

15th North American Caribou Workshop
Whitehorse, Canada
12-16 May, 2014

Can partial-cut harvesting be used to manage terrestrial lichen habitat? A review of recent evidence

Susan K. Stevenson^{1§} & Darwyn S. Coxson¹

¹ University of Northern British Columbia, Ecosystem Science and Management Program,
3333 University Way, Prince George, B.C. V2N 4Z9, Canada, (Corresponding author: Darwyn.Coxson@unbc.ca).

[§] Deceased, August 29, 2014.

Abstract: Recent research suggests that partial-cut harvesting techniques can be used to alter successional trajectories in pine- and spruce-lichen woodlands, allowing forest managers to extend the period of reindeer lichen growth in mid- to late seral boreal forest stands. In Quebec, a fully replicated partial-cutting trial found that terrestrial lichen abundance remained at least as high in the partial cut as in the clearcuts or unlogged stands, and that the partial cut appeared to be on a trajectory to have even more terrestrial lichen due to sustained higher growth rates. In Alberta, a retrospective study found higher terrestrial lichen abundance in an early horse-logged partial cut than in undisturbed adjacent old forests or in clearcuts. Follow-up studies of partial-cut harvesting trials in British Columbia found that group selection plots 10 years after harvesting had lichen cover equivalent to that of undisturbed forest. In contrast, studies on lichen woodlands that have been defoliated by mountain pine beetle showed a major decline in reindeer lichen cover and a corresponding increase in vascular plant cover, similar to the results of previous studies on clear-cut logging impacts. Taken together these studies provide qualified support for the hypothesis that partial-cut harvesting can be used to enhance, or at least maintain, terrestrial lichen mats used as forage by caribou.

Key words: forest management; lichen woodlands; partial-cut harvesting; terrestrial lichens; woodland caribou.

Rangifer, 35, Special Issue No. 23, 2015: 11-26
DOI [10.7557/2.35.2.3461](https://doi.org/10.7557/2.35.2.3461)

Introduction

The changes in stand structure that occur during succession in boreal and sub-boreal lichen woodlands are accompanied by major shifts in the composition of forest floor lichen communities. We review the impacts of three major types of disturbances: fire, partial-cut logging, and canopy mortality due to mountain pine beetle attack. Although data from partial cuts

are most relevant to our objectives, they are the most limited, and there are also valuable lessons to be learned from other successional series.

Post-fire succession in the boreal forest

Ahti (1959) described 5 stages in the development of boreal forest terrestrial lichen communities after fire. 1) The first stage was a bare soil or organic substrate stage in the immediate



Figure 1. *Cladonia mitis* mat in late-successional pine forest (130 years old) in the Omineca River watershed, British Columbia, shows progressive infilling and burial of lichen mat by feather moss fronds. The individual clump shown here is ca. 30 cm in diameter.

post-fire environment. Soil microclimate conditions can be extreme during this period, with soil surface maxima reaching 60°C (Rouse, 1976). 2) This was followed by a crustose lichen stage, with species such as *Trapeliopsis granulosa* abundant. *Polytrichum* moss mats were common during the crustose lichen stage in the Northwest Territories (Maikawa & Kershaw, 1976), along with crustose species such as *Lecidea granulosa* and *L. uliginosa*. 3) From about years 20 - 60 a cup-lichen (squamulose species in *Cladonia* subgenus *Cladonia*, often referred to as *Cladonia* morphotypes) stage develops, with species such as *Cladonia cornuta* and *C. sulphurina* abundant. Skatter *et al.* (2014) noted that reindeer lichens (mat-forming species in *Cladonia* subgenus *Cladina*, often referred to as *Cladina* morphotypes) were abundant 20 - 30 years after fire in Jack Pine stands from northern Saskatchewan. As the forest canopy ages, both cup lichens and rein-

deer lichen mats decline in abundance, due to the constraints of growing in more shaded understory environments where there is a high rate of needle litterfall. 4) Between 60 - 120 years after fire reindeer lichens can reach their greatest period of abundance. Species such as *C. arbuscula*, *C. rangiferina*, and *C. uncialis* are common during this stage (Coxson & Marsh, 2001). 5) In some regions, especially in sites with oceanic climates, *C. stellaris* mats develop as the final lichen successional phase. Regional variants occur, however, with *Stereocaulon paschale* woodlands, for instance, replacing *C. stellaris* woodlands in a zone extending from west of Churchill across to Great Slave Lake, immediately north and south of latitude 60° N (Kershaw, 1977).

As lichen woodlands age, progressive canopy closure can occur, with feather-moss mats gradually coming to dominate the forest floor surface (Maikawa & Kershaw, 1976; Coxson

& Marsh, 2001). As the understory becomes cooler and moister feather-moss mat fronds can infiltrate and eventually bury existing reindeer lichen mats (Fig.1). Coxson & Marsh (2001) documented the shift from dominance by *Cladina* morphotype lichens in mature stands to dominance by pleurocarpous mosses in older stands (Fig. 2) within sub-boreal forests in central-interior BC. The biomass of *Cladina* morphotype lichens, including *C. mitis*, *C. rangiferina*, *C. stellaris*, and *C. uncialis*, in 50 - 100 year old stands exceeded 1700 kg/ha, falling to less than 300 kg/ha after replacement by feather-moss mats had occurred in the stands > 100 years in age (Coxson & Marsh, 2001).

Several regional exceptions to this pattern of canopy closure and domination by feather-moss mats in old-growth lichen woodlands occur. In the clay belt of northwestern Quebec paludification in old stands can lead to reduced vigour and lower tree densities, with the forest floor surface gradually becoming dominated by *Sphagnum* mats (Boudreault *et al.*, 2002; Harper *et al.*, 2003). In cooler oceanic climates, such as in boreal forests in the Grande rivière de la Baleine area of northeastern Quebec, no transition to feather-moss mats occurred even in very old stands, with *C. stellaris* mats dominating the forest floor in stands at least 250 years old (Morneau & Payette, 1989).

