting was observed in 2007 and kinnikinnick cover on the partially burned plot was 30%. Originally, we expected that kinnikinnick would be consumed during fire disturbance and that it would have to re-establish through seed dispersal. Twin-flower had the most aggressive growth form with numerous stems radiating out from a central point in a starfish pattern (Figure 14).

GROWTH RATES

A comparison of growth rates of red-stemmed feathermoss and *Cladina* is provided in Figure 15. Rates for kinnikinnick are shown in Figure 16. Lichen growth rate was generally constant from 2002 to 2007 on each of the 3 microsites, and was highest in canopy gaps and lowest in clearcuts. Moss growth rates were about twice that of lichen growth rates. Initially, moss growth rates were lowest under canopy trees and in cutblocks but increased on both microsites by 2005. On most sites, red-stemmed feathermoss experiences die-back or reduced growth after forest harvesting, a result of the sudden exposure to high light levels and a reduction in forest floor humidity. The increase in moss growth in the recently opened cutblock, suggests that the effects from exposure may be ameliorated, potentially by a landscape level increase in water table. Under the canopy tree, the growth rate for moss in this microsite increased from 4.6 mm/yr in 2003 to 8.9 mm/yr in 2004 and 2005 ($p=0.0002$), the same rate of growth as found under a canopy gap. This suggests that growing conditions

under a dead canopy tree have shifted to approximate conditions found in a canopy gap, at least for red-stemmed feathermoss.

Table 5. Regeneration and vegetation cover in 2007 for 6 permanent plots in the East Ootsa area that were burned by a wildfire in August 2004.

	Mountain pine beetle plots				Harvested plots	
	SBSmc2/01c C04	SBSmc2/02			SBSmc2/01c L03	SBSmc2/02 L01
		C01	C02	C05		
Extent of burn	All	All	All	Partial	All	All
REGENERATION (stems/ha based on 5 m² plot)						
Pine germinants		200	200	1400		
Spruce germinants				200		
Pine 0-10 cm tall	600	3400	1200	3800		800
Spruce 0-10 cm tall				1400		
Pine 10-30 cm tall		3800	1200		1400	200
PERCENT COVER VEGETATION						
<i>Salix</i> sp.	1			<1		
<i>Shepherdia canadensis</i>	3	1		3	5	1
<i>Rosa acicularis</i>	<1					<1
<i>Spiraea betulifolia</i>	4					
<i>Amelanchier alnifolia</i>		<1				
<i>Actostaphylos uva-ursi</i>		1	1	30	<1	
<i>Vaccinium membranaceum</i>	1		<1			25
<i>Vaccinium caespitosum</i>	18	2	4	4	2	2
<i>Linnaea borealis</i>	4	15	10	35	20	
<i>Empetrum nigrum</i>				1		
<i>Cornus canadensis</i>	1	2	1	1	2	1
<i>Arnica cordifolia</i>						<1
<i>Lupinus arcticus</i>	1		<1		1	
<i>Epilobium angustifolium</i>	1	4	1	7	1	<1
<i>Epilobium ciliatum</i>			<1			
<i>Achillea millefolium</i>			<1		1	
<i>Erigeron peregrinus</i>	<1				<1	
<i>Pyrola chlorantha</i>				<1		
<i>Hieracium</i> sp.				<1		
<i>Taraxacum officinale</i>		<1		<1	<1	<1
<i>Calamagrostis Canadensis</i>	1	<1		1	1	
<i>Oryzopsis pungens</i>		1	1	<1	2	<1
<i>Agrostis scabra</i>		<1		<1		1
<i>Carex</i> sp.	3	2		<1	<1	2
<i>Pleurozium schreberi</i>				1		
<i>Polytrichum juniperinum</i>	<1	<1	<1	1		
<i>Lycopodium complanatum</i>	<1					
<i>Cladina mitis</i>				<1		
<i>Cladina rangiferina</i>				1		
<i>Cladonia</i> sp.				<1		
<i>Cetraria</i> sp.				<1		
<i>Peltigera</i> sp.				<1		



Figure 14. Growth of twin-flower on a burned plot in the East Ootsa area, 3 years following fire.

