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RESEARCH PAPER

Origin of the lichen–spruce woodland in the closed-crown forest zone of eastern Canada

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ABSTRACT

Aim We investigate the timing and factors responsible for the transformation of closed-crown forests into lichen–spruce woodlands.

Location The study area extends between 70° and 72° W in the closed-crown forest zone from its southern limit near 47°30′ N to its northern limit at the contact with the lichen–spruce woodland zone around 52°10′ N. A total of 24 lichen–spruce woodlands were selected.

Methods Radiocarbon dating of charcoals at mineral soil contact and within the organic horizons allowed the principal factors causing the degradation of the closed-crown forest to be identified, i.e. light fires, successive fires and the occurrence of a spruce budworm epidemic followed by a fire.

Results Charcoals dated in the organic horizon were less than 200 years old, suggesting a recent transformation of the closed-crown forest following surface fires. Before their transformation into lichen–spruce woodlands, stands were occupied by old, dense forests that originated from fires dating back to 1000 yr BP. The radiocarbon dating of charcoals in the organic horizon indicated that several stands burned twice in less than 50 years, while others burned shortly after a spruce budworm epidemic. Light fires are frequent within the lichen–spruce woodlands according to multiple charcoal layers found within the organic matter horizon.

Main conclusions While closed-crown forests are predicted to expand under climate warming, compound disturbances diminish the natural regeneration of the closed-crown forests in the south and favour the expansion of lichen–spruce woodlands. As black spruce germinates on mineral soils, surface fires accentuate the expansion of the lichen–spruce woodlands southward. Under global warming, warmer springs will lead to earlier low-intensity fires that do not remove as much organic matter, and hence prevent conditions suitable for black spruce regeneration. Also, spruce budworm reduces seed production for a certain time. The occurrence of fire during this period is critical for regeneration of black spruce.

Keywords
Black spruce, boreal forest, charcoal, climate change, disturbances, eastern Canada, ecological succession, fire severity, lichen–spruce woodland.

INTRODUCTION

Throughout the Holocene, the geographical position of each vegetation zone has been influenced by changes in climate (Ritchie, 1987; Prentice *et al.*, 1991). The post-glacial development of vegetation communities has been marked more by changes in stem density than latitudinal displacements of tree populations (Payette & Filion, 1985; Cwynar & MacDonald, 1987; Ritchie, 1987; Davis, 1989; Prentice *et al.*, 1991; Lescop-Sinclair & Payette, 1995). The positions of the boreal vegetation zones have remained relatively stable over the last 3000 years (Prentice *et al.*, 1991; Lavoie & Payette, 1996). Climate warming observed since the end of the 19th century and anticipated for the 21st century will have repercussions on all ecosystems

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including the boreal forest. The mean annual temperature of the earth has increased by around 0.6 °C over the last 100 years. The rate of temperature increase between 1976 and today is double that measured between 1910 and 1945, a phenomenon which is unique over the last 1000 years (Houghton *et al.*, 2001).

Climate change is generally reflected in plant communities by a modification of their composition, as well as by the displacement of plant species within vegetation zones (Cwynar & MacDonald, 1987; Ritchie, 1987; Prentice *et al.*, 1991). In theory, current climate warming should favour a northward expansion of the boreal species with a consequent shift of the southern vegetation zones towards the north. However, the overall trend observed at present is the opposite, i.e. within the closed-crown forest zone there is a degradation of dense forests to woodlands. Closed-crown forests often transform into lichen–spruce woodlands following successive disturbances (Payette *et al.*, 2000; Payette & Delwaide, 2003; Jasinski & Payette, 2005). In eastern Canada, lichen–spruce woodlands are the dominant forest type in the northern part of the boreal forest (Payette, 1992). A short interval between two disturbances can compromise the re-establishment of the closed-crown forest. Disturbances that affect the vitality of trees in the stand, such as an insect infestation, followed shortly thereafter by a fire can greatly increase the probability of a reduced tree regeneration. A reduction in the tree density of a stand can sometimes be caused by a spruce budworm epidemic followed by logging (salvage of dead timber or affected trees) (Dussart & Payette, 2002). The passage of successive fires, that is two fires arriving at an interval too short for the trees to attain maturity and reproduce, can equally cause the drastic reduction of tree regeneration (Sirois, 1988). The transformation of a closed-crown forest to lichen–spruce woodland appears to be a unidirectional process, as to date the reverse process, i.e. the transformation of a lichen–spruce woodland to a closed-crown forest, has not been observed (Payette *et al.*, 2000, 2001; Jasinski & Payette, 2005; Girard *et al.*, 2008). Once transformed to an open stand, the southern lichen–spruce woodlands resemble the lichen–spruce woodlands situated within the lichen woodland zone. The absence of the full re-establishment of closed-crown forest following fire is equally characteristic of the regeneration pattern for the forests found within the lichen woodland zone (Payette *et al.*, 2001).

The lichen–spruce woodlands within the closed-crown forest zone have expanded by 9% to the detriment of the black spruce–feathermoss forests over the last 50 years (Girard *et al.*, 2008). Compound disturbances (over a brief time interval) are responsible for the decrease in the area of the closed-crown forest and subsequent increase in lichen–spruce woodland area (Payette *et al.*, 2000, 2001; Girard *et al.*, 2008). Despite the trend towards an opening of the forests, the forests in the southern region of the closed-crown forest zone are resilient to disturbances, particularly more so than those situated further north. The greater number of forest species [balsam fir (*Abies balsamea* (L) Mill.], white spruce [*Picea glauca* (Moench) Voss], trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.) found within the zone appear to increase the resilience of the closed-crown forest to disturbances (Girard *et al.*, 2008). Within monospecific black spruce stands the interval between different disturbances must be sufficiently long to ensure forest regeneration.

In the boreal forest, succession at a given site does not necessarily produce the same plant community following a disturbance or a series of disturbances (Paine *et al.*, 1998; Walker & Del Moral, 2003). Successive (multiple) disturbances can lead to a change in successional trajectory. The closed-crown boreal forest zone is governed by a disturbance regime that can lead to the transformation of the dominant ecosystems into divergent ecosystems that are capable of maintaining themselves through time (Jasinski & Payette, 2005). Compound disturbances (fire, insect epidemic and logging) can sometimes change the typical successional trajectory to arrive at an alternative stable state, such as lichen–spruce woodland (Payette *et al.*, 2000; Jasinski & Payette, 2005).

