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ARTICLE

Forest productivity after careful logging and fire in black spruce stands of the Canadian Clay Belt

Cécile Leroy, Alain Leduc, Nelson Thiffault, and Yves Bergeron

Abstract: Some regenerating stands of the boreal forest exhibit low juvenile growth after major disturbances, which compromises sustainable forest management objectives. In black spruce – feather moss stands of eastern Canada subject to paludification, careful logging methods could decrease stand productivity with time by preventing a beneficial reduction in organic soil thickness. The aim of this project was to confirm decreases in juvenile growth between stands originating from careful logging and the former stands originating from old fires on the same sites. Stem analyses showed that stands originating from CPRS had significantly better juvenile height growth than the former stands but significantly lower growth than stands originating from recent fire in the study region. If organic matter thickness apparently played a role in the growth differences observed between fire and harvesting, it was not the only factor determining stand productivity. According to our results, cohort status, climatic regime, and quality of the residual organic matter are other factors that seem to drive productivity. Our results show that postharvest management approaches (e.g., site preparation) should be used to increase yields after harvest for the sites to express their full growth potential.

Key words: black spruce (*Picea mariana*), paludification, height growth, careful logging, fires.

Résumé : En forêt boréale, certains peuplements régénérés par des perturbations majeures montrent une faible croissance juvénile. Cela compromet les objectifs de gestion durable de la ressource forestière. Dans les peuplements de la pessière noire à mousses de l'est du Canada sujets à la paludification, les méthodes de coupes limitant les impacts sur les sols et la régénération pré-établie (CPRS, CLAAG) pourraient diminuer la productivité des peuplements dans le temps, en évitant une réduction bénéfique de l'épaisseur de la matière organique. Ce projet avait pour objectif de vérifier s'il existe une diminution de croissance juvénile entre des peuplements issus de coupes à faibles impacts et la génération précédente de peuplements issus de feux anciens, sur les mêmes sites. Des analyses de tiges ont montré que les peuplements issus de CPRS avaient une croissance juvénile en hauteur significativement supérieure aux précédents peuplements, mais significativement inférieure à celle mesurée dans des peuplements post-feux récents dans la zone d'étude. Si l'épaisseur de matière organique semblait jouer un rôle dans les différences de croissance observées entre feu et coupe, ce n'était pas le seul facteur déterminant la productivité du peuplement. Selon nos résultats, la cohorte, le régime climatique et la qualité de la matière organique résiduelle sont d'autres facteurs qui semblent conditionner la productivité. Nos résultats montrent que des interventions de préparation des sites après coupe devraient être utilisées pour permettre aux sites d'exprimer leur plein potentiel de croissance.

Mots-clés : épinette noire (*Picea mariana*), paludification, croissance en hauteur, coupes à faibles impacts (CPRS, CLAAG), feux.

Introduction

In Canada, black spruce (*Picea mariana* (Mill.) BSP) is a major commercial species that supports the forest products industry (Viereck and Johnston 1990; Burton et al. 2010). In boreal forests of Interior Alaska, Labrador, and the Clay Belt of Quebec and Ontario, black spruce stands develop naturally thick forest floors of partially decomposed organic matter (OM) (Taylor et al. 1988; Fenton et al. 2005). In those paludified areas, stand productivity naturally declines as forest floor thickness increases over time (>40 cm) (Simard et al. 2007).

Growth and dynamics of black spruce – feather moss forests in these regions are naturally regulated by the fire regime (Fenton et al. 2005). High-severity fires usually result in dense and productive stands by consuming OM (Fenton et al. 2005; Lecomte et al. 2006). Since the 1970s, timber harvesting has replaced large-scale natural fires as the major forest disturbance in the northern commercial boreal forest (Boucher et al. 2009). In the mid-1990s, to reduce soil erosion and the costs of artificial regeneration after clear-cutting, careful logging around advanced regeneration and soils was implemented, especially in Quebec (Cut with Protection of advanced Regeneration and Soils, CPRS; Boucher et al. 2009) and in Ontario (Careful Logging Around Advanced Growth, CLAAG; Groot 1995). Recently, concerns have emerged regarding those silvicultural practices that are characterized by their low

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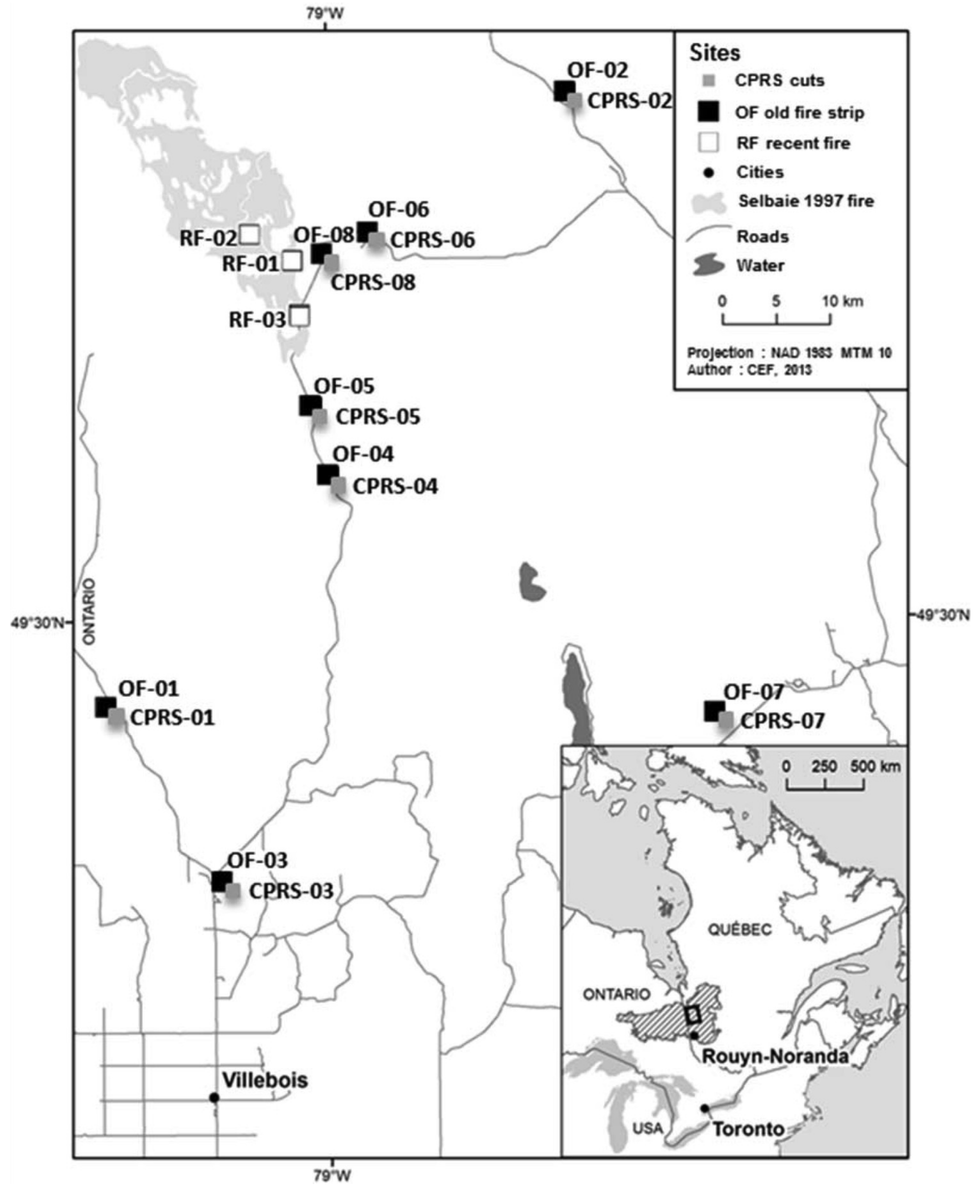
Fig. 1. Location of the study area and sampled sites within the Canadian Clay Belt. Each harvested site (CPRS) is paired with an old-fire site (OF) located in the closest retention strip. The hatched area in the inset corresponds to the Clay Belt and Cochrane Till geological formations.