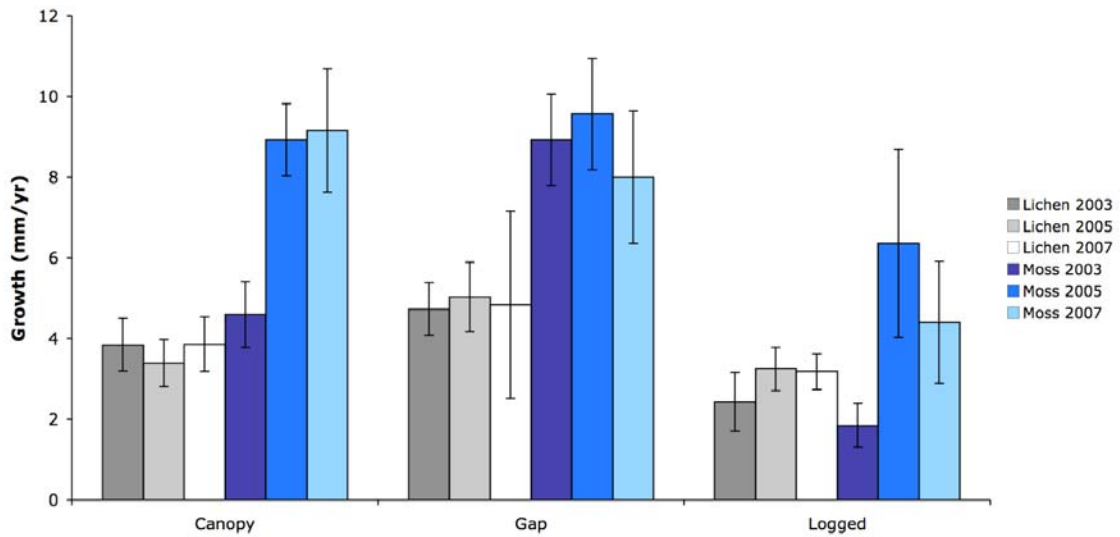


Figure 15. Average annual growth rates for red-stemmed feathermoss and *Cladina* in a gap, under a canopy tree and in a cutblock from 2002 to 2007 on an SBSmc2/01c site in the East Ootsa area. Error bars = ±1 standard error.

The growth rate of kinnikinnick is an order of magnitude greater than rates for mosses or lichens (approximately 80 mm/yr versus 8 mm/yr); however, kinnikinnick also has a high rate of mortality, which may explain why it does not completely displace its forest floor competitors. Our methods may have contributed to some of the variability in kinnikinnick growth rates. We chose stems with long shoots and then continued to measure the current year's growth on the same stem; subsequent growth was often less than the initial growth measured on the stem. When stems died, we replaced tags on long shoots. Therefore, growth rates may have varied depending on how much mortality occurred and how many new stems were added to the sample.

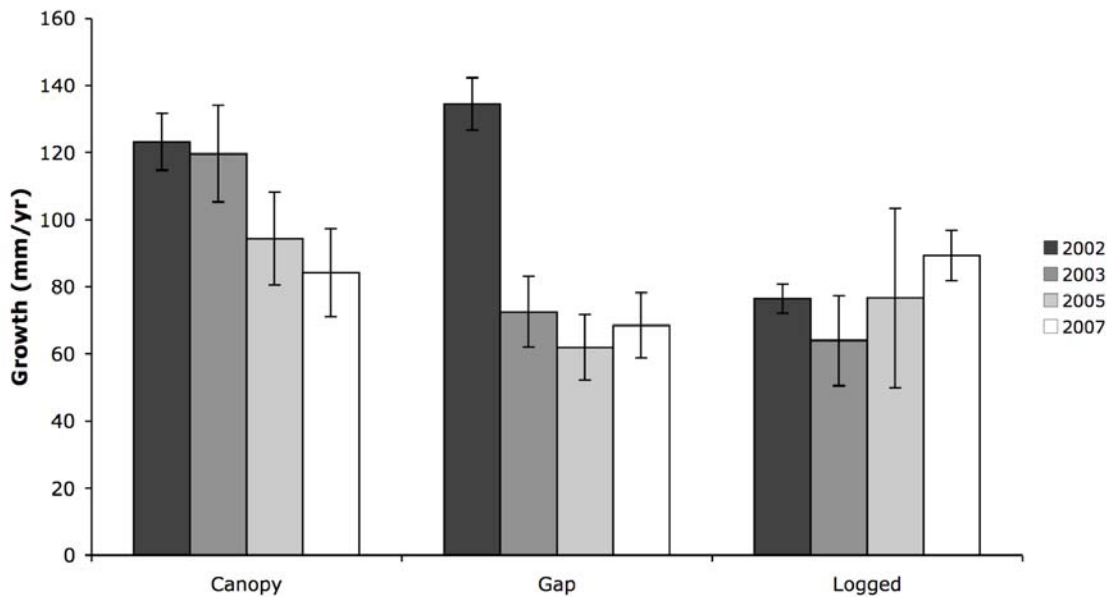


Figure 16. Growth rate of kinnikinnick in a gap, under a canopy tree and in a cutblock from 2002 to 2007 on an SBSmc2/01c site in the East Ootsa area.
Error bars = ± 1 standard error.