The main objective of this study is to determine the origin of the lichen–spruce woodlands along a latitudinal gradient within the interior of the closed-crown forest zone and to identify the disturbance factors responsible for the opening of the closed-crown forest. In order to meet this objective, we have characterized the soils and vegetation of the lichen–spruce woodlands within the closed-crown forest zone. The origin and structure of the lichen–spruce woodlands as a function of their developmental disturbance factors were analysed in sites uniformly distributed across a latitudinal gradient of more than 500 km within the closed-crown boreal forest zone. Two hypotheses were tested during the study: (1) successive fires are the principal cause for the transformation of the closed-crown forest into lichen–spruce woodland and (2) the combination of a spruce budworm epidemic followed by a fire is equally effective in reducing the regeneration of dense forests. Figure 1 summarizes our research hypothesis regarding the successional pathways of the forest vegetation as a function of the disturbances that affect them.

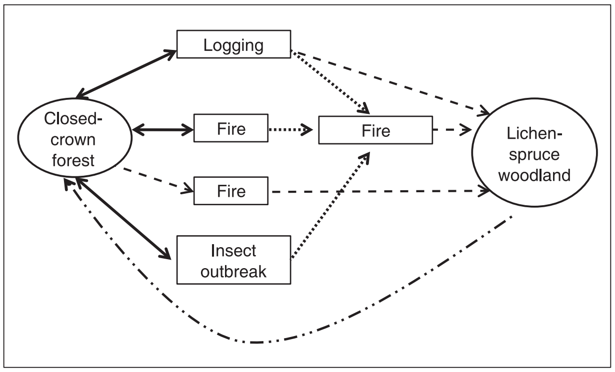

Figure 1 Model of stand disturbances causing the shift from closed-crown forest to lichen–spruce woodland in the closed-crown forest zone. The continuous black arrows indicate good regeneration, whereas the black dotted arrows indicate poor regeneration of the closed-crown forest. The dashed black arrows represent a short interval between two disturbances (compounded disturbances). The dashed and dotted arrow indicates a possible reversion of the lichen–spruce woodland into a closed-crown forest.

STUDY AREA

The lichen–spruce woodlands of the closed-crown boreal forest zone are dominated by black spruce and have a tree cover that is generally less than 40% (Johnson & Miyanishi, 1999; Payette *et al*., 2000). The soil is covered with terrestrial lichens of the genus *Cladonia* such as *Cladonia rangiferina* (L) Nyl, *Cladonia stellaris* (Opiz) Brodo and *Cladonia mitis* (Sandst.) Hustich. The shrub layer is comprised principally of ericaceous shrubs such as *Rhododendron groenlandicum* Retz., *Kalmia angustifolia* L. and *Vaccinium angustifolium* Ait., along with dwarf birch (*Betula glandulosa* Michx.) (Morneau & Payette, 1989; Riverin & Gagnon, 1996; Payette *et al*., 2000; Simard & Payette, 2001).

The study area is in the heart of the closed-crown forest zone and extends from 70° to 72° W and from the southern limit of lichen–spruce woodlands (47°30′ N) north to the contact of the lichen woodland (taiga) zone (52°10′ N). The area is dominated by black spruce but does include limited stands of balsam fir, white birch, white spruce and jack pine (*Pinus banksiana* Lamb.). The forests of the study area are situated on well-drained podzolic soils that have developed on glacial deposits (Table 1). The southernmost section is situated 120 km north-east of Québec City (47°30′ N, 70°–72° W) in the Parc des Grands-Jardins (PGJ) (see Fig. 2) and the Réserve Faunique des Laurentides (RFL). This section is dominated by balsam fir–white birch forests. The average altitude varies between 600 and 800 m above sea level (a.s.l) in the PGJ with some hills reaching over 950 m a.s.l., while the mean altitude of the RFL is around 900 m a.s.l. The mean annual temperature is 0 and –0.5 °C for the PGJ and the RFL, respectively (Boisclair, 1990). An orographic effect exists in this region with the PGJ receiving around 1000 mm of annual precipitation, as compared with 1500 mm for the RFL. Balsam fir–white birch forests dominate the low altitudes of the RFL, with stands of balsam fir and black spruce dominating the higher altitudes. In the PGJ, dense black spruce stands are found in humid and mesic environments, while lichen–spruce woodlands are found in well-drained sites. Logging and spruce budworm epidemics are the principal disturbances in the RFL. During the 20th century, three spruce budworm epidemics devastated the region's forests (1914–19, 1944–51, and 1975–85) (Tremblay, 1999; Payette *et al*., 2000; Simard & Payette, 2001). Nowadays, in the PGJ, fire and spruce budworm epidemics are the principal disturbances, as logging was banned with the creation of the park in 1981 (Dussart & Payette, 2002). The climate of the park is characterized by a mean annual temperature of around 0 °C with approximately 1000 mm of annual precipitation and close to 3.5 m of snow in the winter (Environnement Canada, 2006). The central part of the study area (50° N, 70°–72° W) is situated around 400 km north of Québec City in the region that includes the majority of logging activity occurring in the spruce–moss forests. The northern part of the study region extends just to the limit of the closed-crown forest zone and the beginning of the open forest (52°10′ N, 70°–72° W). The mean annual temperature is around –2 °C while precipitation varies around 800 mm (500 mm of rain and 3 m of snow in the winter) (Environnement Canada, 2006).

Table 1 Transect, GPS location (latitude, longitude), altitude, orientation, drainage, topographic level and deposit for each sampled stand.