impact on soil organic layers, mainly in their ability to maintain forest productivity of harvested stands (Lafleur et al. 2010*a*). These concerns appear especially relevant to current yield tables that are used by forest agencies and are still mainly based on the growth of productive stands originating from fires.

The effects of paludification, fire severity, and different logging methods on black spruce – feather moss stand growth, regeneration, structure, and productivity have been documented extensively, usually through comparisons of sites with varying times since fire and disturbance origins (Pothier et al. 1995; Groot and Adams 2005; Lecomte et al. 2006; Simard et al. 2007; Lavoie et al. 2007*a*; Lafleur et al. 2010a). However, studies that have compared the growth of successive black spruce regeneration in different sites (using chronosequences) raise the issue of potential differences in growing environments among study sites (Simard et al. 2007; St-Denis et al. 2010). To circumvent this limitation, our study aimed to compare successive regeneration growth and productivity on the same sites using a dendrochronological approach. To assess the current full growth potential of black spruce stands in the study area, we also compared the current growth of regenerating CPRS stands with the current growth of recent fire regeneration. Finally, we aimed to identify microsite variables that could explain growth differences, if any.

We expected regenerating CPRS stands to exhibit lower juvenile growth rates than stands regenerating after old or recent fires. Further, we expected the old-fire stands to have lower juvenile growth than recent fire stands because of past climatic conditions that were unfavourable to tree growth (Bergeron and Archambault 1993; Fantin and Morin 2002). We finally hypothesized that OM thickness was the main factor responsible for decreases in growth between regenerating fire and CPRS stands. The effects of other microsite variables were also considered.

Materials and methods

Study area

The study was conducted in northwestern Quebec, in the James Bay administrative region (49°16′N–49°57′N, 78°30′W–79°18′W)

Table 1. Site characteristics in terms of origin, regeneration, and site index.

Origin site	Observed disturbance year (vs. fire-map year)	Stem age (years) in 2010, mean ± SD (min–max)	Height (m) in 2010, mean ± SD	Height (m) at harvest time, mean ± SD	Mean site index	% of layer trees*	Total black spruce stocking (BS stocking > 1 m), %	Black spruce density > 1 m, no.·ha⁻¹
Old fire (OF)								
OF-01	1750 (1825)	179±45 (82–261)	8.3±1.3		4			
OF-02	1765 (1871)	190±26 (139–246)	13.5±3.0		6			
OF-03	1844 (1916)	119±27 (81–167)	13.8±3.7		8			
OF-04	1753 (1725)	161±47 (92–258)	14.3±2.4		6			
OF-05	1770 (1775)	196±38 (101–241)	15.0±3.0		6			
OF-06	1716 (1775)	177±42 (117–295)	13.8±3.4		8			
OF-07	1862 (1825)	144±3 (139–149)	14.2±2.1		10			
OF-08	1775 (1886)	148±36 (105–236)	12.9±2.5		8			
CPRS								
CPRS-01	1994	27±11 (11–51)	1.77±0.67	0.23±0.20	10	63	90 (60)	8750
CPRS-02	1996	49±23 (19–116)	1.69±0.61	0.63±0.36	9	60	100 (70)	4500
CPRS-03	1996	38±14 (12–70)	2.31±0.87	0.57±0.42	10	68	90 (90)	5000
CPRS-04	1997	28±12 (11–62)	2.29±0.78	0.29±0.24	12	65	90 (70)	9750
CPRS-05	1997	36±12 (9–68)	1.98±0.83	0.51±0.30	11	60	100 (80)	6750
CPRS-06	1995	31±13 (12–65)	2.07±1.04	0.39±0.40	10	55	80 (60)	5500
CPRS-07	1997	29±14 (11–71)	1.82±0.58	0.38±0.37	10	75	100 (90)	7750
CPRS-08	1995	42±20 (13–93)	1.90±0.78	0.50±0.40	11	78	80 (70)	4250
Recent fire (RF)								
RF-01	1997	15±3 (11–28)	2.29±0.66		13	10	60 (50)	1500
RF-02	1997	13±5 (10–35)	1.78±0.48		13	15	90 (40)	2500
RF-03	1997	11±1 (7–13)	1.47±0.35		13	22	80 (10)	250

Note: Site index is the estimated stem height (in m) at age 50 (based on Mailly and Gaudreault 2005).
*Number of layer trees/total number of trees × 100

(Fig. 1). The southern portion of the study area was located in the Canadian Clay Belt. The northern portion was covered with Cochrane Till (Veillette 1994). Topography is mostly flat in this area. We located the study sites inside the bioclimatic subdomain of the western black spruce – feather moss forest, where dwarf ericaceous shrubs dominate the understory and sphagnum mosses, feather mosses, and occasionally lichens dominate ground vegetation (Saucier et al. 2009). During the period 1971–2000, mean annual temperature was 0.1 °C, mean annual precipitation was 892 mm, and the mean annual growing degree-days > 5 °C (GDD) was 1249. The mean annual frost-free period lasted about 60 days, with occasional frosts during the growing season (climatic data from the Joutel weather station of Environment Canada (2013)). The geological deposits, topography, vegetation, and cold climate enhance the paludification processes in this region (Lavoie et al. 2005).

Study site selection

To compare the juvenile growth of stands originating from old fires vs. CPRS harvesting on the same sites, we measured the juvenile growth of the harvested stands by sampling adult trees that had been left by harvesting operations in retention strips. These trees originated from old natural forest fires that dominated the natural landscape (Bergeron et al. 2004); they represent the growth patterns of the preharvest natural stands. We compared the juvenile growth of those old natural stands with the current growth of regenerating CPRS stands on the same sites. In doing so, we were able to test for a decrease in stand productivity that was related solely to disturbance origin. We selected 15-year-old cuts (hereafter denoted CPRS) that contained remnants of the previous old-fire stands (hereafter denoted OF).

