Forest Ecology and Management 372 (2016) 44–52

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Short-term response of *Cladonia* lichen communities to logging and fire in boreal forests

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ARTICLE INFO

Article history:
Received 22 January 2016
Received in revised form 29 March 2016
Accepted 3 April 2016

Keywords:
Anthropogenic disturbance
Black spruce
Lichen communities
Natural disturbance
Reindeer lichens
Species persistence

ABSTRACT

Fire is the major disturbance agent in boreal forests that initiates forest regeneration and succession, and plays a major role in determining the composition of terricolous lichen communities. In recent decades however, logging has become an important disturbance agent in boreal forests. In this context, growing concerns about logging effects on endangered species such as woodland caribou (*Rangifer tarandus caribou*) has emerged and drawn attention on how reindeer lichens (i.e. *Cladonia arbuscula*, *Cladonia mitis*, *Cladonia rangiferina*, *Cladonia stellaris*, and *Cladonia stygia*) respond to logging and fire given their importance as winter forage for caribou. We compared critical lichen habitat factors (i.e., forest floor thickness, tree height, and canopy closure) between fire and logged sites and evaluated how *Cladonia* lichen species richness, biomass, and ground cover were related to these habitat factors in the first decades following disturbance. We found no significant differences in habitat factors and no significant differences in lichen species richness or ground cover between logged and fire sites. However, *Cladonia* lichen biomass was significantly higher following logging. These results support the hypothesis that *Cladonia* lichens can persist following logging and suggest that forestry practices that include in their toolbox winter harvesting or machinery traffic restricted to specific trails are likely to preserve undisturbed forest floor habitat conditions with source populations of lichens.

1. Introduction

Fire is considered the major natural disturbance in boreal forests (Payette, 1992; Bergeron et al., 2001). Fires are recurrent phenomena (Heinselman, 1981; Morneau and Payette, 1989; St-Pierre et al., 1992), which initiate forest regeneration and succession (Heinselman, 1981; Payette, 1992), and play a major role in determining the distribution and composition of plant communities in boreal forests (Bergeron and Dubuc, 1989; DeGrandpré et al., 1993; Kenkel et al., 1997). Black spruce stand dynamics are mainly associated with fires of variable frequency, severity and size (Bergeron et al., 2001). Severe fires play an important role, killing ground vegetation and reducing the thickness of the organic layer, hence creating microsites favorable for the establishment of various plant species (Heinselman, 1981; Viereck, 1983). For instance, the exposition of well drained and/or acidic mineral soil following fire provides an ideal substrate for the post-fire colonization of terricolous lichens (Kershaw, 1977). Fire also creates openings in closed-crown forests and contributes to the establishment or renewal of the terricolous lichen mat (Schaefer and Pruitt, 1991; Coxson and Marsh, 2001; Dunford et al., 2006). Consequently, fire has an important effect on both the distribution and abundance of terricolous lichen species in boreal ecosystems (Coxson and Marsh, 2001; Zouaoui et al., 2014), which in turn provide important winter forage for large herbivores, such as the woodland caribou (*Rangifer tarandus caribou*) (Webb, 1998; Lantin, 2003; Dunford et al., 2006; Joly et al., 2010; Lesmerises et al., 2011) which mainly feed on reindeer lichens (i.e., *Cladonia arbuscula*, *Cladonia mitis*, *Cladonia rangiferina*, *Cladonia stellaris* and *Cladonia stygia*).

Over the past few decades, boreal forests have undergone a profound transformation due to human activities, particularly logging which is now the dominant disturbance agent (Burton et al., 2010). As a result, in several regions the area altered by natural disturbances is smaller than that disturbed by logging (Bergeron et al., 2006; Drapeau et al., 2009). Furthermore, logging has been identified as a potential threat to terricolous lichen communities (Goward, 1994; Ryan, 1996; Botting and Fredeen, 2006), because of the removal and disturbance of the lichen mat and modification of the soil microclimate (Dahlman and Palmqvist, 2003;

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http://dx.doi.org/10.1016/j.foreco.2016.04.007
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Gaio-Oliveira et al., 2004). More specifically, logging is thought to negatively affect terricolous lichen establishment through inadequate shade from the remaining trees, slash deposition as well as a deficient amount of exposed mineral soil (Lesica et al., 1991; Frisvoll and Presto, 1997; Miège et al., 2001; Waterhouse et al., 2011). Indeed, in a study on the influence of ground substrate on lichen establishment conducted in Sweden, Roturier et al. (2007) found that lichen cover was significantly higher on bare mineral soil than on other types of substrate, including woody substrates.

In the North American boreal forest, the growing concern of logging effects on biodiversity, particularly on endangered species such as the woodland caribou (Chubbs et al., 1993; Environment Canada, 2011; Rudolph et al., 2012), has drawn attention on how terricolous lichens, especially reindeer lichens, respond to logging and fire in the boreal forest given their importance as winter forage for caribou (Lantin, 2003; Dunford et al., 2006; Joly et al., 2010; Lesmerises et al., 2011). These studies produced, however, conflicting results. Some concluded that soil drying caused by logging could favor lichen growth on sites normally dominated by mosses (Harris, 1996; Racey et al., 1996; Webb, 1998; Johnson et al., 2014), whereas other studies found that the vigorous response of tree regeneration following logging could be detrimental to lichen growth (Coxson and Marsh, 2001; Desponts et al., 2002; Newmaster and Bell, 2002). More recently, Boudreault et al. (2013) suggested that canopy opening after partial cuts provided better growing conditions for terricolous lichens (through increased light and moisture reaching the forest floor), which helped maintain pre-established lichen cover at levels comparable to those in old growth forests. Although the effects of logging on lichen communities remain unclear, silvicultural treatments that change the structural complexity of forest have the potential to create different microhabitats that influence the composition of lichen communities (McMullin et al., 2010).

