

Impacts of silvicultural treatments on arboreal lichen biomass in balsam fir stands on Québec's Gaspé Peninsula: Implications for a relict caribou herd

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Abstract

We investigated immediate, medium and long-term effects of logging on arboreal lichen biomass in old-growth balsam fir forests (*Abies balsamea* (L.) Mill.) in the highlands of Québec's Gaspé Peninsula using three complementary approaches. Firstly, we estimated the immediate loss of lichen biomass following logging and the annual lichen litterfall from remnant trees over 2 post-logging years. Treatments included selection cutting at three intensities (25, 30, 35%), diameter-limit cutting and cutting with protection of regeneration and soils (CPRS). Among studied treatments, we found that CPRS and diameter-limit cutting removed almost all the standing lichen biomass, while selection and partial cut allowed an immediate retention of ~40–60% of the initial lichen biomass. Our results also suggested that the impact of logging on lichen litterfall rates were higher in silvicultural treatments (3–8.5%) compared to controls (1–2%); litterfall rates did not differ after 1 or 2 years post-treatment. Secondly, we evaluated medium-term effects by comparing pre-harvest fruticose lichen biomass data with data collected at the same site 4 years after experimental thinning operations. Mean fruticose lichen biomass did not change 4 years post-harvest. However, *Bryoria* spp. biomass did increase relative to *Alectoria sarmentosa* while *Usnea* spp. remained unchanged. Finally, the long-term logging effects were assessed by evaluating fruticose lichen biomass along a forest chronosequence in stands aged 30, 50, 70 and 90 years. Lichen biomass increased as a function of time for all genera, especially *Alectoria*. Logging activities result in direct losses of lichen biomass, but careful selection cutting that retains large lichen bearing trees and maintains post-harvest conditions not detrimental to lichen growth, particularly for *Bryoria* spp., can ensure a substantial biomass of lichens post-harvest. Such measures may ultimately contribute to maintaining woodland caribou herds that rely on arboreal lichens.

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1. Introduction

Although transition forests may contribute to overall epiphytic diversity (Boudreault et al., 2000), the importance of old-growth forests for non-vascular plants is well recognized (e.g., Lesica et al., 1991; Esseen et al., 1992; Goward, 1994).

The unique structural and microclimatic conditions that are created as a forest ages are facilitating mechanisms that make old-growth forests important for alectorioid lichen species (Rose, 1976; Selva, 1994; Goward, 1998). Among alectorioid lichen species, genera *Alectoria*, *Bryoria* and *Usnea* only achieve noteworthy biomass in late seral stages of forest development (Goward, 1998). Stable substrates are, however, uncommon in young transitional forests; it is only in old growth forests that significant lichen biomass can be found, occurring in vertical, moisture and temporal gradients (McCune, 1993; Arseneau et al., 1997). Conditions such as forest continuity, decomposing trunks, high relative humidity, as well as forest structures and processes common to old growth stands are

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necessary before many lichens attain substantial biomass and begin to reproduce and disperse (Rose, 1976; Lesica et al., 1991; Rheault et al., 2003). Recent studies suggest that logging may induce sharp declines in bryophyte diversity in the short-term (Armleder and Stevenson, 1996; Dettki and Esseen, 1998; Vellak and Ingerpuu, 2005). While some studies have been conducted on lichen community response to forest harvesting in Europe (e.g., Dettki and Esseen, 1998; Esseen and Renhorn, 1998; Vellak and Ingerpuu, 2005), western Canada and the United States (e.g., Rominger et al., 1994, 1996; Rheault et al., 2003; Stevenson and Coxson, 2003), little research has been done on the short and long-term effects of current forest harvesting practices on these lichens in eastern North America, especially in the high elevation boreal forests of eastern Canada (Arseneau et al., 1997).

Given that fruticose arboreal lichens are the basis of the winter diet of some populations of woodland caribou (*Rangifer tarandus caribou*) in North America (Rominger et al., 1996; Terry et al., 2000), detrimental logging impacts on lichen communities may induce indirect negative effects on caribou persistence in managed landscapes. Among the caribou populations that rely on arboreal lichens, the relict herd of Québec's Gaspé Peninsula, in eastern Canada, is well studied (Ouellet et al., 1996; Arseneau et al., 1998; Mosnier et al., 2003). This herd is actually recognized as endangered (COSEWIC, 2002) with less than 140 animals ranging in an area of approximately 1300 km² located in and around the Gaspésie Provincial Park. The high elevation forest stands of the Gaspé Peninsula are considered old-growth and the principal natural disturbance factors affecting the forest dynamics in this region are wind, ice, insect outbreaks, and tree senescence that typically create small openings in the forest canopy (Dansereau, 1999). This area encompasses reserves of balsam fir dominated old-growth stands that support high standing crops of fruticose arboreal lichens (hereafter referred to as lichens) (Arseneau et al., 1998). Although timber harvesting is forbidden in the park, the Matane and Chic-Chocs Wildlife Reserves bordering the park (Fig. 1) are subject to logging. Given their importance in the caribou's winter diet (Rominger et al., 1996; Terry et al., 2000) and the slow growth rate and dispersal ability of lichens (Esseen, 1985; Dettki et al., 2000; Sillett et al., 2000), it is critical to determine the ability of lichens of the genera *Alectoria*, *Bryoria* and *Usnea*, to thrive in and colonize areas directly affected by logging operations (Stevenson and Coxson, 2003).

