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Arboreal forage lichen response to partial cutting of high elevation mountain caribou range in the Quesnel Highland of east-central British Columbia

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Abstract: Group selection silvicultural systems have been recommended for managing mountain caribou (*Rangifer tarandus caribou*) habitat in high elevation Engelmann spruce – subalpine fir forests in east-central British Columbia. We measured the response of arboreal lichen (a key winter forage) to harvesting of 30% of the forested area using three partial cutting treatments, which created small (0.03 ha), medium (0.13 ha), and large (1.0 ha) openings, and a no-harvest treatment. Treatments were replicated on four sites, and monitored over a ten year post-harvest period. The short-term loss of lichen associated with removal of approximately one third of the trees was partially offset by a significant (P=0.01) increase in lichen abundance on trees in the caribou feeding zone (up to 4.5 m) in the three partial cutting treatments relative to trees in the uncut forest. Differences among treatments in the change in lichen composition, as measured by the percentage of *Alectoria sarmentosa* and *Bryoria* spp., were marginally significant (P=0.10). The partial cutting treatments showing a greater likelihood of shifting towards more *Bryoria* spp. than no-harvest treatment (P=0.04). In the year of harvest (1993), larger trees were found to hold more lichen than smaller trees (P=0.04), and live trees supported more lichen than dead trees (P=0.01), but lichen loading was similar among tree species (P=0.51). Tree fall rates were similar among treatments, based on the ten year average (0.6–0.8% of sample trees per year). The results indicate that caribou foraging habitat is maintained in the residual forest when group selection systems that remove only 30% of the trees are applied. Information on the distribution of lichen is useful for developing stand level prescriptions. Providing lichen bearing habitat meets just one of the needs of caribou. A comprehensive approach that considers all factors and their interactions is essential to maintain and recover the threatened mountain caribou.

Key words: arboreal lichen, forest management, group selection silvicultural systems, *Rangifer tarandus caribou*.

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Introduction

Mountain caribou in the Southern Mountains National Ecological Area are designated as threatened by the Committee on Endangered Wildlife in Canada (COSEWIC) and qualify for protection and recovery under the federal Canadian *Species at Risk Act* (SARA). The British Columbia Conservation Data Centre (2007) describes mountain caribou as critically imperilled and have placed them on the endangered and threatened list of species (Red List). The population of mountain caribou was estimated at 1900 animals in 2006 in British Columbia (Hatter, 2006) and this represents 98% of the global population (British Columbia Conservation Data Centre, 2007). There are several planning processes in British Columbia addressing management of these caribou herds. The Cariboo-Chilcotin Land Use Plan (CCLUP), as early as 1995, recognized that mountain caribou were an important management issue in the central interior (Government of British Columbia, 1995). The Mountain Caribou Strategy component of the CCLUP (Youds *et al.*, 2000) delineated areas of no forest harvesting and over 53 000 ha for 'modified harvesting' across the caribou range in east-central British Columbia. This research trial was undertaken to test the hypothesis that group selection silvicultural systems (modified harvesting) are compatible with maintaining caribou habitat in a managed forest environment.

Within the Engelmann Spruce-Subalpine Fir (ESSF) and Interior Cedar Hemlock (ICH) biogeoclimatic zones (Steen & Coupé, 1997) in the central interior of British Columbia, clearcutting on short rotations does not maintain the old growth forest characteristics that caribou require (Mountain Caribou Technical Advisory Committee, 2002). Lichens are widely recognized as the major winter forage of woodland caribou throughout their range (Edwards *et al.*, 1960; Edwards & Ritcey, 1960; Scotter, 1962; Scotter, 1967). In mountainous areas of heavy snowfall in south eastern and east-central British Columbia, caribou eat arboreal (tree-dwelling) lichens almost exclusively during the winter (Terry *et al.*, 2000). Logging can have a drastic effect on available arboreal lichen biomass (Stevenson, 1979; Stevenson, 1985; Stevenson, 1988; Stevenson, 1990; Stevenson & Enns, 1992; Rominger *et al.*, 1994). Clearcutting is not compatible with maintaining mountain caribou habitat as it removes all arboreal lichen. It may take well over a century before the quantity of lichen within a clearcut is comparable to that found in old-growth stands because of the time it takes to develop stand attributes conducive to heavy lichen loading such as defoliated branches, stable environmental conditions and adequate ventilation (Goward & Campbell, 2005). Widespread application of clearcutting reduces the amount of usable caribou habitat, effectively shrinking their range. Large areas with sufficient forage are necessary so caribou can live at relatively low densities in order to successfully evade predators (Bergerud *et al.*, 1984; Seip, 1991).

The impacts of partial cutting on lichen biomass have been studied in Sweden (Esseen *et al.*, 1996) and in north-western North America (Rominger *et al.*, 1994; Stevenson, 2001; Coxson *et al.*, 2003; Stevenson & Coxson, 2003). In the central interior of British Columbia alternatives to clearcutting, specifically single-tree and group selection silvicultural systems are being tested as possible systems to maintain good quality foraging habitat, while allowing some timber harvesting (Armleder & Stevenson, 1996). Testing of partial cutting approaches is necessary to investigate three main concerns: potential increase in the rate of tree fall, potential loss of lichen through increased wind scouring in the residual stand (Terry, 1994), and potential change in the microclimate sufficient to affect lichen growth rates (Kershaw, 1985).