Furthermore, both lichens and bryophytes are a major component of the forest floor communities in boreal forests (Esseen et al., 1997) where they form extensive mixed-species mats. Their relative abundance in mixed-species mats has been found to vary with light intensity and moisture, with lichens frequently overgrowing bryophytes under conditions of high light intensity and low moisture (Morneau and Payette, 1989; During and van Tooren, 1990; Sedia and Ehrenfeld, 2003). Therefore, the composition of the terricolous lichen community is likely to vary with the light and moisture conditions prevailing after fire or logging.

In the last decades, the concept of forest ecosystem management based on natural disturbances has generated lots of interests as it is considered key to the conservation of biodiversity as well as to the preservation of ecosystem structure and functions (Gauthier et al., 2009). In this context, prescribed burning has been considered an appropriate management option in boreal forests to emulate the effects of fire on soil chemistry and stand productivity (Scheuner et al., 2004; Renard et al., 2016). However, before considering prescribed burning as an appropriate management option for lichens (and hence for the woodland caribou), it is of the utmost importance to better understand the response of terricolous lichens to logging and fire.

In this study we compared post-fire and post-logged *Cladonia* lichen communities (with a special focus on reindeer lichens) in the boreal forest of Québec, Canada. More specifically, we analyzed the biomass and ground cover of reindeer lichen and other *Cladonia* species in young (4–13 years, i.e., before complete canopy closure) black spruce stands following logging and fire. We first compared critical lichen habitat factors (i.e., forest floor thickness, tree height, and canopy closure) between fire and logged sites and then evaluated how lichen biomass and ground cover are related to these habitat factors following fire or logging. Then, because bryophytes co-occur with lichens within mixed-species mats and because both group of species may respond differently to particular light and moisture conditions prevailing after fire or logging, we also compared their post-disturbance ground cover. Ultimately, this study aimed at determining if fire and logging had similar effects on *Cladonia* species biomass and ground cover.

2. Materials and methods

2.1. Study regions

Prior to field sampling, potential study sites were first selected using forest maps and then ground truthed. With this method, we selected five study sites. The five study sites were located in three different regions of boreal Québec. Three sites were located in the black spruce (*Picea mariana* [Mill.] BSP)-feathermoss (*Pleurozium schreberi* [Brid.] Mitt.) bioclimatic domain and two sites were in the balsam fir (*Abies blasamea* [L.] Mill.)-white birch (*Betula papyrifera* Marsh.) bioclimatic domain (Robitaille and Saucier, 1998) (Fig. 1). Prior to disturbance the five study sites were dominated by black spruce. Sites were selected in order to pair logged and burnt stands occurring in similar ecological conditions and that were disturbed at similar time periods (Table 1). The regions where these sites were located are characterized by large crown fires that kill the majority of trees and the surface vegetation (Bergeron et al., 2002; Jasinski and Payette, 2005). Before the mid-1990's, stands were logged by clearcutting, but this technique has since been replaced by cut with protection of regeneration and soils (CPRS). CPRS consists of logging all commercial trees (diameter at breast height >9.1 cm) with machinery traffic restricted to parallel trails that cover approximately 25% (33% prior to March 2001) of the logged area (MRNFQ, 2003). Trails are separated by "protection strips" in which only commercial stems (⩾9.1 cm) are logged, leaving pre-logging tree regeneration.

Villebois (VB) region – The site in this region (48°58′–49°50′N and 79°01′–79°30′W) was located approximately 100 km north of Villebois (Fig. 1), in the Clay Belt physiographic region. This region is characterized by a flat topography and is underlain by Cochrane till, a compact till made up of a mixture of clay and gravel, created by a southward ice flow approximately 8000 years BP (Veillette, 1994). Thick (>30 cm) organic deposits are found in many locations. According to the nearest weather station (Joutel, Québec), the average annual temperature was 0.0 °C and average annual precipitation was 909 mm, with 35% falling during the growing season, from 1981 to 2010 (Environment Canada, 2015). The average number of degree-days (>5 °C) was 1241, and the frost-free season lasts about 60 days; frost occasionally occurs during the growing season. Fire frequency in the study area has diminished from a 100-year cycle to an approximately 400-year cycle since the little Ice Age (ca. 1850; Bergeron et al., 2004). The site consisted of a stand burned in 1997 and an adjacent unburned stand logged by CPRS in 1997, located 5 km apart. Pre-disturbance conditions of both stands corresponded to mature forest stands (>120 years) given stand age estimates from forest cover maps. Stands presented the thick organic layer typical of productive forest sites in this region (Lecomte et al., 2005), but were not true peatlands.

Lebel-sur-Quévillon (LB) region – There is one site in this region (48°25′–49°00′N and 76°20–76°79′W) located 50 km southeast of Lebel-sur-Quévillon (Fig. 1), made up of two stands approximately 10 km apart: a stand burned in 1995 and a nearby stand logged by CPRS in 1997. It is characterized by a flat topography with gently rolling hills, underlain by glaciolacustrine and undifferentiated till surficial deposits (Robitaille and Saucier, 1998). According to the nearest weather station (Lebel-sur-Quévillon, Québec), the average annual temperature was 1.0 °C and average annual precipitation was 928 mm, with 35% falling during the growing season, from