Stand	Transect	Latitude (N)	Longitude (W)	Altitude (m)	Orientation	Drainage	Topographic level	Deposit
7	2	47°56′	70°45′	697	SW	2	Top-slope	Till
13	3	48°11′	71°43′	380	S	3	Flat	Till
16	3	48°11′	70°40′	364	SE	2	Mid-slope	Till
18	3	48°11′	70°38′	330	SW	2	Top-slope	Till
26	7	49°11′	71°20′	406	SE	2	Mid-slope	Fluvial–glacial
31	8	49°26′	71°54′	700	W	3	Flat	Fluvial–glacial
33	8	49°26′	71°25′	349	S	3	Flat	Fluvial–glacial
38	9	49°41′	71°23′	348	SE	2	Mid-slope	Till
41	9	49°41′	70°22′	439	E	2	Top-slope	Till
51	11	50°11′	70°56′	392	NE	3	Mid-slope	Fluvial–glacial
56	12	50°26′	70°29′	485	N	2	Top-slope	Fluvial–glacial
61	13	50°41′	70°05′	440	W	3	Mid-slope	Till
62	13	50°41′	71°50′	540	E	2	Top-slope	Fluvial–glacial
63	13	50°41′	70°38′	500	W	3	Low-slope	Fluvial–glacial
69	14	50°56′	71°42′	550	E	3	Mid-slope	Fluvial–glacial
70	14	50°56′	70°15′	560	E	2	Top-slope	Fluvial–glacial
71	14	50°56′	71°11′	450	W	3	Flat	Fluvial–glacial
78	15	51°11′	71°24′	530	E	3	Flat	Fluvial–glacial
79	16	51°26′	70°57′	590	N	2	Top-slope	Fluvial–glacial
81	16	51°26′	71°05′	560	E	2	Top-slope	Esker
86	17	51°41′	70°19′	580	SE	2	Mid-slope	Fluvial–glacial
87	17	51°41′	71°24′	550	NW	2	Mid-slope	Fluvial–glacial
101	19	52°11′	71°05′	720	W	2	Top-slope	Esker
102	19	52°11′	71°42′	640	E	3	Flat	Fluvial–glacial

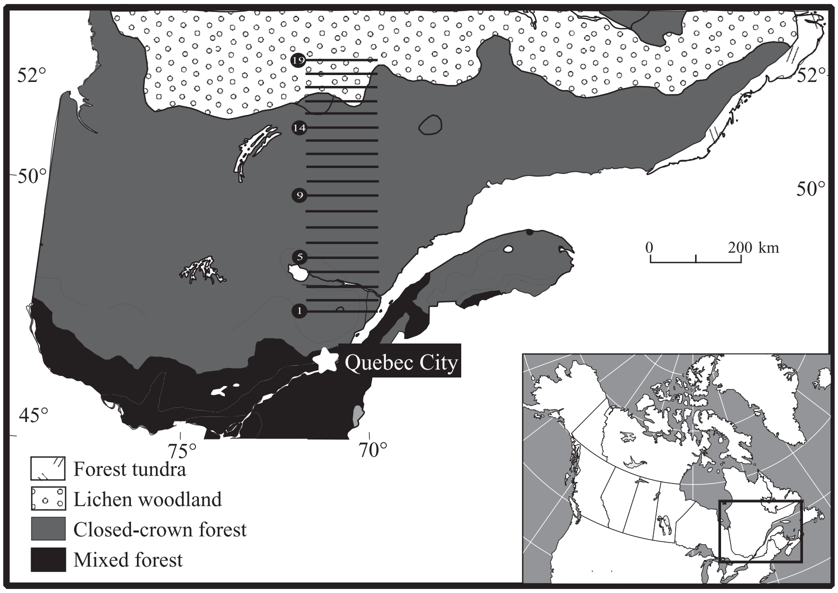

Figure 2 Location of the 19 transects (numbers) in the study area, southern Québec. The main vegetation zones (Payette, 1992) are presented from south to north: the mixed forest zone, the closed-crown forest zone, the lichen–spruce woodland zone (taiga) and the forest–tundra zone.

METHODS

Selection of sampling sites

A transect 1 km wide in latitude and 140 km long in longitude was placed at random with a west–east orientation in the PGJ zone, i.e. the southern limit of the lichen–spruce woodlands (47°30′ N) (Fig. 2). From this first transect, 18 other transects were systematically placed at each 15 min of latitude between 70 and 72° W of longitude up until the northern limit of the closed-crown forest zone (south of the taiga zone at 52°10′ N). The lichen–spruce woodlands and areas of natural (spruce budworm epidemics and fire) and human (logging) disturbances were delineated using air photographs and mapped in GIS software in each transect of the study area in a previous study (see Girard *et al*., 2008). The lichen–spruce woodlands were identified on aerial photographs, verified on the ground, and then digitized. The digitized photographs were then orthorectified using MapInfo Professional (version 7.5, MapInfo Corporation, 2005). In total, 24 sites were selected among the 19 transects.

A 500 m^2 (10 m × 50 m) plot was selected near the geographical centre of each selected lichen–spruce woodland. Within each plot, the diameter at breast height (d.b.h.; i.e. at 1.3 m) was measured for all trees with a diameter greater than 2.5 cm and then classified as either a layer (curved) or seed-origin (straight) stem. Trees with a d.b.h. < 2.5 cm were counted and classified. Finally, the 10 trees with the largest d.b.h. were cut at the base for tree-ring analysis. All of the recovered discs ($n = 240$) were finely sanded in order to make the xylem cells clearly visible under a 40× binocular microscope. The post-fire age of each stand was determined by tree-ring dating of the basal section of the 10 sampled trees. Fire scars were also sampled to determine the date of the last fire by counting the number of tree rings between the scar and the bark.

Along one of the two 50-m plot edges, a vegetation relevé was conducted every 25 cm with the aid of a fine metal pin; each plant species touching the pin was identified and recorded (Mueller-Dombois & Ellenberg, 1974). The relative frequency of each species was calculated by counting the number of times it was recorded along the line and then dividing this value by the total number of points ($n = 200$). The thickness of the organic horizons and the presence of charcoal layers were noted in 11 soil monoliths situated at 5 m intervals along the other 50-m plot edge. In order to reconstruct the fire history of each site, charcoal in the organic horizon and at the mineral soil interface was sampled. Charcoal from the hollows of the organic horizons was not sampled, as it forms a mixed layer where it is not possible to distinguish successive fires. The wood charcoal sampled at each site was obtained from a soil monolith representative of the other soil monoliths in terms of thickness of organic matter and number of charcoal layers identified in the field. The monolith selected at each site was the one that possessed the greatest number of distinctive charcoal layers. Finally, the largest wood charcoal fragments were selected and radiocarbon dated using the accelerator mass spectrometry (AMS) method at the Centre d'Études Nordiques, Université Laval, and Isotrace, University of Toronto, laboratories. The radiocarbon dates were calibrated with the aid of CALIB (version 5.0.2) software (Stuiver & Reimer, 1986).