In their comprehensive study of lichen litterfall, growth and turnover, Stevenson and Coxson (2003) report, based on results from a single site, that group selection and single tree selection systems, removing 30% of the timber, maintained a satisfactory environment for continued lichen growth two years after logging. The Quesnel Highland trial described here was partially cut, in 1993, using a group selection silvicultural system based on 30% removal, with replication of the four treatments over four sites. The treatments varied by opening size: 0.03 ha, 0.13 ha, and 1.0 ha. Over the past ten years, we have measured the abundance of arboreal lichen (*Alectoria sarmentosa* and *Bryoria* spp.) in the residual forest in response to three opening size treatments and a no-harvest treatment. The longer term response includes the rate of tree fall and recruitment of new trees. Additionally, we describe the distribution of lichen by tree species, decay class and diameter class as well as the implications of tree fall and recruitment of new trees to lichen abundance.

Methods

Study area

The four study sites are located 12–28 km east of Likely in east-central British Columbia. Two of the sites, Upper and Lower Grain creeks (UGC and LGC), (52°41'29"N, 121°12'02"W and 52°40'45"N, 121°10'52"W, respectively) are located within the Grain Creek watershed. The other two sites (BBW and BBS) are adjacent to each other in the Blackbear Creek watershed (52°36'37"N, 121°24'30"W). All study sites are submesic to mesic within the Engelmann Spruce–Subalpine Fir wet, cold biogeoclimatic subzone variant (ESSFwc3) (Steen & Coupé, 1997). The elevation of the sites extends from 1440 to 1690 m. Above this elevation, the forest becomes subalpine parkland, then alpine. Slopes are similar at all sites ranging from 24 to 32%, while aspect is northeast at Blackbear Creek, northwest at Lower Grain Creek, and west at Upper Grain Creek.

The forest is dominated by subalpine fir (*Abies lasiocarpa*) and a lesser amount of Engelmann spruce (*Picea engelmannii*). The oldest trees are spruce aged 297 years on the Blackbear Creek site and from 426 to 446 years on the Grain Creek sites. Stands are multi-aged as the fire return intervals are very long; forest replacement typically occurs as individual or small groups of mature and old trees succumb to insects, disease, and tree fall (Steen *et al.*, 2005). Several small (<0.1 ha), wet subalpine meadows are scattered throughout the Lower and Upper Grain Creek study sites. Based on pre-harvest cruise data, gross timber volumes range from 300 to 387 m^3/ha (>17.5 cm diameter at breast height [dbh]). Stem densities are 357 to 736 stems/ha (>12.5 cm dbh), and averaged across the three sites, 29% of the subalpine fir and 12% of the spruce is dead (Steen *et al.*, 2005).

In the forest understory, the thick shrub layer is dominated by white-flowered rhododendron (*Rhododendron albiflorum*) (45% cover) and a lesser component of black huckleberry (*Vaccinium membranaceum*) (7%). The fairly abundant herb layer consists mostly of Sitka valerian (*Valeriana sitchensis*) (10%), oak fern

(*Gymnocarpium dryopteris*) (7%), mountain arnica (*Arnica latifolia*) (5%), rosy twistedstalk (*Streptopus roseus*) (4%), and foamflower (*Tiarella trifoliata*) (3%). The bryophyte layer is fairly continuous covering 40% of the ground.

Experimental design and treatments

The design is a randomized complete block with four sites representing the blocking factor. Each study site is approximately 40 ha and was divided into four - 10 ha treatment units. The four treatments were randomly assigned within each site. One treatment unit was no-harvest (control) while 30% of the area was harvested (including skid trails) in the other three units using one of three group selection treatments that differed by opening size: 0.03 ha (small), 0.13 ha (medium), and 1.0 ha (large). On average, the treatment units contained three - 1.0 ha openings, seventeen - 0.13 ha openings, or sixty - 0.01 ha openings. The partial cutting treatments were harvested using feller-bunchers and grapple skidders. On BBW, UGC and LGC sites harvesting was done on a snowpack of 0.5–1.5 m from December 1992 to January 1993 to minimize forest floor disturbance. The BBS site was cut in the summer of 1992. Permission was obtained from the Workers' Compensation Board of British Columbia to retain safe dead trees in the adjacent forest that would normally be felled during conventional ground-based harvesting.

Field methods

One or two permanent transect lines per treatment unit were set up immediately post-harvest in March of 1993. Transects were 4 m wide and were about 250 m long and were set across slope bisecting openings and residual forest. This captured about 80 trees per treatment unit. Based on four replicate blocks and four treatments, 1225 trees were permanently tagged, and assessed in 1993. Re-assessments were completed in 1997, 2001 and 2003 (10.5 years post-harvest). For each tree (> 10 cm diameter at breast height [dbh]) the following attributes were recorded: species, dbh, decay class (Backhouse 1993), any major breakage on the bole, and lichen abundance. In 2003, diameters of all the trees were re-measured and 30 new recruits were added to the dataset. Lichen abundance was visually rated in classes 0 to 5, and the percentage of *Alectoria* and *Bryoria* species on each sample tree was estimated to the closest 5% (Armleder *et al.*, 1992; Stevenson *et al.*, 1998). Visual estimations of quantity were made by comparing the observed amount of lichen on the tree in the caribou feeding zone (up to 4.5 m above ground) with a series of photographs with known quantities of lichen. Each class corresponds to a range of weights (g) that increases on an approximate logarithmic scale from the lower to the upper weight limit of the class. Similarly, a series of photographs with measured portions of *Alectoria* and *Bryoria* were used to estimate percent composition. All fallen trees were noted during each re-assessment, and the following data were recorded: year of fall, direction of fall, type of break, and decay class at the time of fall.