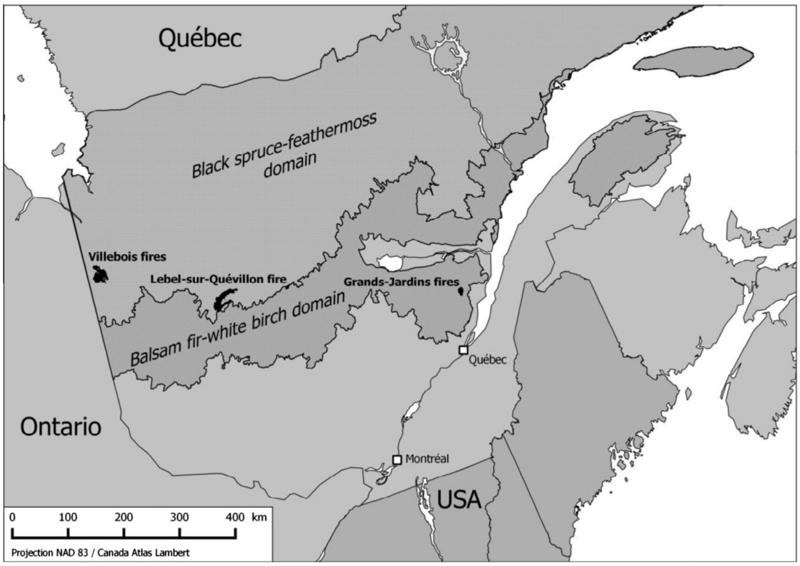

Fig. 1. Location of study areas within Québec.

Table 1
Site characteristics prior to fire or logging disturbance.

Site	Disturbance type	Year of disturbance	Stand age at disturbance	Stand type	Drainage[a]	Surficial deposit[a]
GJ-1	Fire	1999	70	bS(bF)	Good to moderately good	Till
	CPRS	2000	70	bS(bF)	Good	Till
GJ-2	Fire	1991	90	bS(bF)	Good to moderately good	Till
	Clear cut	1991	90	bS(bF)	Good to moderately good	Till
LQ	Fire	1995	>120	bS	Good to moderately good	Till
	CPRS	1997	>120	bS	Good to moderately good	Till
VB	Fire	1997	>120	bS	Good to moderately good	Clay till
	CPRS	1997	>120	bS	Good to moderately good	Clay till

GJ = Parc des Grands-Jardins; LQ = Lebel-sur-Quévillon; VB = Villebois; bS = black spruce; bF = balsam fir; jP = jack pine.
[a] Saucier et al. (1994).

1981 to 2010 (Environment Canada, 2015). The average number of degree-days (>5 °C) was 1376, and the frost-free season lasts about 60 days; frost occasionally occurs during the growing season. Fire frequency in the study area has diminished from a 100-year cycle to an approximately 200-year cycle since the little Ice Age (ca. 1850; Bergeron et al., 2001). The last important fires before the 1995 fire date back to 1905 and 1870 (Kafka et al., 2001); pre-fire conditions in our burned site, therefore, corresponded to mature forest stands (⩾100 years). Pre-harvest conditions of the 1997 logged site corresponded to mature forest stands (>120 years) given stand age estimates from forest cover maps.

Grands-Jardins (GJ) region – Located 120 km north-east of Québec City (47°66′–47°83′N and 70 °70′–71 °78′W), we established two study sites in this region (Fig. 1). One site included a stand burnt in 1991 paired with a nearby unburnt stand that was logged by clearcutting during winter of the same year, whereas the other site included a stand burned in 1999 and a nearby stand logged by CPRS in 1999. In both sites, burned and logged stands were located at least 8 km apart. The region is part of the Laurentian Mountains, within the Canadian Shield, and is characterized by high hills overelain by till, with a mean elevation between 700 m and 900 m. According to the nearest weather station (Forêt Montmorency, Québec), the average annual temperature was 0.5 °C and average annual precipitation was 1583 mm, with 30% falling during the growing season, from 1981 to 2010 (Environment Canada, 2015). The average number of degree-days (>5 °C) was 1033, and the frost-free season lasts about 40 days; frost occasionally occurs during the growing season. Whereas the region is characterized by a long (>450 years) fire cycle (Leblanc, 1998), detailed fire history reconstruction within the Parc national des Grands-Jardins shows that fire was the main natural disturbance with 40% of the park's total area burned by 13 wildfires throughout 20th century (Payette and Delwaide, 2003). The last important fires before the 1991 and 1999 fires date back to 1915 and 1922 (Payette et al., 2000). Hence, pre-fire conditions in our burned sites corresponded to mature forest stands (>80 years). Pre-harvest conditions of our 1991 and 1999 paired logged sites which were adjacent to the park's boundary corresponded to mature forest stands (>80 years) given stand age estimates from forest cover maps.

In the three regions, all stands were established by natural regeneration following logging and fire, and all had open canopy at sampling. Furthermore, although our study combines CPRS and clearcutting for comparison with fire, both types of logging had the same effects on stand structure/opening (i.e. harvesting of all commercial stems) and light conditions at ground level. In addition, both types of harvest also likely had the same effect on forest floor disturbance and understory plant communities (Lafleur et al., 2010). Therefore, we feel confident that at the stand level both types of logging had similar effects on lichen communities.

2.2. Experimental design and sampling

Sampling was conducted during the summer of 2004, i.e. 4 to 13 years after disturbance. At each site, we installed ten 100-m long transects, five in each of the burned and logged areas. The line transects were parallel and spaced 100 m apart, and located a minimum of 30 m from any roads. Along each transect, ten 625-cm^2 sampling quadrats were randomly established. In these quadrats, we first determined the presence or absence of species of *Cladonia* on the ground in order to estimate their frequency. We then visually estimated percent ground cover of reindeer lichens, other *Cladonia* species, and macro bryophyte genera (i.e., *Sphagnum* spp., *P. schreberi*, and *Polytrichum* spp.), and collected lichens for further identification. In each quadrat we measured the thickness of the forest floor (i.e. the organic material covering the mineral soil) with a graduated auger, measured the height of the three nearest live trees using a clinometer, and estimated canopy closure using a densitometer. Lastly, in three 625-cm^2 sampling quadrats along each transect we collected the lichen mat for biomass estimation. More specifically, the entire lichen mats located within the sampling quadrats were brought back to the laboratory where reindeer lichens (i.e. *C. arbuscula*, *C. mitis*, *C. rangiferina*, *C. stellaris*, and *C. stygia*) were sorted from the other *Cladonia* spp. Sorted lichens were then dried at 65 °C for 72 h and weighted. This last procedure allowed us to specifically compare the effects of fire and logging on reindeer lichens and other *Cladonia* species.