Site selection was based on ecosite characteristics, as described on 1:20 000 forest maps produced by the provincial government. We selected mesic to subhydric black spruce – feather moss stands that were established on fine-textured soils, with very low to negligible slopes. In these target areas, we located CPRS that dated from 1994 to 1997 (Table 1). Among the CPRS cutblocks, we included only those in which the last fire occurred 100 to 150 years ago, according to regional wildfire maps (Bergeron et al. 2004), so that trees in the OF retention strips would belong to the first cohort that had established after fire.

We retained eight paired sites containing both CPRS regeneration and OF trees that were provided by retention strips (further identified as CPRS-01 to CPRS-08 and OF-01 to OF-08, respectively) (Fig. 1). We stratified the sampling design in CPRS with a gradient of potential productivity, which was determined by mean site OM layer thickness. OM thickness affects stand productivity at values above 40 cm (Fenton et al. 2005). Sites CPRS-04, CPRS-06, CPRS-07, and CPRS-08 had OM layers less than 40 cm thick. Sites CPRS-01, CPRS-02, CPRS-03, and CPRS-05 exhibited OM layers that were more than 40 cm thick.

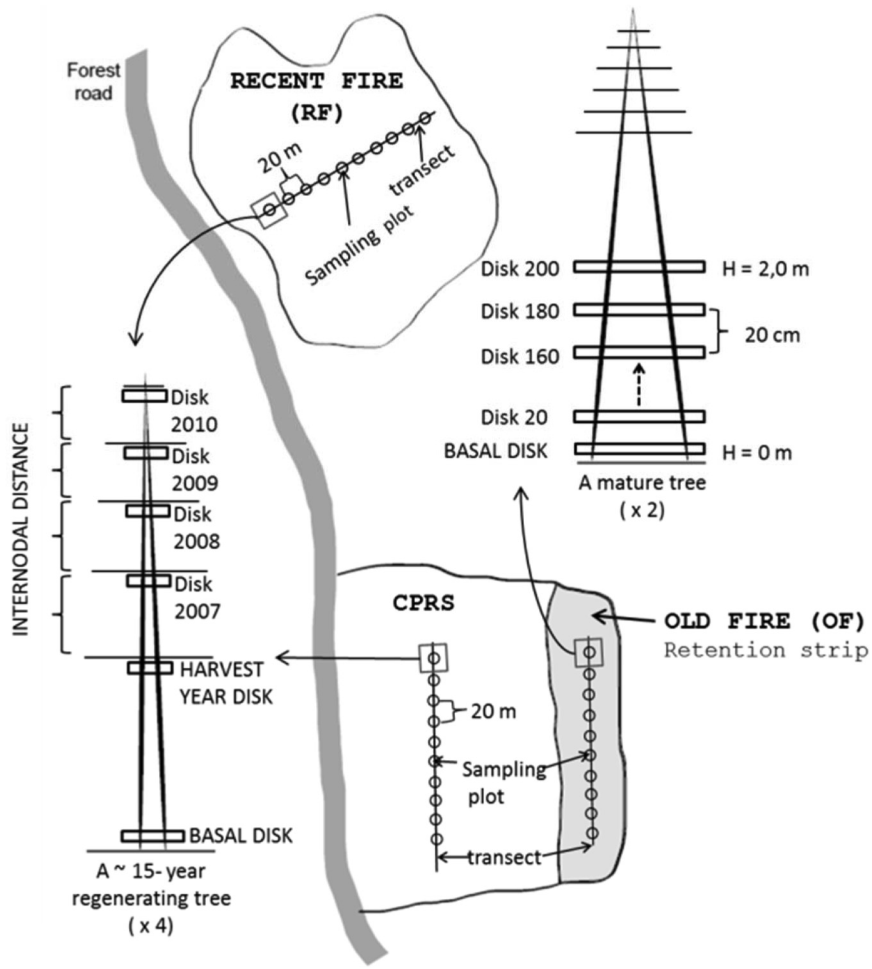
To estimate the full growth potential of the study area, we supplemented the sampling with stands that originated from recent fires (RF), which were of similar age as the CPRS and exhibited the same ecological characteristics. Only one wildfire occurred in 1997 in the study area. We sampled three sites in this wildfire area (RF-01 to RF-03) to encompass a wide range of variability in growth conditions and to obtain a statistically sufficient number of sample trees. RF-01 was selected as an indicator of local maximum potential growth, as the site had a thin OM layer. The site had been planted with black spruce seedlings 1 year after the fire, without prior soil preparation. Sites RF-02 and RF-03 were characterized by natural regeneration (without soil preparation). Site RF-02 was selected for its relatively thin OM layer, and site RF-03 was selected for its thick OM layer (>40 cm).

This also allowed us to check if the growth differences between stands originating from old fires versus CPRS harvesting could be linked to a change in the climatic conditions.

Sampling design and study tree selection

To randomly select study trees that represented the growth potential of each condition, we established a 10 variable-radius plots transect (as opposed to a fixed-area plots transect) on each CPRS, OF, and RF site (Fig. 2). Each plot was 20 m equidistant from the other. In plots that were located within the retention strips, we selected the two dominant merchantable trees that were

Fig. 2. Sampling design used in this study to compare juvenile growth between stands originating from harvesting with protection of advanced regeneration and soils (CPRS) and the former stands originating from old fires (OF) on the same sites. Recent fires (RF) in the study region were also sampled to evaluate growth after the recent fire.



closest to the plot center and representative of the trees that were harvested, according to the point-centered quarter method (Mitchell 2010). These stems had to be ≥7 m in height with ≥9.1 cm DBH (diameter at breast height, 1.3 m), for a total of 20 trees per strip. In CPRS and RF regenerating stands, we selected the most vigorous and tallest four stems that were closest to the plot center. We considered those stems as potential future merchantable stems (for a total of 40 stems per regenerating stand). Field sampling was performed during summer 2011 for the CPRS and OF mature stands and during summer 2012 for the RF regenerating stands.