Data analysis

All data summaries and analyses were performed with SAS (SAS Institute Inc., 1999-2001). The 1993 data set (1225 trees) was used to compare the abundance of lichen among tree species (spruce, subalpine fir), decay classes (alive, dead), diameter classes (10-30 cm, 31-50 cm and > 50 cm) and sites (BBW, BBS, UGC, LGC). In order to estimate lichen loadings, the abundance class had to be converted to an approximate weight and averaged (or summed) over trees. Weights for individual trees were assumed to be equal to the exponential curve evaluated at the lichen class midpoint. The lichen load per tree was as follows for each class: class 0 = 0 g/tree, 1 = 1.25 g/tree, 2 = 16.25 g/tree, 3 = 126.00 g/tree and 4 = 425.00 g/tree). Annual rates of tree fall, and recruitment were tabulated by site and treatment. The percentage of trees by decay class, species, and diameter class, and lichen composition (% *Alectoria* for trees rated lichen class ≥ 2) were also summarized by site and treatment.

The 2003 dataset contains the original tree sample (including 87 fallen trees) and 30 new recruits. Fallen trees were assumed to have no lichen in 2003 unless an amount was recorded on a high stump, and recruits were assumed to have no lichen in 1993.

Logistic regression analyses were use to test for treatment effects immediately after application (in 1993) and by comparing the changes that occurred between the 1993 and 2003 measurement periods. Analysis of the difference between 1993 and 2003 is a type of repeated measures analysis, which accounts for slight variability between the treatments in 1993 and reduces bias due to changes in observers from year to year.

The statistical significance of apparent treatment effects on the amount and composition of arboreal lichen was determined by fitting logistic models that relate lichen response to treatment and site, as well as allowing for the potentially confounding effects of species, live/dead decay class, and tree diameter:

$$\log\left(\frac{p_i(t, s, u, v, dbh)}{p_3(t, s, u, v, dbh)}\right) = \alpha_{it} + \beta_{is} + \alpha\beta_{its} + \gamma_{iu} + \delta_{iv} + (\phi_i + \gamma\phi_{ui}) \times dbh$$

where $p_i(t, s, u, v, dbh)$ is the probability that a tree in the plot receiving Treatment t at Site s falls into one of three levels i (=1, 2, or 3), when the tree is Species u, is in Decay Class v, and has Diameter dbh.

For the purpose of analysis, responses were coded as one of three levels. In particular, the five classes used to rate the abundance of lichen in the field were pooled as follows: Level 1= Lichen Classes 0 and 1, Level 2 = Lichen Class 2, and Level 3 = Lichen Classes 3 and 4. Similarly, the relative abundance of *Alectoria* was classified as 0%-10%, 11%-50%, > 50%, and changes between 1993 and 2003 (in lichen or % *Alectoria*) were classified as an increase, decrease, or no change. Only trees with rated Class 2 and greater were included in the analysis of the proportion of *Alectoria* in response to the harvesting treatments.

The parameter α_{it} is the fixed effect (log-odds) of treatment relative to the control (no-harvest) (i.e., $\alpha_i = 0$ for the control); γ_{iu}, δ_{iv}, $\phi_{i,}$ and $\gamma\phi_{iu}$ are respectively the fixed effects (log-odds) of subalpine fir compared with spruce (i.e., $\gamma_{iu} = 0$ for spruce), a live tree compared with a dead tree (i.e., $\delta_{iv} = 0$ for a dead tree), and a diameter increase of 1 cm ($\phi_{i,}$ is the slope for spruce and $\phi_{i,+}\ \gamma\phi_{iu}$ is the slope for subalpine fir); and β_{is}, $\beta\alpha_{its}$ are the random effects of site and treatment plot (i.e., site × treatment interaction). All random effects were assumed to be independent and normally distributed; variability among lines in the same plot was assumed to be negligible compared with variability among trees, plots, and sites. Model parameters were estimated by the method (Poisson log-linear model) described by Chen & Kuo (2001), using the SAS macro GLIMMIX (Littell *et al.*, 1996). Both a simplified model that excluded species, alive/dead status, and diameter (Model 1: Equation 1 with $\gamma_{iu} = 0$, $\delta_{iv} = 0$, $\phi_i = 0$, $\gamma\phi_{iu} = 0$) and the model that included these effects (Model 2) were fitted to the data. Results were considered significant at $\alpha = 0.05$.