A pedon was dug at each site in order to describe the soil profile using the Canadian soil classification system (Commission Canadienne de Pédologie, 2002). Samples from the organic layers (horizons F, FH and H) and from the mineral soil (horizon B) were collected in order to analyse their chemical properties and determine their pH (H_2O) using the methods described in McKeague (1978). The exchangeable base concentration (K, Ca, Na and Mg), acidity (H^+), and cation exchange capacity (CEC) of the organic material and the B horizon were determined using a plasma mass spectrometer (ICP-MS) (Dreyer *et al*., 1994). Iron and aluminium were extracted from the B horizon using pyrophosphate ($Fe + Al_{pyro}$) and their concentrations determined with a plasma mass spectrometer (ICP-MS) (Ross & Wang,

Table 2 Edaphic characteristics of the organic horizon, B horizon and C horizon. Types of organic matter (F, FH), pH and cation exchange capacity (CEC) are shown for the organic horizon, pH, CEC and Fe + Al (pyrophosphate) concentrations for the mineral horizon (B), and pH and texture of the C horizon are indicated.

	Organic horizon			B horizon				C horizon	
Stand	Type	pH	CEC (%)	pH	CEC (%)	Fe + Al (pyro) (%)	Diagnostic horizon	pH	Texture
7	F	3.85	0.078	5.01	0.695	2.153	Bhfc	5.26	Silty sand
13	F	3.72	0.074	4.66	0.459	3.845	Bhf	5.18	Loam
16	F	3.66	0.069	4.96	0.935	0.219	Bh	5.01	Silty sand
18	F	3.76	0.128	4.78	0.387	3.408	Bhf	4.67	Silty sand
26	F	4.00	0.085	5.14	1.072	2.111	Bhf	5.65	Sandy loam
31	F	4.07	0.090	5.18	2.571	0.483	Bf	5.66	Sand
33	F	3.89	0.095	5.14	3.262	0.476	Bf	6.57	Sand
38	F	3.83	0.103	4.91	1.865	2.145	Bhf	6.22	Sand
41	F	3.74	0.087	5.17	1.639	0.702	Bhf	5.70	Sandy loam
51	F	3.85	0.119	5.12	3.513	0.615	Bf	5.67	Sandy loam
56	F	3.98	0.116	5.18	3.042	0.712	Bhfc	5.60	Sand
61	F	3.74	0.089	5.04	0.696	3.678	Bhf	5.33	Sandy loam
62	F	3.43	0.143	5.02	1.562	2.085	Bhf	5.98	Silty sand
63	F	3.35	0.172	5.35	5.748	1.023	Bhf	5.49	Sandy loam
69	F	3.74	0.142	4.89	4.101	0.564	Bf	5.20	Silty loam
70	FH	3.72	0.235	4.95	4.143	1.657	Bhf	5.31	Silty loam
71	F	3.36	0.165	5.09	2.053	1.515	Bhf	5.56	Silty loam
78	F	3.61	0.143	5.25	2.899	2.506	Bhfc	5.45	Sand
79	F	3.71	0.114	4.96	9.560	4.160	Bhf	5.80	Sandy loam
81	FH	3.33	0.210	4.79	8.378	0.283	Bhc	5.20	Sand
86	F	3.99	0.101	4.75	8.901	1.438	Bhf	5.18	Silty sand
87	F	3.75	0.133	4.91	4.804	1.345	Bhf	5.26	Silty sand
101	F	3.38	0.296	4.96	8.394	0.996	Bhfc	5.21	Sand
102	F	3.83	0.178	4.47	1.343	0.622	Bf	5.22	Sandy loam

1993). The pH (H_2O) and granulometry of the C horizon were also determined.

Statistical analysis

Linear regression analysis was used to correlate the frequencies of abundant species with key site variables. The relationships between latitude, altitude, stand age, mean thickness of the organic matter and the relative frequency of *Cladonia mitis*, *Cladonia stellaris*, *Cladonia rangiferina*, *Betula glandulosa*, Kalmia angustifolia and *Rhododendron groenlandicum* were established in the lichen-spruce woodlands of the closed-crown forest zone using the STATISTICA software package (Statsoft Inc., France, 1984–2006).

RESULTS

Characterization of lichen–spruce woodland soils

The edaphic conditions of each lichen–spruce woodland site were evaluated in order to verify their similarity with all the lichen–spruce woodlands studied. All of the stands distributed along the more than 500-km long latitudinal gradient possessed the same type of soil: a well-drained podzol formed in fluvial–glacial or glacial deposits (Tables 1 & 2). For each soil profile, the stratigraphical positions of the LFH, Ae, B and C horizons were recognizable with a few differences being observed amongst the stands. The pH of the organic horizons averaged 3.72 ± 0.21 (± always refers to standard deviation) and varied little between the soils of the different stands. The cation exchange capacity (CEC) for the organic horizon was also similar amongst the stands (0.13 ± 0.06%). The B horizons (pH of 4.99 ± 0.20) were less acidic than the organic horizons and their cation exchange capacity varied greatly from one stand to another (3.42 ± 2.85%). The concentrations of Fe + Al_{pyro} in this horizon varied between 0.22 and 4.16%. These data indicate that the majority of lichen–spruce woodlands possesses ferro-humic podzols (sites 7, 13 26, 31, 33, 38, 61, 62, 63, 70, 71, 78, 79, 101 and 102), humo-ferric podzols (sites 18, 41, 51 56, 69, 86 and 87) and occasionally humic podzols (sites 16 and 81). The C horizons of the lichen–spruce woodlands were composed entirely of sand and silt, without any trace of clay, which corresponded granulometrically to loam, loamy sand and sandy loam soils. The pHs of the C horizons were higher than the overlying horizons and varied little (5.47 ± 0.40).

