Full length article

Canopy openings created by partial cutting increase growth rates and maintain the cover of three *Cladonia* species in the Canadian boreal forest

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ABSTRACT

In boreal forests partial cutting is often proposed as an alternative to the widespread use of clearcutting to better conciliate forest management with species conservation. A partial cutting experiment was implemented in black spruce boreal forests of western Québec, and the responses of three terricolous lichen species (*Cladonia stellaris*, *C. mitis,* and *C. rangiferina*) to three different treatments of different removal intensities (old unharvested forest stands and old forests treated by partial cutting and clearcutting) were studied. We used transplants of lichens to record growth rate over a period of 15 months, and we also recorded microclimatic variables (thallus temperature, thallus humidity, and photosynthetically active radiation [PAR]) directly at the sampling sites. We observed reduced growth rates in *C. stellaris* and *C. rangiferina* transplants located in untreated control plots compared with transplants located either in stands treated with partial cutting and or stands treated by clearcutting. We also found that lichen growth differed significantly across season, with a higher growth rate during the first summer compared to the other seasons. Lichen cover and frequency (presence or absence) of the three *Cladonia* species did not differ significantly between partial cut plots and control plots. PAR and thallus temperature were significantly lower in control plots, while thallus humidity was significantly higher in control plots. Thallus humidity recorded in the morning (between 6 am and 9 am) showed a reversed pattern, with lower values in control plots compared with partial cutting and clearcutting plots. Our results show that canopy openings in the partial cuttings had a positive influence on the growth of *Cladonia* species, probably through an increase in the quantity of light and humidity reaching the thalli early in the morning. Furthermore, canopy openings resulting from partial cuttings can maintain pre-established lichen cover at levels comparable to what is observed in our unharvested control stands.

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1. Introduction

Terrestrial lichens of the genus *Cladonia* are dominant in many ecosystems of the boreal and arctic zones where they can form extensive mats on the ground (Ahti and Oksanen, 1990). Mat-forming lichens have a great economic importance in Fennoscandia (e.g. handcraft industry; Kauppi, 1979) and ecological importance across the boreal and arctic zones (e.g. forage for caribou and reindeer, CO_2 fixation, nutrient store, control of the flux and energy; Sveinbjörnsson, 1990).

The three principal mat-forming species, *Cladonia mitis*, *C. rangiferina*, and *C. stellaris*, occur across the boreal zone. In natural ecosystems of the eastern Canadian black spruce (*Picea mariana*) boreal forest, terrestrial lichens belonging to the genus *Cladonia* tend to be progressively replaced by feather mosses as time since the last stand-replacing fire increases (Carleton, 1990; Foster, 1985; Taylor et al., 1987). However, a recent study undertaken in the western part of Québec's boreal forest indicates that the importance of terrestrial lichens can increase again with the concomitant opening of the forest canopy in old-growth forests (>200 years) (Zouaoui, 2011). Even if terrestrial lichens are generally less dominant than feather mosses or peat mosses in productive black spruce boreal forests, their continuous occurrence in these ecosystems might represent an important food resource for the forest-dwelling ecotype of woodland caribou (*Rangifer tarundus caribou*) (Kelsall, 1984; Webb, 1998).

Lichens are poikilohydric organisms that are unable to regulate their uptake or loss of moisture, and depend consequently on atmospheric sources for water and inorganic nutrients (Nash,

2008). For this reason, their growth is restricted to periods of sufficient hydration and light (Muir et al., 2006; Palmqvist and Sundberg, 2000). Lichen growth is thus directly related to microclimatic conditions (Dahlman and Palmqvist, 2003; Gaio-Oliveira et al., 2004) and terrestrial lichens are known to be sensitive to microclimatic changes after forest harvesting. For example, Miège et al. (2001) found that 70% removal by volume of trees constituting the dominant forest canopy resulted in higher lichen mortality and decreased forage lichen abundance 3 years after harvesting, compared to treatments with lower volume removal. Disturbances of the forest floor, especially by deposition of slash, and inadequate shade from the remaining trees, were thought to be critical factors (Miège et al., 2001; Waterhouse et al., 2011). Inversely, other studies showed that lichen growth in dense forests is limited by light availability and that, consequently, lichen growth can be stimulated by canopy openings (Muir et al., 2006; Rominger et al., 1994; Sulyma and Coxson, 2001).

Partial cutting aiming to recreate or maintain structural characteristics and microclimatic conditions associated to old forests are often advocated to attenuate the negative impacts of clear cutting on biodiversity (Bergeron et al., 2002; Franklin et al., 2002; Peck and McCune, 1997; Stevenson and Coxson, 2003). Clearcutting is by far the most widespread harvesting method used in boreal forests (Harvey et al., 2002). We implemented a partial cutting experiment with diverse removal intensities (Fenton et al., 2009) to study the response of different organisms to changes in canopy openings in the Abitibi region of northern Québec (Fenton and Bergeron, 2008; Boudreault et al., 2013). The general objective of this study was to evaluate the response of three *Cladonia* species to canopy removal. The specific objectives were (1) to compare lichen growth between transplants located in clearcuttings, in partial cuttings, and in unharvested forests (>100 years), (2) to compare ground lichen cover between clearcuttings, partial cuttings, and unharvested control plots, and (3) to evaluate if variations in growth rates between treatments can be attributed to microclimatic changes between treatments.

2. Methods

2.1. Study area

The study was conducted in the western part of the bioclimatic region of *Picea mariana*-feather moss forest in Québec (50°00″N, 76°00″–80°00″W). The study area is also part of the northern Clay Belt (Rowe, 1972), a broad physiographic unit characterized by lacustrine deposits from proglacial lakes Barlow and Ojibway. Clay soils predominate, the topography is relatively flat, and the forest mosaic is dominated by black spruce. Ground cover in the study area is generally dominated by *Pleurozium schreberi* and *Sphagnum* spp. Meteorological stations located at Matagami, close to our study sites (Fig. 1), indicate mean annual temperature (1971–2000) of −0.7 °C, and mean total annual precipitation (1971–2000) of 906 mm (Environment Canada, 2004).