Results

Distribution of lichen by tree species, decay class and diameter class

Analysis of the distribution of lichen immediately after harvest (1993) showed no significant treatment ($P = 0.20$) or species ($P = 0.51$) effects, while decay class (live / dead) ($P = 0.01$) and diameter ($P = 0.04$) were significant factors (Table 1). The proportion of spruce trees (> 10 cm dbh) in the forest was 17.5% and they held 18.9% of the total lichen biomass, while subalpine fir, the dominant species, held 81.1% of the lichen. Dead trees (17.7% of the sample) contained 12.2% of the lichen while live trees held 87.8%. Small (10-30 cm dbh) subalpine fir trees were the most common size and species of tree in the sample (Fig. 1), and collectively with live medium size subalpine fir (30-50 cm dbh) contain the majority of lichen from all trees sampled (Fig. 2). However, on a per tree basis the small, live subalpine fir trees held about half the amount of lichen as found on the two larger size classes (Fig. 3). The amount of lichen on live spruce trees also increased with size class (Fig. 3). There appeared to be no relationship with species or size class for the amount of lichen per dead tree (Fig. 3). The amount of lichen per tree was substantially lower at the UGC site than the other three sites (Fig. 4). Analysis (Table 2) showed that there was a marginally significant ($P = 0.08$) difference among partial cutting treatments and no-harvest treatment in the proportion of *Alectoria* immediately post-harvest. The trees in the partial cutting treatment with medium-size (0.13 ha) openings were more likely to have more *Bryoria* than those trees in the no-harvest or other two partial cutting treatments. Decay class (live / dead) was highly significant ($P < 0.0001$) (Table 2) with dead trees having more A*lectoria*. (56.3%) than live trees (41.5%) (Fig. 5).

Tree fall and recruitment

A total of 87 trees fell from the original sample of 1225, over 10.5 years. Tree fall rates averaged 0.7% per year of standing trees across all sites and treatments. It ranged from 0.6% to 0.8% per year by treatment (Table 3) and 0.3% to 0.9% among sites. The rate of fall was higher for subalpine fir (0.7%) than for spruce (0.5%). Before falling, the majority of trees were dead (73.5%) compared to live (26.5%). Of the 227 dead standing trees in the sample, 23.4% fell in 10.5 years at a rate of 2.2% per year. The live trees had a much lower fall rate (0.2% per year). Thirty new recruits were recorded in 2003 (27 subalpine fir and 3 spruce).

Response to partial cutting

Results of the logistic analysis of changes in lichen abundance for the whole time period 1993 to 2003 (Table 4) show that there were significant differences among treatments ($P = 0.03$ for Model 2 which included tree species, diameter and decay class). Trees in the residual forest in either small (0.03 ha), medium (0.13 ha), or large (1.0 ha) opening treatments showed more of a shift towards higher lichen classes than did trees in the no-harvest treatments (Fig. 6). Decay class ($P < 0.0001$) and species ($P = 0.02$) exhibited significant relationships with change in lichen class (Table 4). However, ignoring these factors (Model 1) appeared to have little impact on the significance of the treatment effect ($P = 0.05$). Logistic analysis of changes in lichen composition from 1993 - 2003 suggested that there were marginally significant differences among treatments after ten years ($P = 0.06$ for Model 1 and $P = 0.10$ for Model 2); partial cuts showed a greater tendency than the no-harvest treatment to shift towards more *Bryoria* and less *Alectoria* ($P = 0.04$) (Table 5, Fig. 7).

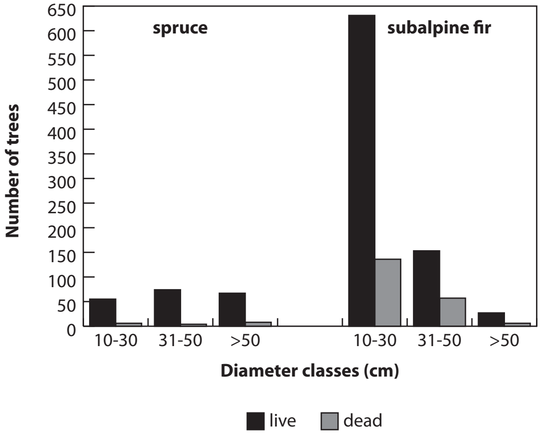

Fig. 1. Distribution of sample trees (n=1225) by species, decay class, and dbh class (1993).

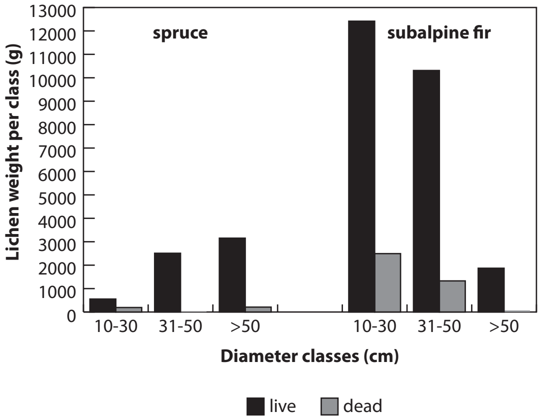

Fig. 2. Total weight of lichen in each combination of species, decay class and diameter class based on 1225 sample trees from all sites and treatments (1993).

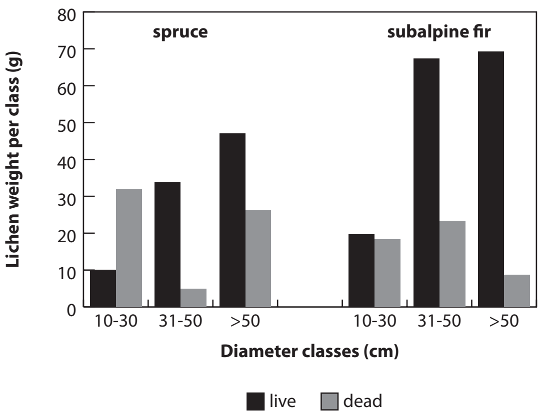

Fig. 3. Mean weight of lichen per tree in each combination of species, decay class and diameter class.