Origin of the lichen–spruce woodlands

All of the studied lichen–spruce woodlands contained a wood charcoal layer at the mineral soil contact (0 cm in Tables 3 & 4)

Table 3 Showing for each lichen–spruce woodland with hummocks and hollows on the soil surface, the mean thickness of the organic matter (± standard deviation), the number of charcoal horizons in the organic matter and the distance between the charcoal horizon and the mineral soil, the mean laboratory number of the ^{14}C date (± standard deviation), the calendar date (cal. yr BP), the stand age (age of the trees), the date of the last fire deduced from fire scars, and an approximation of the date when the closed-crown forest had shifted into lichen–spruce woodland.

Stand	Mean thickness of the organic matter (cm)	Number of charcoal layers in the organic horizon	Distance between charcoal horizon and mineral soil (cm)	Laboratory number	Date (^{14}C yr BP)	Interval (cal. yr BP)	Age (cal. yr BP)	Stand age (years)	Date of the fire scar	Date of lichen-spruce woodland establishment (BP)
7	13.51 ± 7.67	2	4	ULA-367	120 ± 15	58–144	100	51	–	Before 1950*
			0	ULA-331	150 ± 15	170–224	200			
13	23.60 ± 7.55	2	15	ULA-357	5 ± 15	–	Modern	76	–	Before 1920*
			0	ULA-365	160 ± 15	169–222	200			
16	10.50 ± 3.17	2	15	ULA-359	140 ± 15	173–229	200	85	1915	1915
			0	ULA-363	280 ± 15	293–319	300			
18	17.80 ± 5.76	3	13	ULA-364	115 ± 15	58–142	100	46	1951	1951*
			7	ULA-355	175 ± 15	167–217	200			
			0	ULA-333	1390 ± 15	1286–1318	1300			
26	44.00 ± 29.82	2	11	TO-12633	40 ± 50	15–145	100	56	1937	1937*
			0	TO-12647	1150 ± 50	956–1179	1100			
31	7.80 ± 1.33	3	6	ULA-356	10 ± 15	–	Modern	61	1930	1930*
			3	ULA-358	70 ± 15	34–72	50			
			0	TO-12646	1120 ± 50	936–1199	1100			
41	24.00 ± 6.13	2	17	TO-12636	20 ± 50	23–142	100	65	1930	1930*
			0, T	TO-12635	660 ± 60	549–679	600			
			0, B	TO-12634	1640 ± 50	1409–1628	1500			
61	26.90 ± 10.28	2	13	TO-12640	Modern	–	Modern	76	–	Before 1950*
			0	TO-12641	920 ± 50	737–927	800			
62	25.20 ± 6.48	2	13	TO-12618	30 ± 40	31–138	100	65	1927	1927*
			0	TO-12617	2540 ± 40	2488–2644	2500			
70	5.60 ± 1.50	2	4	TO-12616	Modern	–	Modern	63	1931	1931*
			0	TO-12615	90 ± 40	12–148	100			
71	14.36 ± 6.83	2	5	TO-12599	Modern	–	Modern	61	1932	1932*
			0	TO-12598	1490 ± 50	1300–1424	1350			
78	10.02 ± 7.92	3	19	TO-12594	Modern	–	Modern	58	1930	1930*
			11	TO-12593	410 ± 50	421–529	500			
			0	TO-12597	400 ± 40	424–518	500			
86	12.00 ± 5.50	2	10	TO-12608	80 ± 50	11–150	100	78	1919	1919
			0	TO-12607	2650 ± 40	2732–2847	1600			

*Shift may be observed on the 1950s aerial photographs.
T, top; B, base.

Table 4 Showing for each lichen–spruce woodland with flat microtopography, the mean thickness of the organic matter (± standard deviation), the number of charcoal layers in the organic horizon and the distance between charcoal horizon and the mineral soil, the mean laboratory number of the ^{14}C date (± standard deviation), the calendar date (cal. yr BP), stand age (age of the trees), the date of the last fire deduced from fire scars, and an approximation of the date when the closed-crown forest had shifted into lichen–spruce woodland.

Stand	Mean thickness of the organic matter (cm)	Number of charcoal layers in the organic horizon	Distance between charcoal horizon and mineral soil (cm)	Laboratory number	Date (^{14}C yr BP)	Interval (cal. yr BP)	Age (cal. yr BP)	Tree age (years)	Date of the fire scar	Date of lichen-spruce woodland establishment (BP)
33	13.75 ± 5.28	1	0, T	TO-12645	Modern	–	Modern	123	1875/1972	*c.* 1900
			0, B	TO-12644	150 ± 50	163–286	200			
38	20.20 ± 8.03	2	4	ULA-332	170 ± 20	165–222	200	74	–	After 1800
			0	ULA-366	795 ± 15	685–732	700			
51	15.99 ± 4.80	3	9.5	TO-12639	Modern	–	Modern	133	–	Before 1870
			4	TO-12638	40 ± 50	15–145	100			
			0	TO-12637	380 ± 50	315–414/417–509	350/450			
56	14.66 ± 5.21	2	12	TO-12620	0 ± 40	32–83	50	153	–	Before 1800
			0	TO-12619	150 ± 40	58–155/166–284	100/200			
63	17.40 ± 3.07	2	8	TO-12596	Modern	–	Modern	93	1901	1901
			0	TO-12595	590 ± 40	535–654	600			
69	15.60 ± 4.41	2	12	ULA-325	345 ± 15	317–396	350	135	1862	1862
			0	ULA-324	325 ± 15	349–456	400			
79	16.50 ± 5.43	3	14	TO-12603	160 ± 40	60–233	150	65	1937	Before 1850
			4	TO-12604	230 ± 40	139–222/259–324	200/300			
			0	TO-12602	2350 ± 40	2310–2491	2400			
81	9.40 ± 4.36	3	12	TO-12611	10 ± 50	24–141	100	63	–	Before 1850
			8	TO-12610	200 ± 50	59–234	150			
			0	TO-12609	1060 ± 40	924–1057	1000			
87	8.40 ± 4.52	2	4.5	TO-12614	50 ± 50	14–147	100	81	–	Before 1900
			0	TO-12612	550 ± 40	512–566/585–646	550/600			
101	7.50 ± 2.05	2	3.5	TO-12606	230 ± 40	139–222/259–324	200/300	168	–	Before 1800
			0	TO-12605	1020 ± 40	898–1006	1000			
102	11.30 ± 5.02	2	7	TO-12600	Modern	–	Modern	46	1955	Before 1800
			0	TO-12601	180 ± 40	131–230	200			

T, top; B, base.

indicating the occurrence of a fire event at each stand. The charcoal contained in this horizon generally originated from old fires that were of sufficient severity to totally consume the organic material down to the mineral soil. The age of the charcoal obtained from the mineral soil contact of the 24 studied lichen–spruce woodlands generally varied between 350 and 2500 years, except for seven stands (sites 7, 13, 16, 33, 56, 70 and 102) where the charcoal was dated to between 100 and 300 years. The oldest fires to have affected the sites dated more to 700 years ago for 12 sites, from 200 to 500 years for six sites and less than 200 years for the remaining six sites.