In this study, we were interested in identifying the immediate, medium and long-term effects of forest harvesting on lichen abundance in the Gaspé Highlands. Several management perspectives were examined. Firstly, we investigated the immediate effects of five harvesting regimes (selection cutting at three intensities, cutting with protection of advance regeneration and soils, diameter-limit cutting) in old growth stands by evaluating the loss of lichens by logging activities as well as the rate of lichen litterfall in mature balsam fir forests pre-harvest and for 2 years post-harvest. We predicted that as a result of microclimatic changes induced by harvesting, the rate of annual lichen litterfall would be highest in the year following treatment and would stabilize thereafter.

Secondly, we evaluated how selection cutting in two mature stands affected epiphytic lichen abundance. We chose to study selection cutting versus other treatments currently being utilized in these highlands because we suspected that this could be the best alternative for sustainable forest management in this area, as it favours the maintenance of arboreal lichens in harvested stands. We predicted that lichens would remain relatively abundant in these stands as conditions would remain favourable for lichen dispersal and development. We predicted that the relative genus composition would change based on changing environmental conditions. For example, with drier, brighter conditions, we predicted that the reputedly sun-loving *Bryoria* spp. (Brodo and Hawksworth, 1977) would predominate post-harvest, while *Alectoria sarmentosa* (hereafter referred as *Alectoria*), considered a late successional species (Lesica et al., 1991; Arseneau et al., 1997), would decrease.

Finally, we compared the biomass of epiphytic macrolichens in forest age classes 30, 50, 70, and 90 years after stand replacing disturbances. We predicted that the total biomass of alectorioid lichens would increase as the forest aged and that high biomass would only be attained near the end of life expectancy of dominant tree species.

2. Study area

This study was carried out in the highlands of the Gaspé Peninsula, Québec, Canada; an area that includes the Gaspésie Provincial Park and two adjoining Wildlife Reserves (between 48°45' N; 65°20' W and 49°05' N; 66°30' W; Fig. 1). This region experiences a cool and humid climate, a result of altitude and proximity to the Gulf of St. Lawrence. The average annual temperature is below 0 °C for areas above 550 m. The Park and adjoining highland areas also record the highest annual precipitation (up to 1660 mm) in Québec; a third of this precipitation falls as snow and, in the higher elevations, fog is present 200 days out of the year. The forest stands studied occur in the balsam fir (*Abies balsamea*)—white birch (*Betula papyrifera*) ecoregion (Grandtner, 1966), corresponding to the Acadian section of the boreal forest (Rowe, 1972). The elevation range for this study was between 800 and 1000 m asl, corresponding to the mountainous forest vegetation belt. In this region, Arseneau et al. (1997) found that *Alectoria*, *Bryoria* spp. and *Usnea* spp. represented the bulk of epiphytic fruticose lichen vegetation.

3. Methods

Lichen litterfall was evaluated in old-growth balsam fir stands in the area of Lac Solitaire (Matane Wildlife Reserve) and in the Canton Lesseps area (Chic-Chocs Wildlife Reserve). The effect of partial cutting on standing lichen biomass was evaluated at elevations of 700 and 900 m in mature fir stands on Mont Auclair (Gaspésie Provincial Park). Finally, change in lichen community structure associated with a forest chronosequence from 30 to 90 years was documented at study sites located on Mont Auclair (90 years) and from sites located in the Chic-Chocs Wildlife Reserve (30, 50, and 70 years) that all

