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Silviculture to sustain productivity in black spruce paludified forests

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A B S T R A C T

Fire is considered the major disturbance in boreal forests. Nonetheless, in several areas logging has become the primary driver of forest dynamics. In many areas of the boreal forest, stands may undergo paludification (i.e. the accumulation of thick, poorly decomposed organic layers over the mineral soil) in the prolonged absence of fire, which reduces forest productivity. Whereas high-severity fires (HSF) may restore forest productivity by burning the soil organic layer (SOL), low-severity fires (LSF) mainly burn the soil surface and do not significantly reduce SOL thickness. In the Clay Belt region of eastern Canada, an area prone to paludification, forest stands have historically been harvested by clearcutting (CC), but concerns about the protection of soils and tree regeneration lead to the replacement of CC by careful logging (CL). Whereas CC disturbs the SOL and is thought to favor tree growth, CL has little impact on the SOL. Furthermore, it has been suggested that prescribed burning after clearcut (CCPB) could also be used to control paludification. Using a retrospective approach, this study sought to understand how CC, CL, and CCPB compare to LSF and HSF with respect to soil properties, SOL thickness, vegetation ground cover, tree nutrition, and stand height in paludified black spruce stands of the Clay Belt region. HSF led to significantly taller trees than CL and LSF, but did not differ from CC and CCPB. Foliar N was significantly higher in HSF and CCPB sites relative to CL and LSF, with an intermediate value in CC sites. Ground cover of *Rhododendron groenlandicum* was significantly lower in HSF and CC sites relative to LSF, with intermediate values in CL and CCPB sites. *Sphagnum* spp. ground cover was significantly lower in HSF and CCPB sites relative to CL, with intermediate values in CC and LSF sites. High-severity fire sites had a significantly thinner SOL than the four other disturbances. Finally, regression tree analysis showed that SOL thickness represented the best predictor of tree height, whereas segmented regression showed that tree height was negatively correlated to SOL thickness and revealed a cut-off point *circa* 23 cm, which suggests that tree growth is impeded beyond this threshold. These results support the idea that management strategies intending to regenerate paludified forests should primarily aim at reducing organic layer thickness, either through mechanical disturbance or combustion.

1. Introduction

Black spruce (*Picea mariana* [Mill.] BSP) is one of the most wide-ranging and abundant conifers in North America (Burns and Honkala, 1990) and sustains an important forest industry in eastern Canada. Historically, black spruce stands have been harvested by clearcutting because it was thought to be compatible with the ecological requirements of black spruce (Keenan and Kimmins, 1993; McRae et al., 2001). However, in recent decades, concerns were raised about the protection of soils and tree regeneration during forest operations, as clearcutting was thought to damage both. These concerns sparked important changes in harvest methods, and many jurisdictions in Canada replaced clearcutting by careful logging, whose objectives are to protect soils and natural tree regeneration (Harvey and Brais, 2002). More specifically, careful logging consists of logging all merchantable trees with machinery

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traffic restricted to parallel trails that cover approximately 25–33% of the logged area. Trails are separated by "protection strips" in which only merchantable stems are logged, leaving pre-logging tree regeneration (Harvey and Brais, 2002).

In certain areas, however, careful logging may not be as efficient at maintaining forest productivity as previously thought. For instance, in areas prone to paludification (i.e. to the transformation of productive closed-crown forests on dry mineral soil into unproductive forest on organic soil), such as parts of the Clay Belt of northeastern Ontario and northwestern Quebec, the productivity of black spruce stands naturally declines as a thick (>30 cm) organic layer accumulates, the water table rises, soil temperature decreases, and tree root access to the mineral soil is restricted (Simard et al., 2007; Viereck et al., 1993). Furthermore, the understory of paludified black spruce stands is dominated by *Sphagnum* spp. and ericaceous species (e.g., Labrador tea (*Rhododendron groenlandicum* [Oeder] Kron & Judd) and sheep laurel (*Kalmia angustifolia* L.)), both of which contribute to the accumulation of the organic layer (Fenton et al., 2005) and, in the case of ericaceous species, directly limit tree growth (Inderjit and Mallik, 1996; Mallik, 1987; Thiffault et al., 2013). Studies conducted in northeastern Canada have suggested that careful logging, which by definition does not disturb the accumulated organic layer, could contribute to a long-term decline in black spruce stand productivity by favouring paludification (Fenton et al., 2005; Lavoie et al., 2005). In parallel, it has been suggested that harvest methods that severely disturb organic soils, and subsequently result in a reduction in organic layer thickness and (or) accelerate its mineralization, could help restore stand productivity (Lafleur et al., 2010; Simard et al., 2009; Thiffault and Jobidon, 2006). Therefore, while careful logging is likely to leave more residual trees than clearcutting, natural regeneration on clearcut sites may establish in more favourable microsites and have a higher growth rate than the residual stems of the carefully logged sites. In this context, the height advantage of advanced regeneration could disappear over time.

Fire is considered the major natural disturbance in the boreal forest of eastern Canada (Bergeron et al., 2001; Payette, 1992). Forest fires are spatially variable, and soil burn severity varies greatly within and among fires (Johnstone and Chapin, 2006; Miyanishi and Johnson, 2002). In paludified black spruce forests, soil burn severity has significant consequences for tree regeneration (Greene et al., 2007; Johnstone and Chapin, 2006) and growth (Johnstone and Chapin, 2006; Simard et al., 2007), and for the structure, composition and productivity of forests (Lecomte et al., 2006a,b; Simard et al., 2007; Viereck, 1983). High-severity soil burns consume most of the organic forest floor (Dyrness and Norum, 1983; Greene et al., 2005) and promote the establishment of productive stands on mineral soil (Dyrness and Norum, 1983; Simard et al., 2007). In contrast, low-severity soil burns leave the forest floor almost intact, which provides a "head start" to the development of thick organic layers (Fenton et al., 2005; Shetler et al., 2008; Simard et al., 2007). In this context, prescribed burning (i.e. the application of fire for ecosystem management purposes) has been proposed as a means to reduce the thickness of the soil organic layer (SOL; Certini, 2005; Renard et al., 2016), control competing vegetation (McRae, 1998; Wiensczyk et al., 2011), release nutrients locked-up in recalcitrant organic matter, and favor tree regeneration and growth (Certini, 2005; Renard et al., 2016; Ryan et al., 2013; Siren, 1955). In the European boreal forest, prescribed burning was widely used after harvesting to prepare microsites for tree planting, but it is currently rarely used in Canada in a forestry setting due to its operational challenges. However, the inherent properties of prescribed burning as a site preparation technique to emulate wildfire in an ecosystem based management framework are attractive (Bergeron et al., 2007; Nesmith et al., 2011; Ryan et al., 2013). The effects of prescribed burning on soil and vegetation suggest that it could be a potential technique to control paludification and increase black spruce regeneration (Certini, 2005; Ryan et al., 2013). Numerous studies have investigated the short term impacts of prescribed burning that increase SOL temperature and decomposition (Duchesne and Wetzel, 1999; Pietikainen and Fritze, 1995), and could favor black spruce regeneration, notably through a reduction of competing vegetation (McRae, 1998). But these studies were not conducted on deep organic soils like those found in paludified cutovers, neither were they long term studies.

