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Black-spruce–lichen woodlands growth and carbon drawdown potentials as revealed by mature stands

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The afforestation of widely distributed boreal open woodlands such as lichen woodlands (LWs) could provide both a restoration of the closed-crown forest structure in the boreal forest and a mitigation measure against global warming. By comparing natural, mature stands of LW with their dense counterparts — black-spruce–feathermoss stands as a plantation surrogate — this study aims to validate the long-term LW growth support capacity for a high tree density and their carbon sequestration potential after afforestation. Our results reveal that the site potential of LWs can be either lower or equivalent to that of dense stands. This finding contradicts the paradigm of systematic lower tree growth in LWs. The site potential of LWs can be assessed by dominant tree volume at 50 years. This study also shows that the CBM-CFS3 model can simulate the conservative net carbon balance of afforested LW, and, as such, can help reduce uncertainties regarding the long-term net carbon drawdown of afforested LWs.

Introduction

The accounting of the comprehensive impact of actions in the land-use, land-use change, and forestry (LULUCF) sector requires an accurate determination of the real net C drawdown from the atmosphere via biological sequestration, using stand-based calculations for project-level accounting (IPCC 2003, Nabuurs *et al.* 2007). The closed-crown black-spruce–feathermoss (BSFM) forest dominates the continuous boreal forest in the province of Quebec (MRN 2003). While black spruce (*Picea mariana*), the main tree species in this zone, is generally well adapted to wildfires (Viereck and Johnston 1990), post-fire regeneration failure can sometimes occur, resulting in the conversion of closed-crown BSFM to open woodlands (Payette 1992, Gagnon and Morin 2001, Jasinski and Payette 2005), such as lichen woodlands (LWs), which are very common in the boreal zone (Hustich 1966, Girard *et al.* 2008). There is currently no evidence of natural redensification of LWs, i.e., a shift to closed-crown BSFM stands (Payette 1992, Jasinski and Payette 2005). The phenomenon is thus considered as irreversible. The causes for absence of natural redensification seem to be the scarcity of seed trees (Jasinski and

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Payette 2005), poor seed germination on lichen mats (Morneau and Payette 1989, Sedia and Ehrenfeld 2003, Girard *et al.* 2009), and interference from ericaceous shrubs (Thiffault and Jobidon 2006). It has been shown that between 1950 and 2002, 9% of BSFM stands and other closed-crown stands in Quebec's boreal forest were converted to LW after wildfires (Girard *et al.* 2008), indicating a net forest cover loss has occurred, given the irreversibility of the phenomenon. The latest Quebec forest inventory (2002) reveals that approximately 7% (1.6 M ha) of the spruce-moss bioclimatic domain (within the forest management limits) was covered by open woodlands (3rd decennial forest inventory of Quebec's Ministère des Ressources naturelles, MRN).

This progressive transition from closed-crown to open-forest stands has two important consequences from which this study arises. First, there might be a loss of productive forest (Côté *et al.* 2013). Second, there may be a permanent decrease of a potential carbon sink, not simply a transitory reduction, such as that occurs when a regenerative disturbance occurs (Kurz *et al.* 2008, Amiro *et al.* 2010, Dymond *et al.* 2010) . Given that regeneration failures responsible for the BSFM to LW transitions are caused by wildfires that occur when the stand was left almost seedless by a previous disturbance (Payette *et al.* 2000, Jasinski and Payette 2005, Girard *et al.* 2009, Brown and Johnstone 2012) and that global warming scenarios suggest an increased impact from natural disturbances in the boreal region (Flannigan *et al.* 2005, Kurz *et al.* 2008, Amiro *et al.* 2009), this natural long-term opening of the boreal forest could result in a positive feedback loop, thereby decreasing potential C sequestration and fuelling global warming further (Bony *et al.* 2006, Weaver *et al.* 2007, Heimann and Reichstein 2008, Matthews *et al.* 2009, Frank *et al.* 2010). However, the afforestation of open boreal woodlands such as LWs could result in a restoration of the closed-crown forest structure in the boreal forest (Payette 1992, Gagnon and Morin 2001, Jasinski and Payette 2005) and provide a mitigation measure against anthropogenic global warming (Nabuurs *et al.* 2007, Gaboury *et al.* 2009, Montenegro *et al.* 2009, Boucher *et al.* 2012).

Field data for sites having undergone LW afforestation do exist, however are limited in length (15 years of growth) as the studied plantations were established in 2000–2001 (Hébert *et al.* 2006, Hébert *et al.* 2014). The initial results from these sites suggest a slightly lower growth on planted LW as compared with planted BSFM, independent of abiotic conditions (spatially blocked in a split-plot design). This observation may be related to a lower soil temperature in LW due to a higher albedo for the lichen in these stands relative to that of feather-moss in BSFMs, as there is no detected nutritional effect (Hébert *et al.* 2014) nor water status difference (Hébert *et al.* 2006). If this scenario is true, it is logical to ask how growth would change over a longer period as a LW plantation grows and the albedo is reduced as the canopy closes. Planted trees in the LW may also be released from their competition with the well-established shrub species, over this longer period.

However, there are no accurate long-term field measurements of growth and carbon balance in Canada's afforested LW. Gaboury *et al.* (2009) simulated this balance, estimating the potential net C drawdown at 77 t C ha^{-1} for a 70-year-old black spruce plantation in boreal Quebec. A follow-up of these estimates, using a different modelling approach, provided a new set of net C drawdown values for boreal afforestation scenarios, ranging from 58 to 97 t C ha^{-1} (after 70 years) depending on whether larch, black spruce, or jack pine was the planted species (Boucher *et al.* 2012). Other studies used only general assumptions that are difficult to apply to LW and show highly variable mean C drawdown values (Table 1). Bernier *et al.* (2011) studied LWs, but they assessed representative natural stands as the afforested scenario, not plantation surrogates, so this might explain the lower 21–42 t C ha^{-1} estimates relative to Gaboury *et al.* (2009). Nonetheless, given this discrepancy in estimates and the fact that the value of 77 t C ha^{-1} of Gaboury *et al.* (2009) is a simulated value, more precise long-term field data are required.