In the laboratory, the reindeer lichens and other the *Cladonia* species were identified using stereo and compound microscopes, and chemical spot tests with potassium hydroxide (10%), sodium hypochlorite, Lugol's iodine, para-phenylenediamine, chlorhydric acid, and nitric acic. Nomenclature follows Brodo et al. (2001) for the lichens and Ireland (1982) for the bryophytes. Voucher specimens are stored at the Forest Ecology laboratory at the Université du Québec à Montréal.

2.3. Data analysis

In order to characterize the environment in the different disturbance types, the effect of disturbance type (i.e., logging and fire) on tree height, canopy closure, and forest floor thickness was discriminated with mixed-effects ANOVAs, using disturbance type (i.e., logging or fire) as a fixed effect, site as a random effect, and time since disturbance as a covariate. The effect of disturbance type on reindeer lichen and other *Cladonia* species richness, biomass and ground cover, and bryophyte ground cover were similarly discriminated with mixed-effects ANOVAs, using disturbance type (i.e., logging or fire) as a fixed effect, site as a random effect, and time since disturbance as a covariate. Prior to analyses, residuals were tested for normality and homogeneity of variances, and the data was log- or square root-transformed when necessary. Differences were considered significant when $\alpha \leqslant 0.05$.

Subsequently, we assessed the influence of disturbance type and stand characteristics (i.e., tree height, canopy closure and forest floor thickness) on lichen reindeer lichens and other *Cladonia* species biomass and ground cover using regression model selection. We used the Akaike information criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) to compare six statistical models: five tested the effects of disturbance type, time since disturbance and the three stand characteristics taken individually, and one consisted of the combination of disturbance type, time since disturbance, and stand characteristics. We then used model averaging (Burnham and Anderson, 2004) on the entire set of possible models.

Finally, in order to determine if individual species displayed a preference for logged or fire sites, we calculated a predominance index (PI) for each individual species following Söderström (1988). This index corresponds to the difference in species mean frequency between the two types of disturbance divided by the total mean frequency:

$$\mathrm{PI} = A_f - A_h / A_h + A_f$$

where A_f is the mean frequency of species in the fire sites and A_h is the mean frequency of species in the logged sites. Species more frequent in the fire sites will have a value between 0 and 1, and those more than twice as frequent values over 0.33. Corresponding values are -1 to 0 for species more frequent in logged sites, and values lower than -0.33 for those more than twice as frequent. Frequencies for species displaying a preference ($\mathrm{PI} \geqslant |0.50|$) for a disturbance type were submitted to Mann–Whitney *U*-tests to check for significant difference ($p < 0.05$) between disturbance type.

All statistical analyses were conducted using JMP 10.0 (SAS, 2012).

3. Results

3.1. Post-disturbance stand characteristics

Overall, tree height ($p = 0.498$) and canopy closure ($p = 0.356$) did not significantly differ between logged and fire sites (Table 2). Forest floor thickness, however, was significantly ($p = 0.035$) greater in logged (24.5 cm ± 3.7 S.E.) than in fire (14.7 cm ± 2.8 S.E.) sites (Table 2).

3.2. Lichen species richness

A total of 35 terricolous lichen species were observed at the fire sites, five reindeer lichen species and 30 other *Cladonia* species. In the logged sites 32 species (5 reindeer lichen species and 27 other *Cladonia* species) were observed. Five species (i.e., *Cladonia bacilliformis*, *Cladonia bacillaris*, *Cladonia borealis*, *Cladonia cristatella*, and *Clodania foliacea*) were observed in fire sites but not in logged sites, whereas two species (i.e., *Cladonia coccifera* and *Cladonia ramulosa*) were observed in logged sites but not in fire sites. Overall, mean lichen species richness did not significantly differ (p = 0.85) between logged (21.5 ± 1.4 S.E.) and fire (22.2 ± 3.5 S.E.) sites. Appendix A indicates the frequency of each species for each site/disturbance combination.

3.3. Lichen biomass

Reindeer lichen biomass was significantly ($p < 0.001$) higher after logging than after fire (423.9 kg ha^{-1} ± 57.8 S.E. vs. 104.4 kg ha^{-1} ± 12.8 S.E.), whereas there was no significant difference ($p = 0.363$) for the other *Cladonia* species (Fig. 2). When all *Cladonia* species were considered together (i.e. reindeer lichens + other *Cladonia* species), lichen biomass was significantly ($p < 0.001$) higher after logging than after fire (474.7 kg ha^{-1} ± 55.0 S.E. vs. 185.6 kg ha^{-1} ± 30.8 S.E.).

3.4. Lichen and bryophyte ground cover

Disturbance type did not have any significant effect on reindeer lichen ($p = 0.676$) and other *Cladonia* species cover ($p = 0.077$) (Fig. 3). Likewise, disturbance type did not have a significant effect on all *Cladonia* species cover considered together ($p = 0.558$). As

Table 2
Mean tree height (m ± S.E.), canopy closure (% ± S.E.), and forest floor thickness (cm ± S.E.) in logged and fire sites.