The soil surface of the lichen–spruce woodlands in the closed-crown forest zone varies as a function of the microtopography created by the passage of fires. The microtopography can comprise humps and hollows (Table 3) or a flat surface (Table 4). In addition to the charcoal layer situated at the mineral soil contact, the lichen–spruce woodland soils typically contained charcoal layers within the organic horizon. The presence of the charcoal layers within this horizon indicates the passage of superficial or light fires that did not totally consumed the organic material. According to the stratigraphical analysis conducted on similar organic horizons situated in the PGJ, which is situated in the southern region of the study area (Payette *et al.*, 2000), the bottom charcoal layer within the organic horizon corresponds to the fire responsible for the transformation of the closed-crown forest to an open forest; i.e. at some period following the last fire to have burned down completely to the mineral layer.

Thirteen of the 24 stands (stands 7, 13, 16 18, 26, 31, 41, 61, 62, 70, 71, 78 and 86) showed hummock and hollow soil microtopographies. The hummocks were composed of ericaceous remains that can reach 1 m in height, while the hollows contained only a thin carbonized organic layer. The thickness of the organic material varied greatly, with values ranging between 7.80 ± 1.33 cm and 44.0 ± 29.82 cm; the maximum thickness measured was 1.25 m (Table 3). The charcoal layers overlying the first charcoal layer correspond to light fires that only superficially burned the soil surfaces of the lichen–spruce woodlands. Generally two charcoal layers (corresponding to the passage of two fires) were found in the organic horizon at each lichen–spruce woodland, except for three stands (stands 18, 31 and 78) where three different charcoal layers representing three fire events were observed. These fires generally dated to the 1950s and can be delineated on the aerial photographs for this time period (labelled 'modern' in Table 3). Traces of fires that burned forests much denser than the lichen–spruce woodlands studied in 2005 are easily observable on aerial photographs dating back to the 1950s. The transformation from closed-crown forest to lichen–spruce woodland dates back to the period 1900–30 for four stands, to 1930–40 for six stands and finally to around 1950 for three stands.

The surface microtopography of the 11 other lichen–spruce woodland stands (stands 33, 38, 51, 56, 63, 69, 79, 81, 87, 101 and 102) differ from the above-described stands, as their surface soil was much flatter and the ericaceous plants were uniformly distributed amongst the vegetation groundcover. Varying from 7.50 ± 2.05 to 20 ± 8.03 cm in thickness (Table 4), the organic horizons generally contained two distinct charcoal layers and sometimes three (stands 51, 79 and 81). The charcoal layers that were higher up in the organic horizon were typically more than 100 years old, with the exception of charcoal coming from three charcoal layers dated at around 50 yr BP (labelled 'modern' in Table 4). Some of the trees in stands 33, 63, 69, 79 and 102 possessed fire scars dating to 1875, 1901, 1862, 1937 and 1955. In these lichen–spruce woodlands, the timing of the transformation from closed to open forest could not be confirmed by the fire scars (except for stands 33 and 69) or by historical aerial photographs. The fire scars found at these stands (63, 79 and 102) were created by fires that occurred after the establishment of the lichen–spruce woodlands and not during the fire that was responsible for their creation. These lichen–spruce woodlands were established more than 100 years ago and, in the majority of cases, a secondary fire has superficially burned the soil surface. The transformation of closed-crown forests into lichen–spruce woodlands occurred at the start of the 19th century for four stands, with seven others being established between 1850 and 1900.

As four spruce budworm insect epidemics have affected the lichen–spruce woodlands of Québec (1880–90, 1910–16, 1950–66 and 1982–92) (Payette *et al.*, 2000; Simard & Payette, 2001; Filion *et al.*, 2006), sampled fire scars showed that several stands had burned shortly after a spruce budworm epidemic. For example, certain stands (stands 13, 16 and 86) burned shortly after a spruce budworm epidemic that occurred between 1910 and 1916 and others (stands 7, 18, 61 and 102) burned shortly after the 1950–66 epidemic.

Lichen–spruce woodland vegetation

Significant relationships were found between relative frequency of *C. stellaris*, *B. glandulosa*, *K. angustifolia*, *R. groenlandicum* and latitude (Fig. 3). The relative frequencies of *C. stellaris*, *B. glandulosa* and *R. groenlandicum* were higher in the northernmost lichen–spruce woodlands ($r = 0.59$, 0.69 and 0.53, respectively) and relative frequency of *K. angustifolia* was higher in the southernmost lichen–spruce woodlands ($r = -0.64$). No relationship was found between the abundance of *C. mitis*, *C. rangiferina* and latitude ($P > 0.05$). In the lichen–spruce woodlands, there was a strong association between relative frequencies of *C. stellaris*, *B. glandulosa* and altitude ($r = 0.48$ and 0.54, respectively). The relative frequency of these species was higher in the lichen–spruce woodlands located above 500 m of altitude. The abundance of *C. stellaris* increased with stand age ($r = 0.44$) as the abundance of *C. rangiferina* ($r = -0.61$) decreased in the lichen–spruce woodlands that were more than 100 years old. The relative frequencies of *C. mitis*, *B. glandulosa*, *K. angustifolia* and *R. groenlandicum* were not related to stand age. A significant relationship was identified between the abundance of *C. stellaris*, *B. glandulosa* and a decrease of the mean thickness of the organic matter ($r = -0.44$ and -0.49, respectively). The relative frequency of *K. angustifolia* increases with the mean thickness of the organic matter ($r = 0.50$). Finally, *R. groenlandicum* was found in the majority of the lichen–spruce woodlands of the closed-crown forest no matter what the thickness of the organic matter.