TRANSPLANT EXPERIMENT

In a MPB affected stand, the growth of feather moss is favoured over the growth of caribou forage lichens. By following transplants over six growing seasons, we observed mosses expanding when transplanted into lichen colonies, while lichens diminished when transplanted into moss colonies (Figure 17). This pattern probably reflects an increase in moisture availability in forests affected by MPB (the canopy trees no longer pump soil water into the atmosphere). Wetter conditions favour mosses over lichen. The interactions observed in our transplant experiment are occurring at a landscape level. Figure 10 shows moss cover increasing over time in several of the site series examined in this study. Declines

in moss cover on other sites are attributed to the rapid expansion of kinnikinnick, an ecological shift that may be reversing. In contrast, the growth of moss is not expected to reverse, even when the canopy eventually re-establishes and the canopy trees resume pumping water into the atmosphere. Shading by developing canopy trees and the natural water retaining capacity of mosses will likely provide sufficient humidity to allow mosses to continue to expand for many years after the MPB epidemic.

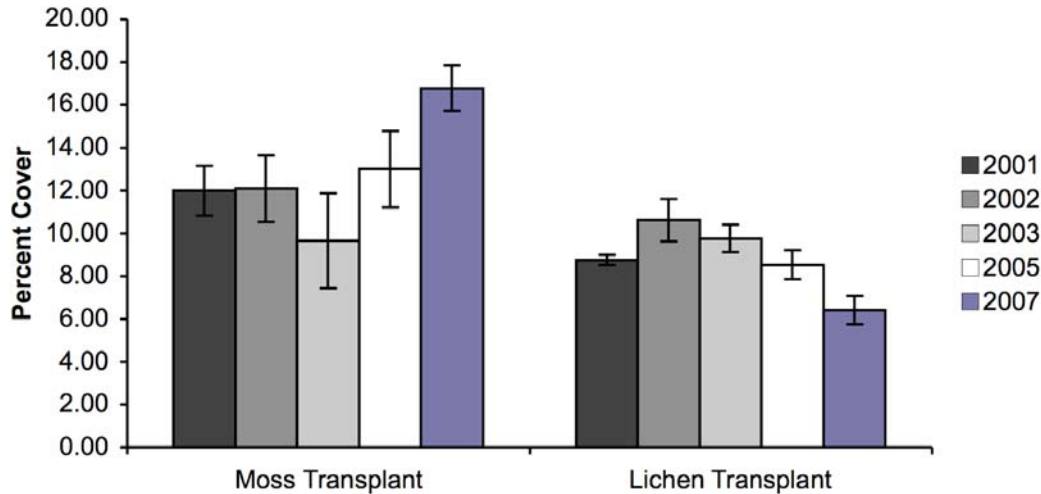


Figure 17. Percent cover of red-stemmed feathermoss and caribou forage lichens in transplanted photoplots on an SBSmc2/01c site in the East Ootsa area from 2001 to 2007. Error bars = ± 1 standard error.

KINNIKINNICK PHOTOPLOTS

Kinnikinnick abundance decreased in five plots situated beneath MPB-killed trees. The cover of kinnikinnick in these plots has diminished from 55% to 22% in five years (Figure 18). Two explanations may be responsible for this decline.

Kinnikinnick is often associated with the litter deposition zone of lodgepole pine trees, especially in edaphically poor habitats. The litter deposition zone of a lodgepole pine tree can be characterized by supporting a continuous rain of needles, reduced incident precipitation, lower light levels, and low canopy tree root-tip density (root-tips become more dense in the soil as you move away from the tree stem, up to a point). Even trees that lean dramatically to one side often support kinnikinnick colonies that correspond to the area traced by the tree canopy. Needle deposition may be important to kinnikinnick health, at least where nutrients are limiting. In drier non-forested plant communities where the distributions of plants are limited more by the availability of water (and less by nutrients), such as the south aspects of ridges, kinnikinnick grows independently of needle litter.

Another possible explanation is that the decrease in kinnikinnick abundance is linked to a landscape level increase in the water table, which is particularly noticeable over morainal till landforms, including the site where these photoplots were established. On many till sites, ponded water was present in 2005 and in 2007 in places that did not have water in previous years. Kinnikinnick may not be able to tolerate these wetter site conditions.