Variable	Disturbance		*p*-value
	Logging	Fire	
Height (m)	3.16 (0.89)	4.74 (1.28)	0.498
Canopy closure (%)	4.2 (1.9)	7.3 (3.3)	0.356
Forest floor thickness (cm)	24.5 (3.7)	14.7 (2.8)	0.035

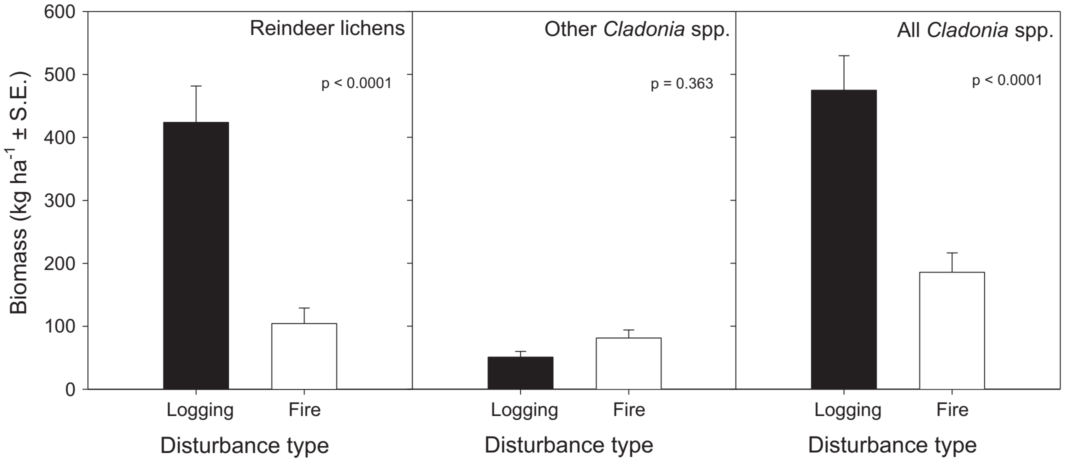

Fig. 2. Mean biomass (kg ha^{-1} ± S.E.) of *Cladonia* lichens in logged and fire sites. Reindeer lichens include *Cladonia arbuscula*, *Cladonia mitis*, *Cladonia rangiferina*, *Cladonia stellaris*, and *Cladonia stygia*.

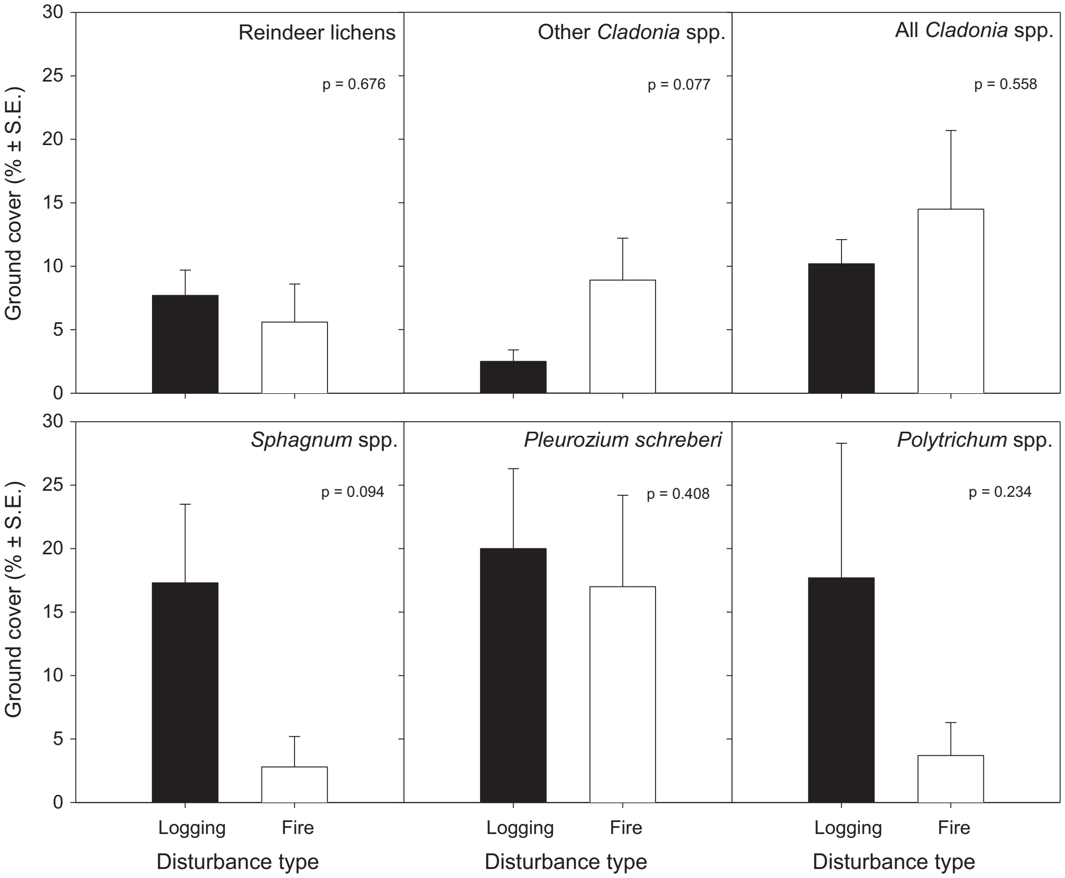

Fig. 3. Mean ground cover (% ± S.E.) of *Cladonia* lichens and bryophytes in logged and fire sites. Reindeer lichens include *Cladonia arbuscula*, *Cladonia mitis*, *Cladonia rangiferina*, *Cladonia stellaris*, and *Cladonia stygia*.

was the case for lichens, bryophyte (i.e. *Sphagnum* spp. [$p = 0.094$], *P. schreberi* [$p = 0.408$] and *Polytrichum* spp. [$p = 0.234$]) ground cover did not differ significantly between logged and fire sites (Fig. 3).

3.5. Relating lichen species richness and ground cover to disturbance type and stand characteristics

Among the five models, the model that best explained reindeer lichen species biomass combined all five variables, followed by disturbance type (Table 3). After model averaging only disturbance type and canopy closure had 95% confidence intervals that excluded 0 (Table 4). Whereas canopy closure had a negative effect on reindeer lichen species biomass, the positive effect of disturbance type indicated that biomass was greater following logging. The model that best explained reindeer lichen species ground cover combined all five variables, followed by canopy closure (Table 3). Model averaging revealed that only canopy closure had 95% confidence intervals that excluded 0 (Table 4), the effect on ground cover being negative.