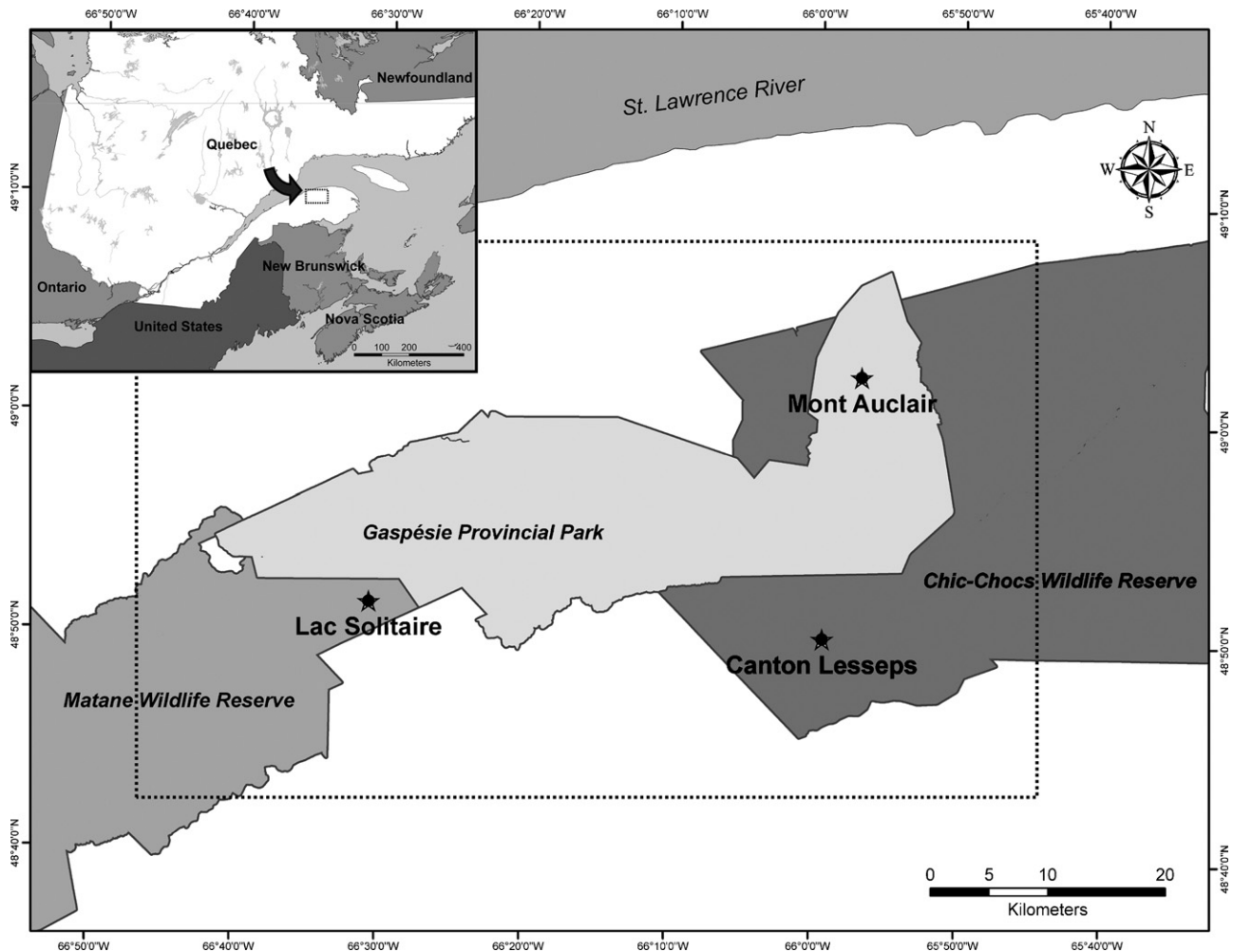


Fig. 1. Location of study area on Québec's Gaspé Peninsula (dotted rectangle) and of study sites: Lac Solitaire (Matane Wildlife Reserve), Mont Auclair (Gaspésie Provincial Park) and Canton Lesseps (Chic-Chocs Wildlife Reserve).

originated from previous clear-cutting activities. For each study site, criteria such as elevation, aspect, disturbance origin, species composition and depositional layer were kept constant to ensure homogeneity among sites. Several studies have shown short-term (~ 10 years) negative edge effects up to 100 m from cutover edges (Esseen and Renhorn, 1998; Kivistö and Kuusinen, 2000; Rheault et al., 2003) so to avoid possible edge effects, study sites were located at least 120 m from stands of other age classes or remnant trees whenever possible. We assumed this buffer would prevent potential bias induced by surrounding habitats.

3.1. Immediate effects

In the summer of 1997, experimental logging (Table 1) was carried out in several old-growth balsam fir stands in the Lac Solitaire (Matane Wildlife Reserve) and Canton Lesseps (Chic-Chocs Wildlife Reserve) areas to investigate the impacts of logging on lichen abundance. Objectives of this simulated thinning were to first assess standing lichen biomass before and following treatment and secondly, to monitor lichen biomass change in remnant trees over time for each given silvicultural

treatment. In the Lac Solitaire area, 23 cut blocks of between 9 and 17 ha (average size ≈ 10 ha) were studied with a distribution of treatments as follows; selection cutting ($n = 6$), cutting with protection of regeneration and soils (CPRS; $n = 6$), diameter-limit cutting (19 cm; $n = 5$) and control blocks ($n = 6$). In the area of Canton Lesseps, 18 blocks of 1 ha each were studied: partial harvest blocks where 35% of the basal area was removed ($n = 6$), partial harvest blocks that removed 25% of the basal area ($n = 6$), and control blocks ($n = 6$). The main differences between the selection cutting and the partial harvesting regimes concern the spatial and age distribution of trees removed. Partial cutting may not strategically maintain clusters of trees nor does it guarantee an uneven-aged stand structure (Table 1). Selection cutting can maintain an uneven-aged stand structure through various techniques whereby small groups or single trees are removed.

We used a regression model (lichen biomass in a single tree = $2.91 \times \text{DBH} - 2.07$; $R^2 = 0.78$) developed for the study area in undisturbed mature forest (Arseneau et al., 1997) to obtain pre- and post-harvest biomass values of standing lichen biomass in the stands studied. This model has been tested with numerous tree samples from the nearby Canton Lesseps and

Table 1
Silvicultural treatment types in stands selected to investigate the impacts on alectoroid lichens at study sites on Québec's Gaspé Peninsula; study sites were located in the Matane Wildlife Reserve (MWR) and Chic-Chocs Wildlife Reserve (CWR)

Treatment type	Description	No. of plots	Size (ha)	Study site
Selection cutting	Partial harvest that removes 30% of the basal area of a stand. Trees are chosen individually or in small groups. Uneven-aged structure is maintained throughout the stand	6	10	Lac Solitaire (MWR)
Cutting with protection of regeneration and soils (CPRS)	Even-aged harvesting system that removes trees >10 cm DBH and protects established regeneration during harvesting operations	6	10	Lac Solitaire (MWR)
Diameter-limit cutting	Partial harvest that removes all merchantable trees with DBH > 19 cm	5	10	Lac Solitaire (MWR)
Partial harvesting (Thinning)	Harvesting that removes 25 or 35% of trees in a stand but not in a manner that maintains an uneven-aged stand structure	6	1	Canton Lesseps (CWR)
Control	No silvicultural treatment performed	6	10	Lac Solitaire (MWR)
		6	1	Canton Lesseps (CWR)

Lac Solitaire areas and the observed and predicted biomass did not differ significantly; we consequently assume this model provides reliable estimates of lichen biomass.

The effects of different harvesting procedures on the rate of lichen litterfall was assessed using litterfall traps placed in old-growth balsam fir stands in the Lac Solitaire and Canton Lesseps areas. Three blocks of each treatment type ($n = 3$) were randomly selected from the Lac Solitaire area and two ($n = 2$) from Canton Lesseps. The CPRS treatment removed all trees so no litterfall traps were placed in these blocks. In each selected block, a 20 m × 20 m quadrat was established and in the summer of 1998 and 1999 nine lichen traps were placed within each to collect lichen litterfall. A lichen trap consists of nylon mosquito netting (1 mm mesh) attached to a 1 m × 1 m wooden frame. These traps were left in place for 2 years (summers 1998–2000) and lichen litterfall was collected after each year (summers 1999 and 2000). Since traps were emptied after year-long periods, the measured biomass represents an annual rate of lichen litterfall.