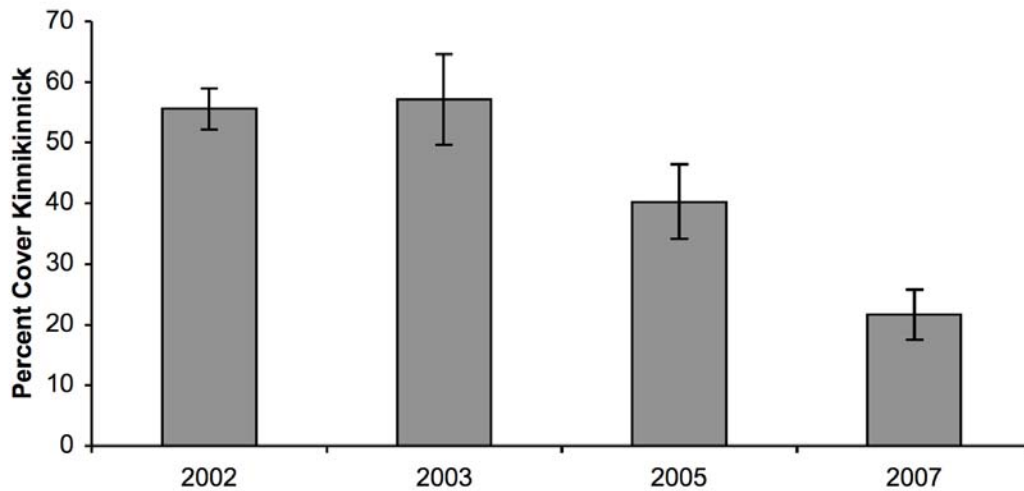


Figure 18. Percent cover of kinnikinnick under mountain pine beetle-killed canopy trees on an SBSmc2/01c site in the East Ootsa area from 2002 to 2007. N=5 for each year. Error bars = ± 1 standard error.

COARSE WOODY DEBRIS

We measured coarse woody debris on plots to assess whether mountain pine beetle and forest harvesting disturbances could impact caribou habitat use by impeding caribou movement (mobility). On harvested sites, increased accumulation of coarse woody debris is the result of slash left on the site and is not expected to increase over time, whereas on mountain pine beetle attacked sites, coarse woody debris is expected to accumulate over time as a result of blowdown of beetle-killed trees.

Overall, coarse woody debris volume, mass and density for mountain pine beetle plots were similar for all 4 years sampled on all biogeoclimatic subzones/site series (Figure 19). Coarse woody debris generally increased slightly or remained constant on most sites except for the ESSFmc/03 and SBSmc2/02 sites where it decreased slightly. The decrease is likely due to Decay Class 5 logs (on the ground and soft) that were overgrown by vegetation or that were otherwise incorporated into the forest floor. This was reflected in a decrease in the number of Decay Class 5 logs and Mobility Class 0 logs (Figure 20). Coarse woody debris volume and mass was generally greatest on ESSFmc plots, followed by SBSmc2 and SBSdk plots.

