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Comparing soil profiles of adjacent forest stands with contrasting tree densities: lichen woodlands vs. black spruce–feathermoss stands in the continuous boreal forest

Rock Ouimet, Jean-François Boucher, Pascal Tremblay, and Daniel Lord

Abstract: We studied mature and adjacent open lichen–spruce woodlands (LWs) and closed-canopy spruce–feathermoss stands (FMs) growing under similar edaphic conditions in the continuous boreal forest zone in Quebec (Canada). A total of six pairs of stands were investigated by profile sampling. Stem density, basal area, and biomass were about four times greater in FMs than in LWs on an area basis. In the humus layer, total stocks of C and N and of exchangeable K, Ca, Mg, Al, and Na were 1.4–2.3 times larger in FM than in LW soils. The first 30 cm and the first metre of mineral soils in LWs and FMs displayed similar available nutrient pools except for total C stocks, which were more than twice as large in FM as in LW soils in these soil layers. For the whole profile, total stocks of C and N and stocks of exchangeable Ca and Mg were 1.3–2.6 times larger in FM than in LW soils. These results highlight the low intrinsic fertility of LW soils, primarily due to the humus layer, but also the importance of the biological control of C, N, and mineral nutrients in these boreal soils.

Key words: lichen woodland, *Picea mariana*, podzols, boreal forest, soil fertility, carbon, nutrient pools.

Résumé : Nous avons étudié des pessières à lichens (LW) ouvertes et des pessières à mousses (FM) fermées adjacentes et croissant dans des conditions édaphiques semblables en forêt boréale au Québec (Canada). Les profils de sol de 6 paires de peuplements ont été échantillonnés. Sur une base surfacique, la densité des tiges, la surface terrière et la biomasse dans les FM étaient environ 4 fois celles des LW. Dans l'humus des FM, les stocks de C et de N totaux et ceux de K, Ca, Mg, Al et Na échangeables étaient de 1.4 à 2.3 fois ceux des LW. Dans les 30 premiers centimètres et le premier mètre de sol minéral des deux types de peuplements, les réserves nutritives étaient similaires, sauf le stock de C total dans les FM qui était plus du double de celui des LW. Dans le profil de sol entier des FM, les stocks de C et de N totaux et ceux de Ca et Mg échangeables étaient de 1.3 à 2.6 fois ceux des LW. Ces résultats démontrent la faible fertilité intrinsèque des sols des LW, principalement à cause de l'humus, et l'importance du contrôle biologique du C, du N et des éléments minéraux dans ces sols boréaux.

Mots-clés : pessière à lichens, *Picea mariana*, podzols, forêt boréale, fertilité du sol, carbone, stocks d'éléments nutritifs.

Introduction

The processes leading to the transition from a closed-canopy black spruce [*Picea mariana* (Mill.) B.S.P.] feathermoss (FM) stand to an open lichen woodland (LW) in the boreal forest are well documented: this change in stand density is mainly driven by lasting impacts of successive disturbances (mainly fire and spruce budworm (*Choristoneura fumiferana* Clemens) outbreaks) occurring during the Holocene and the arising regeneration failure caused by the lack of a viable seed bank, increased frost frequency, or adequate seedbeds (Payette et al. 2000; Gagnon and Morin 2001; Brown and Johnstone 2012; Côté et al. 2014; Payette and Delwaide 2018). LWs are characterized by patches of open forest composed mainly of black spruce and jack pine (*Pinus banksiana* Lamb.), having <25% of canopy cover, and where >40% of the ground layer is covered by terrestrial lichens (*Cladonia* spp.).

R. Ouimet. Ministère des Forêts, de la Faune et des Parcs du Québec, Direction de la recherche forestière, Complexe scientifique, 2700 rue Einstein, Québec, QC G1P 3W8, Canada.

J.-F. Boucher, P. Tremblay, and D. Lord. Département des Sciences fondamentales, Université du Québec à Chicoutimi, 555 boulevard de l'Université, Saguenay, QC G7H 2B1, Canada.

Corresponding author: Rock Ouimet (email: rock.ouimet@mffp.gouv.qc.ca).

The LW and similar types of open woodlands represent a nonnegligible part of the world's boreal forests. In Canada, open woodlands cover several mega hectares (Rowe 1972; Boucher et al. 2012; Canadian Council of Forest Ministers 2013). More specifically in Quebec, open woodlands cover 1.6 million ha, among which LWs are a dominant type (Boucher et al. 2012). Neighbouring FMs and LWs also are a common sight in the closed-canopy boreal forest region in Quebec and elsewhere in Canada, as LWs appear to be trapped in this alternative stable state ever since their creation (Morneau and Payette 1989; Jasinski and Payette 2005; Payette and Delwaide 2018). Because of their geographical proximity, FMs and LWs share the same regional climate and physical characteristics such as surficial deposit, drainage, slope, and aspect (MFFP, 3rd decennial forest inventory). Within the closed-canopy boreal forest zone in Quebec, LWs have even expanded by 9% to the detriment of FM stands over the last 50 yr (Girard et al. 2008). This phenomenon appears irreversible without human intervention (Mansuy et al. 2013).

Forest management objectives aim for these areas to be fully reforested to maintain the annual allowable cut for some regions in the boreal forest (Bureau du forestier en chef 2013). Knowing that LW sites may once have supported denser FM stands (Girard et al. 2009; Côté et al. 2013), one would expect these "neighbours" to have comparable soil fertility levels, that is, a comparable potential for the soil to sustain tree growth. In addition, the persistence of these low-density forested areas for more than 50 yr makes them eligible for afforestation projects in accordance with article 3.3 of the Kyoto Protocol. Therefore, LW afforestation in the province of Quebec has generated great interest as an opportunity for C sequestration (Boucher et al. 2012).