For each treatment, all lichen fragments >2 cm were removed from the traps, dried in an oven at 60 °C for 24 h and then weighed to a precision of ±0.0001 g. We selected only non-decomposing litterfall that was unattached to wood fragments >2 cm diameter. Lichen attached to smaller wood was removed and included in the weighed sample. To determine the annual rate of lichen litterfall post-harvest, we determined what proportion of the post-treatment standing biomass was represented by the litterfall removed from the traps after each year. The average biomass collected from the lichen traps was studied with relation to the estimated standing biomass for all of the sites studied.

3.2. Medium-term effects

In the summer of 1993, 30% of the basal area in two old-growth fir stands (DBH > 10 cm) at 700 and 900 m were removed in order to investigate the influence of altitude and tree height on lichen abundance (see Arseneau et al., 1997). In the summer of 1997, we returned to the same two sites on Mont

Auclair and randomly selected mature residual trees ($n = 7$ –13) for lichen sampling. We climbed trees in order to remove one south-facing branch from the first two height strata (one from 2 to 4 m and another from 4 to 6 m), randomly chosen among available branches, following the same selection criteria used by Arseneau et al. (1997). These branches were then brought to the lab and all fruticose thalli and fragments >2 cm were removed, sorted by genera (*Alectoria*, *Bryoria*, *Usnea*), oven-dried at 60 °C for 24 h before being weighed to a precision of ±0.0001 g. Lichen biomass at the 3 m level was estimated by multiplying the lichen biomass removed from the sampled branch by the number of branches in the 2–4 m height strata; biomass at the 5 m level was similarly obtained using collected lichens and branch numbers in the 4–6 m height strata.

3.3. Long-term effects

Appropriate sites to assess lichen abundance along a forest chronosequence were located on 1:20,000 forest inventory maps; they represent secondary, post-clearcut forests. Due to the inherent difficulties associated with large-scale ecological studies on arboreal lichen abundance, we adapted a method to quantify standing lichen biomass without having to cut trees. All sites were located in the Chic-Chocs Wildlife Reserve, at elevations between 700 and 1000 m. We assumed a relative homogeneity of soils, topography, and climatic conditions by selecting stands of a single habitat type (balsam fir-white birch) and corroborated it in the field. We established a quadrat of equal area (20 m × 20 m) in each stand (30, 50, and 70 years) and randomly selected seven balsam fir trees within each quadrat. Quadrats were selected to minimize any possible edge effects (see study site selection above). Trees sampled at Mont Auclair in 1993 (Arseneau et al., 1997, 1998) were used to document the 90-year-old age class in the chronosequence. We climbed trees and randomly selected one south-facing branch from heights of 1, 3, 5, and 7 m (or closest branch) on each sampled tree. All fruticose lichen thalli and fragments >2 cm were carefully removed from the branches, sorted by

genera (*Alectoria*, *Bryoria*, and *Usnea*), oven-dried at 60 °C for 24 h and subsequently weighed to a precision of ± 0.0001 g.

3.4. Data analyses

All biomass data were checked for normality using the Wilk-Shapiro's test (Zar, 1999). The lichen litterfall data were log-transformed to better respond to conditions of normality and homoscedasticity. Variations in lichen biomass collected from the traps were tested using a MIXED procedure analysis of variance (treatment and year) (SAS 8.0). The thinning data were square root transformed and the variation in biomass of each genus, before and after silvicultural treatments, was evaluated using the MIXED procedure, three-way (branch height, year and site) nested analysis of variance. Standard deviation was corrected for nested design considering within-site and within-treatment variation (Zar, 1999). The variation in fruticose lichen biomass along forest chronosequence was analysed using a two-way (branch height and stand age) analysis of variance.

4. Results

4.1. Immediate effects

The most direct loss of lichen biomass occurred with the CPRS application, which removed all trees, and hence all standing lichen biomass (Table 2). The diameter-limit treatment (DBH > 19 cm) removed 96% of the pre-harvest lichen biomass. The selection cut that removed 30% of the stand's basal area also removed 55% of the standing lichen biomass, while the partial cut (25 and 35%) removed 37 and 40%, respectively, of the standing lichen biomass.

Lichen litterfall rates differed among silvicultural treatments ($F = 7.38$; $p = 0.02$) (Table 2) but it did not differ over time (i.e., after 1 or 2 years) ($F = 0.14$; $p = 0.72$). Lichen

litterfall did not differ between the diameter-limit and the 30% selection cut treatments ($p = 0.68$). However, both treatments had higher proportions of fruticose lichen biomass fallen than controls by factors of 2 ($p = 0.01$) to 4 ($p = 0.02$). Due to windthrow in the experimental site of Canton Lesseps, we could only sample lichen litterfall in one block (i.e., 9 lichen traps) per treatment ($n = 1$) for 25 and 35% partial cut. Accordingly, no statistical tests were performed but our results (Table 2) followed the same trend as those recorded for the Lac Solitaire area, i.e., a slight increase in lichen litterfall following logging.