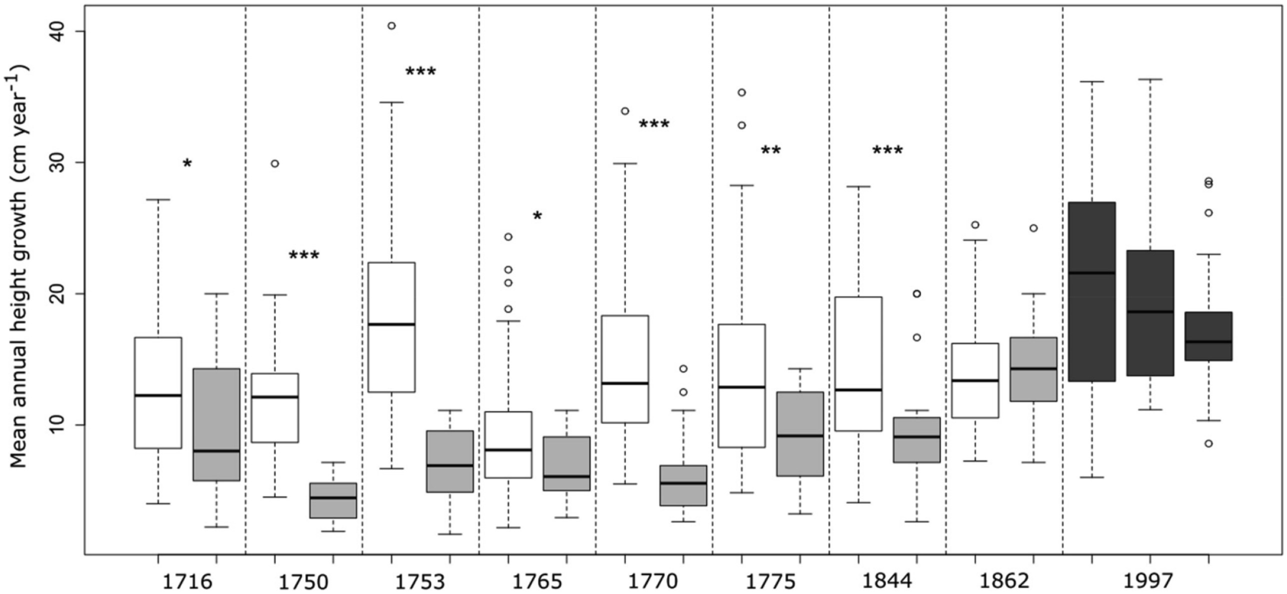
Height growth and site index

The study focused on juvenile growth potential as influenced by stand origin (CPRS, OF, RF). For regenerating stands that originated from CPRS, we studied the mean annual height growth between 2005 and 2010. We made this choice because height growth exhibits little correlation with competition resulting from stand density during earlier years of stand development (Lanner 1985). The 2005–2010 period allowed us to avoid the slow growth recovery period characterizing pre-established regeneration following CPRS (Paquin et al. 1999; Lafleur et al. 2010*b*). Juvenile growth on the RF sites was assessed for the same period (2005–2010). CPRS and RF juvenile height growth is referred to hereafter as "current growth."

For mature trees that were sampled in retention strips, we calculated mean annual height growth that was measured from stem disks collected at heights of 1 and 2 m. These heights corresponded to the range of CPRS and RF mean height regeneration for the period 2005–2010. This technique utilized interpolation of annual growth between heights of 1.0 and 2.0 m (Fantin and Morin 2002). Our approach was supported by the fact that tree height growth measured below a height of 1.0 m is typically a period during which growth does not reflect real site potential (Carpentier et al. 1993). OF juvenile height growth was subsequently referred to as "past growth."

We used stem analyses to reconstruct height growth patterns of the juvenile stage (Fig. 2). For regenerating CPRS and RF trees, we collected the entire stems and measured the internodal distance of each year of growth after disturbance, using apical bud scars. To confirm scar-based dating, we cut, dried and sanded one disk in the upper third of each recognizable internode up to the harvest year (Payette and Filion 2010). We also dated the basal disk on each stem to assess layer and seedling ages. For mature stems that were sampled in OF retention strips, we collected a wood disk every 20 cm, from 0 cm (immediately above the stump) to 2.0 m height on the stems. The stem disks that were obtained from mature trees were dried and sanded. Each disk was precisely dated with a visual crossdating method based on black spruce dendroclimatic chronologies from the study area (Drobyshev et al. 2010). A minimum age was determined for the mature trees by dating the basal disks (Table 1).

Fig. 3. Box-and-whisker plots of mean annual height growth and organic matter (OM) thickness comparisons between paired harvested sites (CPRS, white boxes) and old-fire sites (OF, light grey boxes) and for recent fires (RF, dark grey boxes, right side of figure). Significance of differences is indicated by asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.



Site indices (SIs) are commonly used in forest management to evaluate stand productivity. They provide forest managers with a predicted height that stands are likely to achieve at a given age (50 years old in Quebec). To relate juvenile mean annual height growth to forest management targets, we calculated the corresponding SI values. Because height growth is mainly insensitive to stand density (Lanner 1985), SI is generally considered as a good measure of site growth potential. We calculated SI following Mailly and Gaudreault (2005) (Appendix A).

Explanatory variables of tree growth

As OM thickness is usually strongly correlated with tree growth in paludified areas (Simard et al. 2007), we measured the thickness of the different OM layers according to the von Post classification (fibric, mesic, humic; Saucier et al. 1994) for each sampled stem. In the retention strips, we measured tree rooting depth to estimate OM depth at the time of establishment.

According to Pothier et al. (1995), we hypothesized that initial stand height of the advance growth in CPRS would represent an advantage for the trees. Thus, we determined initial height and age at the time of disturbance for each of the stems that were sampled in CPRS.

As a review of the literature shows that layer growth is slower than growth of seedlings (Doucet and Boily 1986), we attributed a regeneration mode (layering or seedling) to each stem sampled in the CPRS and RF sites. Given that growth substrate (Lavoie et al. 2007*b*) and ericaceous competition (Thiffault et al. 2013) have been documented to affect tree growth, we estimated the percent cover of woody perennials (ericaceous shrubs, tree species), herbaceous species, and feather mosses, sphagnum, and lichens in 4 m^2 circular subplots that were centered on each variable-radius plot used to select study trees (Lafleur et al. 2010*b*). In these subplots, we also counted individual black spruce stems to evaluate regeneration success at the site level (density and stocking). Because of mortality that occurred over time, regeneration density and distribution could not be determined in the retention strips.

Statistical analysis

All analyses were performed in the statistical software package R (R Core Team 2015). Using analyses of variance (ANOVA), we evaluated stand origin effects on mean height growth. The response variables "current growth" for CPRS and RF origins and "past growth" for OF origin were square-root-transformed to meet normality and homoscedasticity assumptions. For each stand origin, we used linear models to check the effects of stem age, height, and OM thickness on growth.

We performed linear mixed models to identify the most important variables that explained growth differences observed between origins at the stem scale with the "nlme" library (Pinheiro et al. 2015). Linear mixed models were the most suitable models given our hierarchical sampling design "tree–plot–site" and its possible effect on tree growth (Burnham and Anderson 2002). We first checked the potential correlations between the different explanatory variables by calculating Spearman correlation coefficients (Legendre and Legendre 2012). We set the correlation threshold above which two correlated variables could not be retained both at |0.5| and retained the biologically interpretable ones. Among them, after trying several variables combinations, we retained the explanatory variables that were significant in the models. We used common models for recent regeneration stands (CPRS and RF origins).