Using a retrospective approach, this study sought to understand how current (careful logging, CL) and former (clearcutting, CC) forest harvesting methods and potential site preparation techniques (prescribed burning, PB) compare to both low- and high-severity fires (LSF and HSF, respectively) with respect to soil chemical properties, SOL thickness, competing vegetation (i.e. ericaceous shrubs) and bryophyte ground cover, tree nutrition, and stand height in paludified black spruce stands of the Clay Belt region of northeastern Ontario and northwestern Québec (Fig. 1). To do so, we this study combined data from four different studies conducted in the Clay Belt region that each independently looked at the effects of CL, CC, CCPB (clearcut followed by prescribed burning), LSF, and/or HSF on soil properties and tree growth. It was hypothesized that because of greater soil disturbance due to compaction and/or combustion, CC and CCPB would reduce the thickness of the SOL, increase soil pH and nutrient availability, decrease the ground cover of competing vegetation, and promote stand growth compared to CL. It was also hypothesized that clearcutting would promote stand growth at a level comparable to that of high-severity soil burns. This study sought to identify the silvicultural treatments most likely to reproduce the growth patterns observed after high-severity soil burns and useful to maintain or restore forest productivity in paludified black spruce stands. In parallel, this study sought to identify, at the tree level, the variables that explain differences in tree height.

2. Methods

2.1. Study area

Located in the Canadian Boreal Shield Ecozone, the Clay Belt of northeastern Ontario and northwestern Québec (Fig. 1) is a large (125,000 km^2) physiographic region characterized by clay deposits (Vincent and Hardy, 1977). While the southern part of the study area is covered by thick (>10 m) glaciolacustrine clay and silt deposited by the glacial Lake Ojibway, the northern part is covered by the Cochrane till, a compact till made up of a mixture of clay and gravel, created by a southward ice flow approximately 8000 years BP (Veillette, 1994). Soils of the study area are mostly classified as Gleysols and Luvisols (Soil Classification Working Group, 1998). Nonetheless, organic deposits (i.e. a surficial deposit consisting of a SOL > 30 cm thick) are found in many locations in both the southern and northern parts of the study area. According to local weather stations, from 1981 to 2010, the average annual temperature was 1.3 °C in Kapuskasing (49°24′N; 82°28′W), Ontario, whereas it was 0.0 °C in Joutel (49°28′N; 78°18′W), Québec (Environment Canada, 2015). During the same period, the average annual precipitation was 830 mm and 909 mm in Kapuskasing and Joutel, respectively, with 30% falling during the growing season, whereas the average number of degree-days (>5 °C) was 1430 in Kapuskasing and 1240 in Joutel. In both locations, the frost-free season lasts about 100 days, with frost occasionally occurring during the growing season.

The study area is dominated by black spruce-feathermoss forests that vary in density and height. Occasional stands of jack pine

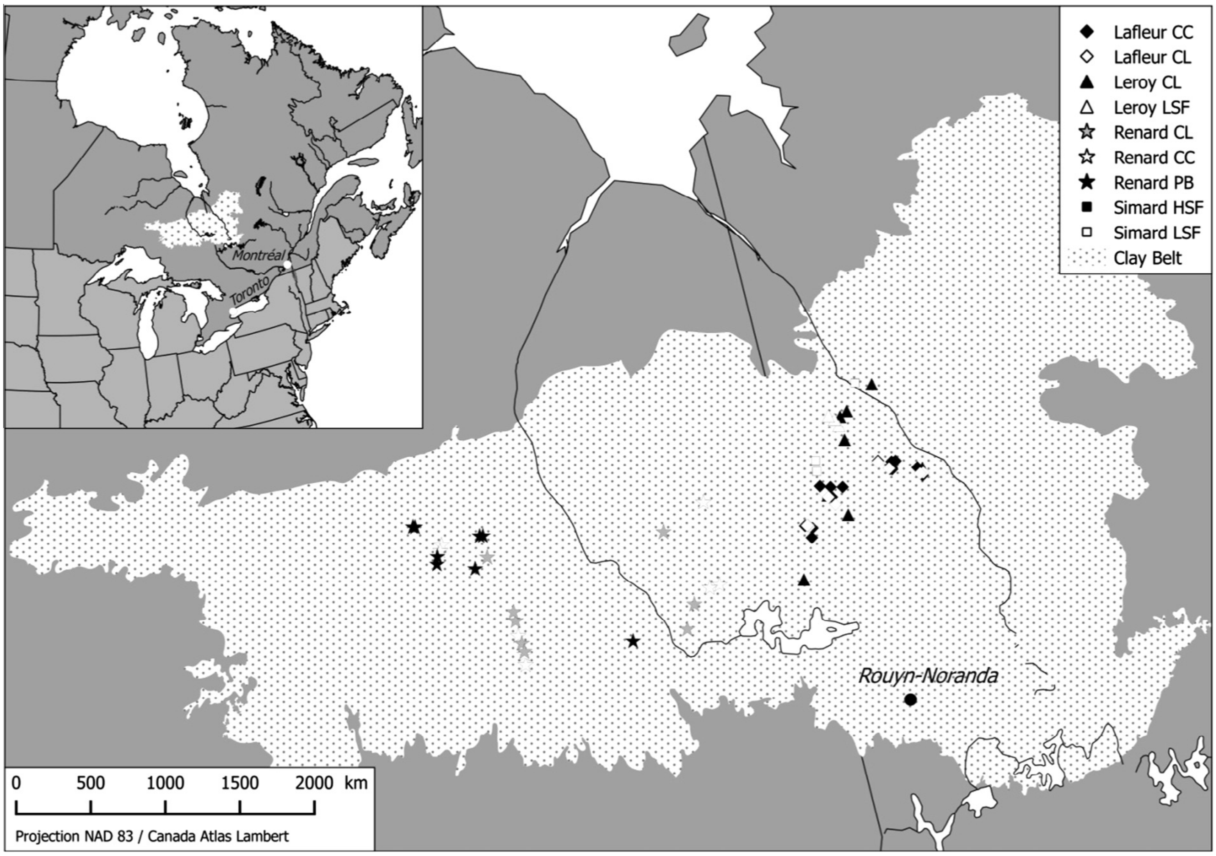

Fig. 1. Location of the Clay Belt and study sites in eastern Canada.

(*Pinus banksiana* Lamb.) and aspen (*Populus tremuloides* Michx.) occur and are often mixed with black spruce (Gauthier et al., 2000; Harper et al., 2003; Taylor et al., 2000). Tamarack (*Larix laricina* [Du Roi] K. Koch), balsam fir (*Abies balsamea* [L.] Mill.), and paper birch (*Betula papyrifera* Marsh.) are a minor component of the forest matrix. Ericaceous shrubs such as *R. groenlandicum*, *K. angustifolia*, and blueberry (*Vaccinium myrtilloides* Michx. and *Vaccinium angustifolium* Ait.) dominate the understory, while the forest floor is dominated by *Sphagnum* spp. (e.g., *Sphagnum recurvum* P. Beauv. sensu lato, *Sphagnum capillifolium* [Ehrh.] Hedw., *Sphagnum fuscum* [Schimp.] Klinggr., *Sphagnum girgensohnii* Russ., and *Sphagnum magellanicum* Brid.) and feathermosses (e.g., *Pleurozium schreberi* [Brid.] Mitt. and *Hylocomium splendens* [Hedw.] Schimp.).

2.2. Data sources

The data used in this study were retrieved from four different studies conducted in the Clay Belt region and each aiming at independently identifying the effects of four types of disturbance (i.e. careful logging, clearcutting, prescribed burning and wildfire) on soil physico-chemical properties and black spruce growth.