LWs are frequently — if not always — described as "poor", unproductive, and of relatively low economic potential, mostly because of their low tree density. This assessment ignores their disturbance history and the fact that these areas may have supported much more tree biomass a few decades ago (Côté et al. 2013). On the basis of standing wood volume at maturity and site quality index, LWs appear less productive than the neighbouring FM stands (Dufour et al. 2016). However, these authors found that the site potential of a certain proportion of LWs was equivalent to that of adjacent FM stands. Considering the dynamics of LW creation, one must assume that current stand density and volume is not an adequate indicator of the potential of LWs to grow fully stocked forest stands, and that other variables such as soil fertility must be considered (Dufour et al. 2016). Until now, only a few studies have presented data on soil fertility indicators or vegetation nutritional status (Girard 2004; Gonzalez et al. 2013; Tremblay et al. 2013; Hébert et al. 2014) of managed and unmanaged LWs. Vegetation nutritional status, as measured by foliar concentrations of tree species (van den Driessche 1974), is generally used in forestry because no soil fertility standards exist for resilient and slow-growing tree species such as black spruce. None of the studies mentioned above firmly concluded that soil fertility levels differed between LWs and FMs, nor did they fully measure the soil nutrient pools. This knowledge gap needs to be filled before conclusions can be drawn about the site potential of LWs to become FM stands.

The main objective of this study was to quantify LW and FM soil fertility as measured by their soil element pools and vegetation nutritional status, using paired stands sharing the same geomorphological characteristics. Sites were selected so as to have comparable species composition, soil type and age since the last-replacing disturbance. The experiment was designed to test the hypothesis that soil element pools do not differ between LWs and FMs.

Materials and Methods

Site description

The experiment was carried out on two sites (Péribonka and Mistassibi) at the junction of the spruce–moss and the balsam fir–white birch bioclimatic domains of the boreal forest north of Lac Saint-Jean, Quebec, Canada (Fig. 1). Mean annual temperature for this region (1971–2000) was 0 °C (±1.3 °C), and mean annual precipitation was 960 mm (33% as snow). Péribonka and Mistassibi comprised four and two experimental blocks (statistical repetitions), respectively, each carefully selected on the basis of the proximity of a pure, high-density FM stand (≥60% tree crown cover) and a LW (<25% tree crown cover) presenting the same topographical and geomorphological characteristics (aspect, slope, surface deposit, and drainage). Both stand types in each block had to be over 70 yr old and show the same age (±10 yr at stump height) to ensure they originated from the same major disturbance. Stand attributes are depicted in Table 1; they are based on stand survey of the experimental sites described in fuller detail in Tremblay et al. (2013). Site quality index, assessed as height of 50-yr-old dominant trees, was determined using equations of Pothier and Savard (1998).

All the selected FM and LW are dominated by black spruce (>75% of basal area) with jack pine, white birch (*Betula papyrifera* Marshall), and trembling aspen (*Populus tremuloides* Michx.) as minor, companion species. The understory includes black spruce advance regeneration, ericaceous shrubs (sheep laurel (*Kalmia angustifolia* L.), and common Labrador tea (*Rhododendron groenlandicum* (Oeder) K.A. Kron and Judd)), and a few *Salix* sp. A dense mat of mosses (*Pleurozium shreberi* (Brid.) Mitt and *Ptillium crista-castrensis* (Hewd.) De Not) covers the ground of FMs. LWs have an important lichen ground cover (>40%) dominated by *Cladonia* spp., and the same moss species found in FMs. Soils are moderately mounded, very well-drained, humo-ferric Orthic Podzols or humo-ferric Ortstein Podzols (Soil Classification Working Group 1998) derived from glacial till or fluvio-glacial