Successional changes in forest floor lichen communities reflect both stochastic factors, such as the availability of propagule sources over time (Hilmo & Sæstad, 2001), and the response of individual lichen species to gradients of temperature, moisture, and light availability (Tegler & Kershaw, 1980; Kershaw, 1985). Generally, early successional lichen species are thought to be more tolerant of heat extremes associated with post-fire surface microclimate, while late-successional lichen species are more sensitive to extremes of desiccation and heat exposure (Kershaw, 1977; Kershaw, 1985). Terrestrial lichen communities are also sensi-

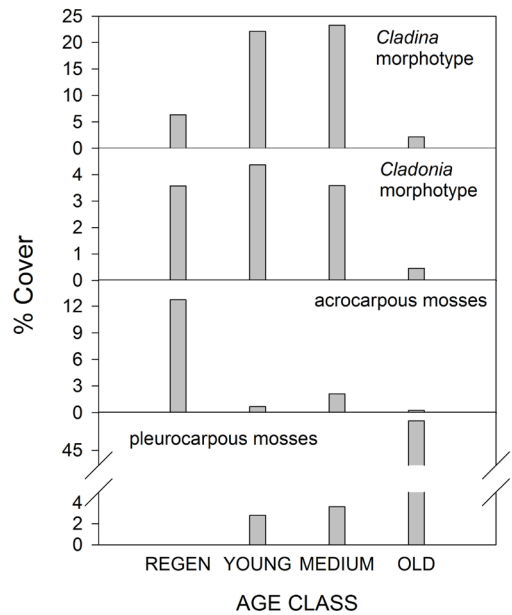


Figure 2. Mean cover (%) by functional group within 50-year age-class intervals (n= 4, 4, 5, and 2 stands respectively) for pine-lichen woodlands in central-interior British Columbia. The *Cladina* morphotype functional group consisted of *Cladonia arbuscula*, *C. rangiferina*, and *C. stellaris* (adapted from Coxson and Marsh, 2001).

tive to stand nutrient availability. Lichens can access stand level nutrient reserves indirectly, from exposure to through-flow precipitation in drip-zones under shrubs and trees (Haughian & Burton, 2015), and for some species directly, using rhizines to mobilize soil or bark nutrient reserves (Cornelissen *et al.*, 2007).

Abundance and viability of terrestrial lichens after partial cutting

Partial-cutting provides a means of bringing about changes in stand structure through removal of selected trees. If the objective of forest managers is to prolong the period of reindeer lichen growth in forest stands, the impact of changes in stand structure from partial-cut harvesting should be greatest in late successional stands, especially if canopy closure has already started to occur. Selective removal of trees in late-seral stands should alter forest floor

microclimates, creating conditions that resemble more closely those found in earlier stages of stand development. We hypothesize these warmer and drier conditions at the forest floor surface after stand thinning should preferentially favour growth of reindeer lichens over that of feather moss mats. Support for this hypothesis derives both from studies of lichen response to changes in stand structure during post-fire succession, and from observed changes in lichen communities after partial-cut harvesting.

Measurements in undisturbed pine-lichen stands have shown a positive relationship between terrestrial forage lichen abundance and various measurements of solar radiation (e.g., Cichowski *et al.*, 2009; Haughian, 2010), or, conversely, a negative relationship between terrestrial forage lichen abundance and various measurements of the tree canopy (e.g., Coxson & Marsh, 2001; Sulyma & Coxson, 2001). At the microsite level, forage lichens are positively associated with canopy gaps and negatively associated with the areas under tree crowns (Sulyma & Coxson, 2001; Haughian, 2010). A significant preference of *Cladina* morphotypes for microsites with greater canopy exposure within older stands was found by Sulyma & Coxson (2001) who analyzed canopy exposure of lichen mats in 100- to 130-year old pine-

lichen woodlands (Table 1). Jonsson Čabrajić *et al.* (2010) similarly showed that in northern Scandinavia the optimum growth of *Cladonia stellaris* and *Cetraria islandica* occurred in forests with <60% canopy cover, corresponding to a basal area of ca 15 m² ha⁻¹, and suggested that the majority of forests in that region are now too dense to maintain optimal lichen growth.

Indirect evidence is provided by examining the response of lichen mats to clear-cut logging. Coxson and Marsh (2001) found that in stands where forest cover had been removed by logging 10 years previous on a deep winter snowpack, reindeer lichens were more abundant on shaded north-facing cut block margins than in the adjacent unlogged forest, reflecting the likely influence of greater light availability and higher humidity (with extended duration of wetting episodes) on lichen growth in these sites. They also noted that regeneration of trees and alders in the developing clearcut would soon curtail the development of lichen mats. The sensitivity of feather moss mats to increases in insolation exposure has previously been observed in large clearcuts, especially on drier sites, where feather mosses often show signs of bleaching and dieback (Kershaw *et al.*, 1994).

Evidence for the maintenance or enhancement of reindeer lichens after thinning or par-

Table 1. Mean microplot values (\pm 1S.E.) for leaf area index in moss- versus lichen-dominated plots in pine lichen woodlands from central-interior British Columbia. Significance values are shown for t-test comparisons between 'Moss' and 'Lichen' plots at each location (from Sulyma & Coxson 2001).

Plot variable	Site	Moss plots	Lichen plots	Significance values
Leaf Area Index (m ² ·m ²)				
	West Germansen	1.617 6 (0.016)	1.551 (0.014)	<i>P</i> < 0.0001
	Germansen Lake	1.700 6 (0.024)	1.637 (0.0126)	<i>P</i> = 0.0004
	Manson	1.961 6 (0.030)	1.787 (0.020)	<i>P</i> = 0.0003

tial removal of canopy structure comes from several studies. Snyder and Woodard (1992) did a retrospective study of lichen abundance in 18 different-aged clearcuts, one 20-year-old horse-logged partial cut, and two unlogged stands within the Subalpine Ecoregion of Alberta. Terrestrial lichen cover, in general, was greater in the partial cut than in the unlogged stands. Lichen cover in the unlogged stands was similar to that in the 20- and 30-year-old clearcuts, but greater than that in the 10-year-old clearcuts. Percent cover of *Cladonia* species palatable to caribou, however, was greater in the partial cut than in the unlogged stands, and greater in the unlogged stands than in the clearcuts (Snyder & Woodard, 1992), suggesting that in this case, partial cutting not only retained preferred forage lichens but actually enhanced them compared to clearcutting.