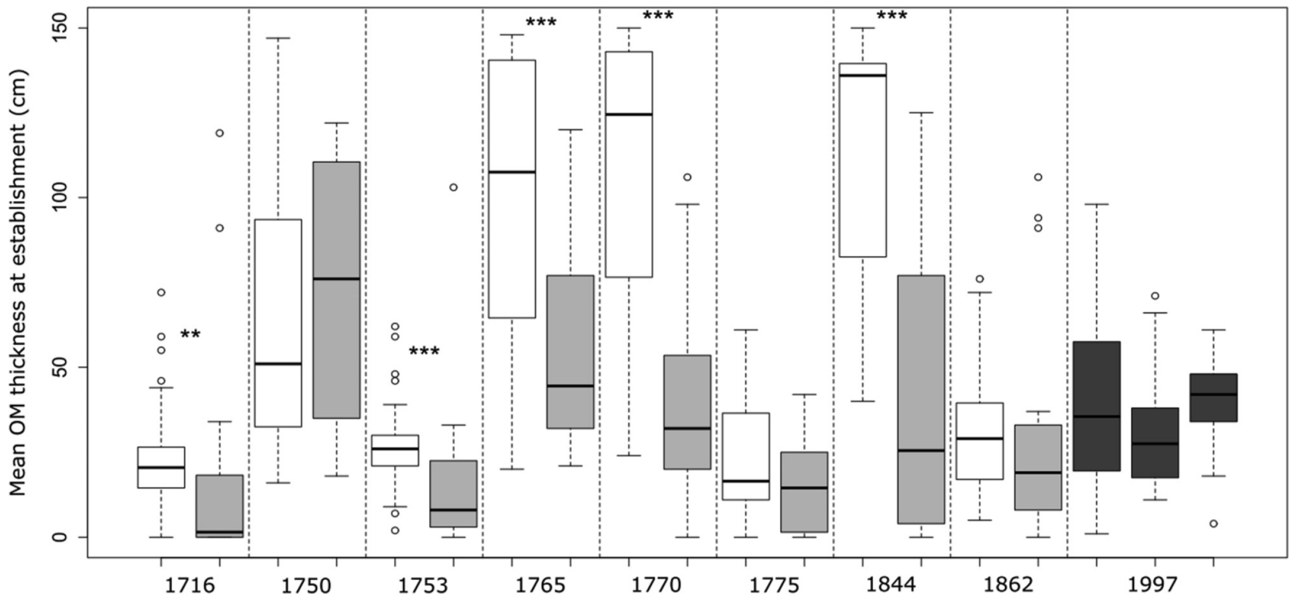
We used maximum likelihood estimation to compare models in terms of fixed effects, according to the Akaike information criterion adjusted for small sample size (AIC_c). The significance of each variable was then checked using the method of multimodel inference based on AIC_c. We conducted these analyses with the "AICcmodavg" library (Mazerolle 2016). The portion of variance that was only linked to some microsite characteristics was also calculated (Burnham and Anderson 2002).

Results

Effect of stand origin on height growth

Stand origin had a significant effect on height growth ($P < 0.001$). Current growth was 13.9 ± 6.6 cm·year^{-1} (mean ± SD) for CPRS stands. Past growth of the OF stands on the same sites was 8.4 ± 0.7 cm·year^{-1}. RF stands' current growth was 18.9 ± 6.3 cm·year^{-1}. Mean height growth of each stand is presented in Fig. 3. Most of the paired CPRS–OF stands showed that CPRS trees grew better than trees belonging to the OF original forest (Fig. 3). CPRS stems had a height growth rate two times higher (SD ± 0.7) than that of OF stems, even if some low-productivity sites showed little

Fig. 4. Box-and-whisker plots of mean organic matter (OM) thickness comparisons between paired harvested sites (CPRS, white boxes) and old-fire sites (OF, light grey boxes) and for recent fires (RF, dark grey boxes, right side of figure). Significance of differences is indicated by asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The x axis is the minimum year of the last fire occurrence, according to regional fire maps (Bergeron et al. 2004); the eight sampling sites are ordered from oldest to youngest.



response (CPRS-01–OF-01 and CPRS-02–OF-02; Fig. 3). Only paired CPRS-07–OF-07 sites showed no significant growth difference between CPRS and OF origins ($0.05 < P < 0.1$). Site index at 50 years (SI_{50}) calculations confirmed that potential productivity of the CPRS stands was significantly better than OF stands' potential productivity (Table 1). Mean CPRS SI_{50} was 10 m compared with 7 m for OF sites. Low OF SI_{50} did not correspond to low SI_{50} in the paired CPRS. RF stands exhibited the highest productivity potential in the study area, with mean SI_{50} = 13 m (Table 1). Comparing the growth of full-sun OF stems (the first cohort of stems on each site) with that of CPRS stems for a given OF SI_{50} revealed that only OF-07 had a better growth than its paired CPRS (Appendix B, Table B1).

Influence of initial stem and stand characteristics

In CPRS stands, stem height at the time of harvesting had a positive significant effect on stem current growth ($P < 0.05$). Pre-established taller stems appeared to grow better, regardless of their age at the time of harvesting ($P > 0.1$). Fire age estimated onsite often differed from that indicated on regional fire maps (Table 1); OF stands were far older than expected from the Bergeron et al. (2004) study in the area. Age analysis of individual trees usually showed asynchronous establishment in the different stands, except for OF-07 (see Table 1). Most trees in OF stands appeared to belong to the second cohort (or elder cohort, depending on time since last fire) of trees that established after fire. As expected, trees originating from old fires established over thinner OM than trees regenerating from the recent fire and CPRS ($P < 0.001$; Fig. 4). OM averaged 25 cm (SE ± 11.1) thicker on the CPRS stands than on the paired OF stands (Fig. 4). OM thickness negatively affected mean annual height growth of CPRS and OF trees (Figs. 5*a* and 5*c*) but did not affect trees originating from the recent fire (Fig. 5*b*). Thickness of the different OM layers had less of an effect on height growth compared with total OM thickness ($0.05 < P < 0.1$ for total thickness; $0.4 < P < 1.0$ for fibric layer thickness). Individual layer thickness was not subsequently considered in the analysis.

Growth model comparison and selection

Given the likely existence of a "site and plot effect" on growth that we could not control, we introduced "nested plots in sites" as a random effect in the models. For CPRS and RF origins models, we retained three nested models:

$$\text{Microsite model} = \sqrt{(H\text{ growth})} \sim \text{Total OM thickness} + \text{RegeMode} + \text{Vaccinium Pc}$$

$$\text{Origin model} = \sqrt{(H\text{ growth})} \sim \text{Origin disturbance} + \text{Total OM thickness} + \text{RegeMode} + \text{Vaccinium Pc}$$

$$\text{Allometric model} = \sqrt{(H\text{ growth})} \sim \text{Origin disturbance} + \text{Total OM thickness} + \text{RegeMode} + \text{Vaccinium Pc} + \text{Initial } H$$

where "H growth" is the current mean annual height growth, "Origin disturbance" is the disturbance from which the stand originated (CPRS or RF), "RegeMode" is the regeneration mode of the stem by seed or by layering, "Vaccinium Pc" is the percentage of ground surface covered by *Vaccinium* spp., and "Initial H" is stem height at the time of disturbance. The microsite model aimed to identify the portion of variance that was only linked to microsite characteristics (Burnham and Anderson 2002). The origin model only contained microsite variables and the stand origin. The allometric model contained the previously mentioned factors, together with the allometric component, i.e., stem height at the time of disturbance.