LW and BSFM within the North American closed-crown boreal forest are often co-occurring stand types that share similar site conditions in terms of climate, soil deposits, drainage, slope, aspect and time elapsed since a last disturbance (Payette 1992, Riverin and Gagnon 1996, Gagnon and Morin 2001, Jasinski and Payette 2005). Therefore, pairs of mature LW and BSFM stands established at those sites offer an opportunity to compare the site potential between these stand types, independent of abiotic conditions as evaluation occurs at tree-level. If tree-level site potential is shown to be comparable between both stand types, it could be assumed that site productivity is a matter of stem density. Fire-established, mature BSFM stands could then be considered as surrogates for afforested LW, as the higher stand productivity of BSFM should only be due to the much lower tree density in LW (Skovsgaard and Vanclay 2008, Madec *et al*. 2012, Côté *et al*. 2013). Given this, data from these BSFM could provide a suitable long-term validation of the C stocks and dynamics simulated so far for LW afforestation projects.

Spruce budworm outbreaks threaten conifer stands of the continuous boreal forest but are not as lethal for black spruce as for balsam fir (Nealis and Regniere 2004, Hennigar *et al*. 2008, Pothier *et al*. 2012). However, black spruce defoliation by budworms has been identified as a factor reducing growth for these trees (Tremblay *et al*. 2011, Krause *et al*. 2012). Furthermore, this budworm defoliation is a disturbance that reduces the LW seedbank thereby favouring the shift from BSFM to LW (Payette *et al*. 2000, Simard and Payette 2005, Girard *et al*. 2009). To date, the differing impacts of spruce budworm outbreaks for BSFM and LW remains unknown.

Given that the existing afforested LWs are only 15 years old (Hébert *et al*. 2014), BSFM that share similar abiotic conditions to the LW may be considered as plausible surrogates of mature afforested LW and provide a valid test for the long-term C stocking potential of afforested LW. Testing this hypothesis first requires confirming that the tree-level growth potential of LW and BSFM is similar on comparable sites. Once confirmed, other objectives can use data from BSFM to validate the simulated C dynamics and stocking of afforested LW. The first objective aims to compare forest C dynamics using generic yield tables with C dynamics using new yield tables based on field measurements of BSFM stands having similar attributes as LW but utilizing a stem density similar to that of plantations. The second objective aims to compare field measurements of carbon stocks at maturity with the published literature and simulated values (to validate the use of available simulation models). Finally, as spruce budworm would be expected to affect the way that LW and BSFM growth is compared, a last objective aims to relate budworm effects on spruce growth to variations of site potential.

Material and methods

Study area and sampling design

The study area is located in the continuous boreal forest subzone of Quebec's boreal vegetation zone, which includes two bioclimatic domains: the spruce–moss and balsam-fir–white-birch (MRN 2003). The first domain, which is also the northernmost one, is extensively dominated by black spruce, often growing in pure stands. Forest dynamics are characterized by fires occurring in cycles extending eastward, as such jack pine can dominate in places where fires are frequent and balsam fir is generally found in areas where fires are relatively scarce. In the second domain, the main stand type is

Table 1. Net C drawdown assumptions used in high-latitude afforestation studies.

Net C drawdown (t C ha^{-1})	Region considered	Reference
21–42	Boreal Quebec (Canada)	Bernier *et al.* (2011)
60	Boreal Canada	Betts (2000)
50–75	Boreal Canada	Betts *et al.* (2007)
55	Boreal latitudes	Claussen *et al.* (2001)
100	Global	Gibbard *et al.* (2005)
170	Boreal Canada	Montenegro *et al.* (2009)

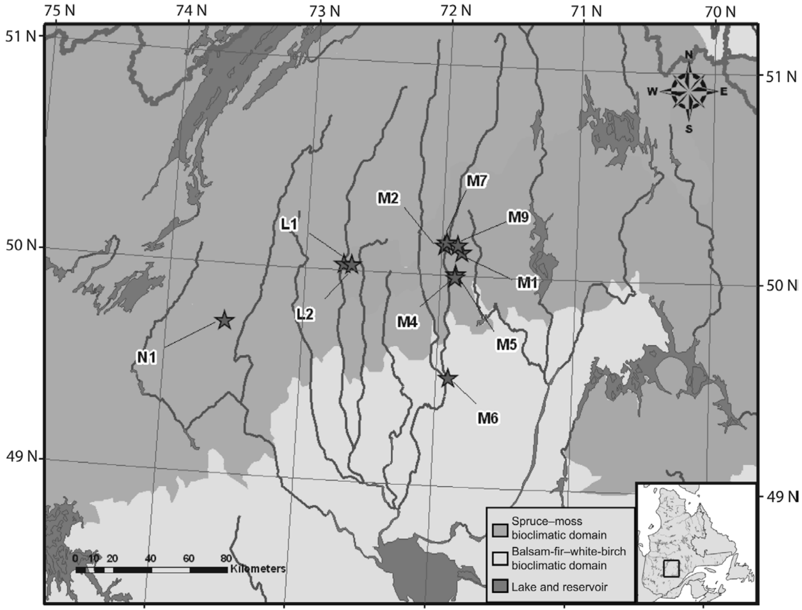

Fig. 1. Locations of blocks and study area.

dominated by conifers (balsam fir and white spruce) in association with white birch. The fire cycle is generally longer than that of the spruce–moss domain, but places exist where fires are rather frequent, allowing black-spruce and jack-pine-dominated stands to occur. LWs are very common throughout the continuous boreal forest, representing 54% of the 1.6 M ha open woodlands. A patchy distribution of LWs spreads from north to south throughout the subzone (i.e., across both domains), although decreasing in extent moving southwards (Girard *et al*. 2008).