Fig. 1. Location of the six study blocks in Quebec, Canada. The black line represents the northern limit of detailed forest mapping (Ministère des Forêts, de la Faune et des Parcs du Québec, 3rd decennial forest inventory (1991–2003)).
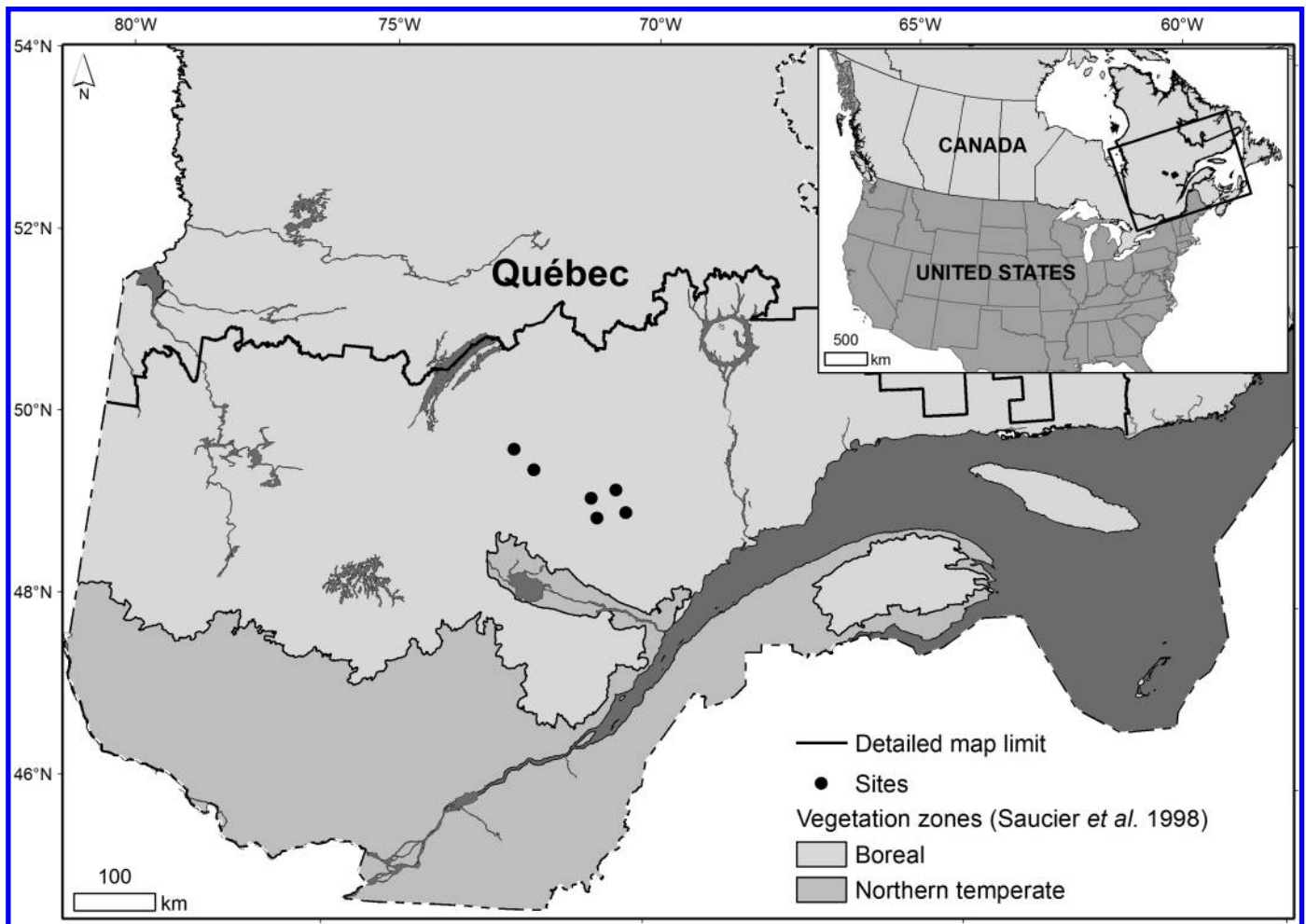
deposits with the regional Archean gneissic lithology. Soil texture is coarse to fine sand in all cases. The coarse fragment (diameter >5 cm) fraction accounts for 0% to 25% of the sampled profiles.

Soil sampling and analysis

In each stand ($n = 12$), a 1 m^3 soil pit was dug out in a representative area in summer 2005 and 2006. Each soil horizon was carefully delimited. Its thickness was measured (to the nearest cm) at three different positions along the profiles and averaged. Color, texture, presence of induration, coarse fragment size (>5 cm), distribution, and proportion of soil pit volume were also noted. Table 2 shows a sample soil profile description for experimental block "Péribonka 4". After these observations and measurements, the soil from each horizon was sampled from the bottom to the top of the profile by inserting a spade at the base of each horizon and gathering the whole horizon with a trowel as shown in Lawrence et al. (2016). A volumetric hammer core sampler (5 cm diameter) was used to take duplicate

volumetric samples of most soil horizons to determine soil bulk density.

In addition, the organic soil layers (L, F, and H) were measured and sampled. To do so, a 0.5 m^2 area adjacent to the face of the soil pit was carefully protected from compaction. Thickness of the different organic layers was measured at three different places (to the nearest cm) and averaged. The whole humus layer was sampled using a volumetric core sampler (at least two samples per soil pit). All the samples were immediately placed in a cooler for the rest of the day before being transferred to the freezer until laboratory processing.

In the laboratory, soil samples were air-dried, lightly milled to break up soil clumps, and sieved through a 2 mm mesh. Only the fine fraction was processed to determine soil properties. Soil pH was measured with water using a 1:2.5 (*w:w*) soil solution. Exchangeable cations (K, Ca, Mg, Mn, Na, Fe, and Al) were extracted with unbuffered NH_4Cl (1 mol L^{-1}, 12 h) solution and measured by inductively coupled plasma emission spectrophotometry (ICP-AES) to determine exchangeable concentrations.

Table 1. Attributes of lichen–spruce woodland (LW) and spruce–feathermoss (FM) stands.