The lichen growth study took place in 2005 and 2006. The weather station recorded more precipitation and lower temperatures during summer 2006 than in summer 2005 (Fig. A1; Environment Canada, 2004). June was particularly warm in 2005 compared to June 2006 with a mean temperature of 16.6 °C and 14.2 °C, respectively. Temperatures during summer months in 2005 were above the mean temperature recorded during the 1971–2000 period, and precipitation was lower than mean precipitation for the same period.

We studied terrestrial lichen growth at three sites (Fénelon, Maicasagi, and Muskuchii) which are located more than 50 km from one another (Fig. 1). The selected sites were dominated by black spruce, had an irregular structure (in terms of vertical structure and diameter distribution), were at least 120 years old, and originated from stand replacing fires that occurred more than 100 years before the study took place (Bescond et al., 2011).

Each site contains a block of stands treated with partial cuttings, a block of stands treated with low retention clearcuttings and a block of stands of old forest stands where no harvest was done, and which was used as a control. The size of each block was at least 25 ha. In clearcutting blocks, all trees with diameter at breast-height >9 cm were harvested. The proportion of basal area removed in the partial cuts was 45% at the Maïcasagi site, 66% at the Muskuchii site, and 85% at the Fénélon site.

Blocks were harvested in 2004, in 2001, and between 1998 and 2000 at Fénelon, Maicasagi, and Muskuchii, respectively. Seventeen circular plots (400 m²) dominated by black spruce were established in each treatment and site combination to study the effects of tree removal on stand dynamics (see Fenton et al., 2009 for more details on the plot selection procedure). General stand characteristics are presented in Table 1.

2.2. Sampling

The effect of treatment on lichen abundance was evaluated for three species: *C. mitis*, *C. rangiferina,* and *C. stellaris*. The percentage cover of the lichens within four 1-m² quadrat in each of the 17 plots that were established within each treatment (clearcutting, partial cutting, and control) was measured five years after harvesting (see Bescond et al., 2011).

Lichen transplants were used to evaluate lichen growth response as a function of canopy openings. To do so, we collected sections of lichen mat approximately 15 cm in diameter for each of the three lichen species studied (*C. mitis*, *C. rangiferina*, and *C. stellaris*). Because it was difficult to find mat sections for all species used for transplants in the same plot, some material was collected from areas located nearby (<10 km). The mat sections were brought back in the laboratory and cleaned. Dead or unhealthy parts of the thalli that appeared darkened or viscous were also removed during the process. The mat sections were thereafter put into circular baskets made with mosquito netting (15 cm diameter by 5 cm depth that were weighed separately before the lichens were put inside). The mat sections were placed in a growth chamber in which the relative humidity was maintained at 40% for 72 h, and then weighed to the nearest 0.0001 g.

In the spring of 2005, 10 plots were selected randomly in each treatment unit (block) at each site. Within these plots, mat sections in baskets (hereafter referred to as transplants) of each species were installed on the ground in the middle of an already established lichen mat. When no lichen mat of the same species was found, specimens from neighbouring areas (<10 km) were transplanted around the basket. Ten transplants of each species were located in each treatment, for a total of 270 transplants. The transplants were brought back to the laboratory in fall 2005. After the lichens were cleaned and dying parts were removed, the transplants were held again in the growth chamber at a relative humidity of 40% for at least 72 h, reweighed, and returned to their previous location in the field. The same procedure was repeated for other seasons (summer 2005: from June 2005 to September 2005: winter 2006: from September 2005 to May 2006, summer 2006: from May 2006 to September 2006).

Humidity, temperature, and light sensors were used to measure microclimate of *C. stellaris*, *C. rangiferina*, and *C. mitis*. This part of the experiment was undertaken at the Fénélon site only. In each treatment, we randomly selected one plot and we instrumented two randomly selected transplants of each species. LogTag HAXO-8 humidity and temperature recorders were used to measure temperature and humidity below the lichen mats. HOBO
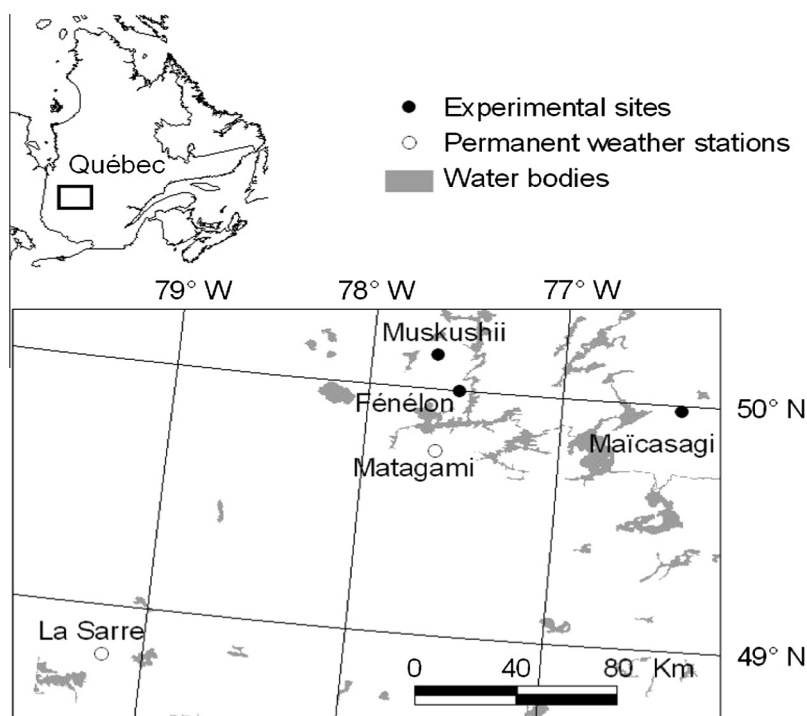
Fig. 1. Map of the study area.

Table 1
Mean ± SD of basal area, stem density, and tree height for each treatment and site.