4.2. Medium-term effects

When considering total fruticose lichen biomass (all genera pooled), mean biomass did not change 4 years after thinning operations at the two sites near Mont Auclair ($F = 0.76$; $p = 0.39$) nor did mean biomass vary according to altitude (700 vs. 900 m; $p = 0.10$), or branch height (3 vs. 5 m; $F = 3.37$; $p = 0.07$) (Fig. 2). However, the response was different among the lichen genera studied. We found that both treatment and branch height significantly affected mean biomass of *Bryoria* spp. Four years post-harvest, *Bryoria* spp. had significantly increased its biomass ($F = 9.87$; $p < 0.01$) (Fig. 3); elevation had no effect on *Bryoria* spp. ($F = 0.19$; $p = 0.67$) while a slight decreased trend can be observed for *Usnea* spp. biomass ($F = 3.24$; $p = 0.08$). *Bryoria* spp. had a significantly higher biomass at the 5 m level at both elevations ($F = 4.29$; $p = 0.04$) (Fig. 3) post-harvest. Biomass of *Alectoria* and *Usnea* spp. did not change as a result of the treatment ($F = 0.01$; $p = 0.92$ and $F = 2.35$; $p = 0.13$, respectively). The biomass of *Alectoria* did not vary as a function of branch height ($F = 1.48$; $p = 0.23$) in opposition to the biomass of *Usnea* spp. ($F = 4.43$; $p = 0.04$) (Fig. 3) which was greater at the 5 m level. Biomass of *Alectoria* differed ($F = 6.00$; $p = 0.02$) between the two elevations studied, with a higher biomass recorded at the 900 m site (Fig. 3).

Table 2

Fruticose lichen biomass (kg/ha \pm S.D.) in old-growth balsam fir stands in the Lac Solitaire (Matane Wildlife reserve) and Canton Lesseps regions (Chic-Chocs Wildlife Reserve) pre- and post-treatments

No. of blocks sampled	Lac Solitaire				Canton Lesseps		
	CPRS	Diameter-limit ^a	Selection (30% BA ^b)	Control	Partial cut (25% BA ^b)	Partial cut (35% BA ^b)	Control
Per treatment.	$n = 6$	$n = 5$	$n = 6$	$n = 6$	$n = 4$	$n = 4$	$n = 6$
For assessment of lichen litterfall	$n = 3$	$n = 3$	$n = 3$	$n = 3$	$n = 1$	$n = 1$	$n = 1$
Pre-treatment	983 \pm 122	766 \pm 82	922 \pm 235	1009 \pm 274	714 \pm 74	835 \pm 80	915 \pm 248
Post-treatment	0	27 \pm 25	413 \pm 128	1009 \pm 274	450 \pm 157	505 \pm 196	915 \pm 248
% Removed	100	96	55	0	37	40	0
Litterfall (1999)	–	1 \pm 0.7 ^c	12 \pm 4 ^c	10 \pm 2 ^c	30 \pm 20 ^d	43 \pm 24 ^d	18 \pm 21 ^d
% Fallen (1999)	–	3.7	2.9	1.0	6.7	8.5	2.0
Litterfall (2000)	–	0.8 \pm 0.2 ^c	10 \pm 2 ^c	13 \pm 7 ^c	17 \pm 9 ^d	16 \pm 8 ^d	19 \pm 12 ^d
% Fallen (2000)	–	3.1	2.5	1.3	4.0	3.5	2.1

^a Diameter-limit = DBH < 19 cm.

^b BA: basal area.

^c Standard deviation was calculated based on 9 traps per block for 3 blocks (i.e., 27 traps).

^d Standard deviation was calculated based on 9 traps in only 1 block (i.e., 9 traps).

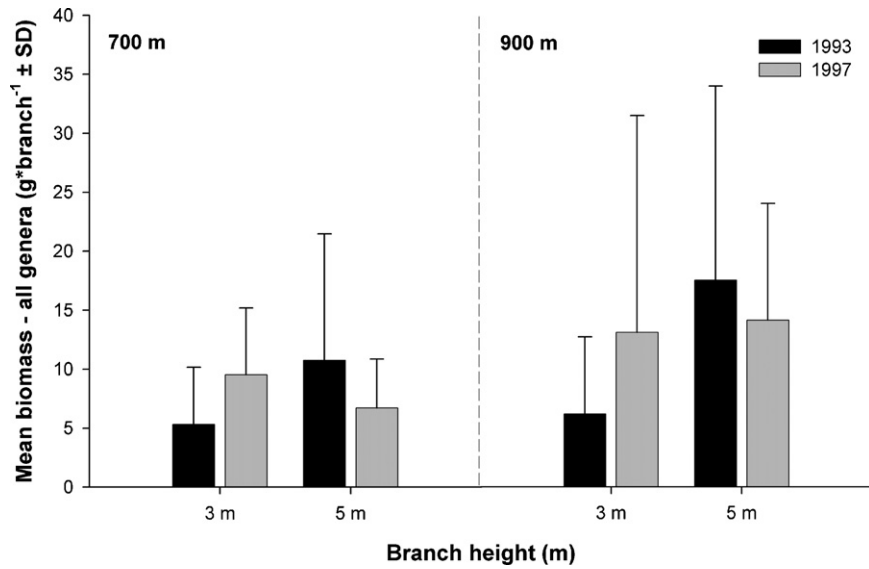


Fig. 2. Mean total fruticose lichen biomass (all genera) at the 700 and 900 m sites in 1993 (before harvest; Arseneau et al., 1997) and in 1997 (4 years post-harvest) in mature balsam fir stands at Mont Auclair, Gaspé Peninsula, Québec.