In 2003–2004, a randomized complete block design (Quinn and Keough 2002) was established in the continuous boreal forest subzone (Fig. 1). Each of the ten blocks embeds two plots established on adjacent but differing stand types (BSFM and LW). Ecoforestry maps were used to select candidate pairs, matching stands of a block in terms of vegetation, tree age, aspect, slope, as well as surficial deposit type and its thickness. Field measurements and observations validated the match for each pair (Table 2). Tree cover density was confirmed as ≥ 80% for BSFM and < 40% for LW. The latter's tree cover is higher than that in the case study by Gaboury *et al*. (2009), which was < 25%, as a compromise had to be established owing to the difficulty in finding very low cover LWs growing next to BSFMs on a same site and originating from the same disturbance. The occurrence of less contrasted pairs, i.e. using 40% tree cover as the maximum value, was high enough to match the needs for this study, considering all the logistical restrictions. Conformity to the chosen criteria was validated in the field and only pairs matching these criteria were selected, ensuring that only the vegetation dynamics (tree density and growth patterns) were different between stands within each pair (block).

Every selected BSFM stand was dominated by black spruce having an even-aged structure and showed a high stem density and a closed canopy with a dense mat of feather mosses (*Pleurozium schreberi*, *Ptillium crista-castrensis*, *Hylocomium splendens*, *Polytrichum* sp.). Ericaceous shrubs (*Ledum groenlandicum*, *Kalmia angustifolia*, *Vaccinium angustifolium*) were sometimes present, covering up to 20% of the ground surface. Selected LWs were open stands dominated by black spruce, their forest floor being more than 40% covered with lichens (*Cladina stellaris*, *C. rangiferina* and *C. mitis*) and more than 25% with ericaceous shrubs.

Sampling

A 400-m^2 circular sampling plot was established

Table 2. Characteristics, pairwise ANOVAR, and stand type comparison of the 20 studied stands.

Block	Stand	Composition[a] & percentage of basal area	Surficial deposit	Deposit thickness (cm)	Forest floor thickness (cm)	Slope (%)	Drainage	Age (years)[b]	Site index (m)[b]	Dominant Vol_{50} (m^3)[b]	Mean DBH (cm)[c]	Density (stems ha^{-1})[c]	Spruce density (stems ha^{-1})[c]	Basal area (m^2)[c]	Volume ($\mathrm{m}^3\ \mathrm{ha}^{-1}$)[c]	Dominants Vol. Age × stand $p > F$[d]
L1	LW	BS 65; JP 35	Glacial	> 100	35	14	Mod.	75.7	10.2	0.0525	5.7	700	525	8.1	28.54	**0.0002**
L1	BSFM	BS 84; TA 13; JP 3	Glacial	50–100	15	35	Well	77.3	13.9	0.1262	12.2	2550	2125	42.3	226.40	
L2	LW	BS 81; WB 19	Glacial	25–50	10	0	Mod.	77.3	6.3	0.0215	3.4	75	75	0.9	2.62	**0.0001**
L2	BSFM	BS 100	Glacial	50–100	10	5	Mod.	76.7	9.9	0.0938	10.7	2850	2825	42.4	199.55	
M1	LW	BS 100	Glacial	> 100	11	16	Mod.	87.7	9.8	0.0685	6.5	650	650	8.4	30.42	**0.0280**
M1	BSFM	BS 88; BF 10; EL 2	Glacial	> 100	16	20	Mod.	86.7	10.6	0.0509	7.6	2675	2375	32.6	133.59	
M2	LW	BS 100	Glacial	> 100	12	8	Mod.	80.7	9.3	0.0601	5.6	425	425	6.5	27.98	**0.0106**
M2	BSFM	BS 80; WB 20	Glacial	25–50	6	23	Well	80.7	14.3	0.2107	15.5	1625	1075	40.4	254.85	
M4	LW	BS 100	Glacial	50–100	6	23	Well	69.3	9.1	0.0620	6.3	275	275	5.6	26.25	0.1170
M4	BSFM	BS 99; BA 1%	Glacial	25–50	5	28	Well	75.7	11.7	0.0942	11.2	2300	2250	41.4	230.27	
M5	LW	BS 100	Glacial	25–50	11	16	Mod.	71.0	8.5	0.0555	6.8	575	575	7.2	24.82	**0.0281**
M5	BSFM	BS 99; WB 1%	Glacial	25–50	4	30	Well	76.7	11.2	0.1454	9.8	2650	2600	44.8	232.92	
M6	LW	BS 75; JP 19; TA 6	Fluvio-glacial	> 100	11	7	Well	60.3	13.5	0.1682	6.1	525	400	11.8	64.29	0.4996
M6	BSFM	BS 75; TA 25	Fluvio-glacial	> 100	9	6	Well	60.3	15.9	0.1839	13.5	2300	1775	41.7	250.58	
M7	LW	BS 97; TA 3	Glacial	25–50	20	46	Well	81.5	11.0	0.0723	4.8	850	825	10.9	40.77	0.1343
M7	BSFM	BS 92; TA 5; WB 3	Glacial	< 50 (outcrops)	20	33	Well	83.0	13.1	0.0950	11.8	2725	2425	41.0	201.42	
M9	LW	BS 100	Glacial	25–50	12	13	Well	87.0	10.6	0.0986	5.3	775	775	13.7	60.23	0.1735
M9	BSFM	BS 100	Glacial	50–100	12	14	Well	89.7	12.3	0.1073	12.7	3375	3375	51.9	264.37	
N1	LW	BS 91; JP 9	Fluvio-glacial	> 100	4	9	Mod.	89.3	10.8	0.0758	5.4	1125	1075	14.7	61.92	**0.0115**
N1	BSFM	BS 93; BF 6; WB 1	Glacial	50–100	7	12	Mod.	95.3	12.6	0.1171	12.9	2825	2550	50.9	310.05	
Mean[e]	LW					15.2		77.9	9.9	0.0735	5.59	598	550	8.79	36.78	
	BSFM					20.6		80.2	12.6	0.1225	11.79	2588	2350	42.95	230.40	
	Diff.					5.4		2.3	2.7	0.049	6.2	1990	1800	34.16	193.62	
	$p > \chi^2$					0.2894		0.6495	**0.0052**	**0.0191**	**0.0002**	**0.0002**	**0.0001**	**0.0002**	**0.0002**	

[a] BS = black spruce; JP = jack pine; TA = trembling aspen; WB = white birch; BF = balsam fir; EL = eastern larch; BA = black ash.