The first study (Simard et al., 2007) was conducted in Québec and compared the effects of low- and high-severity fires on soil properties and tree growth. The study included three pairs of stands, each member of a pair originating from the same fire (i.e. 1907, 1948 and 1949; the sites were 52, 53 and 94 years old at the time of sampling), but with contrasting stem density and residual soil organic layer (RSOL; i.e. the organic layer below the uppermost charcoal layer that was not consumed by the last fire). The stands were classified as originating either from a high-severity fire (HSF) or low-severity fire (LSF), based on the average thickness of the RSOL. Stands where RSOL thickness was >5 cm were classified as LSF, whereas stands where RSOL in <5 cm thick were classified as HSF (Greene et al., 2004; Lecomte et al., 2006b).

The second study (Lafleur et al., 2010), also conducted in Québec, compared the effect of harvest methods (CL and CC) on soil properties and tree growth. The study included 28 stands (18 CC and 10 CL) harvested between 1975 and 1996; the stands were 11–33 years old at the time of sampling.

The third study (Renard et al., 2016) was conducted in Ontario and aimed at comparing the effects of CL, CC, and CCPB on soil properties and tree growth. The study included eight stands both for CL and CCPB, and six for CC. The stands were harvested or prescribed burnt between 1975 and 1995, and were 13–33 years old at the time of sampling.

The last study (Leroy et al., in press) was conducted in Quebec and compared the effects of CL and LSF on soils and tree growth. The study included 8 stands for CL and 3 for LSF. All stands were harvested or burnt in 1997 and were 15 years old at the time of sampling.

2.3. Data sampling

In spite of slight differences with respect to experimental design, this study took advantage of the fact that the four studies collected the same data (with a similar methodology) regarding tree height and foliar nutrition, competing vegetation (i.e. *K. angustifolia* and *R. groenlandicum*) and bryophyte (i.e. *P. schreberi* and *Sphagnum* spp.) ground cover, SOL thickness and soil properties. Tree height was measured on 268–8763 trees per study (Table 1), competing vegetation and bryophyte ground cover in 60–336 locations per study, SOL thickness in 63–441 locations per study, soil chemical properties on 63–84 soil samples per study, and foliar

Table 1
Sample size of the variables for each of the four studies.

Study	Disturbance type[a]	Number of sites	Number of trees	Number of ground cover sampling locations	Number of SOL thickness measurements	Number of soil samples for physico-chemical analyses	Number of sample for foliar analyses
Simard et al. (2007)	LSF	3	129	30	45	45	34
	HSF	3	139	30	18	18	18
Lafleur et al. (2010)	CL	10	2971	120	90	30	87
	CC	18	5792	216	162	54	180
Renard et al. (2016)	CL	8	1640	96	72	24	72
	CC	6	1980	72	54	24	63
	CCPB	8	1605	96	72	24	63
Leroy (in press)	CL	8	320	80	320	37	90
	LSF	3	121	30	121	36	18

[a] CC, clearcutting; CCPB, clearcutting followed by prescribed burning; CL, careful logging; HSF, high-severity fire; LSF, low-severity fire.

nutrition on 52–267 trees per study. More specifically, in all four studies, competing vegetation and bryophyte % ground cover was visually estimated in 5–124-m^2 quadrats per stand, whereas SOL thickness was measured and organic material sampled (at a depth of 10–20 cm, i.e. where the bulk of the roots were located) in 4–19 locations per stand. We refer readers to Simard et al. (2007), Lafleur et al. (2010), Renard et al. (2016) and Leroy et al. (in press) for more details regarding experimental designs and sampling.

2.4. Soil and foliar analyses

In all four studies, soil chemical properties were measured using substrate analysis (C:N, Ntot, exchangeable cations and pH) of the organic layer samples. More specifically, following sampling, organic soil samples were air-dried for 48 h, returned to the laboratory and frozen. Immediately prior to analysis, all samples were air-dried at 30 °C for 48 h and ground to pass through 6-mm sieves. Substrate pH was analyzed in distilled water (Carter, 1993). Total C and N were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation, St. Joseph, MI). Extractable inorganic P was determined by the Bray II method (Bray and Kurtz, 1945), whereas exchangeable cations (including Ca and Mg) were extracted using unbuffered 0.1 M $BaCl_2$ and determined by atomic absorption (Hendershot and Duquette, 1986). Cation exchange capacity (CEC) was defined as the sum of exchangeable cations (Ca, Mg, Na, K, Mn, Fe and Al), and base saturation (BS) as the sum of Ca, Mg, K, Na divided by CEC.

Needle samples were selected from the current year's shoot and were collected from various positions in the crown (mid, top 1/3, and leader). All needles from an individual tree were grouped as one composite sample per tree. These samples were oven-dried at 70 °C for 48 h. After drying, needles were separated from twigs and ground to 0.5 mm for chemical analysis. Total N was determined as it was for the soil samples on a CNS analyzer, while phosphorus was determined following calcination at 500 °C and dilution with hydrochloric acid (Miller, 1998). Phosphorus was analyzed by colorimetry (Lachat Instruments, Milwaukee, WI).

2.5. Data analysis

The effects of disturbance type on stand height, competing vegetation and bryophyte ground cover, SOL thickness, soil chemical properties, and foliar nutrition were determined using one-way mixed effect ANCOVAs. Disturbance type was introduced into these models as a fixed effect, plot and site as random effects, and time since disturbance as a covariate. Prior to analysis, residuals were tested for normality and homogeneity of variances, and were log- or square root-transformed when necessary. Post-hoc comparisons (Tukey HSD) were made to contrast the levels of the fixed variables, and differences were deemed significant when $p < 0.05$.

Then, using the entire dataset, a regression tree approach was used to predict tree height at the microsite level from vegetation ground cover, SOL thickness, soil chemistry and foliar nutrition. Regression trees function by recursively partitioning a dataset into increasingly homogenous subsets. This approach was selected because it is non-parametric, can account for non-linear relationships between variables, and tends to be robust to errors in both the independent and dependent variables (Breiman et al., 1998). In support to the regression tree approach, the use of segmented regression helped identify a SOL thickness threshold above which tree growth is negatively affected. All statistical analyses were performed using JMP 10.0 (SAS, 2012).

3. Results

3.1. Effects of disturbance type on tree height, foliar nutrition, vegetation ground cover, and soil properties

Type of disturbance had a significant ($p = 0.005$) effect on tree height (Fig. 2). High-severity fires sites had significantly taller trees than CL and LSF sites, whereas CC and CCPB sites did not significantly differ from CL, LSF and HSF sites.

Type of disturbance also had a significant effect on foliar N ($p = 0.039$) and P ($p = 0.002$), but not on N:P ($p = 0.077$) (Table 2). Foliar N was significantly higher in HSF and CCPB sites than in CL and LSF sites, with an intermediate value in CC sites. Foliar P was significantly higher in CCPB sites than in CC and CL sites, with intermediate values in HSF and LSF.

Type of disturbance had a significant effect on the percent ground cover of competing vegetation and bryophytes, with the exception of *K. angustifolia* (Fig. 3). Ground cover of *R. groenlandicum* was significantly lower in HSF and CC sites relative to LSF, whereas CL and CCPB sites did not significantly differ from LSF, CC or HSF sites. *P. schreberi* ground cover was significantly lower in CCPB and LSF sites relative to CL sites, whereas CC and HSF sites did not significantly differ from CCPB, LSF and CL sites. Lastly, *Sphagnum* spp. ground cover was significantly lower in HSF and CCPB sites relative to CL sites, whereas CC and LSF did not significantly differ from CCPB, HSF and CL sites.