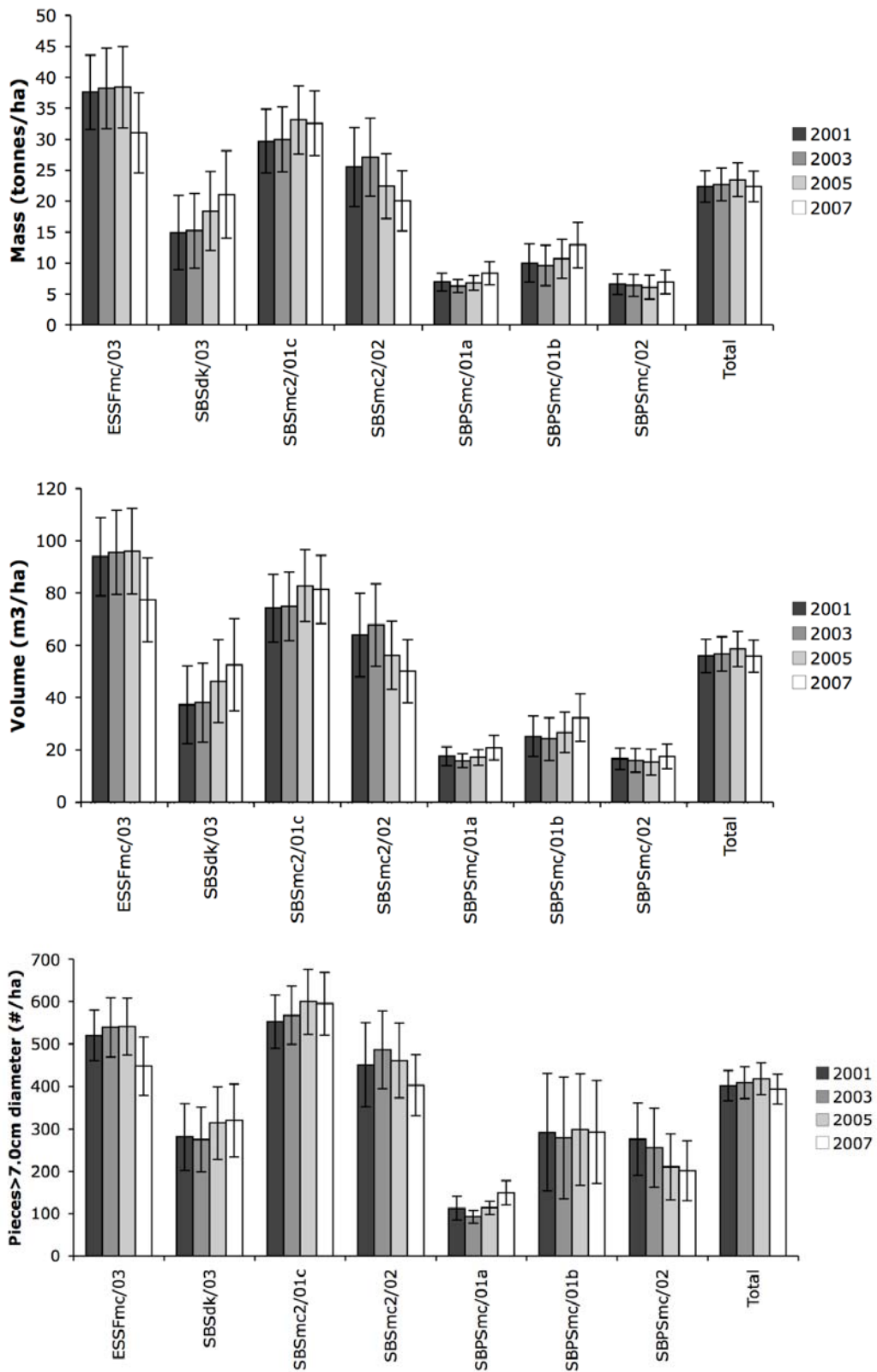


Figure 19. Mean volume, mass and pieces of coarse woody debris by biogeoclimatic zone and year in the East Ootsa and Entiako areas, 2001-2007.

Error bars = ±1 standard error.