	Muskuchii						Fénélon						Maïcasagi					
	Control		Partial cut		Clearcut		Control		Partial cut		Clearcut		Control		Partial cut		Clearcut	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Basal area (m²/ha)	24.1	9.6	6.6	6.4	0.3	0.8	16.7	5.9	3.3	4.0	0.5	1.2	21.9	9.6	9.9	5.1	0.8	1.4
Stem density (no. ha)	1237	528	486	402	19	43	1043	344	218	223	33	84	1092	443	525	195	75	150
Tree height (m)	19.6	1.1	15.9	2.5	–	–	16.0	2.3	11.9	5.0	–	–	19.6	1.4	15.1	2.1	–	–

pendant temperature/light data loggers were used for measurements of photosynthetically active radiation (PAR) and ambient air temperature above the lichen mats (Campbell Scientific). Microclimatic data were recorded during 112 days, from the end of May 2006 to mid September 2006.

2.3. Data analyses

Cover and frequency of *Cladonia* species naturally present in the study plots were analysed with ANOVAs with treatment as a fixed effect and site as a random factor. The response variables were mean cover and frequency (presence or absence) of each species in each plot (average values of the four 1-m² quadrats).

Repeated measures analyses were used to examine between-group differences (treatments) and within-group differences (season of measurement) in lichen biomass. Treatment (partial cut, clearcut, and control plots) and season were fixed factors, and site (Muskuchii, Fénélon, and Maïcasagi) was a random factor. The covariance among repeated measures was modeled with the auto-regressive structure. The response variable was expressed as the biomass of each transplant at the end of each season minus its initial biomass at the beginning of the experiment; these values were thereafter divided by the number of days within each interval to account for differences in length of seasons. Transplants that showed anomalously low growth rates were considered outliers

(biomass >2 SD below the mean biomass of all transplants in each season (Stevenson and Coxson, 2003; Muir et al., 2006)) and were also removed from the data set (4 *C. stellaris* transplants removed from summer 2005, 4 from winter 2006, and 3 from summer 2006; 1 *C. rangiferina* transplant removed from summer 2005, 4 from winter 2006, and 4 from summer 2006; 2 *C. mitis* transplant removed from summer 2005, 2 from winter 2006, and 2 from summer 2006).

We tested for differences between treatments in the growth rates of each species at the end of the experiment with a nested mixed ANOVA with treatment as a fixed effect and site as a random effect. Transplants that showed anomalously low growth rate (GR) were considered outliers (biomass >2 SD below the mean biomass of all transplants of the same species) (Stevenson and Coxson, 2003; Muir et al., 2006) and were removed from the data set (we removed 7, 4, and 4 transplants of *C. stellaris*, *C. mitis*, and *C. rangiferina*, respectively).

Growth rate at the end of the experiment was calculated as:

$$GR = (W2 - W1)/W1 \times 100 \qquad (1)$$

where $W1$ was lichen weight at the beginning of the experiment and $W2$ was lichen weight at the end of the experiment. GR was calculated for the period between June 18, 2005 (W_1) and September 15, 2006 (W_2).

Differences in daily temperature, relative humidity, and PAR among treatments were tested with ANOVAs for each species (data from the two samples per species were averaged). We also tested for differences among treatments in relative humidity in the early hours (from 6 to 9 am). This period is important for lichen photosynthesis because the lichens are generally wet from dew and lighted at the same time (Palmqvist, 2000).

All ANOVAs were performed with the MIXED procedure of SAS (SAS Institute 2002). Denominator degrees of freedom for all analyses were calculated using Satterthwaite's approximation (Littell et al., 1996). The random effects were used as the error term when testing for differences between fixed effects. Significant differences ($p \leqslant 0.05$) within fixed effects were detected with least squares means Tukey's honestly significant difference tests.

3. Results

3.1. Lichen cover

Of the three species examined, *C. rangiferina* was clearly the most abundant in the study plots (Table 2). *C. stellaris* was significantly less frequent in clearcut plots compared with partial cut plots (Table 2), and was significantly less abundant in clearcut plots compared with partial cut plots and unharvested controls (Table 2). *C. rangiferina* was also significantly less abundant in clearcuts compared with both partial cut plots and controls (Table 2).

3.2. Growth of transplants

Repeated measures analyses showed that growth differed significantly across treatments for *C. stellaris* and *C. rangiferina* (Table 3), with growth significantly lower in the control plots than in the partial cut and the clearcut plots (Fig. 2). Most transplants in the control plots lost biomass. 62% of all transplants lost biomass in the control plots compared to 17% and 29% in the clearcut and partial cut plots, respectively. Loss of biomass occurred most frequently in *C. mitis* (48%), followed by *C. rangiferina* (36%) and *C. stellaris* (17%). Growth of the three species differed significantly across seasons (Table 3) and transplants grew faster during the first summer compared to the other seasons (Fig. 2). The significant interactions between treatment and season for the three species (Table 3) indicate a different effect of treatment over time (Fig. 2). Differences between treatments were not significant during winter for *C. stellaris* and were significant only during the second summer for *C. rangiferina*, with lower growth rates in controls for both species. For *C. mitis*, differences in growth among treatments were found only during the first summer and the growth in controls was higher than the growth in clearcuts.

On average, the growth rate of *C. stellaris* at the end of the experiment (mean ± SD: 14.7% ± 13.4) was more than 3 and 7

times higher than the growth rate of *C. mitis* (4.5% ± 14.9) and *C. rangiferina* (1.9% ± 18.6), respectively. Maximum GRs for individual transplants at the end of the experiment were 45% for *C. mitis,* 39% for *C. rangiferina*, and 35% for *C. stellaris*. ANOVA performed on total GR at the end of the experiment revealed significant differences between treatments for *C. stellaris* ($F_{2,82}$ = 19.46, $p < 0.001$) and *C. rangiferina* ($F_{2,80.2}$ = 22.42, $p < 0.001$), but not for *C. mitis* ($F_{2,81}$ = 2.76, $p = 0.07$). GRs for *C. stellaris* and *C. rangiferina* were significantly lower in the control plots than in the partial cut and clearcut plots (Fig. 3a). There was a significant difference among sites for *C. mitis* ($F_{2,83}$ = 13.15, $p < 0.001$), but not for *C. stellaris* ($F_{2,84}$ = 0.87, $p = 0.424$) nor for *C. rangiferina* ($F_{2,82}$ = 1.05, $p = 0.353$). GR of *C. mitis* was significantly lower in the Maïcasagi site, intermediate in the Muskuchii site, and higher in the Fénélon site.