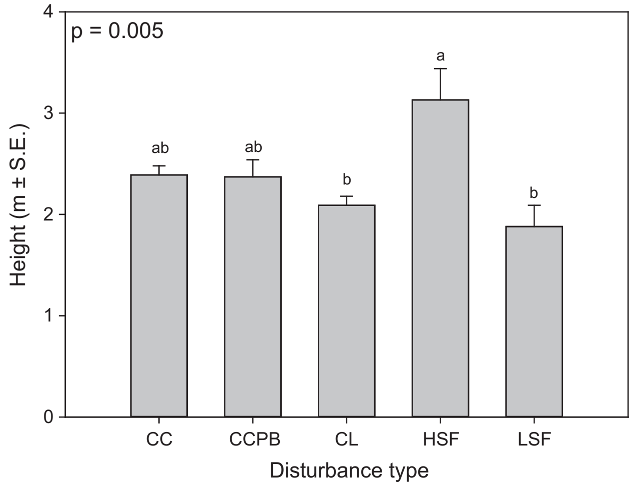

Fig. 2. Mean (±standard error) tree height by disturbance type. Bars with a same letter are not significantly different at alpha = 0.05, according to the Tukey HSD test. CC, clearcutting; CCPB, clearcutting followed by prescribed burning; CL, careful logging; HSF, high-severity fire; LSF, low-severity fire.

SOL thickness differed significantly between disturbance types (Fig. 4). High-severity fire sites had a significantly thinner SOL than the four other disturbances, whereas LSF had a significantly thinner SOL than CL sites.

Table 2
Mean (±standard error) foliar chemistry properties by disturbance type.

Disturbance[a]	N (%)	P ($mg\ g^{-1}$)	N:P
CC	0.85 (0.03)ab	0.89 (0.05)b	10.4 (0.6)
CCPB	0.93 (0.03)a	1.36 (0.12)a	7.2 (0.5)
CL	0.80 (0.02)bc	0.89 (0.05)b	9.8 (0.4)
Fire High	0.96 (0.01)a	1.05 (0.12)ab	9.5 (1.1)
Fire low	0.78 (0.02)c	0.99 (0.19)ab	9.6 (1.7)
F-value	2.695	4.872	2.232
p-value	0.039	0.002	0.077

[a] CC, clearcutting; CCPB, clearcutting followed by prescribed burning; CL, careful logging; HSF, high-severity fire; LSF, low-severity fire. For a given variable, means followed by a same letter are not significantly different at alpha = 0.05, according to the Tukey HSD test.

With respect to soil chemical properties, the type of disturbance had a significant effect on P ($p < 0.001$) and pH ($p < 0.001$) only (Table 3). Whereas P was significantly higher in LSF site relative to the other sites for which data was available (i.e. CC, CCPB, and CL), pH was significantly higher in CCPB sites relative to the other four disturbance types.

3.2. Relating tree height to vegetation ground cover, SOL thickness, soil chemistry and foliar nutrition

The regression tree analysis shows that SOL thickness represented the best predictor of tree height (Fig. 5); trees were subdivided in two groups with SOL <23 cm and >23 cm. The SOL <23 cm

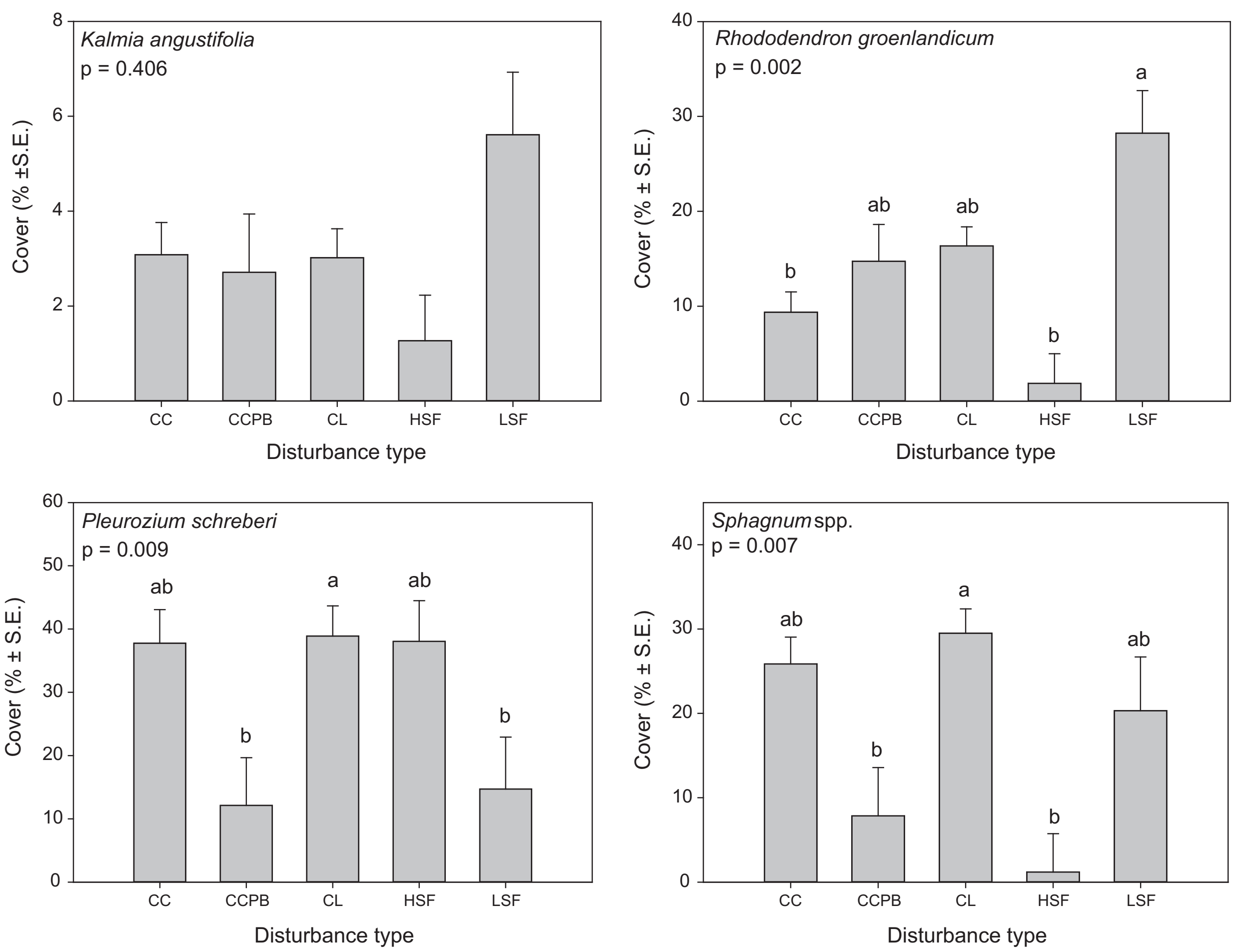

Fig. 3. Mean (±standard error) *K. angustifolia*, *R. groenlandicum*, *P. schreberi* and *Sphagnum* spp. ground cover by disturbance type. For a given species, means followed by a same letter are not significantly different at alpha = 0.05, according to the Tukey HSD test. CC, clearcutting; CCPB, clearcutting followed by prescribed burning; CL, careful logging; HSF, high-severity fire; LSF, low-severity fire.