In a replicated study in Québec black spruce forests, Boudreault *et al.* (2013) compared the abundance and growth rates of three *Cladina*

morphotype species (*C. stellaris*, *C. mitis*, and *C. rangiferina*) in three treatment types: partial cuts, clearcuts, and controls. Both unlogged stands and partial cuts had higher percent cover of *Cladina* spp. than clearcuts. Growth rates of the *Cladina* morphotype species were higher in both the partial-cut and clearcut sites than in the control sites (Fig. 3). In this forest type, it appeared that partial cuts offered the best combination of retention of preharvest forage lichens, and environmental conditions promoting lichen growth after harvest. Interestingly, measurements for *C. stellaris* and *C. mitis* showed negative growth rates (loss of biomass) in the control stands, perhaps indicative of an already declining status for *Cladina* morphotype species in these late seral stands. As Moser *et al.* (1978) noted, however, negative growth rates may be a periodic feature of even healthy lichen mats, during episodes of unfavourable climatic conditions.

One of the most comprehensive studies to

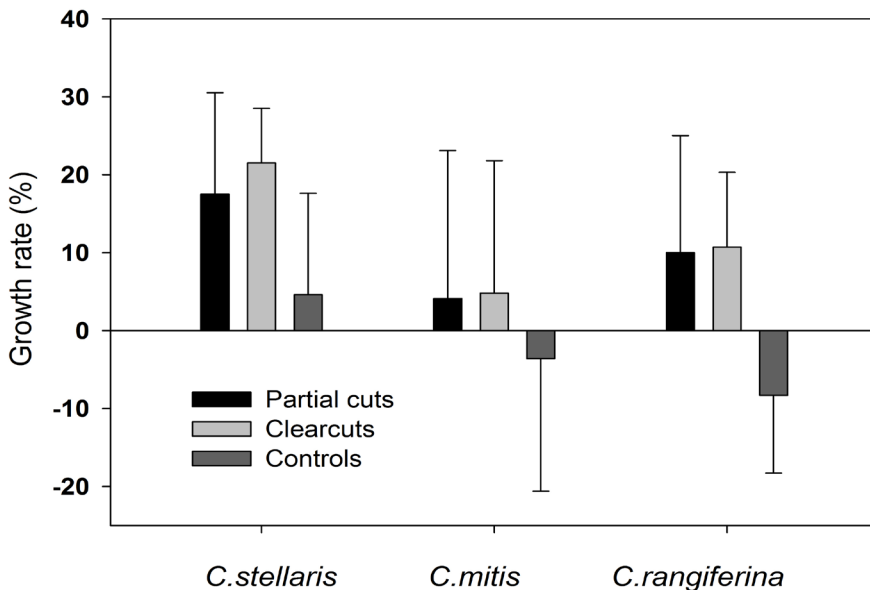


Figure 3. Mean growth rates (+ 1 S.E.) of *Cladonia stellaris*, *C. rangiferina*, and *C. mitis* in black spruce boreal forests of western Québec from spring 2005 to fall 2006. Differences in growth rate that were significant ($P < 0.05$) according to least squares means Tukey's honestly significant difference tests are indicated by different letters (excerpted from Boudreault *et al.*, 2013).

date on the impact of partial-cutting on terrestrial lichen mats was conducted by British Columbia's Ministry of Forests and Range, who began a replicated silvicultural systems study in 1995, described by Miège *et al.* (2001), with follow-up studies described by Waterhouse *et al.* (2011). The study was carried out in the western portion of the range of the Itcha-Ilgachuz caribou herd in British Columbia's central interior plateau. Compared to other forested BC ecosystems, the climate of the Dry, Cold sub-Boreal Pine Spruce biogeoclimatic zone (SBPSxc) and Very Dry Very Cold Montane Spruce biogeoclimatic zone are very dry and cold (Meidinger & Pojar, 1991), with light levels within stands sufficient to allow pine regeneration in the understory (Waterhouse *et al.*, 2010).

Waterhouse *et al.* (2011) described results from their measurements taken in 2004 (8.5 years after logging), reporting on the following treatments:

- Irregular group shelterwood with stem-only harvesting (IGS-SO)
- IGS with whole tree harvesting (IGS-WT)
- Group selection with stem-only harvesting (GS-SO)
- No harvest

The irregular shelterwood prescription called for 50% removal in openings ranging from 20 - 30 m in diameter, and was designed to provide partial shade for terrestrial lichens in the openings. The group selection prescription called for 33% removal in openings about 15 m in diameter, and was designed to maintain arboreal lichens. In stem-only treatments, debris from topping and delimiting was aggregated and left in the harvested openings. In the whole tree treatment, debris from topping and delimiting was piled and burned at the roadside. Post-harvest surveys showed that the actual area cut was 39% in the irregular group shelterwood and 28% in the group selection, and that the opening sizes were within the targeted range.

Although not part of the experimental design, three adjacent clearcuts were also monitored, beginning in 2001.

Cover of forage lichens was significantly lower in the three harvested treatments than in the unharvested control at the first reassessment after harvesting, and subsequently increased. Declines in the harvested units were greater in the openings than in the residual forest stand. In the IGS-SO treatment, healthy forage lichens had declined to 49% of preharvest levels in 1998, and increased to 68% of preharvest levels by 2004. In the IGS-WT treatment, healthy forage lichens had declined to 57% of preharvest levels in 1998, and increased to 71% of preharvest levels by 2004. In the GS-SO treatment, healthy forage lichens had declined to 53% of preharvest levels in 1998, but had nearly reached preharvest levels again by 2004 (Fig. 4). Total moss cover also showed a

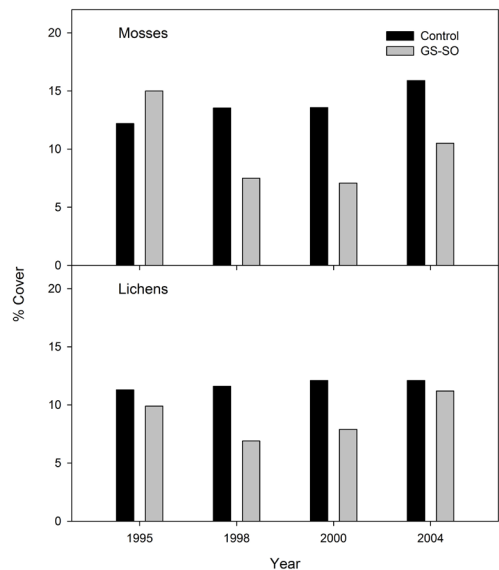


Figure 4. Percent cover of mosses (all moss species) and lichens (preferred forage species) in control versus irregular group shelterwood (stem-only: GS-SO) harvesting plots under pre-harvest (1995) and post-harvest (1998, 2000, 2004) conditions on caribou winter range in west-central British Columbia. Adapted from Waterhouse *et al.*, 2011.