3.3. Microclimatic conditions

The highest and lowest values of PAR for the three *Cladonia* species were observed in clearcut and control plots, respectively (Table 4 and Figs. 4–6). For *C. stellaris* and *C. mitis*, relative humidity was significantly higher in the control plots than in the partial-cut plots (Table 4, Figs. 4 and 6). When microclimatic data recorded between 6 am and 9 am are compared, relative humidity was significantly lower in the control plots than in the harvested plots for *C. mitis* ($F_{2,201}$ = 5.33, $p = 0.006$) and *C. stellaris* ($F_{2,201}$ = 8.250, $p < 0.001$) but not for *C. rangiferina* ($F_{2,201}$ = 0.266, $p = 0.628$). Thallus temperatures were significantly lower in the control plots than

Table 3
Repeated measures analyses of variance comparing biomass of *Cladonia mitis*, *C. stellaris*, and *C. rangiferina* among treatments and seasons.

	dfn, dfd	F	p
Cladonia stellaris			
Between-subject effect			
Treatment	2, 81.1	15.81	**<0.001**
Within-subject effects			
Season	2, 166	71.28	**<0.001**
Treatment × season	2, 166	9.98	**<0.001**
Cladonia mitis			
Between-subject effect			
Treatment	2, 81	0.88	0.418
Within-subject effects			
Season	2, 166	18.54	**<0.001**
Treatment × season	2, 166	7.56	**<0.001**
Cladonia rangiferina			
Between-subject effect			
Treatment	2, 76.2	8.98	**<0.001**
Within-subject effects			
Season	2, 150	41.82	**<0.001**
Treatment × season	2, 150	13.29	**<0.001**

Note: significant values ($p \leqslant 0.05$) are given in boldface.

Table 2
Mean frequency (presence or absence) and mean cover for *Cladonia stellaris*, *C. mitis*, and *C. rangiferina* in partial cut plots, clearcut plots, and control plots. One-way ANOVAs were used to compare the frequency and the cover among treatments. Significant p values are given in boldface. Means with different letters differed significantly ($p \leqslant 0.05$) according to least squares means Tukey's honestly significant difference tests.

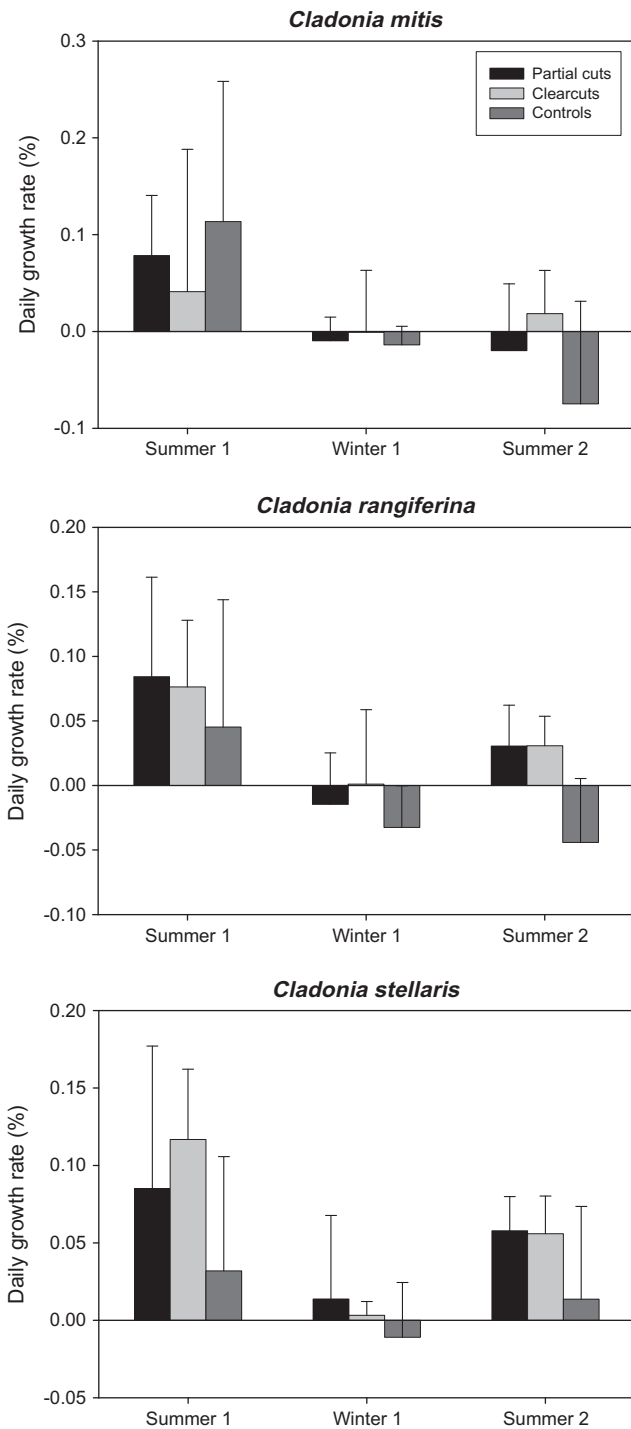|	Control		Partial cut		Clearcut		dfn, dfd	F	p
	Mean	SD	Mean	SD	Mean	SD			
Frequency (presence/absence)									
Cladonia mitis	0.09	0.29	0.05	0.21	0.08	0.27	2, 217	0.94	0.394
Cladonia stellaris	0.07ab	0.26	0.13a	0.34	0.01b	0.01	2, 217	8.42	**<0.001**
Cladonia rangiferina	0.40	0.49	0.36	0.48	0.29	0.45	2, 217	1.77	0.174
Cover (%)									
Cladonia mitis	1.41	4.86	0.54	3.19	1.15	4.52	2, 217	0.49	0.481
Cladonia stellaris	1.04a	4.43	0.94a	3.41	0.05b	0.52	2, 217	4.83	**0.009**
Cladonia rangiferina	4.48a	7.96	3.61a	7.14	2.67b	5.71	2, 217	4.74	**0.010**

Fig. 2. Growth rates of *Cladonia stellaris*, *C. rangiferina*, and *C. mitis* by treatment for each season. Bars are means of growth rates. Error bars are SDs. Growth rate for each period was calculated as the percentage of change in biomass between beginning and end of each measurement interval divided by the number of days within each interval. Summer 1: from June 2005 to September 2005, winter 1: from September 2005 to May 2006, summer 2: from May 2006 to September 2006.