Stand type	Block	Stem density (stem ha^{-1})	Basal area (m^2 ha^{-1})	Stem biomass (Mg ha^{-1})	Height[a] (m)	DBH[a] (cm)	Site quality index	Surface deposit Type[b]	Thickness (cm)	Humus thickness (cm)
FM	Péribonka 1	1375	31.0	149.6	18.7	26.2	16.5	2	>100	14
	Péribonka 2	2025	39.3	186.4	17.9	23.8	15.8	1	>100	32
	Péribonka 3	2325	36.0	162.4	16.5	21.3	14.6	1	>100	14
	Péribonka 4	2100	36.5	160.5	18.2	22.9	16.1	1	>100	30
	Mistassibi 1	2250	39.3	180.0	18.1	20.1	16.0	1	50–100	22
	Mistassibi 2	1300	33.5	163.5	19.1	25.5	16.8	3	50–100	11
LW	Péribonka 1	250	2.7	10.6	10.0	13.5	9.0	2	>100	6
	Péribonka 2	200	7.3	25.4	14.2	21.1	12.6	1	>100	17
	Péribonka 3	450	10.3	37.3	13.9	23.8	12.4	1	>100	13
	Péribonka 4	525	7.3	31.3	13.3	21.2	11.9	1	>100	6
	Mistassibi 1	775	10.8	40.9	12.7	18.6	11.3	1	50–100	15
	Mistassibi 2	750	13.5	50.2	17.5	22.1	13.8	3	50–100	5
LW average		492	8.6	32.6	13.5	20.1	16.1	—	—	10.3
FM average		1896	35.9	167.0	17.7	23.3	12.0	—	—	20.5
Stand type difference (P value)		0.001	<0.001	<0.001	0.010	0.065	0.003	—	—	0.028

Note: Data are from the field inventory. Biomass was computed using equations from Lambert et al. (2005). Site quality index was computed using the equations from Pothier and Savard (1998). Stand data are for merchantable trees (diameter at breast height (DBH, measured at a height of 1.3 m) > 9.0 cm).

[a]For dominant trees.

[b]Surface deposit types: 1, undifferenciated glacial till; 2, glacio-fluvial outwash; and 3, glacio-fluvial.

A subsample of the fine fraction was further ground to 250 μm for total C and N determination. Organic C was measured by dry combustion using a LECO CR-412 (LECO Corporation, St-Joseph, MI, USA). Total (Kjeldahl) N was determined by hot acid digestion (Bremner and Mulvaney 1982). The C/N ratio was calculated with the two concentration values of organic C and total N.

The humus and mineral volumetric samples were air-dried and weighed. A 10 g subsample was oven-dried at 105 °C for 2 h and weighed again to determine water content. The volumetric samples were lightly milled and sieved through a 2 mm mesh to separate the coarse and fine soil fractions and record mass of the fine fraction. A 10 g subsample of the fine fraction was weighed, oven-dried at 105 °C for 2 h and weighed again to determine remaining soil water content. A subsample of the fine fraction was further ground to 250 μm for organic C determination (LECO Corporation, St. Joseph, MI, USA).

Vegetation nutritional status

The nutritional status of black spruce, sheep laurel, and common Labrador tea was also investigated. Foliar samples of the three species were harvested in five randomly selected plots in each stand in September 2006. For sheep laurel and common Labrador tea, the whole foliar biomass of two to three different stems was sampled in each plot. For black spruce, foliar samples were collected in the same plot as the two other plant species; only the current-year and 1-yr-old foliage were sampled on two different individuals. Once harvested,

the samples were stored in a cooler for the rest of the day then placed in a freezer until processing. In the laboratory, foliar samples were oven-dried at 65 °C for 48 h, after which foliage was carefully separated from twigs. The five samples from each species were then pooled and finely ground, and a subsample was used for chemical analysis. Following Kjeldahl digestion (Bremner and Mulvaney 1982), N was analyzed colorimetrically by spectrophotometry (Quickchem 8000, Lachat Instruments, Loveland, CO, USA). Total P, K, Ca, Mg, and Mn were determined by ICP-AES after digestion with concentrated H_2SO_4.

Element stock calculation

Organic matter content (OM, in Mg ha^{-1}) of the humus layer was calculated using eq. 1:

$$(1) \quad OM = \frac{M}{A} \times 100$$

where OM is the organic matter stock (Mg ha^{-1}), M is the dry sample mass (g), and A is the core sampling area (cm^2).

Element content in the humus layer was calculated using eq. 2:

$$(2) \quad Q_H = 10^{-3} \times \sum_{h=1}^{3} \left([x] \times OM \right)$$

where Q_H is the element content in the humus (kg ha^{-1}), h is the humus horizon identification (L, F, and H), and $[x]$ is the element concentration in horizon h (mg kg^{-1}).

Table 2. Soil profile description of the Péribonka 4th experimental block.

Horizon	Depth (cm)	Description
Péribonka 4 LW		
LFH	10–0	Mor; poorly decomposed organic matter (lichen); very abundant fine and medium roots; acidic
Ae	0–7	Fine sand; gray (10YR 5/1D); abrupt wavy boundary; many fine roots; acidic
Bf1cj	7–14	Fine sand; dark reddish brown (5YR 3/3D); lightly cemented; few fine roots; acidic
Bf2	14–29	Fine sand; dark-olive brown (2.5Y 3/3D); many fine roots; acidic
Bf3	29–49	Medium sand; olive (5Y 4/3D); few fine roots; acidic
C	49–99	Medium sand; gray (5Y 5/1D)
Péribonka 4 FM		
LFH	30–0	Mor; poorly decomposed organic matter (mosses); very abundant fine and medium roots; acidic
Ae	0–14	Fine sand; grayish brown (10YR 5/2D); abrupt wavy boundary; acidic
Bf1	14–22	Fine loamy sand; reddish black (2.5YR 2.5/1D); acidic
Bf2c	22–40	Medium sand; dark reddish brown (5YR 3/43D); strongly cemented; acidic
Bf3c	40–55	Coarse sand; dark brown (7.5YR 3/3D); strongly cemented; acidic
C	55–99	Coarse sand; dark brown (10YR 3/3D); acidic

Element content in the mineral soil was calculated using eq. 3:

$$(3) \quad Q_m = 0.1 \times \sum_{h=1}^{z} \left([x]_h \times (D_b)_h \times (E_e)_h \right)$$

where Q_m is the element content in the mineral soil (kg ha^{-1}), h is the horizon number (varies from 1 to z from top to bottom), $[x]$ is the element concentration in horizon h (mg kg^{-1}) on a dry basis, D_b is the bulk density of horizon h (g cm^{-3}), and E_e is the effective thickness of horizon h (cm), that is, the corrected thickness of soil without fragments having a diameter larger than 2 mm.