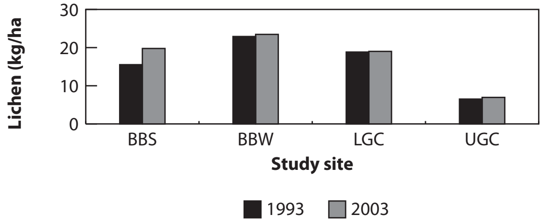

Fig. 4. Estimate of quantity of lichen per site (kg/ha) in the caribou feeding zone (up to 4.5 m) in 1993 and 2003.

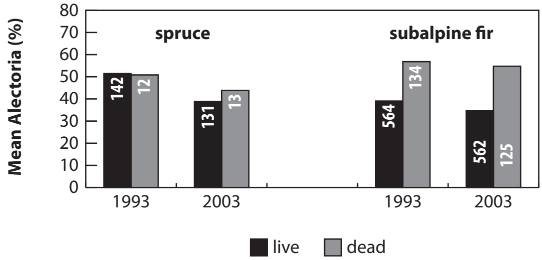

Fig. 5. Composition of lichen (average percentage of *Alectoria*) on dead and live subalpine fir and spruce trees in 1993 and 2003 for trees rated class 2 and higher. Sample size (number of trees) is noted in each bar.

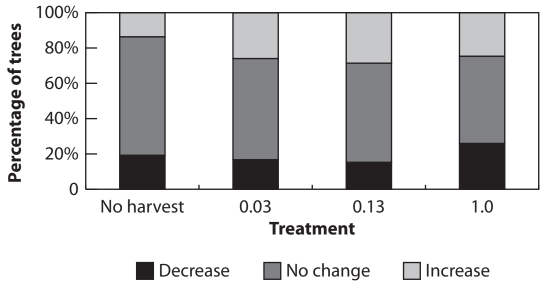

Fig. 6. The percentage of sample trees that showed an increase or decrease or no change in lichen abundance from 1993 to 2003 (percentages differed significantly among treatments, P=0.03).

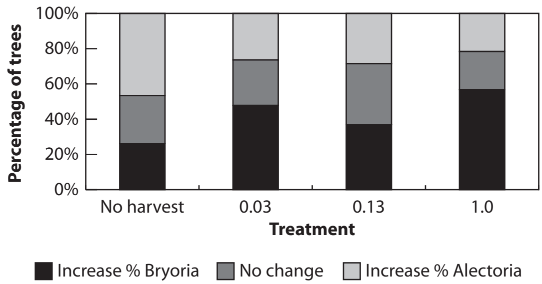

Fig.7. The percentage of sample trees that showed a change in composition (% *Alectoria* / *Bryoria*) from 1993 to 2003 (differences among treatments were marginally significant, P=0.10)

Discussion and management implications

Forests at high elevations are dominated by subalpine fir, have many sizes of trees, and contain numerous dead trees in various stages of decay. Each component contributes to the lichen loading in the forest as a whole. The small subalpine fir trees hold a large quantity of the total lichen but in small amounts per tree. The larger trees in our study tended to hold a larger quantity of lichen in the caribou feeding zone. Campbell & Coxson (2001) also found the lichen load to increase with the size of whole subalpine fir and Engelmann spruce trees. Snow trailing studies have shown that caribou select trees with higher lichen ratings for foraging (Terry, 2000; Kinley *et al.*, 2003); therefore, retention of a portion of the larger trees is vital.

Dead trees are an important component of the stand due to their large number (17.7% of stems in this study) and the total amount of lichen they hold (12.2%). Dead trees hold a somewhat larger proportion of *Alectoria* and lower amounts of *Bryoria* than live trees. Campbell & Coxson (2001) found *Alectoria* to be most abundant in the lower canopy and to utilize summer rainfall events to a greater extent than *Bryoria* to sustain thallus hydration. Perhaps, exposure to summer rainfall events is accentuated in dead trees thus favouring *Alectoria*. Although caribou prefer foraging on *Bryoria* (Rominger *et al.*, 1996), it is important to retain both genera in the stand. In particular during forest operations, safe dead trees should be kept, while ones in advanced stages of decay (unsafe) should be cut. In any case, unsafe ones are likely to fall out of the stand quickly.

Table 1. Logistic regression models of lichen abundance distribution immediately post-harvest (1993). The reference value in the analysis is Lichen Classes 3, 4. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	Lichen Classes 0,1	Lichen Class 2	Lichen Classes 0,1	Lichen Class 2
α (Large)	0.18 ± 0.23	0.07 ± 0.22	0.31 ± 0.24	0.17 ± 0.22
α (Medium)	0.68 ± 0.24	0.45 ± 0.23	0.68 ± 0.24	0.44 ± 0.23
α (Small)	-0.08 ± 0.23	-0.02 ± 0.21	0.09 ± 0.23	0.09 ± 0.22
γ (Subalpine fir)			0.44 ± 0.40	0.39 ± 0.37
δ (Live)			-0.73 ± 0.25	-0.75 ± 0.24
ϕ (Dbh)			-0.015 ± 0.006	-0.011 ± 0.006
γ ϕ (Subalpine fir x Dbh)			0.005 ± 0.012	0.001 ± 0.011