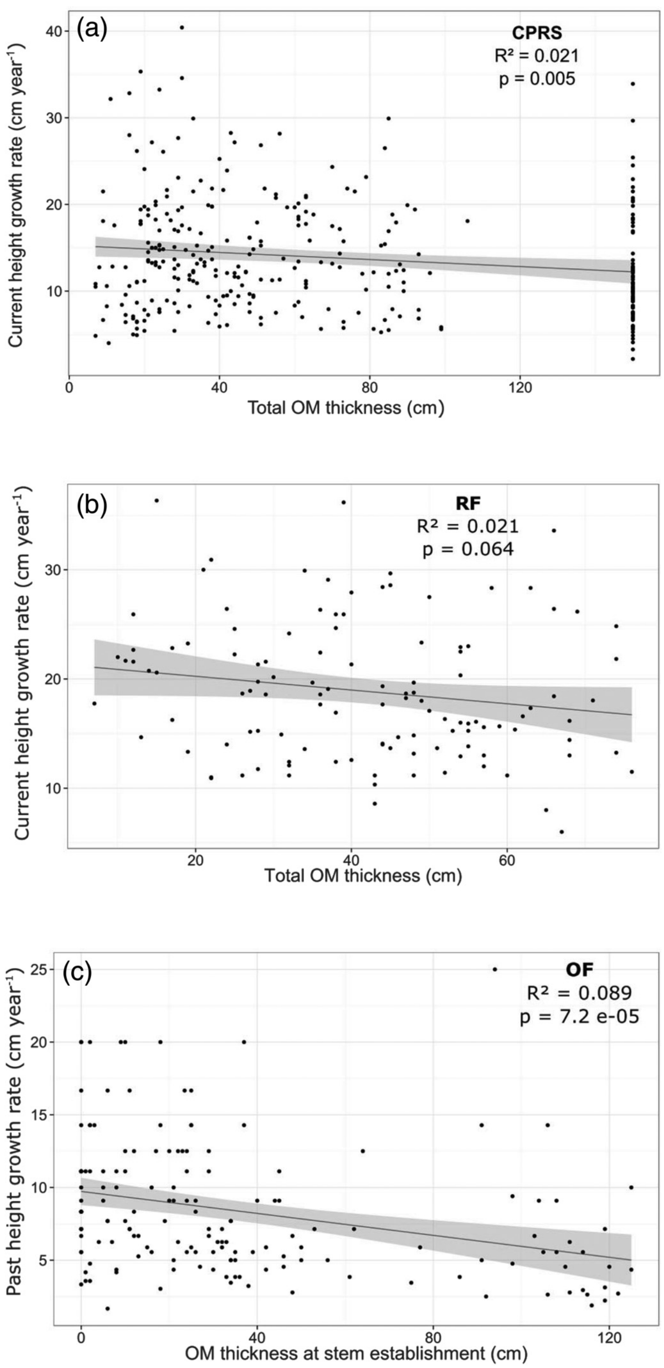
In OF origin stands, we only selected two models to explain past growth as there were too few juvenile growth variables that could be measured in 2011:

$$\text{Status model} = \log(H\text{ growth}) \sim \text{1mDiskYear} + \text{CoverLight}$$

$$\text{OM model} = \log(H\text{ growth}) \sim \text{1mDiskYear} + \text{CoverLight} + \text{OMThickAtEstablishment}$$

where "H growth" is the past mean annual height growth, "1mDiskYear" is the year in which the stem reached 1 m in height,

Fig. 5. Total organic matter (OM) thickness effects on juvenile growth for regeneration that had established in (*a*) harvested (CPRS), (*b*) recent-fire (RF), and (*c*) old-fire (OF) sites (retention strips located in the CPRS). For RF stems, four outliers were excluded from the plot.



"CoverLight" is a criterion that defines whether the young stem grew in full sun or under cover, which was calculated from radial growth data (for further details, see Appendix B), and "OMThickAtEstablishment" is OM thickness at the time of stem establishment. The comparison of the OM model and the status model allowed us to determine which portion of the variance was attributable to the variation in OM thickness.

For recent regenerating stands (CPRS and RF origins), the allometric model that controlled for size effect at the time of disturbance was the best model (AIC_c ω = 1.0; Table 2). Stem height at the time of disturbance explained 57% of the variance in the allometric model. Despite the addition of the variables total OM thickness, RegeMode, and Vaccinium Pc, the stand origin disturbance (CPRS or RF) still accounted for 35% of the variance in the origin model. Multimodel inferences that were based on mixed-model AIC_c criteria for CPRS and RF origins (Table 3) showed that stem height at the time of disturbance and *Vaccinium* spp. cover were weakly significant; they did not have much explanatory weight in the models (confidence intervals close to 0). OM thickness (over 70 cm) had the most significant effect on growth. Overall, this analysis confirmed the significance of the variables stand origin disturbance and regenerating mode (layering or seed). Among the models that were tested, the OM model best explained height growth on OF sites (AIC_c ω = 0.82), again illustrating the effect that OM thickness exerts on productivity (Table 2). OM thickness at the time of stem establishment accounted for 19% of the variance in the OM model. Multimodel inferences for OF sites (Table 3) showed that OM thickness > 25 cm was the most significant driver of growth. Under-cover or full-sun status was also significant, whereas the year in which the stem reached 1 m height was not.

Discussion

Our study refuted the first prediction that CPRS stands would have lower juvenile growth than the former black spruce stands on the same sites. However, it confirmed the second prediction that RF stands experienced better growth than OF and CPRS stands. The results showed that, consistent with our hypothesis, OM thickness played a key role in explaining growth differences between stand origins. Nevertheless, the analysis also demonstrated that OM was not the only factor controlling stand growth.

Comparing past and current juvenile growth of a site

Our results did not show a decrease in site productivity following CPRS, despite the thicker OM layer in which the regenerating stems had rooted in CPRS compared with the estimated OM thickness in OF at the time of stem establishment. Similar results have been reported for two postfire regeneration cohorts on the same sites, which were located in lichen – black spruce woodlands (Côté et al. 2014). One possible explanation is that most OF stems did not belong to the first cohort of trees that had established after fire. Radial growth analysis (Appendix B) indeed showed that more than two-thirds of OF stems that were sampled had not reached "full-sun" growth status, as defined by Wright et al. (2000). Thus, we suspect that these were trees from the second cohort after fire. A drop in productivity of successive cohorts is consistently observed over the study area (Simard et al. 2007). Later cohorts rooted in a thicker OM layer (Simard et al. 2007) and grew under the cover of the previous cohort(s) (Grondin et al. 2000). Mixed models confirmed that OM thickness at the time of stem establishment negatively affected their mean annual height growth, especially when OM thickness exceeded 40 cm.

A second potential explanation for the growth difference that we observed between OF and CPRS stands is related to the unfavourable climate under which OF juvenile growth occurred. Juvenile growth of OF stems mostly took place prior to 1900 during the Little Ice Age (LIA), which was characterized by extremely cold meteorologic conditions, even during summer (Price et al. 2013). This period is associated with a characteristic limitation of tree growth (Bergeron and Archambault 1993; Fantin and Morin 2002). Growth rates that we measured in OF and RF stands are consistent with those that were reported by Grondin et al. (2000) for this region. The supplementary analysis compared the growth of full-sun OF stems and CPRS stems for each OF SI_{50} class (Appendix B). OF stems from the first cohort that grew during the LIA period exhibited slower height growth than CPRS stems did for a similar site potential. This supports the hypothesis of a climatic effect on growth.