Effective horizon thickness was calculated using eq. 4:

$$(4) \quad E_{eh} = E_h(1 - fm)$$

where E_{eh} is the effective thickness of horizon h (cm), E_h is the measured thickness of horizon h (cm), and fm is the coarse fraction in the volumetric sample (>2 mm) (%/100).

The bulk density of all individual soil horizons was estimated through a quantitative relationship by site obtained from the D_b and C concentrations of the volumetric mineral soil samples (see the "Statistical analyses" section below). The Q_m was evaluated for two mineral soil depths (30 and 100 cm). Element stocks in individual horizons were summed to represent the first 30 or 100 cm (measured thickness) of mineral soil. When needed, only a fraction of the last horizon was considered to estimate the value for the first 30 cm of mineral soil. For example, if the Ae, B1, and B2 horizons were 15, 10, and 10 cm thick, respectively, only 5 cm of the B2 horizon was included in the nutrient stock calculations.

Statistical analyses

Bulk density (D_b) of the mineral soil was modelled using the volumetric C concentration (log values) of soil samples to build a generalized least squares model that allows correction of heterogeneity of variances (Zuur et al. 2009). Site and stand type were also included in the model as fixed effects because the goal was to model D_b for these sites only. The model for which the variance function structure had the lowest Akaike information criterion (AIC) scores was selected. The variance function structure was best adjusted by allowing the variance to change according to block and stand type.

The effect of stand type on soil contents, other soil properties, and foliar nutrient concentrations of each

Table 3. Modelled relationship between bulk density (D_b, g cm^{-3}) and total organic carbon (C, g kg^{-1}) concentration in soils for the studied sites ($r^2 = 0.66$; residual standard error = 0.156 g cm^{-3}).

Parameter	Value	Std. error	t value	P value
Intercept	1.532	0.042	36.2	<0.001
Site (Péribonka)	−0.072	0.041	−1.7	0.084
Stand type (FM)	0.084	0.042	2.0	0.049
log(C)	−0.144	0.013	−10.8	<0.001

plant species was analyzed with a one-way analysis of variance using a linear mixed model that included stand type as a fixed effect. Individual blocks at each site were considered as random effects. The standardized residuals of these models were then plotted against all variables to detect possible heterogeneity or trends in their variances. If present, the variance heterogeneity or trend was corrected by adjusting the variance function structure (Zuur et al. 2009). The models for which the variance function structures had the lowest AIC scores were always selected. For all analyses, assumptions of variance homoscedasticity and normality of sample distributions were verified by plotting and analyzing residuals. Adjusted (predicted) means were computed for reporting using R's lsmeans package (Lenth 2016). The analyses were performed with the nlme package (Pinheiro et al. 2017) in version 3.4.1 of the R software environment (R Core Team 2017).

Results

Stand characteristics

Site characterization resulting from ecoforestry map analysis and the field inventory of the studied sites showed that FM and LW stands in each given block had equivalent species composition, age, and geomorphological attributes (surface deposit type, thickness, slope, aspect, and drainage). In addition, soil profile characterization and sampling confirmed that physical soil properties such as texture and stoniness (≥5 cm) were homogenous in each block. Despite these similarities in edaphic variables, and as expected for stands of contrasting regeneration dynamics after disturbance (Jasinski and Payette 2005; Girard et al. 2009), the LW and FM stand types were very dissimilar with respect to merchantable stem density, basal area, biomass, height, site quality index, and humus thickness ($P \leq 0.028$; Table 1). On average, stem density, basal area, and biomass were about four times greater in FMs than in LWs on an area basis. On average, site quality index was 4.1 m higher in FMs than in LWs ($P = 0.003$). The forest floor (humus) also was twice as thick in FMs as in LWs ($P = 0.028$). Height and diameter at breast height (DBH) of dominant trees were also greater in FMs, with average differences of 4.2 m in height (30%) and 3.2 cm (16%) in DBH ($P \leq 0.065$).

Fig. 2. Bulk density (D_b) as a function of total organic carbon concentration in soil, by stand type (open lichen woodland (LW) and closed black spruce–feathermoss (FM)), at the Mistassibi and Péribonka sites. Lines show predicted values according to the model presented in Table 3.
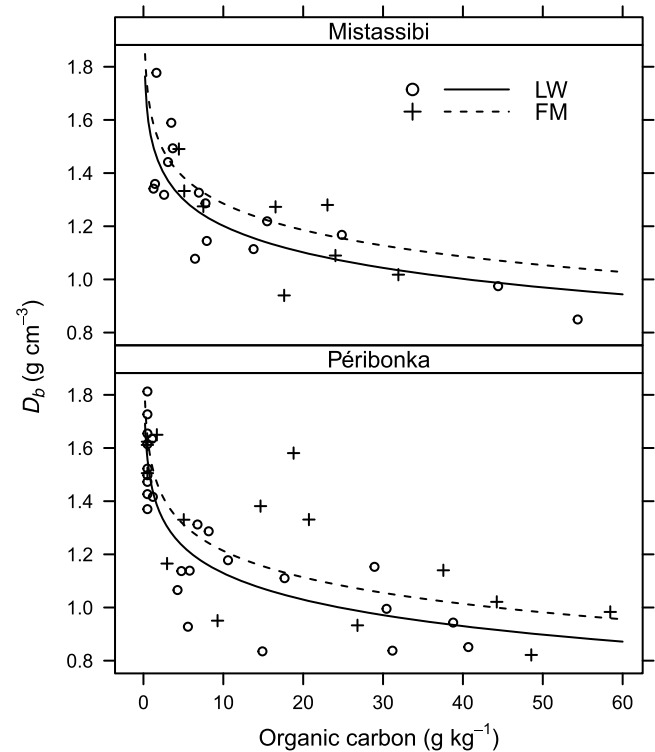
Soil properties