Fig. 3. Gowth rates of *Cladonia stellaris*, *C. rangiferina*, and *C. mitis* at the end of the experiment (a) and annual growth rates of *Cladonia stellaris*, *C. rangiferina*, and *C. mitis* (b) Bars are means of growth rates. Error bars are SDs. Differences of growth rates at the end of the experiment that were significant ($p \leqslant 0.05$) according to least squares means Tukey's honestly significant difference tests are indicated by different letters. Note that analyses were not conducted for annual growth rates.

4. Discussion

In this study, we wanted to evaluate if the ground cover and growth rates of three terrestrial lichen species of the genus *Cladonia* (*C. stellaris*, *C. rangiferina*, and *C. mitis*) differed between treatments of varying tree removal intensity: partial cuts, clearcuts, and unharvested control stands. We found differences in growth rates across treatments, and we also found differences in microclimate among treatments. We first summarize trends that emerged from the analyses and compare them with what was observed in other studies done in comparable regions. We then discuss on how the observed growth responses may be explained by measured environmental factors.

4.1. General trends

Our results show that *C. stellaris*, *C. rangiferina*, and *C. mitis* can grow as well in open habitats (clearcuts) as in semi-open habitats (partial cuts). The growth of these species was particularly low in control forests, where approximately half of the transplants lost weight. We also observed higher growth rates for *C. stellaris* than the other species we studied. den Herder et al. (2003) also found that *C. stellaris* is generally more competitive and exhibits the highest growth rate among seven lichen species in a Finnish pine forest. Moreover, daily growth rates of this species in our study (see Fig. 2) were similar to those measured by den Herder et al. (2003), and were higher than those measured by Gaio-Oliveira et al. (2006) in the middle boreal forest zone of Sweden. In northern open woodland forests in Finland, the growth rate of *C. stellaris* was

in the harvested plots for *C. stellaris* and *C. mitis* (Table 4, Figs. 4 and 6). Thallus temperatures were generally higher than air temperatures in the harvested plots (Figs. 4–6) and lower than air temperature in the control plots. Daily fluctuations in PAR, temperature, and relative humidity across an entire month were lower in the control plots compared with the partial cut and clearcut plots, especially for *C. mitis* and *C. stellaris* (Figs. 4 and 6).
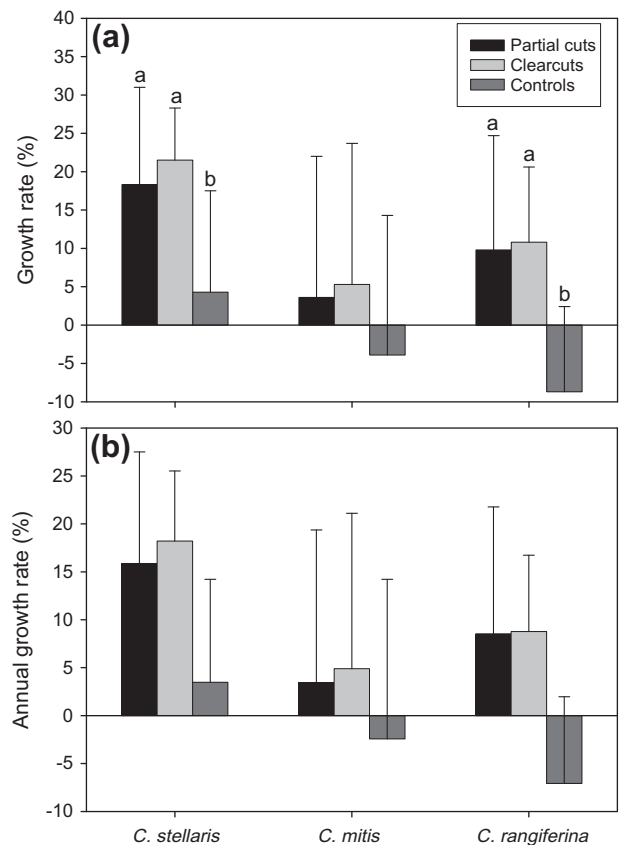
Table 4
Daily mean ± SD of PAR, relative humidity, and temperature for each species from May 2006 through July 2006. One-way ANOVAs were used to test for differences among treatments (control forests, partial cuts, and clearcuts). Significant *p* values are given in boldface. Means with different letters differed significantly (*p* ≤ 0.05) according to least squares means Tukey's honestly significant difference tests.