4.3. Long-term effects

There was very little lichen biomass detected before 50 years and the greatest increase in total biomass occurred during the period from 70 to 90 years (Table 3). Therefore, we restricted the statistical analyses to stands >50 years old. Lichen biomass

increased as a function of time for all genera (*Alectoria*: $F = 8.79$; $p < 0.001$; *Bryoria* spp.: $F = 3.83$; $p = 0.01$; *Usnea* spp.: $F = 3.36$; $p = 0.02$); however, biomass of each genera did not change according to branch height ($p > 0.05$). Lichen biomass accumulation was greatest for *Alectoria* and its relative abundance increased over time (Fig. 4). *Bryoria*'s proportion

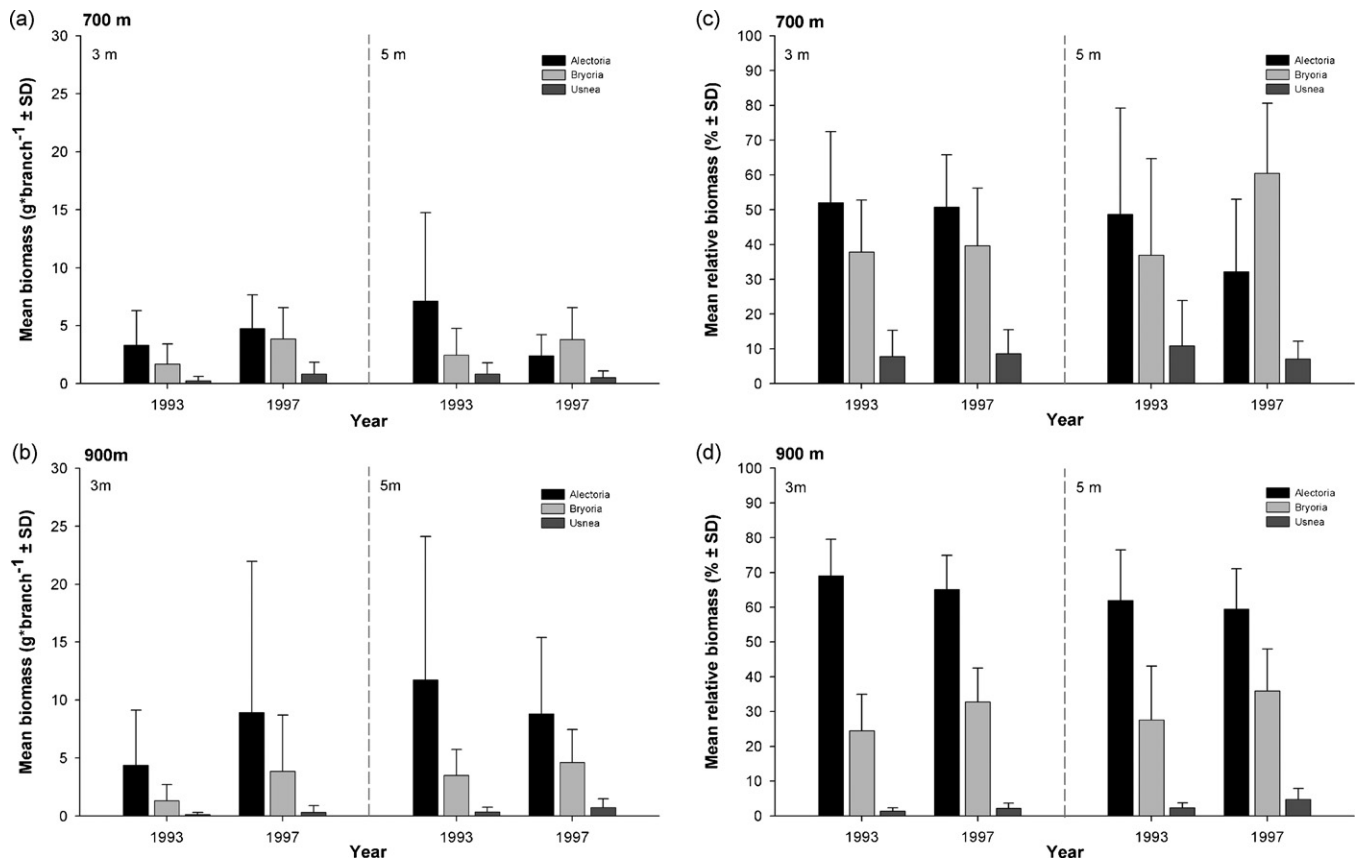


Fig. 3. Mean absolute biomass (a, b) and relative biomass (c, d) of *Alectoria sarmentosa*, *Bryoria* spp. and *Usnea* spp. at the 700 and 900 m sites in 1993 (pre-harvest; Arseneau et al., 1997) and in 1997 (4 years post-harvest) in a mature balsam fir stand on Mont Auclair, Gaspé Peninsula, Québec.

Table 3

Mean biomass (g) and standard deviation (\pm S.D.) for *Alectoria sarmentosa*, *Bryoria* spp. and *Usnea* spp. along a forest chronosequence of 30, 50, 70 and 90 years at study sites on Québec's Gaspé Peninsula

Age (years)	Mean biomass (g \pm S.D.)		
	<i>Alectoria</i>	<i>Bryoria</i>	<i>Usnea</i>
30	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0
50	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0
70	0.2 \pm 0.3	2.4 \pm 2.3	0.5 \pm 0.5
90	14.2 \pm 26.8	6.8 \pm 10.3	1.0 \pm 1.8

decreased as the forest aged in favour of *Alectoria*. *Usnea* was present throughout the chronosequence, but did not attain abundance comparable to *Bryoria* or *Alectoria*.