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.03	0.1000	6	1.56	0.1989
No-harvest *vs* Large	2	0.34	0.7156	2	0.85	0.4374
No-harvest *vs* Medium	2	4.06	0.0303	2	3.93	0.0330
No-harvest *vs* Small	2	0.08	0.9191	2	0.10	0.9029
Large *vs* Medium	2	2.10	0.1442	2	1.12	0.3424
Large *vs* Small	2	0.75	0.4813	2	0.50	0.6098
Medium *vs* Small	2	5.20	0.0134	2	3.00	0.0677
No-harvest *vs* Partial Cut	2	0.96	0.3972	2	1.76	0.1921
Species				2	0.68	0.5089
Live/Dead				2	4.86	0.0078
Dbh				2	3.26	0.0387
Dbh x Species				2	0.11	0.8987

Table 2. Logistic regression models of lichen composition (*% Alectoria*) immediately post-harvest (1993). The reference value in the analysis is *Alectoria* > 50%. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	0%-10% *Alectoria*	11%-50% *Alectoria*	0%-10% *Alectoria*	11%-50% *Alectoria*
α (Large)	-0.35 ± 0.58	-0.11 ± 0.54	-0.34 ± 0.60	-0.09 ± 0.56
α (Medium)	1.43 ± 0.56	0.63 ± 0.55	1.50 ± 0.58	0.66 ± 0.57
α (Small)	-0.16 ± 0.57	-0.26 ± 0.55	-0.18 ± 0.59	-0.27 ± 0.56
γ (Subalpine fir)			-0.09 ± 0.45	0.02 ± 0.36
δ (Live)			1.14 ± 0.21	0.55 ± 0.17
ϕ (Dbh)			-0.005 ± 0.007	-0.007 ± 0.006
$\gamma\,\phi$ (Subalpine fir x Dbh)			0.001 ± 0.014	-0.002 ± 0.011

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.12	0.0918	6	2.19	0.0821
No-harvest vs Large	2	0.19	0.8302	2	0.17	0.8411
No-harvest vs Medium	2	3.22	0.0600	2	3.37	0.0533
No-harvest vs Small	2	0.11	0.8943	2	0.12	0.8889
Large vs Medium	2	4.87	0.0177	2	4.97	0.0163
Large vs Small	2	0.17	0.8484	2	0.17	0.8433
Medium vs Small	2	3.94	0.0347	2	4.12	0.0300
No-harvest vs Partial Cut	2	0.22	0.8008	2	0.24	0.7869
Species				2	0.03	0.9713
Live/Dead				2	16.37	<.0001
Dbh				2	0.85	0.4296
Dbh x Species				2	0.02	0.9757

Table 3. Number of tree falls and recruits per treatment as a percentage of standing trees.

		No-harvest	Small	Medium	Large	Total
Tree falls	1993-1997	7	10	13	11	41
	1997-2001	8	9	14	5	36
	2002-2003	4	2	1	3	10
	Sum 1993-2003	19	21	28	19	87
	Total trees 1993	305	314	318	290	1225
	1993-2003 % of total	6.23	6.69	8.81	6.55	7.09
	% per year	0.59	0.64	0.84	0.62	0.68
Recruits	Sum 1993- 2003	9	6	12	3	30
	Total trees 2003	295	299	302	274	1170

Our results are consistent with those of Coxson *et al.* (2003), who found that the abundance of lichen in the caribou feeding zone (4.5 m) did not vary with tree species. However, Campbell & Coxson (2001) also found by sampling branches throughout whole trees, in uncut forest, that subalpine fir did hold more lichen than Engelmann spruce and the natural clumpy arrangement of subalpine fir was a factor that increased lichen abundance. Trees with higher lichen loading throughout would contribute more potential forage as litterfall or on tree falls. There is a temptation to reforest the harvested openings with spruce that has higher commercial value. However, until more research is available, the recommended regeneration strategy is to plant or acquire natural regeneration, in small groups (with reduced inter-tree distance) with a species mix similar to that found at the site before harvest (Youds *et al.*, 2000).

The removal of one third of the trees, through group selection harvesting, resulted in an immediate loss of lichen. The amount of time required for trees in these openings to develop with sufficient quantities of lichen for forage in the future is not known. However, the sites at Blackbear Creek which originated about 297 years ago, through natural regeneration following wildfire (Steen *et al.*, 2005), have similar lichen abundance to Lower Grain Creek established about 446 years ago and much more lichen than Upper Grain Creek (426 years old). The elapsed time since tree removal is just one of many factors that determine the lichen holding capacity of the forest. Goward & Campbell (2005) describe three important

Table 4. Logistic regression models for the change in lichen abundance from 1993 to 2003, including fallen and recruited sample trees. The reference value in the analysis is the increase. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	Decrease	No change	Decrease	No change
α (Large)	-0.86 ± 0.38	-0.81 ± 0.35	-0.84 ± 0.37	-0.81 ± 0.34
α (Medium)	-0.93 ± 0.37	-0.90 ± 0.35	-1.11 ± 0.36	-0.99 ± 0.34
α (Small)	-0.23 ± 0.37	-0.84 ± 0.35	-0.34 ± 0.36	-0.90 ± 0.34
γ (Subalpine fir)			-1.08 ± 0.41	-0.78 ± 0.34
δ (Live)			-2.19 ± 0.23	-1.23 ± 0.22
ϕ (Dbh)			0.000 ± 0.006	-0.005 ± 0.005
γ ϕ (Subalpine fir x Dbh)			0.004 ± 0.012	0.007 ± 0.010