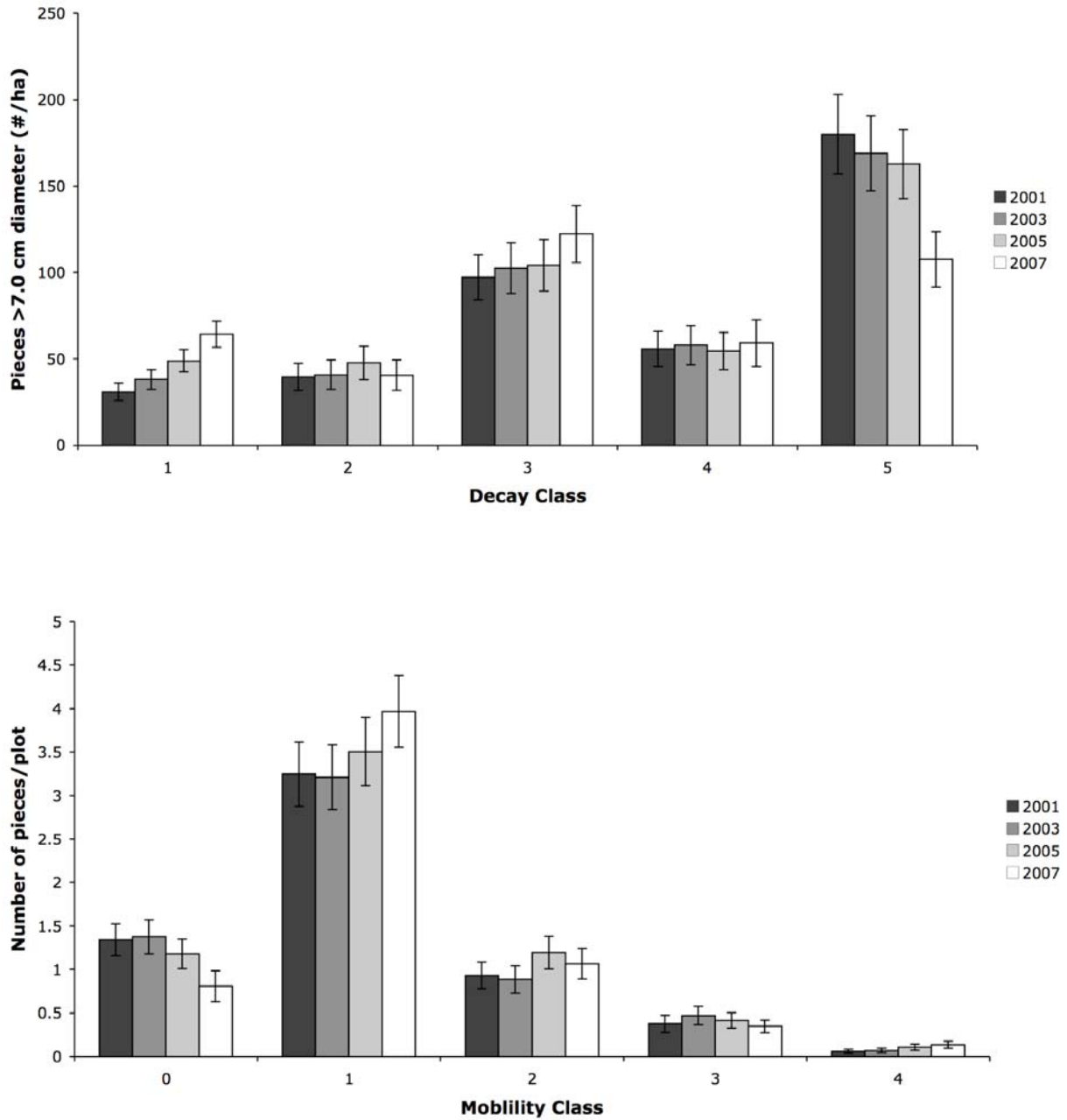


Figure 20. Mean pieces of coarse woody debris on mountain pine beetle plots in each decay class and mobility class by biogeoclimatic zone and year in the East Ootsa and Entiako areas, 2001-2007. Error bars = ±1 standard error.

Decay Class and Mobility Class of coarse woody debris pieces indicate that most coarse woody debris pieces are presently in the later stages of decay and have little effect on mobility with most pieces in Decay Class 5 and Mobility Class 1 or 0 (Figure 20). There was a slight increasing trend in Decay Class 1 (fresh blowdown) from 2001 to 2007, suggesting that a limited amount of blowdown is occurring each year but that that large-scale blowdown of mountain pine beetle attacked trees has not yet occurred.

Overall Mobility Index has generally increased gradually from 2001 to 2007 (Figure 21). The Mobility Index pattern appears to be similar to the pattern of volume and mass of coarse woody debris, except on ESSFmc plots. Mobility Index on ESSFmc plots is lower than on SBSmc2/01c plots, whereas volume and mass are higher, suggesting that elevation of coarse woody debris (off the ground) on ESSFmc plots is generally low.

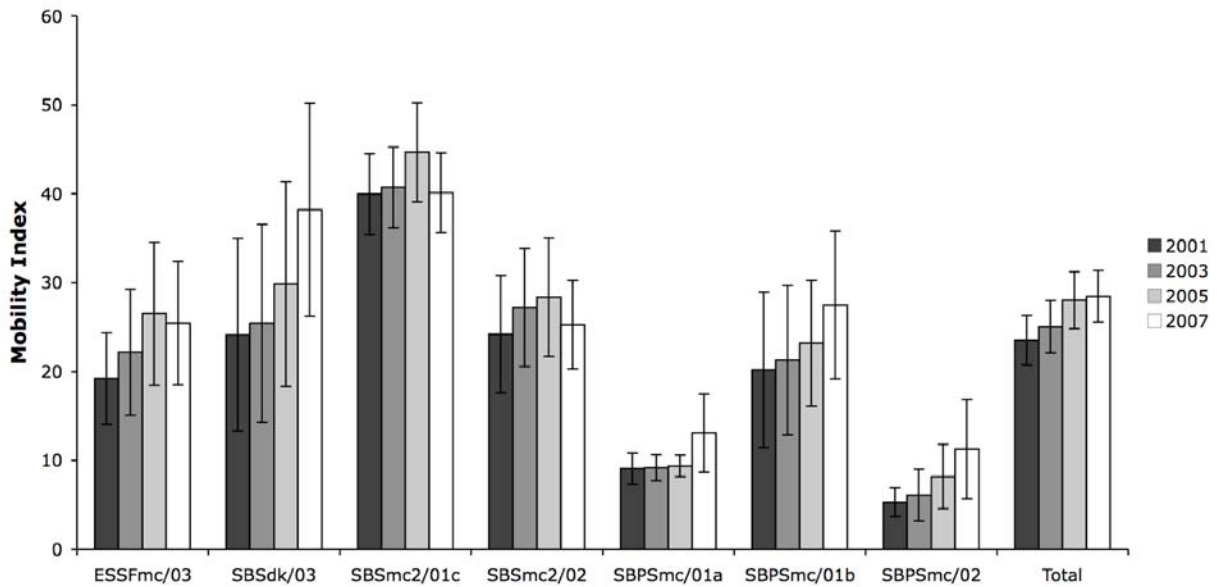


Figure 21. Mean mobility index of coarse woody debris by year for mountain pine beetle sites in the East Ootsa and Entiako areas, 2001-2007.