Table 3
Model selection results for reindeer lichen and other *Cladonia* species biomass and ground cover. Models are classified using Akaike's information criterion (AICc), including difference in AICc (ΔAICc) and Akaike weight (W).

Model	AICc	ΔAICc	W
(A) Reindeer lichens			
Biomass			
DT + TH + FF + CC + TSD	1159.08	0.00	0.81
Disturbance type (DT)	1162.17	3.09	0.17
Canopy closure (CC)	1167.81	8.73	0.01
Forest floor thickness (FF)	1170.13	11.05	<0.01
Tree height (TH)	1177.05	17.97	<0.01
Time since disturbance (TSD)	1177.19	18.11	<0.01
Ground cover			
DT + TH + FF + CC + TSD	6710.78	0.00	0.68
Canopy closure (CC)	6712.31	1.52	0.32
Tree height (TH)	6721,78	11.00	<0.01
Time since disturbance (TSD)	6735.12	24.34	<0.01
Disturbance type (DT)	6736.17	25.39	<0.01
Forest floor thickness (FF)	6736.47	26.69	<0.01
(B) Other *Cladonia* species			
Biomass			
DT + TH + FF + CC + TSD	944.46	0.00	0.99
Time since disturbance (TSD)	958.62	14.16	<0.01
Forest floor thickness (FF)	982.20	37.74	<0.01
Tree height (TH)	984.51	40.05	<0.01
Disturbance type (DT)	988.82	44.36	<0.01
Canopy closure (CC)	989.80	45.34	<0.01
Ground cover			
DT + TH + FF + CC + TSD	6001.62	0.00	0.99
Time since disturbance (TSD)	6082.54	80.92	<0.01
Disturbance type (DT)	6092.17	90.55	<0.01
Forest floor thickness (FF)	6123.19	121.57	<0.01
Canopy closure (CC)	6148.47	146.85	<0.01
Tree height (TH)	6155.68	154.06	<0.01

Table 4
Reindeer lichen and other *Cladonia* species biomass average estimates, unconditional standard errors and confidence intervals (CI) based on model averaging; 95% confidence interval of coefficients in bold excluded 0.

Dependent variable	Independent variable	Estimate	SE	95%CI
(A) Reindeer lichens				
Biomass	Disturbance type	127.4	46.8	34.1, 220.7
	Tree height	24.5	19.8	−15.1, 64.0
	Forest floor thickness	2.7	5.3	−7.7, 13.2
	Canopy closure	−23.5	7.5	−38.5, −8.5
	Time since disturbance	−18.3	11.9	−42.1, 5.5
	Intercept	392.2	178.3	37.0, 747.4
Ground cover	Disturbance type	0.5	0.7	−0.8, 1.9
	Tree height	−0.4	0.3	−1.0, 0.07
	Forest floor thickness	−0.1	0.1	−0.2, 0.0
	Canopy closure	−0.3	0.1	−0.4, −0.1
	Time since disturbance	0.2	0.2	−0.1, 0.6
	Intercept	9.4	2.2	5.1, 13.8
(B) Other Cladonia				
Biomass	Disturbance type	4.3	12.2	−20.0, 28.7
	Tree Height	24.0	5.2	13.7, 34.4
	Forest floor thickness	−2.1	1.4	−4.8, 0.7
	Canopy closure	−5.0	2.0	−8.9, −1.1
	Time since disturbance	18.9	3.1	12.7, 25.1
	Intercept	−112.9	46.6	−205.7, 20.0
Ground cover	Disturbance type	−3.6	0.4	−4.5, −2.7
	Tree Height	−0.2	0.2	−0.6, 0.1
	Forest floor thickness	−0.0	0.0	−0.0, 0.0
	Canopy closure	−0.1	0.1	−0.2, 0.0
	Time since disturbance	1.0	0.1	0.7, 1.2
	Intercept	−0.9	1.4	−3.7, 1.9

By far, the model that best explained the biomass and ground cover of other *Cladonia* lichen species combined all five variables, i.e., disturbance type, time since disturbance, tree height, forest floor thickness, and canopy closure (Table 3). For biomass, model averaging revealed that tree height, canopy closure and time since disturbance had 95% confidence intervals that excluded 0; tree height and time since disturbance had a positive effect other *Cladonia* species biomass, whereas canopy closure had a negative effect (Table 4). For ground cover, model averaging indicated that disturbance type (negative effect, i.e. fire sites > logged sites) and time since disturbance (positive effect) had 95% confidence intervals that excluded 0.

3.6. Predominance index

The Mann–whitney *U*-tests revealed that six species displayed a significant preference for logged sites (reindeer lichens: *C. arbuscula*, *C. stellaris*, *C. stygia*, *C. coccifera*, *Cladonia digitata*, and *C. ramulosa*) and five for fire sites (*C. bacilliformis*, *C. bacillaris*, *C. borealis*, *C. cristatella*, and *C. foliacea*) (Appendix A).

4. Discussion

In this study, we sought to discriminate the effects of logging and fire on terricolous lichen species richness, biomass and ground cover, and determine whether biomass and ground cover would be more responsive to habitat factors or type of disturbance. Except for reindeer lichen species biomass, which was significantly higher in logged than burned sites, we found no significant differences in lichen species richness, biomass or ground cover between these disturbance types. Likewise, we found no significant difference in bryophyte ground cover between logged and burned sites. Furthermore, our results indicate that reindeer lichen species biomass was more responsive to disturbance type (positive effect: logged sites > fire sites) and canopy closure (negative effect), whereas ground cover was more responsive to canopy closure (negative effect). For other *Cladonia* species, biomass was more responsive to tree height (positive effect) and time since disturbance (positive effect), and ground cover to time since disturbance (positive effect).