similar pattern of decline and then recovery in the GS-SO treatment, though values remained well below that of the control stands in 2004. This recovery to levels below that of control stands is consistent with a negative response of moss mats to reduced canopy cover, reflecting, among other factors, the loss of stored carbon reserves in feather moss-mats when rewetting follows intense desiccation events (Wilson & Coxson, 1999).

Dwarf shrub cover, initially at 8 - 10%, declined slightly in the partial cuts immediately after harvest, then increased to slightly (2 - 6%) above preharvest levels. Herb cover was only 2 - 3% in the preharvest stand, and increased to 3 - 4% in the partial cuts by 2004. Cover of dwarf shrubs and herbs had a significant negative relationship with cover of healthy forage lichens at all measurement times. Seven to eight years post-harvest in the adjacent clearcuts, forage lichen cover was low (2.8%), dwarf shrub cover was similar (16.9%), and herb cover was high (17.4%), compared to the partial cuts.

Lessons from mountain pine beetle attacks

The mountain pine beetle epidemic has killed at least 726 million m³ of timber in BC's interior forests, affecting more than 17.5 million ha and killing most of the mature lodgepole pine in the Central Plateau region of the province (British Columbia Ministry of Forests, Lands and Natural Resource Operations, 2012). Cichowski (2011) reviewed literature on the potential effects of the epidemic on caribou. In addition to the western portion of the Itcha-Ilgachuz winter range (Waterhouse, 2011), data on the effects of mountain pine beetle mortality on terrestrial lichens are available from three other study areas: the Tweedsmuir-Entiako winter range (Cichowski *et al.*, 2008), the Kennedy Siding winter range (Seip & Jones, 2009), and the northeastern portion of the Itcha-Ilgachuz winter range (Cichowski *et al.*, 2009). The level of pine mortality was

moderate to high in all four areas, ranging from 46 - 75% in the Itcha-Ilgachuz to 78 - 96% in the Tweedsmuir-Entiako (Cichowski, 2011).

Cover of terrestrial forage lichens in unlogged stands decreased after the mountain pine beetle attack in all four study areas. In the Tweedsmuir-Entiako, mean lichen cover was 16% in 2001, 13% in 2003, 11% in 2005, and 10% in 2007. The rate of lichen decline had diminished or stopped in most site series by 2007 – about 7 or 8 years after the initial attack (Cichowski *et al.*, 2008). In the northeastern portion of the Itcha-Ilgachuz range, mean lichen cover declined from 20.5% on plots established in 2005 and 2006 to 16.4% in 2008 (Cichowski *et al.*, 2009). In the western portion of the Itcha-Ilgachuz, terrestrial lichen cover in the no-harvest controls for the silvicultural systems study of Waterhouse *et al.* (2011) declined from the 2004 pre-mountain pine beetle cover of 11.3% to 9.7% in 2008, but this change was not statistically significant (Waterhouse, 2011). At Kennedy Siding, terrestrial lichen cover was 24% in 2006, 17% in 2007, and 12% in 2008 and 2009 (Cichowski, 2011).

Concurrently, cover of dwarf shrubs increased in all four study areas. On most sites in the Tweedsmuir-Entiako range, kinnikinnick (*Arctostaphylos uva-ursi*) cover increased from about 30% to about 60% between 2001 and 2007 (Cichowski *et al.*, 2008). In some, but not all, subzones, the rate of increase levelled off after 2005, and dieback of kinnikinnick was observed in some plots. Informal observations in 2010 suggested that the kinnikinnick dieback was continuing and was more widespread (Cichowski, 2011). In the northeastern portion of the Itcha-Ilgachuz, kinnikinnick cover increased significantly from 3.6% in 2005-06 to 6.2% in 2008, and twinflower (*Linnaea borealis*) cover increased significantly from 3.4% to 8.5% (Cichowski *et al.*, 2009). In the western portion of the Itcha-Ilgachuz, mean percent cover of dwarf shrubs increased from 10.1% in

2004 to 17.3% in 2008 (Waterhouse, 2011); species that increased included kinnikinnick, twinflower, crowberry (*Empetrum nigrum*) and grouseberry (*Vaccinium scoparium*) (Cichowski, 2011). At Kennedy Siding, velvetleaf huckleberry (*Vaccinium myrtilloides*) exhibited a 17.5% increase in cover from 2006 to 2008 (Seip & Jones, 2009). Moss cover generally declined (northeastern Itcha-Ilgachuz, Kennedy Siding) or remained the same (Tweedsmuir-Entiakio, western Itcha-Ilgachuz) in mountain pine beetle-attacked stands (Cichowski, 2011).

The death of some, but not all, of the trees in the forest canopy, either through mountain pine beetle attack or through partial cutting, may affect terrestrial lichen abundance in several ways. The amount of light reaching the forest floor is increased. There is increased deposition of needles and woody debris on the forest floor, although the timing of deposition differs between insect mortality and logging, and with logging method. Water relationships may also change. Surface drying increases with increased irradiance, but soil moisture may increase as there are fewer canopy trees to transpire moisture into the atmosphere. Significant changes in surface temperature and humidity profiles can occur with loss of canopy cover. Greater insolation exposure in sites with dry continental climates can lead to cooler night-time temperatures and more intense early morning dewfall, triggering wetting events in those lichen species capable of rehydration from dewfall and/or high humidity events alone, similar to those observed by Bidussi *et al.* (2013) for epiphytic lichens in interior BC. However, these same sites with reduced canopy cover will typically experience lower mid-day humidity and thus more intense mid-day drying of forest floor moss and lichen mats. All these changes may affect lichens directly, or may affect them indirectly by altering relationships between the lichens and their competitors.