Error bars = ± 1 standard error.

Mobility Index was generally lower on harvested plots than on mountain pine beetle plots in 2001 and 2007 except for ESSFmc/03 plots where Mobility Index was greater on harvested plots (Figure 22). This was in contrast to volume, mass and density, which were generally greater on harvested plots than on mountain pine beetle plots in 2001 and 2007 (Figure 23). The difference is likely due to shorter piece lengths on logged plots, which results in a lower Mobility Index.

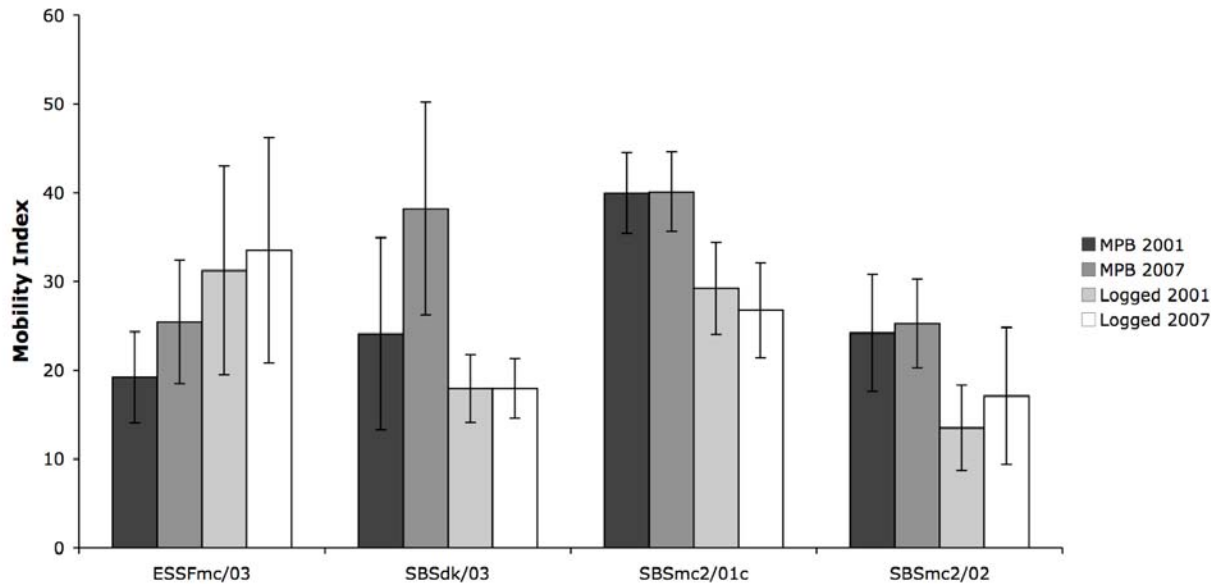


Figure 22. Mean mobility index for mountain pine beetle (MPB) and logged sites by biogeoclimatic zone and year in the East Ootsa and Entiako areas, 2001-2007. Error bars = ± 1 standard error.

Currently, the amount of coarse woody debris is generally low on all sites and is not enough to impede animal movements. Some new pieces of coarse woody debris were documented on harvested plots; these were either residual trees in the harvested area or trees from the adjacent forest. On mountain pine beetle plots, blowdown has increased on some plots, but the majority of trees are still standing (see Stand Structure and Regeneration). Between 2001 and 2007, there has been a gradual accumulation of new coarse woody debris; however, a greater rate of accumulation is expected to occur in the next 5-20 years.

Fall down rates of dead mountain pine beetle-killed trees will vary with ecological conditions. Lewis and Hartley (2005) expect 25%-50% of beetle-killed trees to fall within 8 years, and 90% of trees to fall within 15 years of attack in SBSmc and SBSwk biogeoclimatic subzones in British Columbia. They anticipate that beetle-killed trees will persist slightly longer on drier sites and that smaller diameter trees will fall sooner than larger diameter trees. In southern Oregon, mountain pine beetle-killed trees began to fall after 5 years, 50% of trees fell within 9 years, and 90% fell by 14 years post-attack (Mitchell and Priesler 1998). In the Chilcotin and Kamloops regions in British Columbia, 52% and 26% of beetle-killed trees had fallen by 18 years following attack respectively (Hawkes *et al.* 2004).