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.55	0.0484	6	2.96	0.0277
No-harvest *vs* Large	2	3.50	0.0461	2	3.60	0.0432
No-harvest *vs* Medium	2	4.25	0.0265	2	5.91	0.0084
No-harvest *vs* Small	2	3.22	0.0587	2	3.68	0.0413
Large *vs* Medium	2	0.03	0.9684	2	0.31	0.7396
Large *vs* Small	2	2.12	0.1436	2	1.64	0.2172
Medium *vs* Small	2	2.37	0.1169	2	2.90	0.0768
No-harvest *vs* Partial Cut	2	4.61	0.0202	2	5.60	0.0102
Species				2	3.79	0.0227
Live/Dead				2	50.44	<.0001
Dbh				2	0.69	0.5041
Dbh x Species				2	0.21	0.8130

factors for development of an abundant lichen community which generally increase over time: availability of defoliated branches (attachment sites), stable environmental conditions and openness of the forest (increased ventilation). Other factors such as aspect, slope, slope position, presence of open water, and distance from inoculation source are also important.

The re-establishment of trees and the subsequent inoculation with lichen after a large wildfire may be comparatively slow compared with a group selection system. The openings (particularly those greater than 0.1 ha) can be successfully regenerated through planting (Lajzerowicz *et al.*, 2006) or by natural regeneration, over a somewhat longer period (Steen *et al.*, 2006). Close proximity to the uncut forest should ensure inoculation with lichen fragments that will establish when substrate and climate conditions are conducive for attachment and growth. The recommended cutting cycle of 80 years means that trees will have 240 years to grow and accumulate forage lichen before being harvested again (Youds *et al.*, 2000; Stevenson *et al.*, 2001).

Loss of lichen bearing trees over the entire ten year period has been low and there was little difference in tree fall rates among the treatments (0.6 – 0.8% of the standing trees per year). The subalpine fir trees that died some years ago (decay class 4), perhaps due to western balsam bark beetle (*Ceratocystis dryocoetidis*) (Steen *et al.*, 2005), are now falling out of the stand. The relatively low rates are consistent with other British Columbia studies (Coates, 1997; Huggard *et al.*, 1999; Waterhouse & Armleder, 2004). Typically,

Table 5 Logistic regression models for the change in lichen composition (% *Alectoria*) from 1993 to 2003, including fallen and recruited sample trees. The reference value in the analysis is the increase. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	Decrease	No change	Decrease	No change
α (Large)	1.03 ± 0.41	0.38 ± 0.42	0.92 ± 0.41	0.36 ± 0.42
α (Medium)	0.62 ± 0.41	0.68 ± 0.41	0.63 ± 0.40	0.70 ± 0.41
α (Small)	1.31 ± 0.41	0.44 ± 0.43	1.16 ± 0.41	0.40 ± 0.43
γ (Subalpine fir)			-1.10 ± 0.44	-0.02 ± 0.54
δ (Live)			0.45 ± 0.22	0.14 ± 0.23
ϕ (Dbh)			0.007 ± 0.007	0.013 ± 0.008
γ ϕ (Subalpine fir x Dbh)			0.015 ± 0.013	-0.010 ± 0.016

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.46	0.0564	6	2.06	0.1008
No-harvest *vs* Large	2	3.22	0.0597	2	2.62	0.0957
No-harvest *vs* Medium	2	1.68	0.2101	2	1.82	0.1862
No-harvest *vs* Small	2	5.26	0.0134	2	4.22	0.0278
Large *vs* Medium	2	1.46	0.2551	2	1.19	0.3220
Large *vs* Small	2	0.26	0.7715	2	0.21	0.8127
Medium *vs* Small	2	2.74	0.0863	2	2.15	0.1400
No-harvest *vs* Partial Cut	2	4.37	0.0256	2	3.77	0.0396
Species				2	4.61	0.0101
Live / Dead				2	2.03	0.1311
Dbh				2	1.22	0.2944
Dbh x Species				2	2.00	0.1352

the first few years following harvest are the most susceptible to endemic wind throw (Stathers *et al.*, 1994). Coates (1997) and Huggard *et al.* (1999) found increased rates overall in partial cuts relative to uncut forests within the first couple of years post-harvest. In a longer term study of five years, Waterhouse & Armleder (2004) found no treatment differences between uncut and partially cut forest. In our study, the high proportion of dead fallen trees (73.5%) and much higher rate of tree fall for standing dead compared to standing live (10 times) is similar to that reported by Waterhouse & Armleder (2004). Huggard *et al.* (1999) found the rate of fall for subalpine fir was higher than that of Engelmann spruce. Veblen (1986) notes the greater stability of Engelmann spruce leads to its long-term presence in ESSF forests.