Table 2. AIC_c results for mean annual height growth explanatory models for the three stand origins.

Models	*K*	AIC_c	ΔAIC_c	AIC_c weight (ω)	Cumulative weight (ω)	Log-likelihood	Model R^2
CPRS and recent-fire (RF) sites							
Allometric model	10	1003.97	0.00	1	1	−491.73	0.55
Origin model	9	1031.69	27.72	0	1	−506.64	0.49
Microsite model	8	1037.29	33.32	0	1	−510.48	0.49
Null model: 1	4	1043.44	39.48	0	1	−517.68	
Old-fire (OF) sites							
OM model	7	151.75	0.00	0.82	0.82	−68.41	0.76
Status model	6	154.76	3.02	0.18	1	−71.04	0.75
Null model: 1	4	173.56	21.81	0.00	1	−82.62	

Note: AIC_c, Akaike information criterion adjusted for small sample size.

Table 3. Multimodel inference results based on AIC_c of each model for the three stand origins.

Variables	Multimodel inference estimate (regression coefficient)	SE	95% CI (lower limit, upper limit)
CPRS and recent-fire (RF) models			
Vaccinium Pc	−0.01	0	−0.01, 0
Initial *H*	0.01	0	0, 0.01
RegeMode: seedlings	0.22	0.08	0.07, 0.38
Total OM thickness >70 cm	−0.32	0.14	−0.59, −0.05
Total OM thickness 35–70 cm	−0.07	0.10	−0.26, 0.12
Origin disturbance: CPRS	−0.88	0.21	−1.30, −0.46
Old-fire (OF) models			
OMThickAtEstablishment >25 cm	−0.19	0.08	−0.36, −0.03
CoverLight: cover	−0.28	0.09	−0.45, −0.11
1mDiskYear	0	0	0, 0.01

Note: AIC_c, Akaike information criterion adjusted for small sample size; SE, standard error; CI, confidence intervals.

Estimating the actual juvenile growth potential of the study area

Current juvenile growth in CPRS was not reduced compared with past juvenile growth in the previous stands, but it was slower than the juvenile growth that we measured for regeneration following a recent fire. This fire occurred during the same period and, thus, under a similar climate in the study area. Fire severity varies both across and within fires (Miyanishi and Johnson 2002). It would be unwise to generalize what was observed in this particular fire to other fire events, but we sampled a wide range of variability with the plots on the study site. Given that it was partially consumed by fire, OM was significantly thinner in RF stands compared with CPRS stands. OM thickness had a negative effect on tree growth; although it did not strongly differentiate growth among stand origins, it was the most limiting "microsite" explanatory variable of height growth for a given origin.

Despite being characterized by a thicker OM layer, RF sites generally exhibited better growth than CPRS sites. Within RF sites, OM thickness did not significantly affect height growth, which indicates that it was not the only microsite factor limiting growth. Stand origin had a significant effect on growth when the models controlled for OM thickness, regeneration mode, initial stem height at the time of disturbance, and *Vaccinium* cover. Other variables that are known to vary with stand origin disturbance (e.g., soil nutrient availability or pH) should be measured to identify the specific mechanisms conditioning tree growth. Indeed, we observed significant differences between CPRS and RF soils from the forward-looking measures made 15 years after disturbance (see Appendix C). Soils from the RF stands were more fertile (lower C–N ratio), were less acidic, and had higher nutrient concentrations than soils from the CPRS stands. We assume that charcoal resulting from the incomplete OM combustion during fire partially explained soil responses (Wardle et al. 1998) for young stands (Brais et al. 2015). The beneficial effects of charcoal on soil fertility can indeed be measured up to 30 years after disturbance (Saarsalmi et al. 2012).

Management implications

The results have direct management implications for silviculture and the management of boreal sites that are characterized by OM accumulation following major disturbances. First, the results demonstrate that there is a positive relationship between initial height of advance regeneration and postharvest growth rates on paludified sites, as has been observed in other studies conducted on productive mesic sites (Pothier et al. 1995). The use of harvesting approaches that aim to conserve tall vigorous stems should be promoted, keeping in mind that the size effect was weak compared with other production factors. The results also confirm that black spruce layers are able to survive and maintain their growth potential during a long period of suppression (up to several decades); there was no effect of stem age at the time of disturbance on stem growth potential.

Analyses of juvenile growth also indicate that in the presence of thick post-CPRS organic layers (>40 cm depth), some form of site preparation should be prescribed that could reduce OM thickness, so that the remaining regenerating stems could exhibit enhanced growth (Prévost and Dumais 2003). Severe mechanical treatments can reduce OM thickness (Henneb et al. 2015), expose soil layers that favour growth for conifer seedlings (Lafleur et al. 2010*b*), and reduce competition by ericaceous species (Thiffault and Jobidon 2006). On more productive sites, where OM thickness is of moderate depth (<40 cm), mechanical site preparation could be avoided, especially in the presence of a sufficient density of vigorous advance regeneration. However, productivity would therefore probably be slightly below expectation (St-Denis et al. 2010).

In the study area, annual allowable cut calculations for black spruce stands are based on a site index of 12 m height at 50 years (Bureau du forestier en chef 2013). According to Mailly and Gaudreault's (2005) SI calculation, RF sites should reach a SI of 13, whereas CPRS sites should reach a mean SI of 10. The target set by forest managers might have been a little optimistic against the mean potential SI of 10 that was observed in the OF strip retention stands. These results had already been observed by Simard et al.

(2007) using a chronosequence approach. Even if the growth performances of the study area are not yet alarming for forest managers, they remain a concern. It would be appropriate to conduct another inventory campaign on the same sites in a decade to check if stems' potential SI improved enough to reach a SI of 12, which is still possible for most of the sites.

Conclusion

Our study aimed to describe the effects of a current and generalized harvesting practice in boreal forests (CPRS or CLAAG) on tree growth. It compared past and current juvenile growth of two generations of trees growing on the same sites that were subject to paludification (paired plots located in CPRS and associated retention strips) and also included plots that had been established in a recent wildfire site. We expected a decrease in juvenile growth after harvest compared with the juvenile growth of the previous stands, but the CPRS that we studied did not exhibit such a trend. In fact, the growth rate of current regeneration strata was higher than the juvenile growth rate of the previous stands (of fire origin). However, these results must be extrapolated with caution, as most of the sampled trees in the retention strips had grown under the cover of one or several cohorts of dominant trees, in a harsh climatic regime. By comparing post-CPRS growth with the growth of trees regenerating in recent fires, we noted that harvesting did not promote optimal growth rates for the region (Grondin et al. 2000).

The thickness of OM in which stems had established was a key factor explaining sapling growth. Our results, however, suggest that other factors such as microsite quality (e.g., soil physicochemical characteristics) were also important and should be considered in future research and forest management practices (Renard et al. 2016).