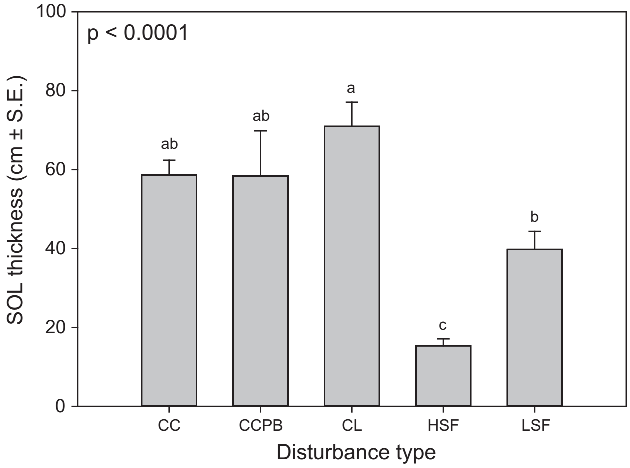

Fig. 4. Mean (±standard error) soil organic layer (SOL) thickness by disturbance type. Bars with a same letter are not significantly different at alpha = 0.05, according to the Tukey HSD test. CC, clearcutting; CCPB, clearcutting followed by prescribed burning; CL, careful logging; HSF, high-severity fire; LSF, low-severity fire.

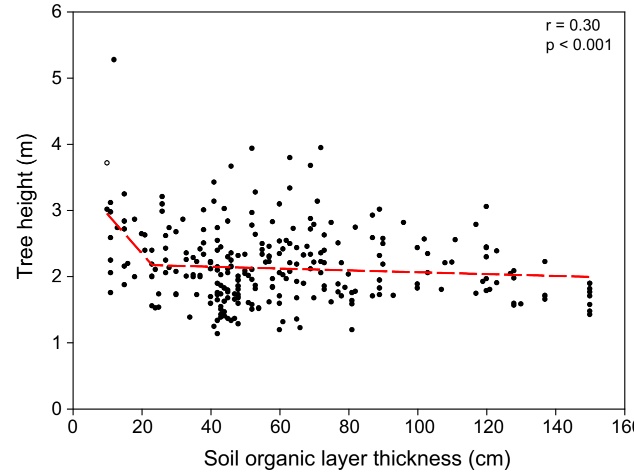

Fig. 6. Black spruce height in relation to soil organic thickness.

Table 3
Mean (± standard error) soil chemical properties by disturbance type.

Disturbance[a]	Ntot (%)	C:N	P ($mg\ g^{-1}$)	pH	CEC
CC	1.23 (0.06)	43.6 (2.8)	0.03 (0.0)b	4.24 (0.09) b	82.2 (12.6)
CCPB	1.18 (0.10)	44.8 (4.9)	0.02 (0.01) b	5.08 (0.15) a	117.7 (22.3)
CL	1.11 (0.06)	46.5 (2.9)	0.03 (0.01) b	4.29 (0.09) b	125.3 (14.9)
HSF	1.00 (0.16)	51.2 (8.2)	No data[b]	3.96 (0.29) b	51.3 (39.9)
LSF	1.00 (0.11)	47.2 (5.4)	0.10 (0.01) a	4.36 (0.19) b	60.0 (39.7)
F-value	1.288	0.296	11.390	6.128	2.002
p-value	0.286	0.879	<0.001	<0.001	0.106

For P and pH, means followed by a same letter are not significantly different at alpha = 0.05, according to the Tukey HSD test.
[a] CC, clearcutting; CCPB, clearcutting followed by prescribed burning; CL, careful logging; HSF, high-severity fire; LSF, low-severity fire.
[b] Because of missing data for high-severity fire, ANOVA on P was performed using CC, CCPB, CL and LSF only.

group cm did not display additional division, whereas the SOL >23 cm group was further divided in two groups with foliar N <0.83% and >0.83%. While the foliar N >0.83% group was not further divided, the foliar N <0.83% group was divided in two groups with foliar N:P <12.2 and >12.2. The four terminal leaves were significantly ($p < 0.001$) different, with trees belonging to the SOL <23 cm group being taller that the trees from the three other groups (Fig. 5). Soil chemical properties therefore appeared less significant predictors of tree height.

Segmented regression showed that tree height was negatively correlated to SOL thickness and, as suggested by the regression tree, revealed a cut-off point *circa* 23 cm which suggests that tree growth is impeded beyond this threshold (Fig. 6).

4. Discussion

Over the past decades, the interest in developing forest management strategies based on "near-nature" treatments (Bergeron et al., 1999; Kuuluvainen and Russel, 2012) have led to numerous studies aiming at comparing the effects of natural and anthropogenic soil disturbances on plant growth and nutrition, and soil

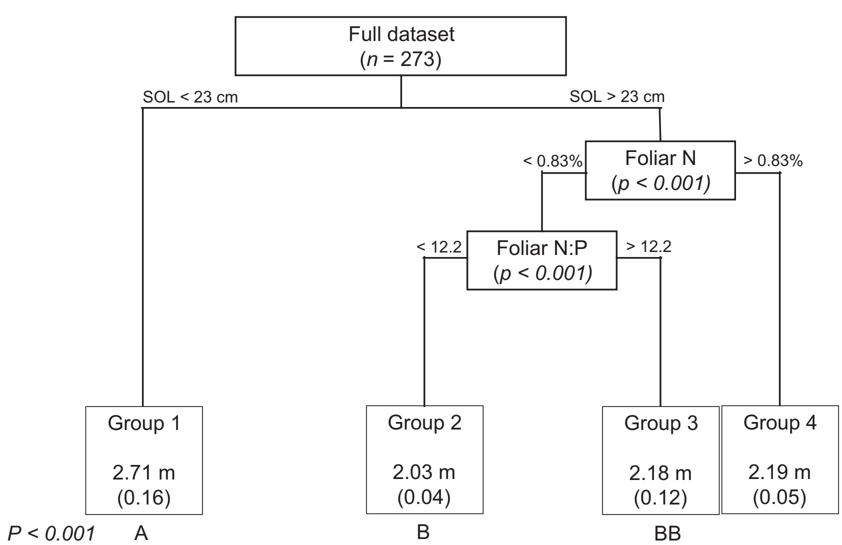

Fig. 5. Graphical representation of the regression tree model. The regression tree reveals that soil organic layer (SOL) thickness is the strongest predictor of tree height. The four terminal leaves (height [m ± S.E.]) were significantly ($p < 0.001$) different, with trees belonging to the SOL <23 cm group being taller that the trees from the three other groups.

properties (Lorente et al., 2012a; McRae et al., 2001; Ruel et al., 2004; Thiffault et al., 2007, 2008). Whereas most of these studies concluded that both types of disturbance differed with respect to their effects on plant growth, nutrition, and soil environment, none have compared these effects along gradients of soil disturbance severity, and few controlled for time since disturbance. In this respect, this study innovates by showing that to some extent, severe natural (fire) and anthropogenic (clearcut and prescribed burning) soil disturbances have similar effects on tree growth and nutrition, and that likewise low-severity soil disturbances, whether from fires or silvicultural operations (careful logging), also produce similar effects. It also shows that in paludified black spruce forests, high-severity soil disturbances improve tree nutrition and initiate more productive stands compared to low-severity soil disturbances. This illustrates the importance of taking soil disturbance severity into account when managing forests at the stand and landscape levels (Simard et al., 2009).