5. Discussion

5.1. Immediate effects

The immediate impact of logging on lichen biomass differed markedly among treatments. Clearly, the complete removal of host trees, as with the CPRS treatment, not only removes old growth associated lichens but also the associated habitat of mature trees, senescent trees and large snags. The conversion of large tracts of old growth to young managed stands may therefore eliminate, for at least 70 years, the conditions necessary to support a rich and abundant lichen flora (Longton, 1992; Dettki and Esseen, 1998). The diameter-limit treatment that removed 96% of the stand's basal area also removed the largest (and likely oldest) trees in the stand. Since epiphytes are strongly influenced by local combinations of plant cover, topography, and microclimates (Hoffman and Kazmierski, 1969; Arseneau et al., 1997, 1998), this treatment may also drastically impact climatic conditions, especially light intensity, on both the stand and microsite levels.

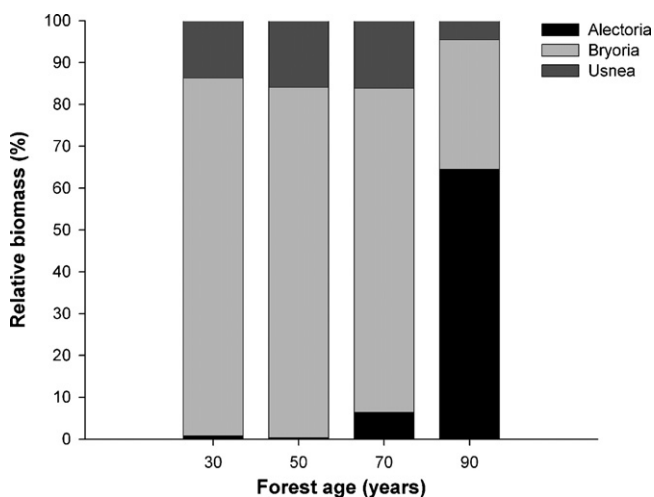


Fig. 4. Proportional biomass of *Alectoria sarmentosa*, *Bryoria* spp., and *Usnea* spp. occurring on tree branches in a forest chronosequence aged 30, 50, 70, and 90 years on Québec's Gaspé Peninsula.

Selection (30%) and partial (25 and 35%) cuttings underwent similar logging intensities and allowed an immediate retention of \sim 40–60% of the initial lichen biomass. These results suggest that selection and partial cutting may mitigate lichen loss and may have implications for successful caribou management in the area.

Our results suggest that litterfall rates increased markedly during the first few years post-harvest, particularly following partial cuttings. This *a priori* negative result may be explained by the greater biomass of lichens that persists following partial cutting. Although not significant, a declining trend in litterfall rates was observed in all treatments in the years post-harvest (except in CPRS, where no lichen remained), indicating that environmental conditions were likely stabilizing post-disturbance. The post-harvest litterfall rates for the selection cut with 30% basal area removed are considerably less than rates for the two partial cuts at 25 and 35% (see Table 2). Stevenson and Coxson (2003) looked at litterfall rates in an Engelmann spruce-subalpine fir forest in north-central British Columbia that had undergone selection harvesting and found that *Bryoria* and foliose lichen litterfall were significantly greater in the year following harvest than in the subsequent year. They were unable, however, to attribute this loss to the treatment since the control exhibited the same pattern. A trend consistent with that of Coxson et al. (2003) suggested a greater decline in standing crop of canopy lichens in the single-tree selection area. Our results suggest that the uneven-aged group-selection cut maintained more favourable environmental conditions for lichen retention than the partial cut. In addition, the close alternation of lichen propagule sources with regularly recruited host trees in the regeneration strata is likely to maintain high and regular lichen productivity in uneven-aged, managed forests. Such results support Dettki and Esseen (1998) and Coxson et al. (2003) conclusions that, although negative impacts are sometimes observed, partial cutting should be preferentially chosen over clearcutting in order to maintain macrolichen communities most similar to natural forests.

Reproductive constraints of alectorioid lichens must be considered when planning selection cutting operations. These lichens disperse primarily via thallus fragmentation and, due to the large size of their fragments, they disperse at shorter distances than do species that rely on soredia or other smaller propagules (Esseen et al., 1996). Peck and McCune (1997) suggested that dispersal over distances $>$ 35 m is negligible. In order to optimize the lichen colonization and growth within logging treatments, especially selection cutting, we believe that harvesting operations should integrate such conclusions when planning residual tree density and residual stand configuration.

5.2. Medium-term effects

Overall total lichen biomass retained in trees did not change 4 years following a partial cut in Mont Auclair, a result similar to that found in subalpine spruce-fir stands of interior British-Columbia following the harvest of 30% of the stand's basal area (Coxson et al., 2003). These results also agree with conclusions of Rolstad et al. (2001) that moderate selective cutting in

Norwegian forests may prove to be an acceptable management option to sustain viable lichen assemblages.

Despite the increase in lichen litterfall observed on a short-term basis, the relative stability in lichen biomass in the medium-term suggests the growth rate may have increased. Indeed, some studies postulate that green tree retention may enrich post-harvest lichen communities (McCune, 1993; Dettki, 2000) and suggest that scattered remnant trees remaining post-harvest – a result of selection cutting – may attenuate microclimatic extremes in the early years following harvest, and may help to preserve legacy populations of host trees and lichens (Peck and McCune, 1997). Directly, they may provide canopy habitat that maintains a suitable environment for the establishment and growth of alectoroid species. They may also maintain a source of propagules from persistent populations of species associated with old growth that, in turn, can accelerate establishment and increase growth rates of lichens in the regeneration cohort at a greater rate than in stands lacking nearby propagule sources. We can speculate, therefore, that strategic clustering of retained trees (group-selection method) can provide a better microclimate and fewer windfalls than a uniform thinning operation. In this study, it is unclear whether dispersal potential was favoured more than growing conditions but we speculate that the environmental conditions created by the partial harvest caused the increased abundance of the *Bryoria* spp. pioneer species.