[b] Mean from the three harvested dominant trees. Vol_{50} refers to the mean tree volume of dominants at 50 years.

[c] Mean of all the commercial trees in the plot (DBH > 9 cm).

[d] Results of block by block ANOVAR, within-subject the Greenhouse-Geisser test. Values set in boldface indicate significant difference (α = 0.05) in volume growth between BSFM and LW.

[e] $p > \chi^2_1$ refers to a Wilcoxon mean comparison between LW and BSFM. Values set in boldface indicate significant difference (α = 0.05).

in each of the 20 stands. Diameter at breast height (1.3 m, DBH) was measured on every tree using a caliper. Three individual, dominant black spruce trees were felled in order to assess the growth potential of the site (Pardé and Bouchon 1988, Mailly and Gaudreault 2005). These trees had to display a single stem (no fork), no obvious leaf area reduction, no decay and no sign of juvenile growth suppression. Veteran trees were also avoided. Stem discs were sampled at stump height (0 m), 0.3 m, 0.6 m, 1.0 m, 1.3 m, 2 m, and at each successive complete metre in order to conduct stem analysis. Discs were then taken to the laboratory and rubbed with fine sandpaper to obtain a clear reading surface.

Four cross-oriented radius paths were marked, according to cardinal point direction, on each of the sanded face of discs sampled at 0 to 1.0 m stump height. The same procedure was used for the discs collected above 1.0 m stump height but with only two opposite radius paths. The year of the last completely formed ring was established from the date of field sampling and the occurrence of latewood. From this information, the year corresponding to the first ring on each disc was determined, counting down from the last ring using a binocular microscope at a magnification up to 100×. Ring widths along each radius path were measured using the WinDendro™ software (Regent Instruments, Quebec City, Canada) coupled to a high-resolution digital scanner. Tree rings that were difficult to measure were analyzed using a binocular microscope at 100× as well as a dendrometric table. Measurements between the paths of a disc, discs of a tree, trees of a stand and between stands were cross-dated using Cofecha software (Holmes 1983) to ensure that every tree was aged correctly.

Stem analysis data processing

Height growth was computed from the stem analysis data following Carmean's method (Dyer and Bailey 1987) allowing extrapolation of cross area and volume between sections and development of increment time-series. Cumulative volumes by age series were compared individually in each block, performing univariate repeated analysis of variance (ANOVAR) to compare growth patterns between stands (BSFM *vs*. LW) for each block. Since the sphericity assumption of the variance-covariance matrix is unlikely met, degrees of freedom for the *F*-test were adjusted based on the Greenhouse-Geisser ε, which is known to make the test much more conservative (Quinn and Keough 2002). Age, site index (height at 50 years) and volume at 50 years were obtained from stem analysis and a global comparison between BSFM and LW was performed with a Wilcoxon non-parametric test, using blocks as observations. All other univariate tests were performed this way. This non-parametric test was preferred although the assumptions for parametric testing were generally fulfilled, because it is likely more robust with a small number of observations (n = 10 per stand type).

As spruce budworm outbreaks are known to affect black spruce in the study area (Hardy *et al*. 1986, Tremblay *et al*. 2011), the effect of outbreaks on the growth of the harvested dominant trees was quantified. To do so, the *Impact* routine from the dendrochronological program library (http://ltrr.arizona.edu/research/software) was used. It calculates the percentage of growth reduction by dividing the mean annual volume increment during the event by the mean value during a reference period. For the outbreak growth reduction period, the mean volume increment from 1976 to 1979 (Morin and Laprise 1990) was used whereas the six previous years (1970–1975) served as the reference period. Using these measurements of outbreak impact as response variable, an ANOVA was performed to check for the effect of stand type.

Stand volume calculation

Stem density, DBH and mean basal area were calculated from merchantable tree size (DBH > 9 cm). These data were used for plot-level volume calculation performed with the Artemis-2009 simulator (ver. 2.5.1), running on the Capsis 4.2.2 platform (http://capsis.cirad.fr/), which estimates individual tree height, taking into account species and stand-specific characteristics such as climate (Fortin *et al*. 2009, Fortin and Langevin 2012). It computes volume at tree level and integrates at plot level, accounting for errors associated with the use of estimated height (Fortin *et al*. 2007).

Carbon stock evaluation

DBH measurements of all woody stems reaching 1.3 m high were used for determining the carbon stock sequestered in trees. Individual tree biomass was computed using species-specific equations, taken from: (1) Fradette (2013) for black spruce and jack pine total biomass in LW, (2) Tremblay *et al*. (2006) for above-ground biomass of *Sorbus* sp. in both stand types, and (3) Lambert *et al*. (2005) for all other above-ground biomass equations. In the latter cases, root biomass was calculated from above-ground biomass using equations from Li *et al*. (2003). Carbon stocks for both stand types were calculated as half of these total dry mass (IPCC 2003). The same allometric biomass equations were also used for calculating total biomass of the above-mentioned dominant trees sampled for stem analysis. DBH values at 50 years (dry wood DBH) were used to have comparable data of the whole tree growth potential for both stand types.

Carbon stock simulation

In order to compare the carbon stock dynamics from the natural BSFM in this study with that from a LW afforestation simulation, the afforestation scenario from Gaboury *et al*. (2009) was repeated, but using the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3; Kurz *et al*. 2009) instead of the CO2FIX carbon model. First, an initial growth period of a dense natural black spruce stand having a site index of 12 m using natural stand yield tables (MRN 2000) was simulated for 70 years, followed by a fire which shifted the stand to a LW. A natural development of this LW was then simulated for 75 years, using a site index of 9 m at low density leading finally to a clear-cut, leaving debris at stump level (tree-length logging). Scenarios were then specifically simulated from this common starting point.

For the Gaboury *et al*. (2009) afforestation scenario, a growth and yield table of black spruce plantation having a site index of 6 m (at 25 years) and a density of 2000 stems ha^{-1} was used (MRN 2000). For all other simulations, site-specific growth and yield tables were constructed as follows. From the mean cumulative volume of the three dominant trees, a Richards growth function (Richards 1959) was fit to the data due to the occurrence of a break in the last years (up to five) before the mean age, as the mean computation was reduced from three to two samples. These series were transformed into ratios of the volume at the age of the stand at sampling time, i.e. the mean age of the three felled dominant trees. Ratios were multiplied by the stand volume at sampling age calculated by the Artemis model as described above, so that the yield curve matches the merchantable volume measured in the plot.