Although a certain amount of arboreal lichen in the stand is lost through tree fall, in the short-term it provides a concentrated supply of lichen which is actively sought out by caribou (Rominger & Oldemeyer, 1989; Rominger & Oldemeyer, 1991; Terry *et al.*, 2000; Kinley *et al.*, 2003). This important source of forage should be encouraged by maintaining a high proportion of subalpine fir in the stand, retaining the standing dead where safe during harvesting operations and using long cutting cycles to recruit live and dead lichen bearing trees over time.

Over the ten year study period, partial cutting using any of the opening sizes increased the frequency of a higher abundance rating for arboreal lichen relative to the no-harvest treatment ($P=0.03$). Therefore, losses through in situ decomposition, fragmentation and foraging are being exceeded by growth rate gains to a greater extent in the partial cut treatments. Using the same lichen estimation technique, Coxson *et al.* (2003) found no differences in lichen loading two years post-harvest among no-harvest, single tree and group selection (30% cut) treatments on one site in the Cariboo Mountains to the northeast of our study site. Rominger *et al.* (1994) reported no difference in quantity of lichen on branches taken from two pairs of partial cuts and no-harvest blocks, 8 -10 years after cutting. In *Picea abies* dominated Scandinavian forest, Esseen & Renhorn (1998) reported wind scouring of *Alectoria sarmentosa* up to two tree lengths from newly created edges. At distances of 20-30 m from edges the lichen biomass recovered and ultimately reached higher levels of abundance than those in forest interior sites. Greater post-harvest light exposure while being protected from the winds at the immediate edge may explain this increase (Esseen & Renhorn, 1998). Coxson *et al.* (2003) reported higher light levels in the group selection treatment compared to uncut forest. This may also explain the trend we recorded of increased frequency of higher lichen ratings in our partial cutting relative to the uncut forest. The edge effect was also expected to be greater in the boreal forest study where harvest openings were much larger (Esseen & Renhorn, 1998) allowing greater wind fetch resulting in further wind penetration into the uncut forest.

In addition to light availability, lichens are sensitive to wetting and drying cycles (Kershaw, 1985) and degree of ventilation in the stand (Goward & Campbell, 2005). In our study, Stathers *et al.* (2001) measured canopy wetness, relative humidity and air temperature (1.5 m above ground) in one opening of each size (0.03 ha, 0.13 ha and 1.0 ha) and the no-harvest treatment on the Blackbear winter block. These variables were very similar among treatments so were considered to be a function of the overlying air mass. In a more refined study, Coxson *et al.* (2003) measured lichen thallus temperature and hydration and found the cumulative duration of thallus hydration (required for photosynthetic activity) to be greater in the uncut forest than in a group selection treatment (especially on south aspect branches). This finding was supported in a companion study (Stevenson & Coxson, 2003) that found growth rates of *A. sarmentosa* and *Bryoria fuscenscens* were higher in a no-harvest treatment compared to the edges of a group selection cut. If this trend is happening on our study area, the effect must be spatially limited and not reflective of the entire residual stand. It is possible that the group selection treatments have increased the overall ventilation of the stands enabling species of *Bryoria* normally occurring higher in the canopy to colonize and grow in the lower portions of the canopy (Goward & Campbell, 2005).

Coxson *et al.* (2003) hypothesize that the lichen community could shift on the group selection edges to greater abundance of *Bryoria* and reduction in *Alectoria* over a longer period of time. Studies by Rominger *et al.* (1994) and Stevenson (2001) suggest a possible shift to *Bryoria* in partially harvested stands. Our findings are consistent with this hypothesis. After ten years, we found, based on samples throughout the residual forest, a marginally significant difference among treatments ($P=0.10$), with partial cutting treatments showing a greater likelihood of an increase in the proportion of *Bryoria* than the no-harvest treatment ($P=0.04$).

Terry *et al.* (2000) studied winter habitat selection by mountain caribou including foraging strategies. They concluded that 400-500 stems ha-1 should be maintained in managed forests to provide adequate lichen forage. The stem density in the residual forest (Steen *et al.*, 2005) after the first entry in our low volume removal group selection meets this recommendation and in time more lichen bearing trees will recruit as the openings regenerate. Also, the lichen bearing capacity of the residual forest has not been negatively affected by any of the partial cutting treatments. Therefore, application of group selection silvicultural systems on long cutting cycles (80 years) and with low levels of removal (30%) as tested in this study and recommended for 'modified harvesting' areas (Youds *et al.*, 2000) should maintain enough lichen for foraging caribou.

Removal of one-third of the forest, even if tempered by increased abundance in the residual portion, may diminish the attractiveness of the habitat for caribou. This concern fostered development of an adaptive management trial, involving a 1200 ha of partial cutting area and a 2000 ha unharvested area, to determine whether caribou would utilize habitat changed by group selection (Armleder *et al.*, 2002). Providing lichen bearing habitat meets just one of the needs of caribou. Other potentially adverse factors that need to be managed include: habitat fragmentation in conjunction with creation of early seral range for other ungulate species (Seip, 1992), predation (Bergerud *et al.*, 1984; Bergerud & Elliot, 1986; Seip, 1992) and motorized winter recreation (Kinley, 2003; Powell, 2004). Some of these factors are inter-related. For example, while partial cutting may retain sufficient forage lichen, the access created by timber harvesting could lead to increased snowmobile use and consequently increased detection, encounter and kill rates of caribou by wolves (Powell, 2004). A comprehensive approach that considers all factors and their interactions is essential to maintain and recover the threatened mountain caribou.

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