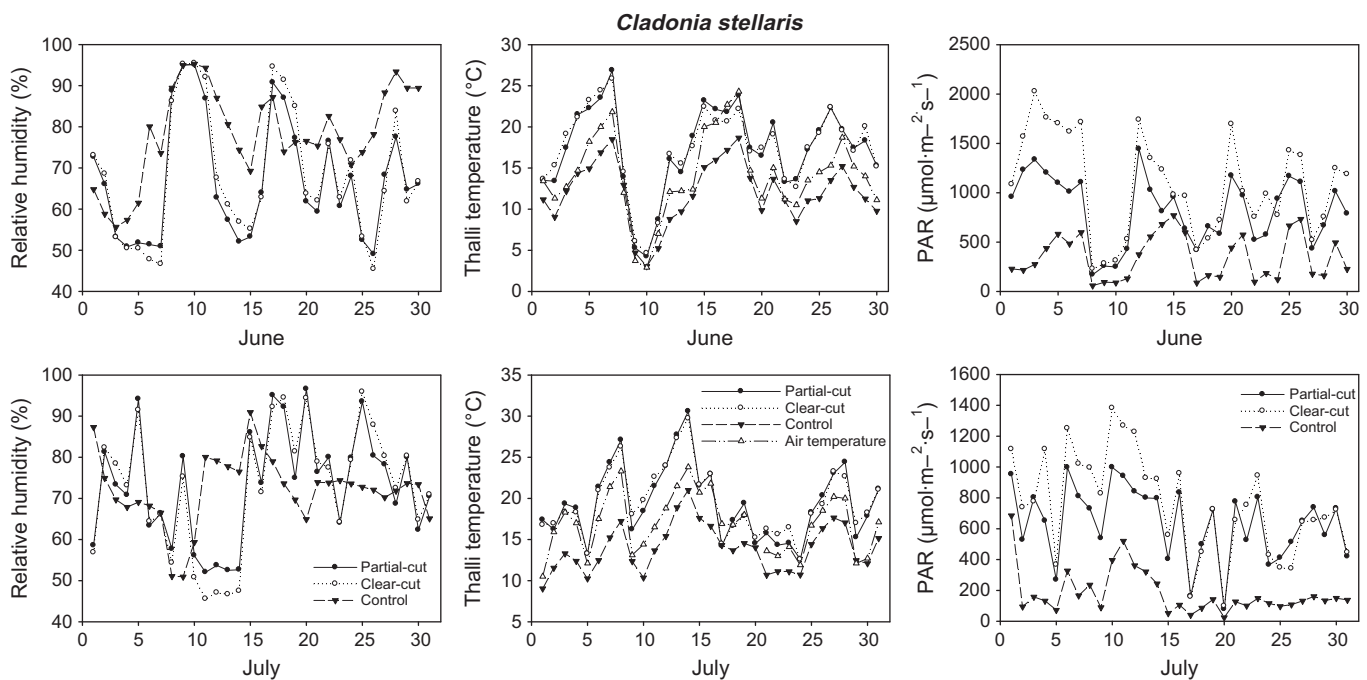|	Control		Partial cut		Clearcut		F	p
	Mean	SD	Mean	SD	Mean	SD		
PAR								
Cladonia mitis	1539.94b	1375.19	2681.13a	1267.95	–	–	13.40	**<0.001**
Cladonia rangiferina	450.05c	234.46	2033.36b	1038.35	2745.43a	1440.57	38.72	**<0.001**
Cladonia stellaris	347.77c	229.942	830.39b	345.618	1082.81a	512.222	28.88	**<0.001**
Relative humidity								
Cladonia mitis	81.30a	7.66	73.74b	16.26	77.91ab	15.94	5.07	**0.007**
Cladonia rangiferina	78.70	12.39	77.69	15.53	81.62	16.97	1.25	0.289
Cladonia stellaris	74.65a	10.62	69.68b	14.08	70.29ab	15.24	3.52	**0.032**
Temperature								
Cladonia mitis	13.09c	3.75	19.21a	4.55	16.96b	4.72	34.23	**<0.001**
Cladonia rangiferina	16.65	4.67	17.53	4.48	16.99	4.67	0.69	0.503
Cladonia stellaris	13.03b	3.62	18.58a	5.10	18.61a	4.80	33.91	**<0.001**

Fig. 4. Summary of microclimate data for *Cladonia stellaris* during June and July 2006 at the Fénélon site. The lines are the average of all sensors within a plot. The *x*-axis represents day numbers.

26% per year (Crittenden, 2000), which was much higher than what we observed in our natural old forests (3.5%) but only slightly higher than the growth rates we found in partial cuts (15.9%) and clearcuts (18.2%) in our study. Comparisons with other studies conducted nearby our study area (Boudreau and Payette, 2004; Kershaw and Rouse, 1971b; Ouzilleau and Payette, 1975; Scotter, 1963) are challenging because growth rates were not estimated based on mass increments in these studies. It is likely that the growth rates observed in our study are higher than the growth rates for the same species in northern woodland forests dominated by terrestrial lichens, where caribou forage pressure and self-shading may limit lichen growth (Crittenden, 1991; Sveinbjörnsson, 1990).

4.2. Influence of environmental factors

Canopy removal influences epiphytic lichen development through changes in microclimatic conditions. We expected a decrease in relative humidity, and thus a reduction of the hydration period, for all species where the canopy was more open. Because lichen growth is limited by the duration of hydration periods and by the irradiance level during these periods (Gauslaa et al., 2007), a reduction of the hydration period diminishes the time available for photosynthetic activity and lichen growth (Lange et al., 1986; Palmqvist and Sundberg, 2000). We observed a significant reduction of relative humidity for *C. mitis* and *C. stellaris* in the harvested plots compared to the control plots. However, the reduction in relative humidity was not associated with a concomitant reduction in growth rates. Moreover, growth rates of *Cladonia* species were not higher during summer 2006 than during summer 2005 (Fig. 2) even though precipitation was more abundant and temperatures lower in 2006 than in 2005 (Fig. A1). Boudreault et al. (2013) found a reverse pattern for epiphytic species in the same sites, with higher growth rate during the year with more precipitation. Compared to epiphytic lichens, *Cladonia* species may be favoured by their habitat and morphology to tolerate relatively dry meteorological conditions. The greater capacity of the soil substrate to retain moisture during droughts compared
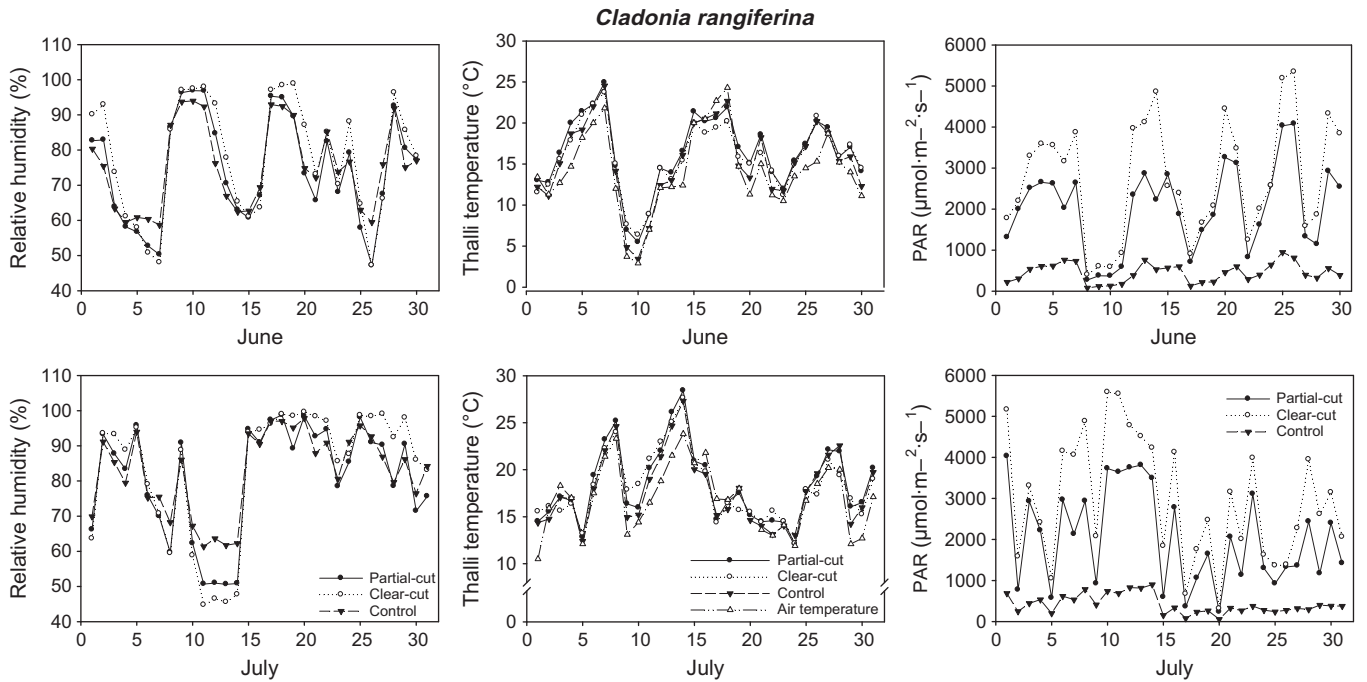
Cladonia rangiferina