Soil bulk density (D_b) was strongly related to soil C concentration and, to a lesser extent, stand type ($P \leq 0.049$; Table 3). There was only a slight difference in D_b values between the two site types. The model's low residual standard error (0.156 g cm^{-3}) allowed a reasonable extrapolation of D_b for individual horizons in the profiles sampled in both site types (Fig. 2).

Soil pH tended to be 0.17 ± 0.1 unit lower in FMs than in LWs, and this difference was apparent both in the humus and mineral soil layers ($P \leq 0.091$; Fig. 3). Soil C/N ratio varied according to both stand type and depth ($P_{\text{stand type} \times \text{soil depth}} < 0.001$). The C/N ratio tended to remain stable at all depths in LW soils (mean: approximately 24 ± 0.11), but it tended to increase with depth in FM soils (from 23 to 36 ± 0.34). Humus C/N ratios were similar in both stand types (70 ± 5; $P = 0.242$).

Soil element content

The analysis of element contents in the humus layer showed that LWs and adjacent FMs had different stocks of total C and N as well as of exchangeable K, Ca, Mg, Al, and Na ($P \leq 0.072$; Table 4). On average, stocks were 1.4–2.3 times larger in FM than in LW soils.

In the first 30 cm of mineral soil, total C and exchangeable Al stocks were about 2.7 times larger in FM than in

Fig. 3. Soil pH (left) and C/N values (right) at various depths, by stand type (open lichen woodland (LW) and closed black spruce–feathermoss (FM)). Curves show mean (adjusted) values. The points above the line at depth 0 show mean (adjusted) values for the humus layer. Differences between stand types were significant both in the humus and mineral soil ($P = 0.048$ and 0.091, respectively, with respect to pH; and $P = 0.242$ and 0.028, respectively, with respect to C/N ratio).
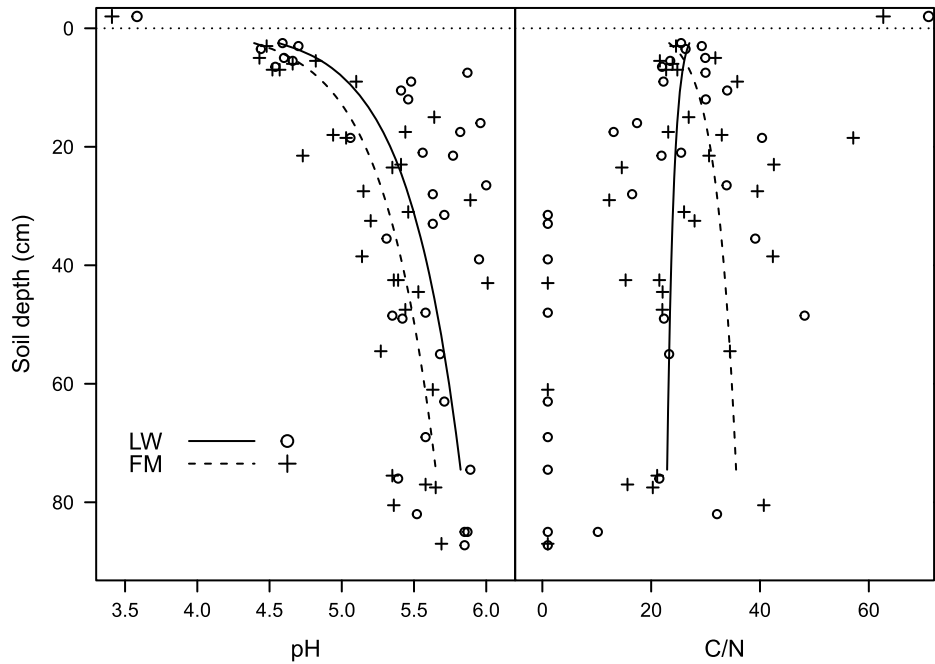

Table 4. Comparison of element stocks between open lichen woodland (LW) and adjacent closed black spruce–feathermoss (FM) stands for the humus layer, the first 30 cm of mineral soil, the first 1 m of mineral soil, and the whole profile (humus + 1 m of mineral soil).