Results

Stand characteristics

The stand pairs all dominated by black spruce, were very uniform in terms of vegetation composition, soil characteristics, and age (Table 2). They were all established on glacial deposits, of either till or fluvio-glacial sediments. An apparent deposit mismatch can be observed in the N1 stand pair owing to the map codification, but a soil investigation in the field revealed that deposit thickness, as well as soil horizon thickness and texture, were comparable. The tree density in the BSFM stands ranged from 1625 to 3375 stems ha^{-1} with a mean of 2588 ± 456 (SD) stems ha^{-1}. The LW tree density was much lower, ranging from 75 to 1125 stems ha^{-1} and a mean of 598 ± 298 (SD) stems ha^{-1}. Generally speaking, tree-level productivity indices were lower in open stands, by 2.7 ± 1.2 (SD) m for site index and 0.049 ± 0.049 (SD) m^3 ha^{-1} for dominant tree volume at 50 years, suggesting a lower site potential in LW.

Growth and yield

The ANOVAR performed block by block on the cumulative volume growth revealed that site potential is not always different between LW and BSFM stands (Table 2). Four blocks (M4,

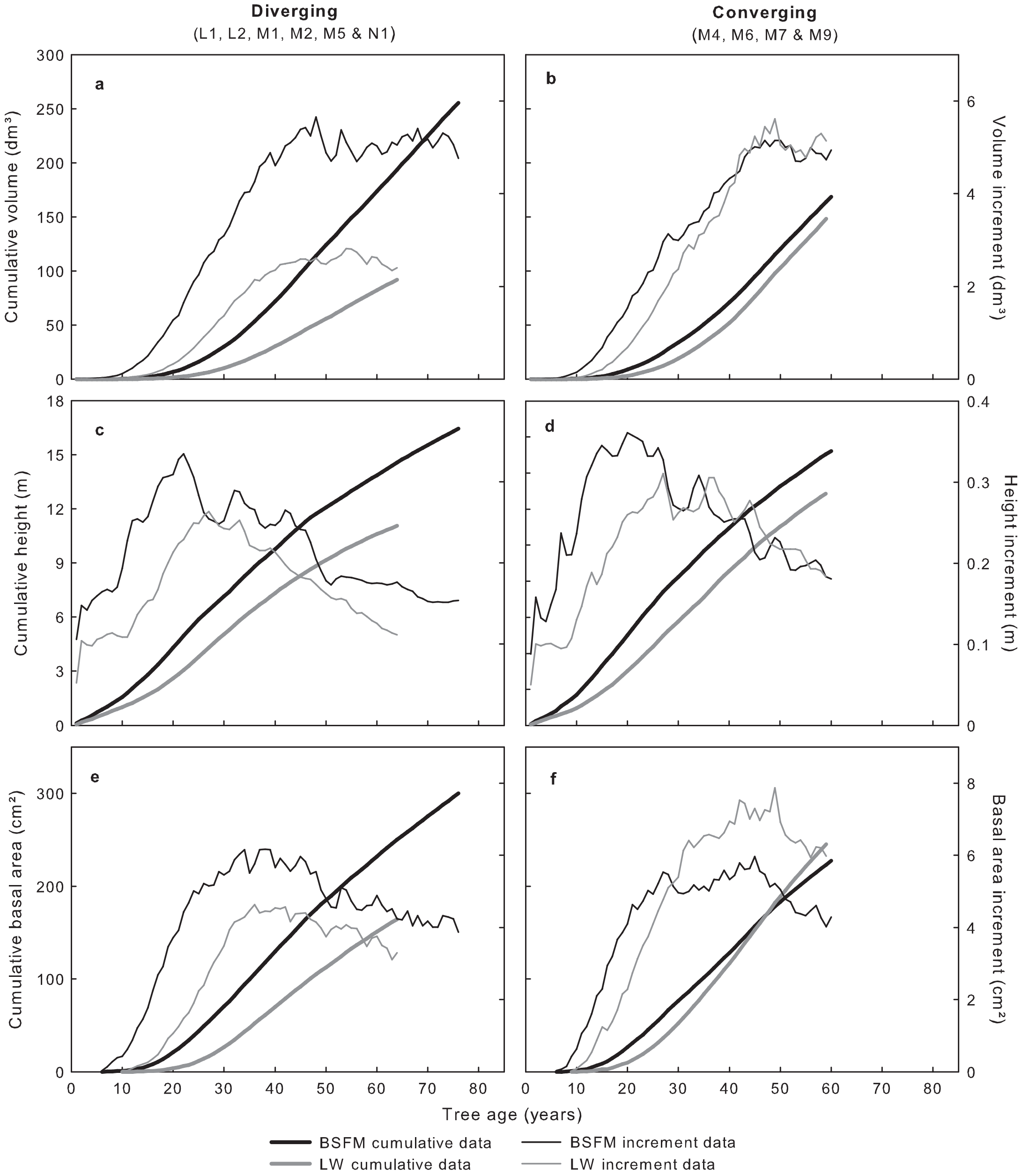

Fig. 2. Mean growth development by age of dominant black spruce growing in two groups (converging and diverging) of blocks. Annual increment and cumulative data are shown in each panel.