Fig. 5. Summary of microclimate data for *Cladonia rangiferina* during June and July 2006 at the Fénélon site. The *x*-axis represents day numbers.
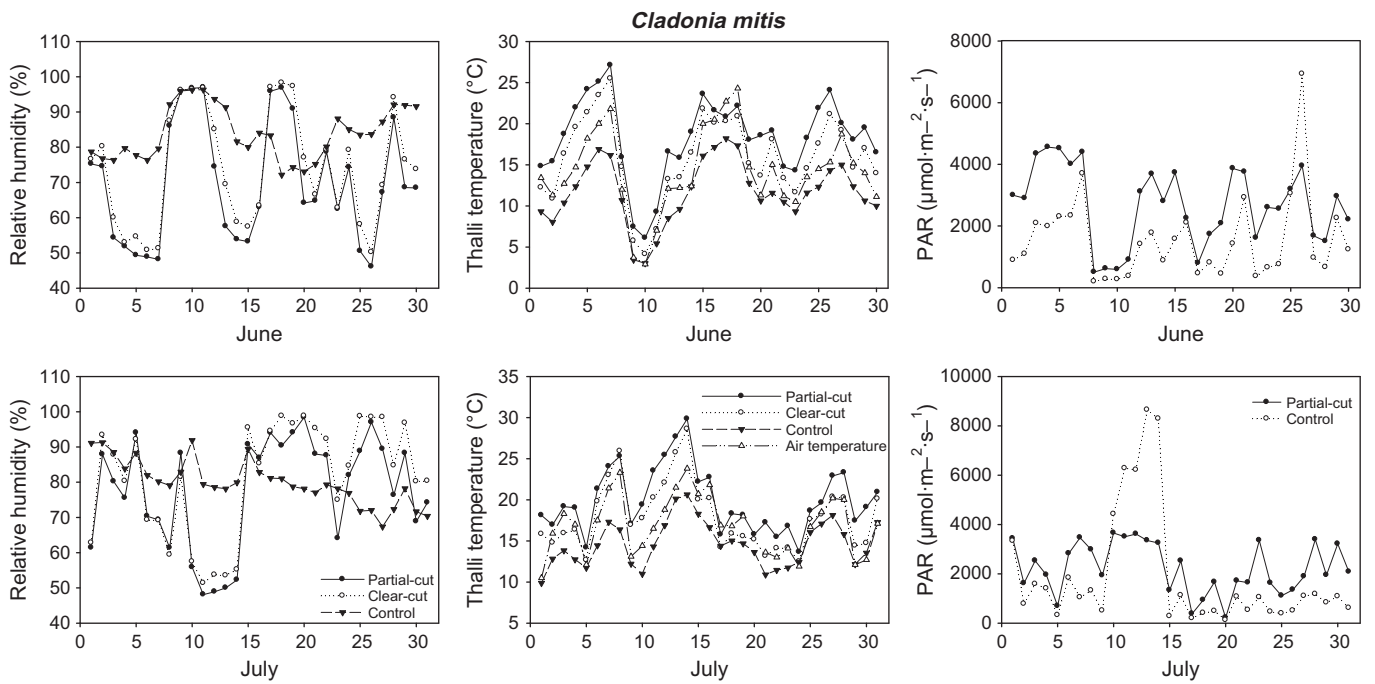
Cladonia mitis

Fig. 6. Summary of microclimate data for *Cladonia mitis* during June and July 2006 at the Fénélon site. The lines are the average of all sensors within a plot. Solid lines are for partial cut plots, short dashed lines are for clearcut plots, and long dashed lines are for control plots. The *x*-axis represents day numbers.