Soil layer	Stand type	C (Mg ha^{-1})	N (kg ha^{-1})	K (kg ha^{-1})	Ca (kg ha^{-1})	Mg (kg ha^{-1})	Mn (kg ha^{-1})	Fe (kg ha^{-1})	Al (kg ha^{-1})	Na (kg ha^{-1})
Humus	LW	43.6 (11.2)	724 (181)	38 (16)	121 (41)	13.7 (6.0)	1.3 (0.7)	3.5 (0.5)	31.1 (3.3)	3.1 (0.8)
	FM	**70.7**[†] (12.8)	**1302**[*] (181)	**72**[*] (16)	**201**[†] (41)	**32.0**[†] (8,7)	2.2 (0.9)	5.1 (0.6)	**42.9**[*] (3.3)	**5.6**[*] (0.8)
First 30 cm of mineral soil	LW	37.4 (19.4)	1208 (155)	35 (5)	27 (8)	6.1 (2.2)	0.8 (0.3)	16.9 (4.9)	114 (51)	9.6 (2.6)
	FM	**97.4**[*] (19.4)	2006 (547)	35 (5)	39 (22)	8.7 (2.6)	0.9 (0.3)	47.1 (21.6)	**328**[†] (86)	9.1 (2.5)
First 1 m of mineral soil	LW	60.2 (16.6)	2701 (326)	94 (12)	117 (21)	26.5 (11.7)	4.5 (1.5)	28.0 (8.6)	205 (90)	33.0 (4.4)
	FM	**144.5**[*] (30.6)	3961 (750)	80 (12)	131 (44)	30.9 (11.8)	3.8 (1.4)	57.8 (30.8)	461 (135)	29.3 (4.0)
Whole profile	LW	106.8 (21.5)	3425 (399)	123 (13)	103 (31)	46.3 (20.0)	7.3 (2.2)	36.6 (15.6)	240 (96)	34.4 (4.1)
	FM	**277.1**[***] (29.9)	**5991**[*] (1081)	126 (13)	**133**[*] (31)	**85.8**[*] (20.0)	6.5 (2.1)	69.6 (21.0)	517 (140)	32.7 (3.9)

Note: Differences between LW and CF are statistically significant at [†], $P \leq 0.10$; [*], $P \leq 0.05$; [**], $P \leq 0.01$; [***], $P \leq 0.001$. Data presented are adjusted means, with standard error in parentheses. Significant differences between stand types are highlighted in bold.

LW soils ($P \leq 0.086$; Table 4). For other elements, soil contents did not differ significantly between LWs and FMs at this soil depth ($P \geq 0.219$).

In the first 1 m of soil, on average, only total C differed significantly between stand types, with values 2.4 times larger in FM than in LW soils ($P = 0.022$; Table 4). There were no other significant differences in element contents between LW and FM soils at this depth ($P \geq 0.121$).

When considering the whole profile (humus and 1 m mineral soil), total C and N, and exchangeable Ca and Mg stocks were 1.32.6 times larger in FM than in LW soils ($P \leq 0.050$; Table 4). There were no other significant

differences in element contents between LW and FM soils for the whole profile ($P \geq 0.164$).

Plant foliar nutrient status

For the three sampled plant species, foliar N and K concentrations were consistently 6% to 22% higher in FM than in LW stands ($P \leq 0.056$; Table 5). Sheep laurel and common Labrador tea both had higher foliar Mn concentrations in FMs than in LWs ($P \leq 0.001$). In addition, sheep laurel foliage had higher Mg concentrations in FMs than in LWs ($P = 0.037$), and common Labrador tea foliage had slightly higher P concentrations in FMs

Table 5. Comparison of element concentration in foliage between open lichen woodland (LW) and adjacent closed black spruce–feathermoss (FM) stands for black spruce (*Picea mariana*), sheep laurel (*Kalmia angustifolia*), and common Labrador tea (*Rhododendron groenlandicum*).

Species	Stand type	N (g kg^{-1})	P (g kg^{-1})	K (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})	Mn (g kg^{-1})
Black spruce	LW	5.97	0.89	3.87	4.69	0.87	1.35
	FM	**6.40****	0.98	**4.72****	4.53	0.90	1.39
SE		0.35	0.05	0.31	0.59	0.04	0.18
Average values for black spruce[a]		9.38 (0.18)	1.43 (0.04)	5.40 (0.12)	3.49 (0.15)	1.13 (0.02)	—
Sheep laurel	LW	13.34	0.97	3.93	4.45	0.83	0.36
	FM	**14.08**[†]	1.03	**4.47***	4.55	**0.92***	**0.46*****
SE		0.20	0.04	0.25	0.20	0.03	0.03
Common Labrador tea	LW	12.18	1.01	4.27	5.14	1.07	0.49
	FM	**14.30***	**1.17**[†]	**5.05*****	5.29	1.22	**0.64*****
SE		0.47	0.07	0.12	0.22	0.05	0.07

Note: Difference between LW and CF is statistically significant at [†], $P \leq 0.10$; *, $P \leq 0.05$; **, $P \leq 0.01$; and ***, $P \leq 0.001$. Data presented are adjusted means with accompanying SE in parentheses. Significant differences between stand types are highlighted in bold. SE, standard error.

[a]Average values (and SE between parentheses) for black spruce foliage (current and 1 yr old) in Quebec and Ontario (excluding the Clay Belt and the Appalachians) obtained from the Canadian Tree Nutrient Database (Paré et al. 2012) ($n = 93$ to 108, depending on the nutrient).

than in LWs ($P = 0.056$). In both stand types, for all nutrients analyzed except Ca (which appeared to be above the average concentration), foliar concentrations were much lower than average values reported in the literature for black spruce in Quebec and Ontario.