M6, M7 and M9) showed similar growth of dominant trees in both stands while growth was different among the other blocks. This difference allowed for defining two groups based on the growth tendency between stands of each block. The "diverging" group showed volume growth curves to diverge throughout the measured period, as annual volume increments from the two stands deviated from one another for almost the first 40 years before reaching a plateau, thereafter keeping a constant difference (Fig. 2a). The second "converging" group showed volume increments to be slightly lower for the LW in the first 30 years before becoming equal to that for BSFM at about 40 years, making the total volume growth curves parallel (Fig. 2b). Differences among these groups were also apparent in the height growth component; the height increment of the LWs being lower in the diverging group, making cumulative height curves of both stand types deviate in a continual manner (Fig. 2c). For the converging group, height increment was lower for LW at the beginning but equal at 25 years, making cumulative height curves parallel (Fig. 2d). However, the difference among groups was striking in terms of basal area. Here again, the stands in the diverging group deviated in a continual manner (Fig. 2e), while in the converging group, basal area annual increment of the LW was lower than for the BSFM in the first 25 years but caught up and exceeded BSFM trees for the last 35 years (Fig. 2f). Cumulative volume development did not differ between the two groups for the BSFMs (ANOVAR inter-subject Group effect $F = 0.0015$, df = 1, $p = 0.9692$; intra-subject Age × Group effect $F = 0.1006$, Greenhouse-Geisser df = 1.0879, $p = 0.7747$), while there was a significant difference for the LWs (ANOVAR inter-subject Group effect $F = 10.8742$, df = 1, $p = 0.0027$; intra-subject Age × Group effect $F = 14.5974$, Greenhouse-Geisser df = 1.1015, $p = 0.0005$), showing that the converging/diverging group distinction is due to differences in LW site potential alone. The total biomass of dominant trees at 50 years also differed between BSFM and diverging LW (Wilcoxon $\chi^2_1 = 18.6397$, $p < 0.0001$), but not between BSFM and converging LW (Wilcoxon $\chi^2_1 = 0.4987$, $p = 0.4801$).

Spruce budworm outbreaks affected black spruce growth in the studied area, with an obvious sign of growth reduction during the last outbreak period in both stand types (Fig. 3). Owing to the grouping of blocks (converging *vs.* diverging), the statistical analysis of spruce budworm outbreak impact was adapted: a split-plot ANOVA was run instead of the originally planned randomized complete block ANOVA. Blocks were nested in the group factor and stand type was the factor replicated in each block. The block factor was randomized and interaction between groups and stand types was also tested. The split-plot ANOVA (Table 3) revealed that volume increments during the outbreak were significantly influenced by stand type but not by the divergence level between BSFM and LW (groups). Mean growth increment for each stand type showed a stronger relative impact of spruce budworm in BSFM (Fig. 3). On average, BSFM annual growth increment during the 4-year budworm reduction period was 70% of the preceding 6-year period, while it was 80% in LW. This percentage was also negatively correlated with tree density in LW (Pearson's $r = -0.744$, $p = 0.0136$) but not in BSFM (Pearson's $r = 0.222$, $p = 0.5375$).

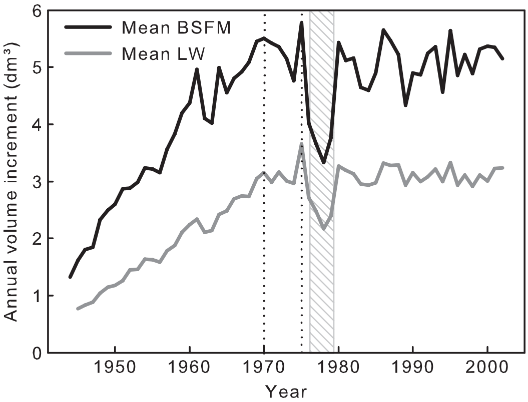

Fig. 3. Mean annual volume increment of dominant black spruce growing in LW and BSFM. The grey shaded period refers to a growth reduction related to a spruce budworm outbreak, while the period between dotted lines is the reference period used for calculating the impacts from the outbreak.

Carbon stocks

On average, BSFM stands stock over four times more carbon in tree biomass than LWs when all species are considered (Table 4). The same ratio applies when accounting for only black spruce, which represents 92% of total biomass carbon

Table 3. Summary of a split-plot ANOVA showing the tested fixed effects (REML) on the percentage of volume growth during the spruce budworm impact period.

Source	df	*F*-ratio	*p* > *F*
Group	1	0.1731	0.6883
Stand type	1	6.1732	**0.0166**
Group × stand type	1	0.3481	0.5580

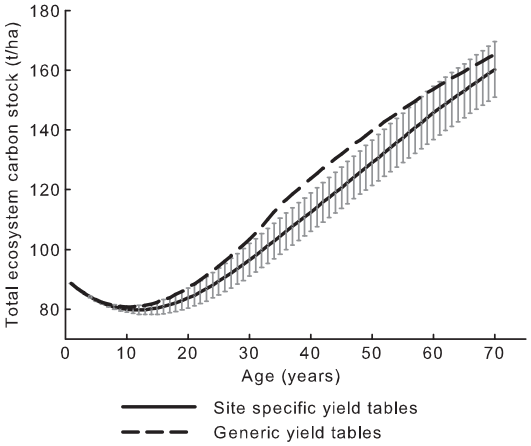

Fig. 4. Total carbon stock of BSFMs in this study (“site-specific yield tables”) along with the carbon stock of planted LW, as hypothesized in Gaboury *et al.* (2009, “generic yield tables”) and simulated with CBM-CFS3. Vertical bars are 95% confidence intervals.

stock in LW and 84% in BSFM. A comparison between the simulated black spruce biomass carbon stock and measurements revealed that CBM-CFS3 overestimated biomass carbon by 7.1% in LW but has an underestimate of 74% for the lowest tree density LW (L2, 75 trees ha^{-1}). In BSFM, the model underestimated biomass carbon by 14.2%.

The afforestation simulation scenario, using the same assumptions and yield tables as Gaboury *et al*. (2009), followed a slightly higher carbon stock growth curve than the one using yield tables based on the BSFM carbon stocks measured in the field (Fig. 4). During the first 70 years of development, which is the same period as studied by Gaboury *et al*. (2009), carbon stock for the afforestation scenario begins and ends within the 95% confidence interval of the BSFM mean, but it is slightly over these limits in the middle portion of the curve.