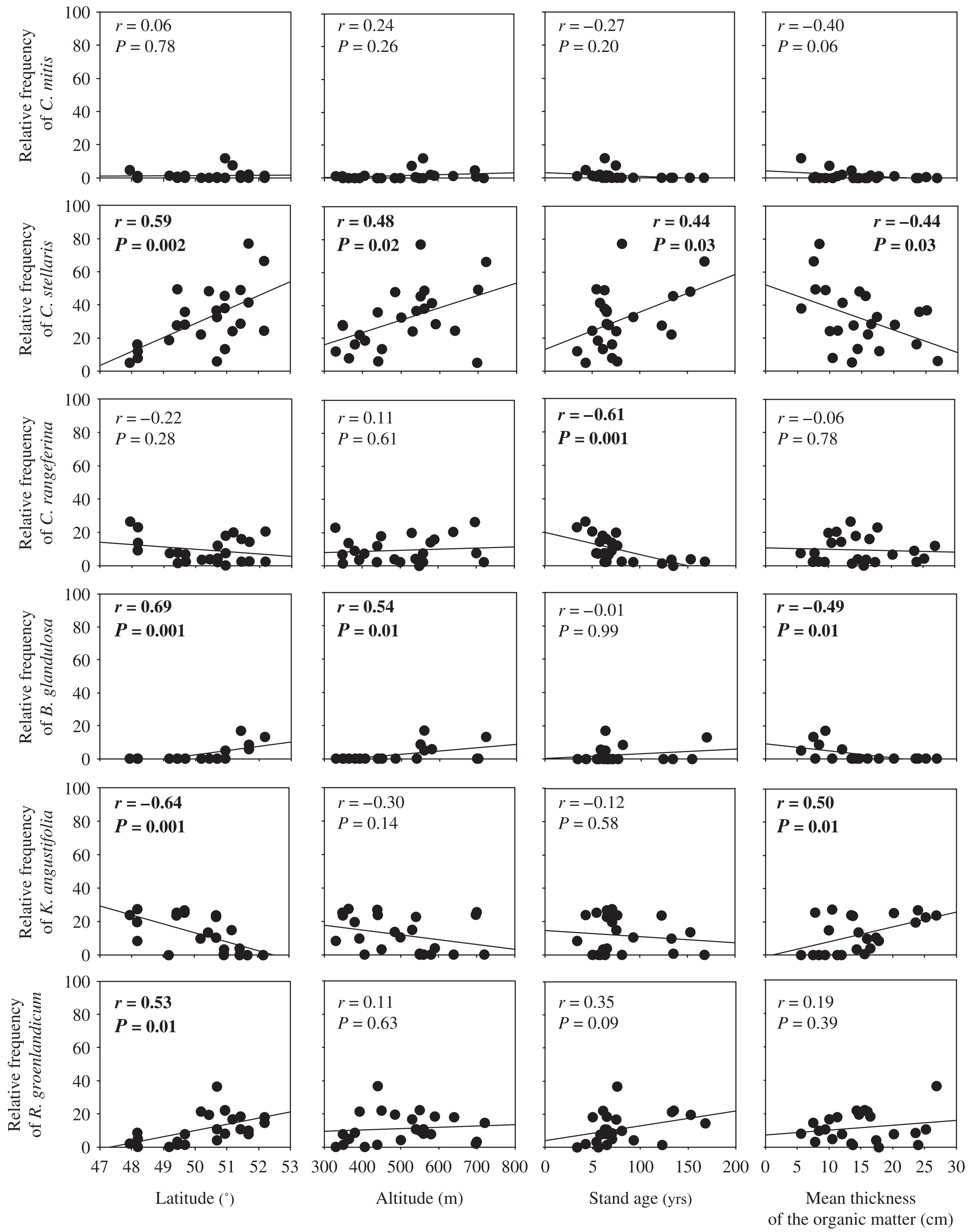

Figure 3 Relationship between latitude, altitude, stand age, mean thickness of the organic matter and relative frequency of *Cladonia mitis*, *Cladonia stellaris*, *Cladonia rangiferina*, *Betula glandulosa*, *Kalmia angustifolia* and *Rhododendron groenlandicum* in the lichen–spruce woodlands of the closed-crown forest zone. Values of r and P are in bold when $P < 0.05$ ($n = 24$ stands for each regression except for the mean thickness of the organic matter where $n = 23$ (outlier when $\times = 44$ cm).

DISCUSSION

The vegetation zones of the boreal forest acquired their current configuration over the last 5000 years (Davis, 1981; Prentice *et al*., 1991). Following the last deglaciation and the concurrent climate warming, vegetation species migrated northwards. Given the southern position of the closed-crown boreal forest zone, the surface area of the closed-crown forest (spruce–moss forest) may expand towards the north with current and future climate warming (Houghton *et al.*, 2001). However, an inverse trend is currently being observed in Québec: the lichen–spruce woodlands, a forest type typical of the subarctic, have actually been expanding within the closed-crown forest zone since at least the end of the 19th century (Girard *et al.*, 2008).

In the boreal forest, ecological succession is influenced by natural disturbances (fire and insect epidemics) (Heinselman, 1981; Johnson, 1992; Payette, 1992; Bergeron, 1998). Following a fire, the ecological succession generally leads towards a dense forest that resembles the pre-fire stand. Similar to other studies, our research indicates that ecological succession can lead to the establishment of an ecosystem that is different from the one that existed before the disturbance (Paine *et al.*, 1998; Payette *et al.*, 2000, 2001; Payette & Delwaide, 2003; Jasinski & Payette, 2005; Girard *et al.*, 2008). The occurrence of successive disturbances over a short time interval can lead to a drastic reduction in the natural regeneration of black spruce stands, resulting in the creation of lichen–spruce woodlands instead of dense forests. These ecosystems appear to be resilient to disturbances and relatively stable through time, as no transformations back to closed-crown forests have been observed to date (Jasinski & Payette, 2005). In our study, three things were found to be responsible for the transformation of the closed-crown forest into lichen–spruce woodlands: light fires, successive fires and the occurrence of a spruce budworm epidemic followed by a fire.