Four years post-harvest, we found that *Bryoria* spp. biomass significantly increased at both the 700 and 900 m sites and also in the higher stratum (4–6 m) within sampled trees (Arseneau et al., 1997), at the expense of shade-preferring *Alectoria*. We speculate that the brighter, drier environment encountered at these higher strata is detrimental to *Alectoria* but favourable to *Bryoria* spp. This agrees with studies that have demonstrated that *Alectoria* spp. are more abundant in old-growth forests while *Bryoria* spp. dominated second-growth forests in western North America (e.g., Lesica et al., 1991; Radies and Coxson, 2004). Following partial cutting, Rominger et al. (1994) also reported that a decrease in *Alectoria* is usually compensated for by an increase in *Bryoria* spp. Finally, the biomass of *Usnea* spp. remained relatively stable throughout the study, suggesting that the intensity of this partial cutting operation had a low, if any effect, on this genus during the period of study. However, Radies and Coxson (2004) observed that some *Usnea* species are more frequent and abundant in old-growth unmanaged forests than in second-growth stands.

5.3. Long-term effects

From the chronosequence study, we see that the largest accumulation of lichen biomass was recorded in the 90-year age class (Table 3). Since balsam fir dominated stands in this class range from 90 years onward, we speculate that lichen biomass will plateau in this class at the same time that trees are senescing (~100 years). Stand structures can account for differences in lichen biomass between old growth versus young stands. As a forest matures, tree growth slows, dominant branches emerge, microclimate in the crown starts to stabilize,

and leaching of exposed bark produces favourable substrates for many lichen species (Brodo, 1973). Favourable microclimates, suitable germination substrates, stable canopy architecture, and long-term branch stability-common traits in mature forests-all allow sufficient time for propagule dispersal and lichen growth (McCune, 1993). Clearly then, rapid changes in stand structure – and therefore lichen microhabitat – disfavour accumulations of lichen biomass.

5.4. Limits and scope

The results of this study are based on sample sizes that may appear low compared to similar studies (e.g., Uliczka and Angelstam, 1999; Dettki and Esseen, 1998). Although time and budget restrictions frequently lead to relatively small samples in epiphytic lichen studies (e.g., Boucher and Stone, 1992; Arseneau et al., 1998; Boudreault et al., 2000), our sampling effort proved satisfactory for highlighting significant differences in lichen abundance that highlights a number of major impacts of various forestry practices on epiphytic lichen communities in the short, intermediate and long-terms.

6. Management implications

Disturbance modifies environmental conditions in a forest stand and will affect the ability of certain forest species to thrive and reproduce in changing ecological situations. However, natural disturbance events and harvesting have different impacts on forest soils, regeneration and growth (Brinkley and Richter, 1987; Brais et al., 1995). Suitable microclimate and substrate are particularly important to lichen biology and must be considered when designing management guidelines for remnant old growth stands. It is well-known that under even-aged management practices, mature stands – as well as old-growth stands – are threatened (Boudreault et al., 2000; McRae et al., 2001; Löfman and Kouki, 2003). Our results clearly demonstrate that such conversion of old-growth, uneven-aged forest into young, rotational, even-aged stands can have dramatic effects on lichen production (Armleder and Stevenson, 1996). Supporting Stevenson and Coxson (2003), we suggest that of the five silvicultural treatment studied, strategic selection harvesting regimes are the best adapted to maintain lichen biomass and diversity. Otherwise, forests managed under harvesting regimes that eventually eliminate, or substantially reduce, the number of large and old lichen-bearing trees (such as cutting with protection of regeneration and soils) will be unable to sustain initial lichen biomass and therefore, will be unable to provide winter habitat for caribou (Stevenson et al., 2001). Moreover, the natural disturbance regimes that prevail at these altitudes in the study area justify the use of selection cutting as the main logging technique.

With respect to medium-term effects following partial cutting, we observed a slight shift from shade-preferring *Alectoria* toward *Bryoria* spp.; such a dynamic may be positive from a caribou management perspective. Indeed, Rominger et al. (1996) showed that *Bryoria* spp. was preferred by woodland caribou and suggests that this genus should be

considered a management priority in intensively managed landscapes. Other studies also consider *Bryoria* spp. as an important predictor of habitat use by woodland caribou (Terry et al., 2000; Johnson et al., 2001). We also demonstrated that intensive harvesting methods, i.e., CPRS, may directly impact caribou herds by decreasing arboreal lichen availability. In our study area, CPRS may also have a negative indirect effect by increasing habitat quality, e.g., increased fruit production and moose (*Alces alces*) presence for predators of caribou such as black bears (*Ursus americanus*) and coyotes (*Canis latrans*) in regenerating stands (Crête and Desrosiers, 1995; Mosnier et al., submitted for publication).

Considering the conservation status of the resident caribou herd in the Gaspésie Provincial Park, there is a critical need for change towards an ecosystem-based forest management strategy. However, since the long-term impacts of selection harvesting techniques on lichen growth and dispersal are not exhaustively examined, choices of harvesting techniques in caribou winter habitat areas should be fairly conservative. As concluded by Coxson et al. (2003), retention strategies for lichens and the organisms that depend on them should consider cumulative landscape-level effects as well as the harvesting strategy proposed. In situations where uneven-aged management strategies cannot be applied, another consideration for managers would be a moderate extension of the rotation period. Kuusinen and Siitonen (1998) suggested that epiphytic lichen diversity could be increased in a *Picea abies* dominated boreal forest in Finland by prolonging the stand rotation to >120 years and by increasing the diversity of habitats in the stand. In our study area, we are confident that such a moderate extension of the rotation period would not decrease long-term timber production significantly, and would likely result in an increase in aesthetic, wildlife and biodiversity values (Curtis, 1997).

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