4.1. Tree height and foliar analysis

This study supports the hypothesis that clearcutting promotes stand growth at a rate comparable to that of high-severity soil burns. More specifically, stands originating from both CC and CCPB were on average as tall as stands originating from HSF. Though not significantly, CC and CCPB stands were approximately 20% taller than stands originating from CL and LSF. These results strongly support that severe silvicultural soil disturbance (whether mechanical and/or chemical), such as those occurring during clearcutting and prescribed burning, can promote tree growth to levels similar to high-severity fires and that the key explanation may lay in the modification of soil properties by disturbance. Such interpretation is in line with the conclusions from studies that have investigated the impacts of mechanical site preparation severity on regeneration growth in boreal stands (Thiffault et al., 2004a; Thiffault and Jobidon, 2006).

Furthermore, the effects of soil disturbance severity were also reflected in foliar nutrition. Trees originating from severe soil disturbance (i.e. CC, CCPB and HSF) had higher foliar N concentration, and, with the exception of CC, higher foliar P concentration, than trees originating from low-severity soil disturbance (i.e. CL and LSF). Therefore, greater levels of foliar N and P in trees from CC, PB and HSF may explain improved growth compared to CL and LSF (Lafleur et al., 2010, 2011a; Macdonald and Lieffers, 1990; Maynard et al., 2014). In addition, the results regarding N:P suggest that N was more limiting to tree growth than P. This is in contradiction with some studies (e.g. Walbridge and Navaratnam, 2006) that suggest that in forested peatlands, P is more limiting than N. In boreal ecosystems, one of the main N inputs is derived from N_2 fixation by cyanobacteria hosted by feathermosses such as *P. schreberi* (DeLuca et al., 2002; Lagerström et al., 2007; Limpens et al., 2006). Released in the substrate as organic N, this N source is subsequently available for plant growth (Näsholm et al., 2009), including black spruce (Kielland et al., 2006). Moreover, in terrestrial ecosystems, the weathering of primary and secondary minerals is the ultimate source of P (Walker and Syers, 1976). As organic matter accumulates over the mineral soil, forested peatlands become isolated from the underlying influence of the mineral soil, and P gradually becomes less available for plant growth (Dimitrov et al., 2014; Simard et al., 2007). Because substantial additional inputs of P are unlikely to occur in forested peatlands ecosystems, both biological and soil P stores should be tightly conserved. The strong P resorption efficiencies observed in black spruce by Chapin and Kedrowski (1983) may explain why, in contradiction with other studies, N deficiency appeared more acute than the P one.

4.2. Soil properties and SOL thickness

It was hypothesized that because of greater soil disturbance, CC and CCPB would reduce the thickness of the SOL, and increase soil pH and nutrient availability compared to CL. While CC and CCPB effectively reduced SOL thickness by approximately 20% compared to CL, the difference was not significant. Actually, only LSF (44% reduction) and HSF (78% reduction) managed to significantly reduce SOL thickness compared to CL. Furthermore, with the exception of significantly higher soil pH at CCPB sites compared to other sites, we did not observe any significant differences in soil chemical properties (i.e. N_{tot}, C:N, cationic exchange capacity) between disturbance types.

Numerous studies conducted in the boreal forest reported thinner forest floor after fire compared to harvest (e.g. Kishchuk et al., 2014b; Simard et al., 2001). Forest floor removal by fire can impact long-term site productivity through the loss of soil organic matter and modifications to nutrient supply (Certini, 2005). For instance, N losses (especially through volatilization) have been frequently reported in various ecosystems (e.g., Boerner et al., 2009; Johnson and Curtis, 2001; Kishchuk et al., 2014b; Maynard et al., 2014; Nave et al., 2011; Wan et al., 2001). Nave et al. (2011) calculated that forest floors would require 100–130 years to recover lost N, which could contribute to N limitation in boreal forests. Nevertheless, postfire stands usually contain high amount of deadwood and plant remains, whose decomposition contributes to replenish soil organic matter and nutrient stocks over time (Seedre et al., 2011). In addition, following fire soil C and N had been shown to increase over time owing to sequestration by biochar and organic matter forms and the establishment of N-fixing plants (Johnson and Curtis, 2001), which could explain why we did not observe any significant differences in soil N_{tot} concentration between treatment types. Also, charcoal production generally enhances soil N availability due to its capacity to adsorb tannins and other phenolics (DeLuca et al., 2006), a mechanism of particular importance in ericaceous-dominated ecosystems (Wardle et al., 1998).

Furthermore, several studies showed that base cations (i.e. K^+, Ca^{++}, Mg^{++}) are usually higher in the forest floor following fire than after harvest (Simard et al., 2001; Thiffault et al., 2007). Cation exchange capacity has been shown to be an important indicator of boreal forest soil response to disturbance (Kishchuk et al., 2014a). The incorporation of highly condensed and aromatic C forms of charred organic material into the soil after fire is critical to soil long-term exchangeable cation availability (Thiffault et al., 2008).

In a recent review on the effects of natural and anthropogenic disturbances on soils and tree nutrition, Maynard et al. (2014) showed that soil total N and base cations tend to increase following harvest. That increase may be attributed to the incorporation of harvest residues into the forest floor, which act as a long-term source of nutrients (e.g., Harmon et al., 1990; Thiffault et al., 2007). The exchangeable base cation pools built from the nutrient flush following disturbance is of crucial importance for nutrient cycling and tree nutrition during the subsequent rotation, as is the capacity of soil to store this pool. In that respect, Thiffault et al. (2007, 2008) showed that harvesting did not emulate the enhancement of soil Ca^{++} and Mg^{++} pools or the deposition of charred organic material with high exchange capacity associated with wildfire, raising concerns about the long-term availability of these nutrients on harvested sites.

Hence, whereas fire reduces forest floor depth and generates a pulse of plant-available nutrients in the soil that can be taken up by regenerating vegetation, harvesting in contrast leaves a large portion of the forest floor undisturbed and does not generate the same nutrient pulse observed after fire. For instance, fire causes substantial losses of N through volatilization (Neff et al., 2005), whereas clearcutting may increase soil acidity and the loss of base cations. Despite these potential differential effects, this study indicates that CC in these relatively unproductive black stands has not resulted in significant short- to mid-term changes in soil properties (at least, none that we could detect).

4.3. Competing vegetation and ground cover

By restricting circulation of skidding machinery to evenly spaced trails, while leaving understory vegetation and soils intact between trails, CL may be accompanied by rapid proliferation of the existing ericaceous understory (Lorente et al., 2012b). This takes advantage of full-light conditions and interferes with advance conifer regeneration (Mallik, 2003). Ericaceous shrubs may compete directly with conifers for nutrients (Castells, 2008; Thiffault et al., 2004b, 2013), but also compete indirectly by modifying humus quality (Joanisse et al., 2009) and imposing potential allelopathic effects (e.g., Inderjit and Mallik, 2002; Zhu and Mallik, 1994). In contrast, by affecting the organic layer in which ericaceous shrub rhizomes proliferate (Hébert and Thiffault, 2011; Mallik, 1993), CC and CCPB are likely able to limit shrub proliferation and hence, their interference with conifer growth. Likewise, HSF may kill ericaceous root systems, whereas LSF might stimulate aggressive vegetative reproduction through stem-base sprouting and rhizomatous growth (Mallik, 2003).