Although studies in undisturbed lichen

woodlands consistently show a positive relationship between terrestrial forage lichen abundance and canopy openness, mountain pine beetle mortality, which increases light transmission, has been associated with declines in terrestrial lichen cover. In the northeastern portion of the Itcha-Ilgachuz range, Cichowski *et al.* (2009) found that the greater the increase in light transmission following the mountain pine beetle epidemic, the greater the decrease in terrestrial lichen abundance. Between 2001 and 2007 in the Tweedsmuir-Entiakio Range, more mountain pine beetle mortality was associated with a greater decrease in lichen cover, but once the effect of mountain pine beetle mortality was taken into account, higher light levels had a positive effect. A separate examination of trends between 2005 and 2007 indicated that changes in light transmission or interception had a significant effect on changes in lichen abundance, suggesting that by seven to eight years after the initial attack, increased light was beginning to create favourable conditions for lichen recovery (Cichowski *et al.*, 2009).

Armleder and Waterhouse (2008) and Waterhouse *et al.* (2011) have asserted that lichen morphotypes that have been growing in subdued light are adversely affected by a sudden increase in exposure to light. Lichens of the same species growing under different light conditions exhibit both morphological and physiological differences. Lichens have the capability of responding to changes in the light regime by increasing the production of phenolic compounds believed to have a protective function; in *Cladina* morphotypes newly exposed to enhanced levels of ultraviolet light, accumulation of phenolics increased and the penetration of ultraviolet radiation into the lichen thallus was more strongly attenuated than in lichens not exposed to enhanced levels of radiation (Bufoni Hall *et al.*, 2002). Gauslaa *et al.* (2012) noted that a rapid transition to high light exposure in desiccated lichens (this in work on

Lobaria pulmonaria) resulted in chlorophyll degradation, an interaction that was exacerbated under low relative humidity conditions. This same high light exposure while the lichens were desiccated gradually, however, triggered changes in the photochemistry of the lichens that improved their tolerance of excess irradiance in the desiccated state (Stepigova *et al.*, 2008).

It is therefore possible that the increase in light levels brought about by beetle mortality of canopy trees reported by Cichowski *et al.* (2009) induced mortality in some lichens, and that those that survived had acclimatized to increased light levels seven to eight years after the initial beetle attack. Differences in increased light exposure could also explain why forage lichens in 15-m wide openings recovered faster than those in 30-m wide openings between 2000 and 2004 (Waterhouse *et al.*, 2011), but were then adversely affected by a further increase in light exposure from mountain pine beetle attack between 2004 and 2008, while those in the 30-m wide openings were not (Waterhouse, 2011). Gauslaa *et al.* (2006) noted that lichen response to changing canopy conditions is a delicate balance between growth potential (more with increasing light) and desiccation damage, which is greater under high light conditions.

Interactions with understory shrubs and woody debris

Mortality of canopy trees from mountain pine beetle attacks is followed by a period of two or three years during which the needles fall from the dead trees, covering ground vegetation and producing a pulse of nutrients. Although lichens do not generally dominate areas immediately under the crown-radius projection of canopy trees (Haughian, 2010), they may be affected by vegetation changes within those areas. Kinnikinnick, a major competitor with forage lichens, often forms circular colonies

(skirts) in the high needle litter deposition zone beneath live lodgepole pine trees. Cichowski *et al.* (2008) observed that the rapid expansion of kinnikinnick in the Tweedsmuir-Entiako study area following mountain pine beetle attack corresponded to the massive needle deposition by canopy trees and to the increased availability of nutrients, light and water. They suggested that the needle-pulse combined with the increase in available nutrients allowed kinnikinnick to expand beyond its 'skirt' at the base of trees, into areas normally too poor in nutrients to support kinnikinnick. Needle deposition throughout their study area has slowed down, and 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.

Over time, woody debris levels will increase after mountain pine beetle outbreaks as branches gradually break off the dead trees and the trees begin to fall, but the mountain pine beetle-affected stands reviewed by Cichowski (2011) had not yet reached this stage. After stem-only partial cutting, there is a pulse of litter that is not confined to pre-existing needle-fall zones, and is composed of both logging slash and needlefall. It is therefore more likely to cover lichen mats than the needles that fall from beetle-killed trees, and was identified by Miège *et al.* (2001) as a factor adversely affecting post-harvest lichen abundance. By 2008, however, the difference between the group selection and the two irregular group shelterwood treatments, which differed in level of removal and opening size, was far greater than the difference between stem-only harvesting and whole-tree harvesting (Waterhouse *et al.*, 2011), and the authors observed that woody debris left over from stem-only harvesting may have ameliorated microclimate conditions for the lichens.

Lichen management using partial cuts

Current literature supports the concept that partial cutting can be used to maintain, and in some cases perhaps enhance, the preharvest lichen community. This maintenance strategy of partial-cut harvesting has gained acceptance as a viable management approach in BC, especially in the relatively dry and cold Montane Spruce Zone (Meidinger & Pojar, 1991). Partial cutting with the objective of maintaining lichen forage is a key part of the management approach on more than 181,000 ha in the range of the Itcha-Ilgachuz caribou herd (Armleder & Waterhouse, 2008), and was recommended by McNay (2011) for high-elevation plateaus in the Montane Spruce Zone in B.C. Specifically, McNay (2011) recommended an irregular group shelterwood system with openings not exceeding two tree lengths wide by three or four tree lengths long for the purpose of maintaining a sustainable supply of terrestrial forage lichens. He added the following caveat: "Practitioners are advised that while this specific silvicultural regime has been shown to maintain terrestrial forage lichens, further monitoring may be necessary to prove the regime does not subject caribou to greater spatial overlap with an early-seral predator-prey system" (McNay, 2011: p. 68).

Particular care should be taken with respect to the adverse impacts of logging slash (needles and woody debris) on terrestrial forage lichens, as described by Gough (2010). The exclusion of woody debris that occurs under a branch and stem harvesting system probably has mixed impacts on terrestrial forage lichens. In a comparison of several different clearcut harvesting methods in Alberta, Kranrod (1996) found that stump-side delimiting in combination with winter harvest and without scarification left more terrestrial lichen cover the summer after timber harvest than any other treatment combination. He observed that environmental conditions under piles and at pile edges were

moderated, and appeared to provide suitable microenvironments for lichens, whereas lichens present in road-side delimiting sites without cover often appeared to be suffering damage from exposure.