At the scale of the Holocene, the degradation of the closed-crown forest into a lichen–spruce woodland is a relatively recent phenomenon within the closed boreal forest (Jasinski & Payette, 2005). The physiognomy of humps and hollows on the soil surface of a large number of lichen–spruce woodlands is characteristic of the passage of a light fire. Light fires leave an important quantity of soil organic material (Johnstone & Kasischke, 2005; Jayen *et al.*, 2006; Kemball *et al.*, 2006; Lavoie *et al.*, 2007; Lecomte *et al.*, 2006). This organic material, composed of partially or non-decomposed lichens and mosses, forms a germination bed that is unfavourable for black spruce seeds (Johnstone & Kasischke, 2005; Jayen *et al.*, 2006). Black spruce regenerates best on mineral soil, conditions that are generally created following a severe fire (Vincent, 1965; Viereck & Johnston, 1990). Several stands that are currently occupied by lichen–spruce woodlands have not burned for over 1000 years. Since that time, the forest stands developed a thick organic horizon that recent fires could only marginally burn, thus creating humps and hollows with the residual organic matter. With the occurrence of additional fire events, the ground surfaces of the lichen–spruce woodlands have become flatter and have almost eliminated the humps of organic material. The presence of charcoal layers in the organic matter of all the studied lichen–spruce woodlands suggests that light fires have been frequent since the end of the 19th century. Most of the natural fires probably occurred in the spring time or at the start of summer when the litter layer is still frozen or too thick to burn completely. Also, a thick lichen mat on the ground decreases soil temperature and may delay spring thawing (Kershaw & Rouse, 1971). Climate warming has also made it more likely for fires to occur early in the spring (Westerling *et al.*, 2006), thus favouring light fires, the accumulation of organic material and, consequently, an expansion of the lichen–spruce woodlands within the heart of the closed-crown forest zone.

Several lichen–spruce woodlands in the closed-crown forest zone possessed traces of successive fires, i.e. several fires occurring within a short temporal interval. The radiocarbon dating of wood charcoal buried within the organic matter indicates that several stands burned at least twice in less than 50 years. In addition to being superficial, these fires occurred within a time interval that was too short for black spruce to reach maturity and produce adequate seeds for regeneration (Viereck & Johnston, 1990). The transformation of a moss forest into a lichen–spruce woodland can equally be caused by the compounded disturbances of a spruce budworm infestation followed by a fire (Holling, 1992; Payette *et al.*, 2000; Girard *et al.*, 2008). Indeed, if an epidemic is followed shortly after by a fire, the production of seeds will be inadequate to ensure a dense post-fire regeneration of the stand. The combination of these two disturbances constitutes the third cause for the transformation of the closed-crown forest into a lichen–spruce woodland. Combined insect infestation and fire disturbance events have created several lichen–spruce woodlands within the closed-crown forest zone of eastern Canada.

Most of the studied lichen–spruce woodlands established following fires that occurred over the last 100 years. The analysis of aerial photographs taken in the 1950s allowed us to directly observe the transformation of closed-crown forests into lichen–spruce woodlands by observing the density of burned stands on the photographs before, during and after the disturbances (also see Girard *et al.*, 2008). The species composition of the groundcover vegetation also confirms the recent establishment of lichen–spruce woodlands within the closed-crown forest zone. For the lichen–spruce woodlands formed in the last 100 years, several species that are typically dominant on the forest floor of the closed-crown forest were found, including *Polytrichum* sp., *Amelanchier* sp., *Abies balsamea*, *Kalmia angustifolia* and *Pleurozium schreberi* (data not shown). These plants are the vestiges of the old forest and indicate that the stands were denser before the last fire.

Dwarf birch, which is a widespread subarctic species, colonizes the ground layer of the lichen–spruce woodlands in the PGJ (47°30′ N) and the lichen–spruce woodlands situated north of 51° N. The populations of dwarf birch in the PGJ reflect conditions colder than those of today. Widespread occurrence of lichen–spruce woodlands in this area favoured the maintenance of dwarf birch populations in this region for the past several thousand years (Lavoie & Richard, 2000; Jasinski & Payette, 2005). Extreme conditions like summer frosts, water deficiency and low tree density as found in lichen–spruce woodlands create favourable conditions for the expansion and regeneration of dwarf birch. However, the colonization of the lichen–spruce woodlands within the closed-crown forest zone by dwarf birch indicates that its distribution range is expanding towards the southern boreal forest. This southward expansion is favoured by the creation of newly open areas such as the lichen–spruce woodlands and the conditions created by them.

The succession of lichen species also suggests a recent degradation of the closed-crown forest. A slow succession of lichen species occurs on soil surfaces following a fire and begins with *C. mitis*, followed by *C. stellaris* (Morneau & Payette, 1989). This succession was also observed in the studied lichen–spruce woodlands. The groundcover of stands established over 100 years ago were gradually dominated by *C. mitis* and then, by *C. stellaris*.

CONCLUSION

We used complementary techniques including the radiocarbon dating of wood charcoal, the dating of fire scars and the analysis of aerial photographs from the 1950s to reconstruct the timing and disturbance factors responsible for the transformation of dense forests into open forests. The transformation of closed-crown forests into woodlands appears to be a recent phenomenon within the closed-crown forest zone, produced primarily following a suite of successive disturbances. Three important factors causing the transformation of the closed-crown forests into lichen–spruce woodlands were identified: light fires, successive fires and the occurrence of a spruce budworm epidemic followed by a fire. We did not observe any cases of a moss forest transforming into a lichen–spruce woodland following a disturbance.

Our first research hypothesis stipulated that successive fires would be the primary factor causing the transformation of the closed-crown forest. While successive fires are indeed one of the causes, the closed-crown forest was found to be degraded principally by the passage of recent light fires. These light fires leave a considerable organic mass on the ground, thus creating unfavourable microsites for the germination of black spruce seeds, consequently favouring the creation of lichen–spruce woodlands. The physiognomy of the hummocks and hollows of the soil surface of the spruce forests also indicates that these forests have not burned for a long time (sometimes more than 1000 years) before the occurrence of the light fires. Several stands were burned at the moment of, or shortly after, a spruce budworm epidemic, thus confirming our second research hypothesis. A short time interval between these two disturbances does not allow for a strong natural regeneration, as the spruce does not have adequate time to reach sexual maturity and produce sufficient seeds following the occurrence of the first disturbance.

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