Discussion

LW growth potential

In this study, growth indicators used to compare site potential of LW and BSFM revealed that LW are generally less productive at the tree level. Due to the similarities between the two adjacent stand types in terms of site characteristics (soil deposits, drainage, slope, aspect, time elapsed since the last disturbance), the lower site potential in LW than in BSFM is unlikely to be explained by these site characteristics. This study, however, delves deeper into the question of the intrinsic lower productivity of LWs, with new insights

Table 4. Biomass carbon stock measured in the field versus simulated values from CBM-CFS3 scenarios at the age of sampling (*see* Table 2). Abbreviations: LW: lichen woodlands; BS: black spruce; BSFM: black spruce–feathermoss.

Block	LW biomass C stocks (t ha^{-1})				BSFM biomass C stocks (t ha^{-1})			
	All species measured	BS measured	BS simulated	Simulated – measured BS (%)	All species measured	BS measured	BS simulated	Simulated – measured BS (%)
L1	28	22	21	–5	116	88	76	–14
L2	19	19	5	–74	101	99	80	–19
M1	25	25	26	4	88	76	55	–28
M2	21	21	25	19	131	83	85	2
M4	14	14	23	64	107	100	87	–13
M5	23	23	23	0	119	112	89	–21
M6	31	21	32	52	124	75	73	–3
M7	31	30	31	3	107	92	77	–16
M9	34	34	37	9	122	122	97	–20
N1	39	36	35	–3	125	114	101	–11
Mean	26.5	24.5	25.8	7.1	114.0	96.1	82.0	–14.2
SD	7.5	6.9	9.1	37.0	13.1	16.2	13.1	8.9

revealed by looking at the growth and yield over decades. It shows that LW lags behind BSFM for the first 30 years at all sites, in agreement with studies looking at the short-term establishment phase of regeneration following silvicultural treatments and centered on ericaceous shrubs impacts (Mallik 1993, Thiffault *et al*. 2004, 2005, Thiffault and Jobidon 2006, Hébert *et al*. 2010a, 2010b). However, two growth patterns are possible thereafter: either volume increment continues to diverge for another 10 years, when LW tree growth remains approximately half of that found in BSFM, or it starts to converge until the disparity is substantially reduced after another decade, followed by a period of parallel growth. In this latter converging group, the difference in cumulative volume between both stand types is small, the volume of dominant trees in LW being 90% of that for trees in BSFM at 60 years; this difference is expected to decrease thereafter as the absolute difference of 15 dm^3 remains constant from year to year. In the diverging group, the volume of dominant trees in LW at 60 years is 47% of that for dominants in BSFM, and the disparity widens continuously. This finding of two subgroups of LWs, based on long-term site potential, suggests that site productivity cannot be assessed based solely on tree density, but also requires long-term growth patterns (Payette 1992, Riverin and Gagnon 1996, Côté *et al*. 2013).

Detailed growth analysis of stand types from the converging group revealed noticeable morphological differences between dominant trees growing in LW and BSFM. In this group, dominant trees from both stand types produced a similar stem volume, indicating equivalent site potential. One could argue that BSFM potential was underestimated as a higher tree density and competition may reduce dominant volume growth. However, LW growth potential may also be underestimated, as stem analysis neglects root volume, and there is evidence that black spruce root growth (Vincent *et al*. 2009) and total volume (Fradette 2013) increase even as tree density decreases. The present study addressed this tradeoff. The dominant tree biomass at 50 years, determined using allometric equations that includes roots, confirms that trees in productive LWs grow as fast as those in BSFMs. Besides, the morphological distribution of converging BSFMs and LWs stem volume was different; from 50 years onwards, dominant trees in LW were shorter but their basal area was greater. As a result, while 50-year dominant tree volume was equal between stand types, mean measured site index at this age was 11 m in LW but 13 m in BSFM. The site index therefore seems to underestimate site potential in LW, at least in those stands of the converging group.

In a search for explanations for the differential site potential among LWs, the impact of the last spruce budworm outbreak was investigated. However, there was no significant difference between stand groups (diverging *vs*. converging) in the magnitude of the growth reduction. As mentioned previously, differences between groups can be observed as early as at 20–30 years, but on average the outbreak occurred at 51 years of stand age. As such, we conclude that the spruce budworm outbreak had no influence on the convergence or divergence patterns between the growth of trees in LW and those in BSFM. However, the split-plot ANOVA revealed that the percentage of growth during the outbreak was affected by the stand type, with the growth reduction being relatively smaller in LW than in BSFM. Density seems to be the driver of this relationship, but in an asymptotic way, since it only had a significant effect on the density range of LWs, and not in that of BSFMs. Although it was not initially an objective of this study, this is probably the first time that an effect of stand tree density on the severity of a spruce budworm outbreak was observed. According to Dymond *et al*. (2010), future (currently occurring) spruce budworm outbreaks will be an important issue for the carbon dynamics of eastern Canadian forests in the near future. No other causes for this different site potential in LWs could be unraveled in this study, but possible avenues related to variable stressful growth conditions of open canopy micro-climates include hydraulic limitations, photoinhibition, and frost risks (Bazzaz and Carlson 1982, Grime *et al*. 1986, Bazzaz and Wayne 1994, Pearcy and Sims 1994, Groot 1999, Osmond *et al*. 1999, Archibold *et al*. 2000, Sperry 2000).

Carbon stocks and sequestration rates

As our results showed, tree-level site potential in LWs can occasionally be as high as that for plantation-density BSFM stands, i.e. 40% of all LWs in this study. Therefore, the latter may be considered valid surrogates for elevated site potential afforested LWs, meaning that tree density is the main differentiating factor between productive LWs and BSFM stands in terms of C stocking. This is also supported by the fact that natural BSFMs, with a tree density comparable to that in plantations, do not present an optimized tree distribution (as in plantations) nor do they benefit from the favourable growth conditions associated with scarification during the juvenile growth phase (Hébert *et al.* 2006). In addition, planted seedlings are produced from seed orchards or seeds harvested from trees specifically selected for their high growth potential. Furthermore, BSFMs in this study had an even-aged structure that therefore excludes the presence of older trees and their associated carbon stock. However, older trees would be present in LW that was not harvested prior to tree planting; this understory planting scenario should be the primary prescribed treatment mode as suggested by Boucher *et al.* (2012) and (Hébert *et al.* 2014). Altogether, these features prevent possible overestimates when comparing BSFM stand growth with that of afforested LWs having an inherently low site potential and constitutes a conservative comparison with afforested LWs that have a high site potential.