Waterhouse *et al.* (2011) observed that slash on the ground and suspended low above the ground adversely affected lichens, but high suspended slash and areas adjacent to slash piles may provide refugia for lichens. An important point raised by Waterhouse *et al.* (2011) was that whole-tree (WT) and stem-only (SO) harvesting systems have the potential of affecting lichens differently. Whole tree skidding is likely to cause more damage to the lichen mat than skidding of delimiting stems, and results in roadside processing areas that are severely disturbed. The slash generated from on-site processing covers lichens. Percent cover of logging slash had a significant negative relationship with abundance of healthy forage lichens at all measurement times, but forage lichen abundance in the two irregular group shelterwood (IGS) treatments did not differ significantly from one another at any time. The authors noted that slash deposited on the ground crushed lichen, while low suspended slash prevented light and precipitation from reaching lichen mats. The influence of slash on lichen regrowth may be broadly similar in other disturbance features, such as seismic lines, which at a microsite level can lead to increased canopy openness. However, as discussed below, linear disturbance features have other attributes which can significantly reduce their value as habitat for caribou.

Harvesting with a high level of retention and small patch size, as recommended by Gough (2010) is a key component of any successful partial-cutting lichen retention strategy. Terrestrial forage lichens in the 30% removal treatment of Waterhouse *et al.* (2011) recovered to preharvest levels, whereas lichens in the 50% removal treatment with 30-m openings did

not (Waterhouse *et al.*, 2011). Sulyma (2002) provided a summary of the predicted interactions between harvesting methods, harvesting season, site preparation, and regeneration method (Table 2). Sulyma recommended that harvesting occur during the winter season to minimize disturbance of lichen mats during harvesting with whole tree removal preferred to minimize the amount of residual debris left after harvesting.

The broader context of caribou habitat management

Caribou populations are affected by many factors other than the abundance of terrestrial forage lichens, and forest harvesting can affect caribou in ways other than through its impact on lichens. Here we discuss mainly the impacts of forest harvesting on terrestrial forage lichens, but a landscape-level management plan should take into consideration the entire array of human-mediated influences on caribou populations.

A cornerstone of present-day caribou management in North America has been to consider interactions between habitat modifications and predator response. Current findings suggest that factors which increase predator populations, for instance, creation of early seral habitats which favor growth of moose or deer populations, or those which allow more ready predator dispersal, such as the creation of road networks, can have major detrimental impacts on caribou (Apps *et al.*, 2013; Whittington *et al.*, 2011). Care must also be taken that partial-cut harvesting intensity does not exceed the threshold at which a flush of early seral vegetation might occur (Frey *et al.*, 2003).

The design of partial-cut logging blocks must also include considerations of changes in road access which would be required and future use of these roads. At a small scale, within blocks, planned skid trails would optimally be winter access only, minimizing disturbance

of ground cover and limiting future use. The design of access roads for hauling timber from partial-cutting harvest blocks raises further issues of predator access and changes in landscape patterns. Previous studies suggest that the impacts of linear features such as roads and seismic lines may be greatest in the late-winter period, when woodland caribou were found by Dyer *et al.* (2002) to cross active roads 6 times less frequently than simulated road networks. Dyer *et al.* (2001) also found significant avoidance effects in woodland caribou, up to 500 m, from roads and seismic lines, although these effects should decline with time as vegetation recolonizes deactivated roads and seismic lines. A strategy for road deactivation, road access restrictions, and restoration of road corridors, if required, is therefore a vital part of any partial-cutting harvest design in caribou winter habitat, in common with other linear disturbance features in caribou habitat.

Conclusion

The use of partial-cut logging to reduce canopy closure in mid- to late-seral lichen woodlands provides a short- to mid-term strategy for maintaining or even enhancing forage lichen availability for caribou. This strategy would best be considered in landscapes where there are few mid-seral stands that can replenish caribou habitat in coming decades. Under these circumstances, partial-cut harvesting may be used as a tool to maintain lichen forage availability in locations where it might be lost due to successional change. Eventually, however, these stands will require resetting by stand level disturbance factors such as wildfire to develop future lichen communities. Partial-cutting, therefore, cannot be used as a long-term substitute for natural disturbance dynamics that maintain a broad age-class distribution of stands after disturbances such as fire.

Acknowledgments

We would like to thank the Government of the Yukon, Forest Management Branch, for funding support for an earlier draft of this review.