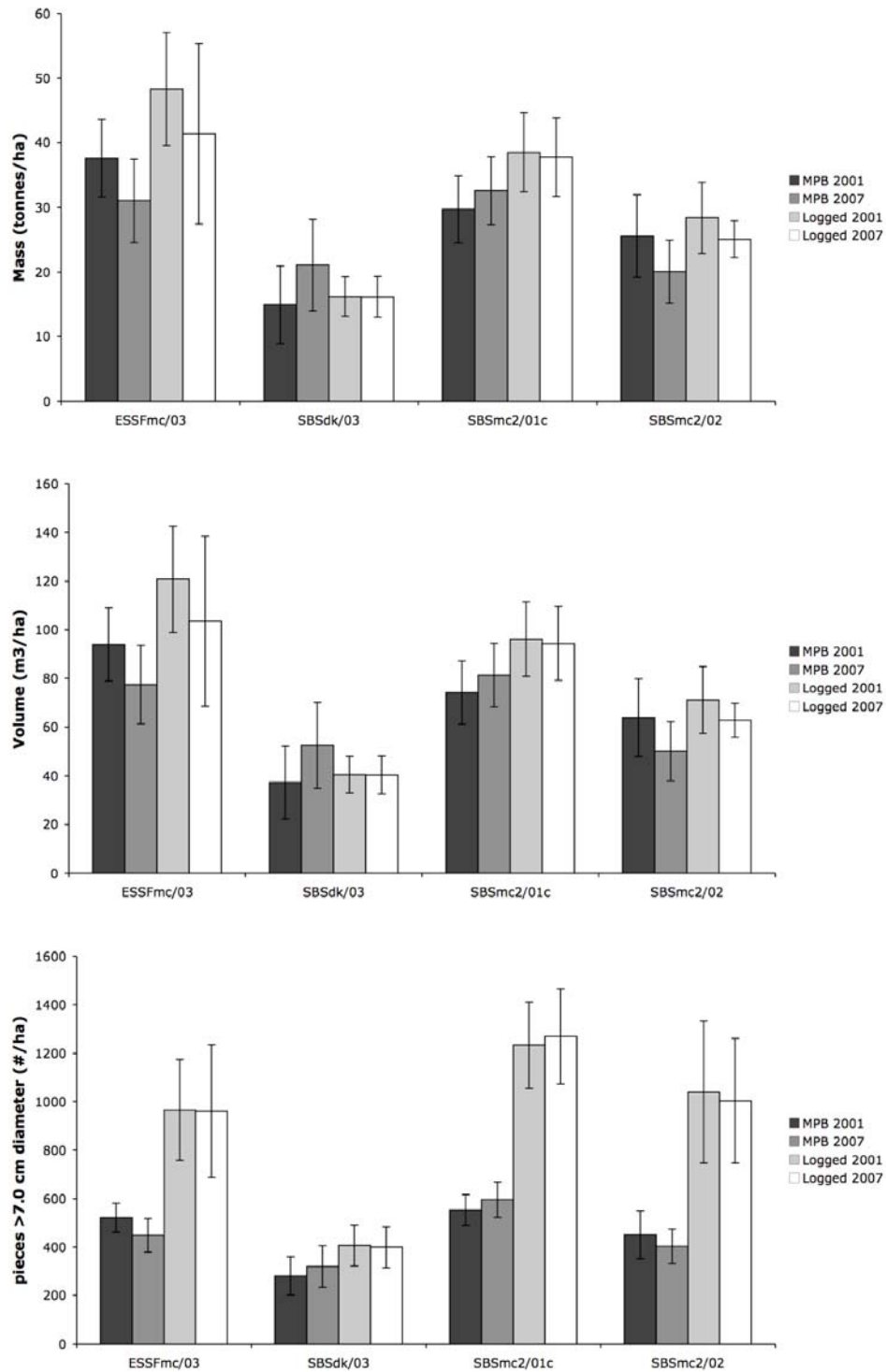


Figure 23. Mean volume, mass and pieces of coarse woody debris for mountain pine beetle (MPB) and logged plots in 2001 and 2007 in the East Ootsa and Entiako areas.
 Error bars = ±1 standard error.

FUTURE WORK

This report marks the seventh year of this multi-year study that has documented changes in forest floor vegetation following beetle attack and forest harvesting over six growing seasons. Many insights have been gained over this time period resulting in new understanding about the ecology of sub-boreal forests of British Columbia. The mountain pine beetle epidemic has caused a landscape level shift in the understory plant communities of pine forests in the East Ootsa and Entiako areas, and our research has documented these changes. As changes to the forest floor composition continue to progress, we plan to resample our permanent sample plots every two years to document the impacts of the mountain pine beetle epidemic on caribou forage lichens and the role of coarse woody debris as a mobility barrier. In addition, a study has been initiated to record movement patterns and habitat use of the Tweedsmuir-Entiako caribou population using GPS and VHF radio collars, and another study has been initiated to document vegetation response to a recent fire in Entiako Park. Research on caribou habitat use and response of vegetation to fire will compliment this study in determining the impact of the mountain pine beetle epidemic on caribou and the vegetation of their winter range.

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