Discussion

Element stocks and standing biomass

These results for mature and adjacent FM and LW stands reveal significant differences in soil element stocks for some essential plant nutrients. For example, total N and exchangeable K, Ca, and Mg pools in the humus were significantly larger in FMs than in LWs. As nutrient stocks are related to stand yield and productivity, our results suggest that vegetation, through its accumulated litter, exerts a strong biological control on soil nutrient pools (Bastianelli et al. 2017). The retroactive feedback of vegetation on soil nutrient pools of FM vs. LW soils may then be seen as a process not of nutrient consumption (immobilization), but rather of enrichment, working in two different ways. First, the greater biomass in FM soils acts as a nutrient sink because immobilization in the biomass prevents nutrients from leaching out of the root-accessible zone. Second, the greater biomass in FMs creates more litter and fine roots, which in turn yield organic compounds and mineral nutrients that improve the soil's physicochemical properties. Dufour et al. (2016) showed that the higher stand productivity of FMs compared with LWs was related to differences in stem density. However, they reported that 60% of the LW stands in their study expressed a lower productivity than their FM counterparts at the individual stem level. The differences in nutrient stocks in humus and soils could at least partly explain these growth differences.

The soil nutrient pools may also be influenced by lichen cover abundance. Lichens contain low concentrations of major nutrients, accumulate at slow rates in the litter (Sedia and Ehrenfeld 2005), have low primary productivity (Kershaw 1975), and hinder fine root development in trees (Pacé et al. 2017). This can affect soil temperature, humidity, and the resulting decomposer activity because lichens are highly reflective and have low thermal conductivity (Bonan and Shugart 1989; Haughian and Burton 2018). Therefore, lichen cover appears to play only a small role in nutrient cycling within the LW ecosystem (Moore 1980; Auclair and Rencz 1982).

Results obtained from the humus layer show that the forest floor was twice as thick in FMs as in LWs (Table 1; Hamel et al. 2004; Girard et al. 2011). Mosses may play a significant role in humus C accumulation. On average, moss-derived C can account for 31% of soil C stocks accumulated in the organic layer in FM ecosystems (Bona et al. 2013). Hamel et al. (2004) also found a positive relationship between humus thickness and site quality index for black spruce. Considering the ability of black spruce to develop adventive roots from the stem as a measure of humus thickness growth (Krause and Morin 2005), a thicker humus in FMs suggests that a larger root biomass may develop directly in this layer, which is richer, as shown by its larger N, K, Ca, and Mg stocks. Moreover, black spruce takes up N mainly from the forest floor (Houle et al. 2014). When they do not develop directly in humus, black spruce root systems usually develop at the humus – mineral soil interface (Sims et al. 1990; Desrochers and Gagnon 1997). This root system distribution enables black spruce to better fill its nutritional needs. The nutrient distribution and stocks observed in the present study would favour black spruce tree growth

in FM stands over LWs. The hypothesis of higher fertility of FMs is supported by the higher foliar N and K concentrations observed for the three plant species. This investigation is the first to reveal differences in element pools between LWs and FM stands. Based on measured nutrient stocks and foliar nutrient status, it appears that soils in LWs are less fertile than in FM stands.

Role of soil carbon

Because these ecosystems are evolving under the same climatic and edaphic environment, LWs are considered as an alternative stable state of former FM stands (Jasinski and Payette 2005). If a LW was created a long time ago, it did not receive much organic input through litterfall and root turnover. This would have led to soil C depletion, as was observed in this comparison study. It appears the replenishment of soil C stock via the production of annual litter may not be sufficient to increase the soil microbial biomass in LWs. Therefore, the low rate of litter production in LW soils may favour K-strategist organisms. These microorganisms can feed on more decomposition-resistant organic compounds such as lignin, cellulose, and humified compounds (Weil and Brady 2016).

Because the source of both C and N is ultimately the atmosphere, the amount of C and N accumulated in the whole soil profile can indicate the importance of biological control of soil C. Given that both LWs and FMs are found in the same environmental and edaphic conditions, the smaller available nutrient pool in the humus and lower soil C content in LWs, caused by past fire disturbances and by the associated humus consumption and low tree densities, may be one of the main factors causing low soil fertility. The apparent C loss in soils of former FMs that have become LWs can also be related to its coarse texture and its very low fine mineral particle fraction, which is a key feature for long-term soil C stabilization (Feller and Chenu 2012).

Conclusion

The comparison of soil nutrient stocks in adjacent LWs and FM stands in the continuous boreal forest ecozone showed that LWs have much lower stocks of total C, total N, and available K, Ca, and Mg in the humus. Plants in LWs also have lower foliar nutrient concentrations, mainly for N and K. Therefore, it appears that LW soils are less fertile than FM soils.

The differences in soil exchangeable nutrient pools of LWs and FMs were mainly found in the humus layer, indicating a strong biological control of C, N, and mineral nutrients in these boreal soils. However, the first 30 cm and first metre of mineral soils in LWs and FMs displayed similar available nutrient pools. As the mineral soils are similar, LW afforestation could be considered as a viable option in the long term in some regions, provided that major disturbances such as fire frequency and intensity can be controlled. Simulations

have shown that it can take only 8–12 yr for LWs to become a net C sink when understory planting is the chosen silvicultural approach (Boucher et al. 2012). Early observations in field experimental trials show some potential for LW afforestation in the boreal forest ecozone (Hébert et al. 2006; Fradette 2012; Hébert et al. 2014).

In general, LWs correspond to the IPCC (2006) definition of nonforested land; this makes them eligible for afforestation/reforestation operations aimed at increasing timber productivity or C density (Hébert et al. 2014). As LW soils are C depleted, the potential exists for increasing soil C sequestration in these ecosystems (Boucher et al. 2012). In addition, the study of site fertility in younger LWs is warranted as their pools of nutrients and C may not yet be lost.

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