References

- Ahti, T.** 1959. Studies on the caribou lichen stands of Newfoundland. — *Ann. Bot. Soc. 'Vanamo'* 30: 1-43.
- Apps, C.D., McLellan, B.N., Kinley, T.A., Serrouya, R., Seip, D. & Wittmer, H.** 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. — *Journal of Wildlife Management* 77: 1409-1419. <http://dx.doi.org/10.1002/jwmg.601>
- Armleder, H. & Waterhouse, M.** 2008. Mountain pine beetle and northern caribou: The Itcha-Ilgachuz experience. — *BC Journal of Ecosystems and Management* 9: 102-105.
- Bidussi, M., Goward, T. & Gauslaa, Y.** 2013. Growth and secondary compound investments in the epiphytic lichens *Lobaria pulmonaria* and *Hypogymnia occidentalis* transplanted along an altitudinal gradient in British Columbia. — *Botany* 91: 621-630. <http://dx.doi.org/10.1139/cjb-2013-0088>
- Boudreault, C., Bergeron, Y., Gauthier, Y. & Drapeau, P.** 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. — *Canadian Journal of Forest Research* 32: 1080-1093. <http://dx.doi.org/10.1139/x02-027>
- Boudreault, C., Zouaoui, S., Drapeau, P., Bergeron, Y. & Stevenson, S.** 2013. Canopy openings created by partial cutting increase growth rates and maintain the cover of three *Cladonia* species in the Canadian boreal forest. — *Forest Ecology and Management* 304: 473-481. <http://dx.doi.org/10.1016/j.foreco.2013.05.043>
- British Columbia Ministry of Forests, Lands and Natural Resource Operations.** 2012. *Beetle facts: Infestation information*. Available from: http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/Updated-Beetle-Facts_May2012.pdf (Accessed 10 April 2014).
- Buffoni Hall, R.S., Bornman, J.F. & Björn, L.O.** 2002. UV-induced changes in pigment content and light penetration in the fruticose lichen *Cladonia arbuscula* ssp. *mitis*. — *Journal of Photochemistry and Photobiology B: Biology* 66: 13-20. [http://dx.doi.org/10.1016/S1011-1344\(01\)00270-6](http://dx.doi.org/10.1016/S1011-1344(01)00270-6)
- Cichowski, D.** 2011. *Literature Review — Research on Mountain Pine Beetles and Caribou*. Report prepared for B.C. Ministry of Environment, Williams Lake by Caribou Ecological Consulting, Smithers, B.C. Available from: http://a100.gov.bc.ca/appsdata/acat/documents/r22847/Cichowski_1303238545657_e822d6b-59c6854aeb61e99363115a4aa9016b33c-98cf2984cbb2bfb8c0cea71c.pdf (Accessed 10 April 2014).
- Cichowski, D., Macadam, A. & Haessler, S.** 2009. *Mountain pine beetle/lichen project, Quesnel TSA: Year 4—2008/09*. Report prepared for B.C. Ministry of Environment, Williams Lake, B.C. FIA-FSP Project Y091176. Available from: http://www.for.gov.bc.ca/hfd/library/FIA/2009/FSP_Y091176c.pdf (Accessed 10 April 2014).
- Cichowski, D., Williston, P. & Haessler, S.** 2008. *The response of caribou terrestrial forage lichens to mountain pine beetles and forest harvesting in the East Ootsa and Entiako area: Annual Report – 2007/08 – Year 7*. A report to Morice-Lakes Innovative Forest Practices Agreement, Prince George, B.C., the Bulkley Valley Centre for Natural Resources Research and Management, Smithers, B.C., and Ministry of Environment, Prince George, B.C. 46p. Available from: <http://www.sernbc.ca/pdf/Caribou/Year%207%20Report%20on%20the%20Response%20of%20Caribou%20Terrestrial%20For>

- age%20Lichens%20to%20MPB.pdf (Accessed 10 April 2014).
- Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. & During, H.J.** 2007. Comparative Cryptogam Ecology: A Review of Bryophyte and Lichen Traits that Drive Biogeochemistry. — *Annals of Botany* 99: 987-1001. <http://dx.doi.org/10.1093/aob/mcm030>
- Coxson, D. S. & Marsh, J.** 2001. Lichen chronosequences (post-fire and post-harvest) in lodgepole pine (*Pinus contorta*) forests of northern-interior British Columbia. — *Canadian Journal of Botany* 79: 1449-1464. <http://dx.doi.org/10.1139/b01-127>
- Dyer, S.J., O'Neill, J.P., Wasel, S.M. & Boutin, S.** 2001. Avoidance of industrial development by woodland caribou. — *Journal of Wildlife Management* 65: 531-542. <http://dx.doi.org/10.2307/3803106>
- Dyer, S.J., O'Neill, J.P., Wasel, S.M. & Boutin, S.** 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. — *Canadian Journal of Zoology* 80: 839-845. <http://dx.doi.org/10.1139/z02-060>
- Frey, B.R., Liefers, V.J., Munson, A.D. & Blenis, P.V.** 2003. The influence of partial harvesting and forest floor disturbance on nutrient availability and understory vegetation in boreal mixedwoods. — *Canadian Journal of Forest Research* 33: 1180-1188. <http://dx.doi.org/10.1139/x03-042>
- Gauslaa, Y., Coxson, D.S. & Solhaug, K.A.** 2012. The paradox of higher light tolerance during desiccation in rare old forest cyanolichens than in more widespread co-occurring chloro- and cephalolichens. — *New Phytologist* 195: 812-822. <http://dx.doi.org/10.1111/j.1469-8137.2012.04221.x>
- Gauslaa, Y., Lie, M., Solhaug, K.A. & Ohlson, M.** 2006. Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. — *Oecologia* 147: 406-416. <http://dx.doi.org/10.1007/s00442-005-0283-1>
- Gough, A.** 2010. Effects of historical timber harvesting practices on caribou forage lichen abundance near Marsh Lake, Yukon: Phase 1 final report. — Unpublished report prepared for Forest Management Branch, Government of Yukon. 56 pp. Available from: http://www.emr.gov.yk.ca/forestry/pdf/Lewes_Lake_Caribou_Lichen_Report.pdf (Accessed 10 April 2014).
- Harper, K., Boudreault, C., DeGrandpré, L., Drapeau, P., Gauthier, S. & Bergeron, Y.** 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. — *Environmental Reviews* 11: S79-S98. <http://dx.doi.org/10.1139/a03-013>
- Haughian, S.R.** 2010. *Understory vegetation-environment relationships of lichen rich forests in north central British Columbia*. — M.Sc. thesis. University of Northern British Columbia, Prince George, B.C.
- Haughian, S.R. & Burton, P.** 2015. Microhabitat associations of lichens, feathermosses, and vascular plants in a caribou winter range, and their implications for understory development. — *Botany*. <http://dx.doi.org/10.1139/cjb-2014-0238>
- Hilmo, O. & Sæstad, S.M.** 2001. Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. — *Biological Conservation* 102: 251-259. [http://dx.doi.org/10.1016/S0006-3207\(01\)00100-8](http://dx.doi.org/10.1016/S0006-3207(01)00100-8)
- Jonsson Čabračić, A.V., Moen, J. & Palmqvist, K.** 2010. Predicting growth of mat-forming lichens on a landscape scale – comparing models with different complexities. — *Ecography* 33: 949-960. <http://dx.doi.org/10.1111/j.1600-0587.2009.06079.x>
- Kershaw, K.A.** 1977. Studies on lichen-dominated systems. XX. An examination of