4.1. Post-disturbance stand characteristics

As has been found in other studies, fire resulted in thinner forest floor than logging (e.g., McRae et al., 2001; Simard et al., 2001). While fire is a chemical disturbance during which the forest floor is consumed through the oxidation of organic matter, logging is a mechanical disturbance during which the forest floor is compacted by machinery traffic. Thus, in contrast to fire, which results in a net loss of soil material, little is lost during logging. In addition, wildfire generates a pulse of soil nutrients that can be taken up by the regenerating vegetation (Simard et al., 2001; Thiffault et al., 2007). In contrast, CPRS leaves the forest floor mostly undisturbed and does not generate the same nutrient pulse observed with wildfire (McRae et al., 2001). Despite these different effects on the forest floor, it has been established in black spruce forests that post-fire and post-logged stands may show similar density and height 10–30 years following disturbance (Lafleur et al., 2010).

From these results, one could expect that lichens and bryophytes were likely to have experienced similar light and moisture levels in fire and logged sites. However, notwithstanding the differences in forest floor thickness, one could also expect that through the differences in the type of disturbance (i.e., chemical vs. mechanical) experienced by the forest floor, lichen and bryophytes communities could have been impacted differently in fire and logged sites.

4.2. Lichen species richness

Our results show that *Cladonia* species richness did not differ between the two types of disturbance. In a study on plant diversity on logged and burned sites in Alaska, Rees and Juday (2002) found that lichen species richness was greater in logged sites during early stand development stages (i.e. 2–18 years after disturbance). Their results suggest that lichens are eliminated by fire and/or persist following logging. Nonetheless, in forest ecosystems, stumps and decaying wood left on the forest floor following disturbances constitute important growth substrates for lichens (Söderström, 1988; Nascimbene et al., 2008). In response to canopy opening, these substrate become dryer (Hagemann et al., 2010) as more solar energy reaches the ground and surface temperature increases (Carlson and Groot, 1997). The high tolerance of lichens to relatively low moisture content of the substrate (Williams et al., 1978) may have favoured the rapid establishment of new species, which may explain why in this study reindeer lichen species and overall *Cladonia* species richness was similar in recently (i.e. 4–13 years) burned and logged sites.

4.3. Lichen biomass

Our results show that reindeer lichen species biomass was four times greater in logged sites compared to fire sites, whereas other *Cladonia* species biomass did not differ between the two types of disturbance. Nonetheless, because in both the logged sites (89%) and fire sites (56%) most of the lichen biomass consisted of reindeer lichens, overall *Cladonia* lichen biomass was significant greater in logged sites. These results are consistent with several studies (e.g. Coxson and Marsh, 2001; Collins et al., 2011) who observed a reduction in lichen biomass following fire, and with Coxson and Marsh (2001) who also observed greater lichen biomass after logging compared to fire.

4.4. Lichen and bryophyte cover

Our results show that lichen and bryophyte ground cover were not significantly different between post-logged and post-fire sites, which suggests either that lichen mats may persist on sites impacted by machinery trafficking during logging or that forest floor disturbance during logging creates similar types of microhabitats as fire for invading species. Our results are consistent with Boudreault et al. (2013) who observed that canopy openings resulting from partial cutting could maintain pre-established lichen cover at levels comparable to what was observed in unlogged control stands. They are also similar to those of Coxson and Marsh (2001) who observed that damage to lichen communities was minimal following winter logging, whereas the ground

Table A1

Terricolous lichen species frequency (%) per site and disturbance type, and predominance index (PI).