Our results indicate that growth rates used in the simulated sequestration rate for afforested black spruce (this study) as well as in previous simulations by Gaboury *et al.* (2009) and Boucher *et al.* (2012) were conservative, as the predicted 195 m^3 ha^{-1} at 80 years (MRN 2000) in planted LWs with black spruce is clearly lower than the 230 m^3 ha^{-1} measured in this study with natural BSFM stands of the same age. To our knowledge, it is the first time that measured growth yields of natural BSFM stands provide support to the use of generic growth yield tables for plantations. Growth yield being a strong determinant of C sequestration rate (Gaboury *et al.* 2009), these measured tree volumes in natural BSFM stands further validate the conservative approach used in the simulated C accountings for afforested LWs (Fig. 4, Gaboury *et al.* 2009, Boucher *et al.* 2012).

More field validation of the simulations presented in Gaboury *et al.* (2009) and Boucher *et al.* (2012), which also further support the conservative approach therein, comes from comparisons with measured carbon stocks in the biomass through use of specific allometric equations (Lambert *et al.* 2005, Fradette 2013) in the present study (Table 4). The average difference between both scenarios (intact LWs and surrogates of plantations with BSFM stands) resulted in net carbon stocks (114.0 – 26.5 = 87.5 t C ha^{-1}, SD = 12.5) somewhat higher than those stemming from the simulations of Gaboury *et al.* (2009) and Boucher *et al.* (2012) that produced values at maturity of between 60 and 70 t C ha^{-1}. New simulations of carbon stocks based on measured tree growth patterns indicate that compared with measured values, the amount of carbon stocked in the biomass of 80 year-old LWs is overestimated by 7% with the CMB-CFS3 simulations, while simulated carbon stocks in BSFMs are underestimated by 14%. This simulated versus measured biomass carbon stock comparison, altogether with the measured growth yields, also demonstrates the suitability of using CBM-CFS3 along with the generic yield tables for evaluating the net carbon balance of LW afforestation projects.

Implications for high-latitude afforestation

This study is the first to provide a measured estimate of carbon stock in mature black-spruce stands that have a stem density in the same range as that of plantations. It suggests that previous estimates, not using appropriate BSFM surrogate, may underestimate carbon stocks in afforested LWs. For example, the measured carbon of tree biomass was on average 114.0 ± 13.1 (SD) t ha^{-1} at a mean age of 80 years (density cover > 80%), while it was 51.2 t ha^{-1} in Bernier *et al.* (2011) (density cover 40%–60%). As our CBM-CFS3 simulations reached 135 years without showing any carbon stock peak, the C stocks measured in this study should still increase for decades as forest ages beyond 80 years.

While the financial cost of an eventual afforestation program might be an issue (Madec *et al.* 2012, Tremblay *et al.* 2013), it would be advised to account for probable intrinsic site conditions. This study shows that site potential in boreal LWs is variable, with two marked growth rate groups. What makes a LW potentially productive or not is currently unknown, but this study provides clues as to how to identify high potential LWs in order to prioritize them over less productive sites. Site index alone is a less accurate indicator than the dominant tree merchantable volume at 50 years, as the site index underestimates the wood volume growth potential and could lead to mistakenly rejecting a productive LW for afforestation. The differentiation of both productive and unproductive groups is clear, as high potential LW trees had a volume of about 100 dm^3 at 50 years, while low potential trees had a volume of 50 dm^3. Also, there is a tendency for the total basal area to be higher in the converging group (10.5 *vs.* 7.6 m^2 ha^{-1}), suggesting a denser tree cover (Jennings *et al.* 1999) that may help to mitigate the albedo-related forcing effect, which appears to be stronger when afforestation occurs on the most open LWs (Bernier *et al.* 2011).

This study supports the use of CBM-CFS3 as an appropriate tool for predicting carbon balance from LW afforestation projects. Although predictions were revealed to be more or less accurate in highly productive BSFMs, such as the ones in this study (230 m^3 ha^{-1} at 80 years) as well as in very low density LWs, the predictions still support conservative management strategies. Given that the quality of growth and yield data is also an issue (Mansuy *et al.* 2013), this study shows that CBM-CFS3 can be adequately fed by generic yield tables, as the modelled output of predicted carbon stocking for the afforestation scenario fell within the carbon stocking range of a natural BSFM stand.

Conclusions

Site potential of lichen woodlands (LWs) can be either lower or equivalent to that in dense black-spruce–feathermoss stands (BFSMs), thus contradicting the paradigm of systematic lower tree growth in the former. Stem analysis from dominant trees revealed that the annual volume increment in LW was comparable to that in BSFM at some sites, while it was lower at others. The future development of an efficient indicator for site potential, aiming to identify the most productive LWs for afforestation, would help in optimizing carbon drawdown in forest management. This study also validated the use of generic black-spruce yield tables for assumptions related to growth when simulating C dynamics in LW afforestation projects. These simulations seem, in fact, to be rather conservative and, as such, the carbon drawdown from boreal afforestation might be greater than that suggested by the models.

Given the potentially large availability of high-latitude LWs in North America and Russia (Shvidenko *et al.* 1997, Gaboury *et al.* 2009, Boucher *et al.* 2012), these findings can help push the concept of high-latitude afforestation closer to being an environmentally and economically efficient action for C offsetting (Boucher *et al.* 2012). However, other uncertainties related to high-latitude afforestation still needs to be addressed, in particular those associated with albedo change impacts, variations in volatile organic compound production, and the net present value of a given afforestation project (Bernier *et al.* 2011, Boucher *et al.* 2012, Ehn *et al.* 2014). But one of the most recognized issue, the reversal risk associated to wildfires, is better depicted in the light of this study. Knowing that low growth rate may worsens the impacts of fire losses (Mansuy *et al.* 2013), it shows that some of the LWs — for the least those that have a high site potential — should not be more impacted by fire than planted BSFMs, since their growth potentials are similar. This finds even more support in recent work suggesting that the higher density afforested LWs may be less susceptible to fires than open LWs (Cavard *et al.* 2015).

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