- some aspects of the northern boreal lichen woodlands in Canada. — *Canadian Journal of Botany* 55: 393-410. <http://dx.doi.org/10.1139/b77-050>
- Kershaw, K. A.** 1985. *Physiological Ecology of Lichens*. Cambridge Univ. Press. Cambridge, U.K. 293pp.
- Kershaw, M., Wiltshire, R. & Hollsted, C.** 1994. *Critical silvics of feathermoss as related to vegetation management*. — Technical Note TN-29, Ontario Ministry of Natural Resources. 16pp. Available from: https://www.mnr.gov.on.ca/stdprodconsume/groups/lr/@mnr/@nws/documents/document/mnr_e005383.pdf (downloaded 10 April 2014).
- Kranrod, K.A.** 1996. *Effects of timber harvesting methods on terrestrial lichens and understory plants in west-central Alberta*. — M.Sc. thesis. University of Alberta, Edmonton. 138pp.
- Maikawa, E. & Kershaw, K. A.** 1976. Studies on lichen-dominated systems. XIX. The postfire recovery sequence of black spruce – lichen woodland in the Abitau Lake Region, N.W.T. — *Canadian Journal of Botany* 54: 2679-2687. <http://dx.doi.org/10.1139/b76-288>
- McNay, R.S.** 2011. Silviculture options for use in ranges designated for the conservation of northern caribou in British Columbia. — *BC Journal of Ecosystems and Management* 12: 55-73.
- Meidinger, D. & Pojar, J.** 1991. *Ecosystems of British Columbia*. BC Ministry of Forests, Victoria, British Columbia.
- Miège, D., Goward, T., Waterhouse, M. & Armleder, H.** 2001. Impact of partial cutting on lichen diversity in lodgepole pine forests on the Chilcotin Plateau in British Columbia. — BC Ministry of Forests, Research Branch, Victoria, B.C. Working Paper 55.
- Morneau, C. & Payette, S.** 1989. Postfire lichen–spruce woodland recovery at the limit of the boreal forest in northern Quebec. — *Canadian Journal of Botany* 67: 2770-2782. <http://dx.doi.org/10.1139/b89-357>
- Moser, T.J. & Nash III, T.H.** 1978. Photosynthetic patterns of *Cetraria cucullata* (Bell.) Ach. at Anaktuvuk Pass, Alaska. — *Oecologia* 34: 37-43. <http://dx.doi.org/10.1007/BF00346239>
- Rouse, W.R.** 1976. Microclimatic Changes Accompanying Burning in Subarctic Lichen Woodland. — *Arctic and Alpine Research* 8: 357-376. <http://dx.doi.org/10.2307/1550439>
- Seip, D. & Jones, E.** 2009. *Response of woodland caribou to partial retention logging of winter ranges attacked by mountain pine beetle*. — Report on FIA/FSP Project Y091010 (2008-09). Available from: http://www.for.gov.bc.ca/hfd/library/FIA/2009/FSP_Y091010a.pdf (Accessed 10 April 2014).
- Skatter, H.G., Kansas, J.L., Charlebois, M.L. & Balicki, B.** 2014. Recovery of terrestrial lichens following wildfire in the boreal shield of Saskatchewan: Early seral foraging availability for Woodland Caribou (*Rangifer tarandus caribou*) — *Canadian Wildlife Biology and Management* 3: 1-14.
- Snyder, J. & Woodard, P.M.** 1992. *Lichen regeneration rates in Alberta following various types of logging and wildfire disturbances: final report*. — Unpublished report, University of Alberta, Edmonton. 118pp.
- Stepigova, J., Gauslaa, Y., Cempirkova-Vrablikova, H. & Solgaug, K.A.** 2008. Irradiance prior to and during desiccation improves the tolerance to excess irradiance in the desiccated state of the old forest lichen *Lobaria pulmonaria*. — *Photosynthetica* 46: 286-290. <http://dx.doi.org/10.1007/s11099-008-0050-8>
- Sulyma, R.** 2002. *Adaptive management of forestry practices in pine-lichen woodlands in north-central British Columbia, Site 1* (98-

- Mile, Mackenzie) and Site 2 (Malaput – Vanderhoof) Pretreatment Assessments.* — Unpublished Report. Forest Floor Contracting, Fort St. James, B.C. 32pp. Available from: https://www.for.gov.bc.ca/hfd/library/fia/2006/LBIP_2418011d.pdf (Accessed 10 April 2014).
- Sulyma, R. & Coxson, D.S.** 2001. Microsite Displacement of Terrestrial Lichens by Feather Moss Mats in Late Seral Pine-Lichen Woodlands of North-central British Columbia. — *The Bryologist* 104: 505-516. [http://dx.doi.org/10.1639/0007-2745\(2001\)104\[0505:MDOTLB\]2.0.CO;2](http://dx.doi.org/10.1639/0007-2745(2001)104[0505:MDOTLB]2.0.CO;2)
- Tegler, B. & Kershaw, K.A.** 1980. Studies on lichen-dominated systems. XXIII. The control of seasonal rates of net photosynthesis by moisture, light, and temperature in *Cladonia rangiferina*. — *Canadian Journal of Botany* 58: 1851-1858. <http://dx.doi.org/10.1139/b80-214>
- Waterhouse, M.** 2011. *Lichen and vegetation response to mountain pine beetle damage in partial cuts and mature forests in the West Chilcotin in 2008. EP1208 File Report.* — Unpublished draft on file at Ministry of Forests, Lands and Natural Resource Operations, Williams Lake, B.C. 23pp.
- Waterhouse, M.J., Armleder, H.M. & Nemec, A.F.L.** 2011. Terrestrial lichen response to partial cutting in lodgepole pine forests on caribou winter range in west-central British Columbia. — *Rangifer Special Issue* 19: 119-134. <http://dx.doi.org/10.7557/2.31.2.1996>
- Waterhouse, M. J., Wallich, E. C., Daintith, N. M. & Armleder, H. M.** 2010. Planted stock performance 10 years after partial cutting in west-central British Columbia. — *Forestry Chronicle* 96: 118-129. <http://dx.doi.org/10.5558/tfc86118-1>
- Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J. & Musiani, M.** 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. — *Journal of Applied Ecology* 48: 1535–1542. <http://dx.doi.org/10.1111/j.1365-2664.2011.02043.x>
- Wilson, J.A. & Coxson, D.S.** 1999. Carbon flux in a subalpine spruce-fir forest: pulse release from *Hylocomium splendens* feather-moss mats. — *Canadian Journal of Botany* 77: 564-569. <http://dx.doi.org/10.1139/b99-002>