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Appendix A

Site index (SI) calculation

The site index (SI) of each stem is usually calculated as being the height that is reached by the stem after a given number of years (50 years in Quebec) of free growth (unsuppressed growth). SI is calculated using mature stem height growth patterns to define the major inflections of age–height growth curves that reflect a growth recovery (Curtis 1964; Grondin et al. 2000; Subedi et al. 2009). This method is usually used for mature stand SI calculation. Mailly and Gaudreault (2005) developed a method to predict future SI in young stands.

For CPRS and RF stands, SI was calculated on only 392 of the 440 sampled stems, as the stems had to meet Mailly and Gaudreault's (2005) criterion to be used: stem height at the time of disturbance was less than 1 m, so that the stem was no longer growth suppressed at this height.

For OF stands, SI was calculated for 158 of the 160 sampled stems that were less than 50 years old when they reached 1 m in height (Mailly and Gaudreault 2005).

Table B1. Comparison of old-fire (OF) and CPRS mean height growth per OF SI_{50} class. Only OF stems showing juvenile growth in full light were considered.

OF mean SI_{50} (sites)	No. of OF stems considered	Full-light OF past growth (cm·year^{-1}), mean ± SD	CPRS current growth (cm·year^{-1}), mean ± SD
4 (S01)	1	4.35±NA	12.24±5.36
6 (S02, S04, S05)	8	7.78±2.77	14.42±7.72
8 (S03, S06, S08)	14	12.05±5.36	13.83±6.31
10 (S07)	17	14.57±4.62	13.90±4.66

Appendix B

Under-cover or full-light growth index calculation

Knowing if the OF stems grew under direct light allowed us to better discern an effect of the past climate on growth because it would place them in growth conditions close to those following recent wildfire. We used a binary variable indicating whether the stem appeared to have been grown in full light or under the cover of a previously established stand.

The "juvenile growth under sun or cover" characteristic was based on a simple criterion. Radial growth of 0.45 mm·year^{-1} is considered the critical threshold above which a tree can be considered to have experienced full-sun juvenile growth (Wright et al. 2000). OF-07 stems appeared to originate from the first tree cohort after fire (see Table 1), based on synchronous establishment of all stems over a 10-year period after fire (Simard et al. 2007). Therefore, we used the data on annual radial growth measured between the heights of 0 to 40 cm on the OF-07 stems to confirm that the 0.45 mm·year^{-1} threshold was consistent in our study area. We considered that stems (at heights of 0–40 cm) with a mean radial growth < 0.45 mm·year^{-1} had grown under cover.

To perform this analysis, we used 130 of the 160 OF stems. Some stems were excluded from the analysis when the stem disks taken at stump level (immediately above main roots insertion) were found to be rotten. Of the OF stems that were used in this analysis, 90 had a mean annual radial growth rate below the threshold suggested by Wright et al. (2000).

To assess climate effects on past OF stand growth, we calculated the 1–2 m mean height growth for each SI_{50} of OF stands by considering only the first cohort stems. We then compared it with the CPRS growth (Table B1).

Appendix C

Prospective analysis of organic soil nutrient contents

To check if regeneration growth after disturbance (CPRS or RF) could be correlated with soil chemical properties (as reported by Lafleur et al. 2010), we measured selected properties (C–N ratio, total N, P, Ca, and Mg, and pH) of OM samples. These were measured at the site scale in the three RF sites and in four of the eight CPRS sites. We collected five to 10 samples per organic horizon layer (fibric, mesic, and humic) and per site. We did not analyze OF soils as their current chemical properties were no longer representative of their juvenile period.

After collection, samples were kept frozen until analysis. Subsamples were oven-dried (60 °C for 24 h), ground to pass through 6 mm sieves, and weighed. Total C and N concentrations were estimated by dry combustion using a LECO furnace and CNS-2000 analyzer (LECO Corporation 2002). We chose the C–N ratio as a soil fertility indicator. Extractable inorganic P was determined by spectrophotometry (colorimetry) on a continuous flow analyzer

Table C1. Values (mean ± standard deviation) of soil chemical properties after cutting with protection of regeneration and soils (CPRS) and following recent fire (RF) in paludified black spruce stands. ANOVA results (*P* values) are summarized at the bottom of the table.

Disturbance organic layer	C–N ratio	N_{tot} (%)	P_{avail} (mg·g^{-1})	K (cmol(+)·kg^{-1})	Ca (cmol(+)·kg^{-1})	Mg (cmol(+)·kg^{-1})	pH
CPRS							
Fibric	65.4 (14.1)	0.76 (0.17)	0.111 (0.038)	2.1 (0.8)	11.6 (3.3)	4.4 (1.5)	4.00 (0.24)
Mesic	36.2 (10.0)	1.16 (0.33)	0.056 (0.028)	0.3 (0.2)	12.7 (10.7)	3.6 (2.5)	4.14 (0.51)
Humic	31.6 (13.1)	0.82 (0.27)	0.048 (0.032)	0.3 (0.2)	3.1 (1.9)	1.3 (0.8)	4.04 (0.29)
RF							
Fibric	54.3 (7.7)	0.90 (0.19)	0.152 (0.038)	2.4 (0.7)	17.8 (3.2)	6.4 (1.5)	4.31 (0.19)
Mesic	38.8 (7.1)	1.15 (0.15)	0.078 (0.027)	1,0 (0.6)	22.8 (10.3)	6.3 (2.3)	4.39 (0.40)
Humic	27.5 (4.8)	1.10 (0.19)	0.051 (0.028)	0.4 (0.2)	18.1 (12.3)	4.6 (2.3)	4.68 (0.45)
***P* value**							
Horizon (H)	<0.0001	<0.0001	<0.0001	<0.0001	0.0027	<0.0001	<0.0001
Origin (O)	0.0537	0.0213	0.0008	0.0021	<0.0001	<0.0001	<0.0001
H × O	0.0831	0.1935	0.1857	0.3898	0.3761	0.6507	0.3887

(LACHAT^{Tm}) after extraction in Bray II acidic solution (Bray and Kurtz 1945). Exchangeable Ca and Mg were extracted using unbuffered 0.1 mol·L^{-1} $BaCl_2$ and determined by atomic absorption spectroscopy (Hendershot and Duquette 1986). Bulk pH was determined by potentiometry on a pH meter (Orion 2 Star) with a combined electrode in distilled water (2.0 ± 0.04 g of organic soil for 20 mL of water) and in $CaCl_2$ (400 μmol·L^{-1} of $CaCl_2$ 0.5 mol·L^{-1} added to previous samples) (Carter 1993).

We compared the soil properties for each stand origin and for each OM horizon with two-way ANOVA models.

Analyses (Table C1) revealed significant differences in the chemical properties between OM layers and significant differences between CPRS and RF stand origins. The interaction between OM layer and stand origin was not significant for any of the measured properties (Table C1).

The deepest and most decomposed organic layers had the lowest C–N ratios. Organic soils of the RF site exhibited lower C–N ratios than those of the CPRS sites. Soil pH increased with organic layer depth in RF sites, but values remained similar across the soil profile on CPRS sites. In general, RF soils were less acidic than CPRS soils. Nutrient availability (N, P, K, Ca, Mg) was higher in RF than in CPRS sites and usually decreased with organic layer depth, except for Ca, which was more available in the mesic layer (Table C1).

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