Species	GJ-1		GJ-2		LQ		VB		PI[a]
	Logging	Fire	Logging	Fire	Logging	Fire	Logging	Fire	
Reindeer lichen species									
Cladonia arbuscula (Wallr.) Flotow	43.3	3.3	40.0	0.0	33.3	6.7	36.7	0.0	−0.88*
Cladonia mitis (Sandst). Mong.	3.3	0.0	23.3	66.7	13.3	56.7	20.0	26.7	−0.43
Cladonia rangiferina (L.) Nyl.	46.7	3.3	10.0	20.0	43.3	30.0	40.0	16.7	−0.33
Cladonia stellaris (Opiz) Brodo	43.3	3.3	10.0	6.7	50.0	0.0	36.7	0.0	−0.87*
Cladonia stygia (Fr.) Ahti	23.3	3.3	20.0	0.0	53.3	0.0	23.3	0.0	−0.95*
Other Cladonia species									
Cladonia bellidiflora (Ach.) Schaerer	0.0	0.0	0.0	16.7	10.0	0.0	0.0	0.0	0.25
Cladonia bacilliformis (Nyl.) Sarnth.	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	1.00*
Cladonia bacillaris (Ach.) Nyl.	0.0	0.0	0.0	6.7	0.0	6.7	0.0	0.0	1.00*
Cladonia borealis S. Stenroos	0.0	0.0	0.0	16.7	0.0	6.7	0.0	13.3	1.00*
Cladonia botrytes (K.G. Hagen) Willd.	0.0	13.3	6.7	26.7	0.0	10.0	0.0	0.0	0.76
Cladonia caespiticia (Pers.) Flörke	0.0	13.3	0.0	16.7	6.7	6.7	6.7	20.0	0.62
Cladonia cariosa (Ach.) Sprengel	13.3	10.0	26.7	20.0	13.3	3.3	16.7	20.0	−0.35
Cladonia carneola (Fr.) Fr.	20.0	6.7	36.7	23.3	20.0	3.3	10.0	26.7	−0.18
Cladonia cenotea (Ach.) Schaerer	16.7	0.0	33.3	26.7	20.0	0.0	20.0	0.0	−0.54
Cladonia cervicornis subsp. *verticillata* (Hoffm.) Ahti	0.0	23.3	40.0	30.0	0.0	6.7	0.0	30.0	0.20
Cladonia chlorophaea (Flörke ex Sommerf.) Sprengel	0.0	6.7	20.0	23.3	0.0	6.7	0.0	0.0	0.29
Cladonia coccifera (L.) Willd.	0.0	0.0	0.0	0.0	10.0	0.0	6.7	0.0	−1.00*
Cladonia coniocraea (Flörke) Sprengel	6.7	10.0	13.3	10.0	0.0	6.7	6.7	3.3	−0.06
Cladonia cornuta subsp. *cornuta* (L.) Hoffm.	30.0	0.0	33.3	10.0	20.0	10.0	13.3	16.7	−0.45
Cladonia crispata var. *crispata* (Ach.) Flowtow	0.0	0.0	0.0	16.7	6.7	3.3	0.0	0.0	0.50
Cladonia cristatella Tuck.	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	1.00*
Cladonia deformis (L.) Hoffm.	0.0	0.0	0.0	6.7	3.3	0.0	0.0	0.0	0.34
Cladonia digitata (L.) Hoffm.	16.7	0.0	13.3	6.7	20.0	0.0	43.3	0.0	−0.87*
Cladonia ecmocyna Leighton.	0.0	0.0	0.0	0.0	6.7	0.0	0.0	3.3	0.34
Cladonia fimbriata (L.) Fr.	26.7	13.3	26.7	23.3	16.7	10.0	16.7	13.3	−0.18
Cladonia foliacea (Willd) Schaerer	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	1.00*
Cladonia gracilis subsp. *turbinata* (Ach.) Ahti	0.0	6.7	0.0	50.0	10.0	6.7	3.3	20.0	0.72
Cladonia multiformis G. Merr.	0.0	0.0	20.0	20.0	0.0	10.0	0.0	6.7	0.29
Cladonia ochrochlora Flörke	30.0	23.3	23.3	10.0	23.3	10.0	23.3	6.7	−0.33
Cladonia phyllophora Hoffm.	0.0	0.0	0.0	13.3	10.0	6.7	10.0	30.0	0.43
Cladonia pleurota (Flörke) Schaerer	3.3	0.0	16.7	26.7	10.0	0.0	10.0	0.0	−0.04
Cladonia pyxidata (L.) Hoffm.	0.0	0.0	20.0	10.0	6.7	6.7	0.0	6.7	−0.07
Cladonia ramulosa (With.) J.R. Laundon	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	−1.00*
Cladonia rei Schaerer	10.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.20
Cladonia squamosa (Scop) Hoffm.	0.0	0.0	23.3	26.7	26.7	6.7	16.7	20.0	−0.11
Cladonia sulphurina (Michaux) Fr.	16.7	6.7	10.0	10.0	13.3	6.7	13.3	10.0	−0.23
Cladonia uncialis (L.) Weber ex F.H. Wigg.	33.3	30.0	70.0	76.7	20.0	0.0	23.3	26.7	−0.04
Number of species	18	16	22	32	25	22	21	19	

[a] Values between 0 and 1 indicate species more frequent in the fire sites, whereas values between −1 and 0 indicate species more frequent in logged sites. $^*p \leqslant 0.05$ (Mann–Whitney *U*-test).

cover of *P. schreberi* was reduced. After disturbance, Lesica et al. (1991) suggested that the combination of more light reaching the forest floor, increased soil temperature, decreased humidity and a decline in litterfall would promote *Cladonia* species to the detriment of *P. schreberi*. Hence, carryover and enhancement of terricolous lichen richness and cover can be accomplished if the forest floor is not unduly disturbed during logging and *Cladonia* species reestablish quickly once the canopy cover is removed (Harris, 1996). The lack of statistical differences in terricolous lichen cover between logged and burned sites also suggest that landscapes managed for timber supply do not support less forage conditions for woodland caribou than do wildfires. However, in the last decades, the spatial extent of old-growth forests at regional scales in the boreal forest has decreased (Drapeau et al., 2009) which may have cumulative effects on the regional availability of lichen cover and abundance, and hence, woodland caribou seasonal movements (Lantin, 2003; Dunford et al., 2006).

Finally, despite a relatively low number of replicates for each type of harvest (i.e. one clearcutting sites and 3 CPRS sites), our results suggest that clearcutting could potentially have a stronger negative effect on total lichen cover (i.e. the combination of *Cladonia*) than CPRS, and that concentrating soil disturbance to specific trails, such as what occurs in sites harvested by CPRS, leaves a lichen cover that is comparable to what is observed after fire. However, these hypotheses have yet to be tested.

5. Conclusion

This study suggests that in the boreal forest, logging creates, in the first decades following disturbance, habitat conditions for *Cladonia* lichens similar to those of fires in terms of tree height and canopy opening, but not with respect to forest floor thickness. This resulted in similar lichen ground cover after logging and fire. Nonetheless, *Cladina* biomass differed between the two types of disturbance, with higher biomass in logged sites, which indicates that lichens established prior to logging may persist. This implies that forestry practices that include in their toolbox winter harvesting or machinery traffic restricted to specific trails such as CPRS harvesting are likely to preserve undisturbed forest floor habitat conditions with source populations of lichens. This in turn, is likely to facilitate lichen recolonization in disturbed areas and maintain or reconstruct functional lichen communities in managed landscapes. Hence, it seems unlikely that forage conditions for woodland caribou may be less in current managed landscapes than in burned landscapes. However, it remains unclear how after a second harvest rotation, lichen source populations in harvested stands will persist since they origin from past fire events.

Acknowledgements

We are grateful to Maude Beauregard, Karelle Jayen and Daniel Lesieur for their assistance in the field and in the laboratory. Financial support was provided by the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, a Discovery Grant (Y. Bergeron) and a Discovery Grant (P. Drapeau), from the Natural Science and Engineering Research Council of Canada (NSERC) and a grant from the Programme de recherche en Équipe (P. Drapeau and collaborators) by the Fonds de Recherche Nature et Technologies du Québec (FQRNT).

Appendix A

See Table A1.

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