with aerial tree structures, and reduced evaporation rates due to the thickness and the density of the *Cladonia* carpet, may also have extended hydration periods after dew or precipitation events (Kershaw and Rouse, 1971a,b). Differences in lichen humidity among treatments during the early morning hours may be explained by greater dew accumulation and more precipitation reaching the ground in opened-canopy forests; conversely, in closed canopy conditions, dew or precipitation are intercepted by tree branches before reaching the ground (Geiger, 1966). This

phenomenon might explain the higher growth rates in open environments. Microclimate data also indicate that lichen temperatures for *C. mitis* and *C. stellaris* were significantly higher in the harvested plots than in the control plots. It is likely that elevated temperatures in this study did not offset carbon gain from photosynthesis (Palmqvist, 2000), and that temperatures experienced by the lichens even in the harvested plots are well within the range of temperatures experienced by the lichens in their natural microhabitats (see Kershaw and Field, 1975).
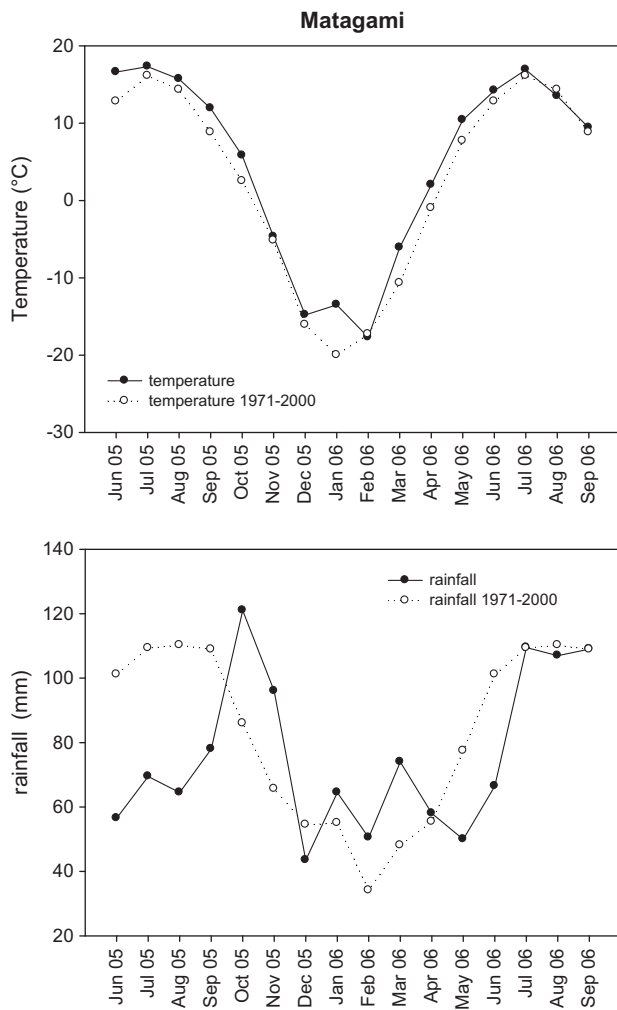
Fig. A1. Mean temperature and monthly rainfall recorded at the Matagami weather station during the study. Solid lines are for years 2005-2006 and dashed lines for mean temperature and mean rainfall during the 1971-2000 period.

Our results thus suggest that growth rates of the three species were favoured by an increase in canopy openness in the harvested plots. Webb (1998) found opposite results for *C. stellaris,* with higher growth rates in unharvested forests than in clearcuts, and argued that the increase in insolation at the ground level as a result of logging was responsible for this decline. On the other hand, other studies have shown that photosynthesis in lichens is often light limited (Gaio-Oliveira et al., 2004; Gauslaa et al., 2006; Palmqvist, 2000), and that canopy openings may increase lichen growth. Our results suggest that growth rates of the three species studied were probably limited by the low light levels prevailing in the forests used as controls in our study. Another factor that can restrict *Cladonia* biomass accumulation in dense forests is competition with feather moss (*Pleurozium schreberi*), which prefers moist and shadowy sites (Helle et al., 1983; Sulyma and Coxson, 2001).

4.3. Influence of canopy removal on the maintenance of terrestrial lichen cover

Even if species growth did not differ between partial cuts and clearcuts, partial cuts can contribute to maintaining a higher cover of terrestrial lichens than did clearcuts. For instance, the abundance and frequency of *C. stellaris* was much lower in clearcuts

than in partial cuts. At least two reasons may explain this pattern. First, disturbance of the soil surface by harvesting (Bescond et al., 2011) and the probability that pre-established lichens be dislodged or buried are greater in clearcuts than in partial cuts. Second, the high number of branches present on the ground in clearcuts (Bescond et al., 2011) may compromise lichen recruitment and establishment (Miège et al., 2001).

Because lichen species growth was favoured by partial cuts, we expected that cover and frequency of *Cladonia* species 5 years after harvesting would be higher in partial cuts than in old forest control plots. However, the cover of species was similar between partial cuts and control forests. Such results suggest that some taller vascular plants that were favoured by canopy openings (e.g., *Vaccinium myrtilloides, Kalmia angustifolia* (Bescond et al., 2011)) may have outcompete lichens for light. Disturbances to the soil surface in partial cuts, even if reduced compared with clear-cutting, may also have delayed potential lichen abundance response to the increased amount of light reaching the ground (Miège et al., 2001; Waterhouse et al., 2011).

5. Conclusion

Our results showed that canopy openings in the partial cuts had a positive influence on *Cladonia* growth rates. It is likely that the increase in the quantity of light and humidity reaching the thalli early in the morning (Palmqvist, 2000) was favourable for lichen growth in the partial cuts. We also found that five years after harvesting, partial cuts maintained a higher cover of terrestrial lichens than did clearcuts. Hence, canopy openings resulting from partial cuts not only provide better growing conditions for terrestrial lichens but maintain pre-established lichen cover at levels comparable to what is observed in our old forest control plots.

In recent years, partial cuts in the boreal forest have been proposed as an alternative to clearcuts to maintain a forest cover adapted for organisms associated with old forest characteristics (Drapeau et al., 2003; Fenton et al., 2009). This is the case of the woodland caribou, an endangered species for which partial cuts could maintain an irregular forest structure (Courtois et al., 2007). In addition to the protection cover provided by partial cuts, our results show that they can offer, comparatively to clearcuts, good forage conditions for woodland caribou through maintenance of a relatively high cover of pre-established terrestrial lichens and adequate growth conditions for expanding terrestrial lichens.

Appendix A.

See Fig. A1.

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