Treatment effects were different on bryophytes than they were on ericaceous shrubs. When compared to treatments involving harvesting alone (CL or CC), prescribed burning (CCPB) had a negative effect on *P. schreberi* and *Sphagnum* cover. It thus appears that these two species can resist the increased disturbance severity caused by conventional clearcutting, compared to that of a harvesting approach restricted to specific skid trails. Both species are highly sensitive to the burning technique that was applied after clearcutting. Following the same trend, *Sphagnum* cover was greatly reduced following high-severity (natural) fires. However, *P. schreberi* thrived equally well following this high-severity disturbance as they did following CL, the least intensive treatment of our gradient. This is surprising, as late successional mosses such as *Dicranum* spp., *H. splendens* and *P. schreberi* were shown to be replaced by pioneer moss species such as *Polytrichum* spp. following surface fires (Marozas et al., 2007).

4.4. Relating tree height to SOL thickness

Results from this study strongly suggest that black spruce growth is limited by SOL >30 cm thick. This is similar to Drobyshev et al. (2010) who also suggested a 20–30 cm threshold with respect to the effects of SOL on black spruce growth. This threshold likely corresponds to the SOL thickness beyond which tree root access to the mineral soil is severely restricted (Simard et al., 2007; Viereck et al., 1993). Beyond this threshold, black spruce likely mainly relies on organic N (Kielland et al., 2006) and P resorption (Chapin and Kedrowski, 1983) for nutrition and growth.

4.5. Management implications

Globally, this study supports the idea that management strategies intending to regenerate paludified forests should primarily aim at reducing SOL thickness, either through mechanical disturbance or combustion. Harvesting methods that disturb the surficial layers, such as traditional clearcutting, ideally followed by prescribed burning, should be preferred to careful logging practices on sites prone to paludification such as those found in the east-Canadian Clay Belt. Although a larger proportion of the advance regeneration might be damaged during CC harvesting with or without prescribed burning compared to CL, the increased growth of the remaining seedlings and saplings, combined with the establishment of new seedling following germination of seeds on good microsites, should compensate for the reduced stocking and density. In-fill planting in appropriate microsites could then be used to reach stocking standards. However, as legislation might not permit the use of clearcutting in some jurisdictions, such as in Quebec, careful logging should be followed by intense mechanical site preparation to disrupt the organic layer and reduce its thickness (Henneb et al., 2015; Lafleur et al., 2011b). Any treatments that will further promote increased nutritional status should be beneficial to conifer growth.

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References

Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. For. Chron. 75, 49–54.
Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31, 384–391.
Bergeron, Y., Drapeau, P., Gauthier, S., Lecomte, N., 2007. Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. For. Chron. 83, 326–337.
Boerner, R.E.J., Huange, J., Hart, S.C., 2009. Impacts of fire and fire surrogate treatments on forest soil properties: a meta-analytical approach. Ecol. Appl. 19, 338–358.
Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Sci. 59, 39–45.
Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1998. Classification and Regression Trees. Chapman and Hall/CRC, Boca Raton, USA.
Burns, R.M., Honkala, B.H., 1990. Silvics of North America. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC.
Carter, M.R., 1993. Soil Sampling and Methods of Analysis. CRC Press, Boca Raton, FL.
Castells, E., 2008. Indirect effects of phenolics on plant performance by altering N cycling: another mechanism of plantplant negative interactions. In: Zang, R.S., Mallik, A.U., Luo, S.M. (Eds.), Allelopathy in Sustainable Agriculture and Forestry. Springer, New York, pp. 137–156.
Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.
Chapin III, F.S., Kedrowski, R.A., 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64, 376–391.
DeLuca, T.H., Zackrisson, O., Nilsson, M.-C., Sellstedt, A., 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419, 917–920.
DeLuca, T.H., MacKenzie, M.D., Gundale, M.J., Holben, W.E., 2006. Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. Soil Sci. Soc. Am. J. 70, 448–453.
Dimitrov, D.D., Bhatti, J.S., Grant, R.F., 2014. The transitional zones (ecotone) between boreal forests and peatlands: ecological controls on ecosystem productivity along a transition zone between upland black spruce forest and a poor fen in central Saskatchewan. Ecol. Model. 291, 96–108.
Drobyshev, I., Simard, M., Bergeron, Y., Hofgaard, A., 2010. Does soil organic layer thickness affect climate-growth relationships in the black spruce boreal ecosystem? Ecosystems 13, 556–574.
Duchesne, L.C., Wetzel, S., 1999. Effect of clear-cutting, prescribed burning and scarification on litter decomposition in an Eastern Ontario jack pine (*Pinus banksiana*) ecosystem. Int. J. Wildland Fire 9, 195–201.
Dyrness, C.T., Norum, R.A., 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Can. J. For. Res. 13, 879–893.
Environment Canada, 2015. Canadian Climate Normals 1981–2010 http://climat.meteo.gc.ca/ (accessed 18.12.15).
Fenton, N., Lecomte, N., Légaré, S., Bergeron, Y., 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. For. Ecol. Manage. 213, 151–159.
Gauthier, S., De Grandpré, L., Bergeron, Y., 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. 11, 781–790.
Greene, D.F., Noel, J., Bergeron, Y., Rousseau, M., Gauthier, S., 2004. Recruitment of *Picea mariana*, *Pinus banksiana* and *Populus tremuloides* across a burn severity gradient following fire in the southern boreal forest of Québec. Can. J. For. Res. 34, 1845–1857.
Greene, D.F., Macdonald, S.E., Cumming, S., Swift, L., 2005. Seedbed variation from the interior through the edge of a large wildfire in Alberta. Can. J. For. Res. 35, 1640–1647.

Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, S., Noël, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., Swift, L., 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Can. J. For. Res. 37, 1012–1023.
Harmon, M.E., Ferrell, W.K., Franklin, J.F., 1990. Effects of carbon storage of conversion of old-growth forests to young forests. Science 247, 699–702.
Harper, K., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S., Bergeron, Y., 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environ. Rev. 11, S79–S98.
Harvey, B., Brais, S., 2002. Effects of mechanized careful logging on natural regeneration and vegetation competition in the southeastern Canadian boreal forest. Can. J. For. Res. 32, 653–666.
Hébert, F., Thiffault, N., 2011. The Biology of Canadian Weeds. 146. *Rhododendron groenlandicum* (Oeder) Kron and Judd. Can. J. Plant Sci. 91, 725–738.
Hendershot, W.H., Duquette, M., 1986. A simple barium chloride method for determining cation exchange capacity and exchangeable cations. Soil Sci. Soc. Am. J. 50, 605–608.
Henneb, M., Valeria, O., Fenton, N.J., Thiffault, N., Bergeron, Y., 2015. Mechanical site preparation: key to microsite creation success on Clay Belt paludified sites. For. Chron. 91, 187–196.
Inderjit, Mallik, A.U., 1996. Growth and physiological responses of black spruce (*Picea mariana*) to sites dominated by *Ledum groenlandicum*. J. Chem. Ecol. 22, 575–585.
Inderjit, Mallik, A.U., 2002. Can *Kalmia angustifolia* interference to black spruce (*Picea mariana*) be explained by allelopathy? For. Ecol. Manage. 160, 75–84.
Joanisse, G.D., Bradley, R.L., Preston, C.M., Bending, G.D., 2009. Sequestration of soil nitrogen as tannin-protein complexes may improve the competitive ability of sheep laurel (*Kalmia angustifolia*) relative to black spruce (*Picea mariana*). New. Phytol. 181, 187–198.
Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta-analysis. For. Ecol. Manage. 140, 227–238.
Johnstone, J.F., Chapin III, F.S., 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9, 14–31.
Keenan, R.J., Kimmins, J.P., 1993. The ecological effects of clear-cutting. Environ. Rev. 1, 121–144.
Kielland, K., McFarland, J., Olson, K., 2006. Amino acid uptake in deciduous and coniferous taiga ecosystems. Plant Soil 288, 297–307.
Kishchuk, B.E., Quideau, S.A., Wang, Y., Prescott, C.E., 2014a. Long-term soil response to variable-retention harvesting in the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment, northwestern Alberta. Can. J. Soil Sci. 94, 263–279.
Kishchuk, B.E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T., Sidders, D., 2014b. Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada. Can. J. For. Res. 45, 141–152.
Kuuluvainen, T., Russel, G., 2012. Natural disturbance emulation in boreal forest ecosystem management – theories, strategies, and a comparison with conventional even-aged management. Can. J. For. Res. 42, 1185–1203.
Lafleur, B., Fenton, N.J., Paré, D., Simard, M., Bergeron, Y., 2010. Contrasting effects of season and method of harvest on soil properties and the growth of black spruce regeneration in the boreal forested peatlands of eastern Canada. Silva Fenn. 44, 799–813.
Lafleur, B., Paré, D., Fenton, N.J., Bergeron, Y., 2011a. Growth and nutrition of black spruce seedlings in response to disruption of *Pleurozium* and *Sphagnum* moss carpets. Plant Soil 345, 141–153.
Lafleur, B., Paré, D., Fenton, N.J., Bergeron, Y., 2011b. Growth of planted black spruce seedlings following mechanical site preparation in boreal forested peatlands with variable organic layer thickness: 5-year results. Ann. For. Sci. 68, 1291–1302.
Lagerström, A., Nilsson, M.-C., Zackrisson, O., Wardle, D.A., 2007. Ecosystem input of nitrogen through biological fixation in feather mosses during ecosystem retrogression. Funct. Ecol. 21, 1027–1033.
Lavoie, M., Paré, D., Fenton, N., Groot, A., Taylor, K., 2005. Paludification and management of forested peatlands in Canada: a literature review. Environ. Rev. 13, 21–50.
Lecomte, N., Simard, M., Bergeron, Y., 2006a. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Ecoscience 13, 152–163.
Lecomte, N., Simard, M., Fenton, N., Bergeron, Y., 2006b. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems 9, 1215–1230.
Leroy, C., Leduc, A., Thiffault, N., Bergeron, Y., in press. Forest productivity after careful logging and fire in black spruce stands of the Canadian Clay Belt. Can. J. For. Res. http://dx.doi.org/10.1139/cjfr-2015-0484 (in press).
Limpens, J., Heijmans, M.M.P.D., Berendse, F., 2006. The nitrogen cycle in boreal peatlands. In: Wieder, R.K., Vitt, D.H. (Eds.), Boreal Peatland Ecosystems. Springer, New York, pp. 195–230.
Lorente, M., Parsons, W.F.J., McIntire, E.J.B., Munson, A.D., 2012a. Wildfire and forest harvest disturbances in the boreal forest leave different long-lasting spatial signatures. Plant Soil 364, 39–54.
Lorente, M., Parsons, W.F.J., Bradley, R.L., Munson, A.D., 2012b. Soil and plant legacies associated with harvest trails in boreal black spruce forests. For. Ecol. Manage. 269, 168–176.
Mallik, A.U., 1987. Allelopathic potential of *Kalmia angustifolia* to black spruce (*Picea mariana*). For. Ecol. Manage. 20, 43–51.
Mallik, A.U., 1993. Ecology of a forest weed of Newfoundland: vegetative regeneration strategy of *Kalmia angustifolia*. Can. J. Bot. 71, 161–166.
Mallik, A.U., 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keystone species change. Crit. Rev. Plant Sci. 22, 341–366.
Marozas, V., Racinskas, J., Bartkevicius, E., 2007. Dynamics of ground vegetation after surface fires in hemiboreal *Pinus sylvestris* forests. For. Ecol. Manage. 250, 47–55.
Maynard, D.G., Paré, D., Thiffault, B., Lafleur, B., Hogg, K.E., Kishchuk, B., 2014. How do natural disturbances and human activities affect soils on tree nutrition and growth in the Canadian boreal forest? Environ. Rev. 22, 161–178.
Macdonald, S.E., Lieffers, V.J., 1990. Photosynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix laricina* from drained and undrained peatlands. Can. J. For. Res. 20, 995–1000.
McRae, D.J., 1998. Effective control of bracken fern by prescribed fire. In: Ontario forest Research institute (Ed.), Third International Conference on Forest Vegetation Management. Canadian Forest Service, pp. 199–201.
McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environ. Rev. 9, 223–260.
Miller, R.O., 1998. High-temperature oxidation: dry ashing. In: Kalra, Y.P. (Ed.), Handbook of Reference Methods for Plant Analysis. Soil and Plant Analysis Council. CRC Press, Boca Raton, FL, pp. 53–56.
Miyanishi, K., Johnson, E.A., 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Can. J. For. Res. 32, 1285–1295.
Näsholm, T., Kielland, K., Ganeteg, U., 2009. Uptake of organic nitrogen by plants. New. Phytol. 182, 31–48.
Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.W., 2011. Fire effects on temperate forest soil C and N storage. Ecol. Appl. 21, 1189–1201.
Neff, J.J., Harden, J.W., Gleixner, G., 2005. Fire effects on soil organic matter content, composition, and nutrients in boreal onterior Alaska. Can. J. For. Res. 35, 2178–2187.
Nesmith, J.C.B., Caprio, A.C., Pfaff, A.H., McGinnis, T.W., Keeley, J.E., 2011. A comparison of effects from prescribed fires and wildfires managed for resource objectives in Sequoia and Kings Canyon National Parks. For. Ecol. Manage. 261, 1275–1282.
Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, UK, pp. 144–165.
Pietikainen, J., Fritze, H., 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Biol. Biochem. 27, 101–109.
Renard, S.M., Gauthier, S., Fenton, N.J., Lafleur, B., Bergeron, Y., 2016. Retrospective study to assess site preparation techniques effects on paludification process and black spruce regeneration. For. Ecol. Manage. 359, 147–155.
Ruel, J.-C., Horvath, R., Ung, C.H., Munson, A.D., 2004. Comparing height growth and biomass production of black spruce trees in logged and burned stands. For. Ecol. Manage. 193, 371–384.
Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11, e15–e24.
SAS, 2012. JMP Version 10. SAS Institute Inc., Cary, NC.
Seedre, M., Shrestha, B.M., Chen, Y.H., Jogiste, K., 2011. Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging. J. For. Res. 16, 168–183.
Shetler, G., Turetsky, M.R., Kane, E., Kasischke, E., 2008. *Sphagnum* mosses limit total carbon consumption during fire in Alaskan black spruce forests. Can. J. For. Res. 38, 2328–2336.
Simard, D.G., Fyles, J.W., Paré, D., Nguyen, T., 2001. Impacts of clearcut harvesting and wilefire on soil nutrient status in the Quebec boreal forest. Can. J. Soil. Sci. 81, 229–237.
Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., Paré, D., 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. 17, 1619–1637.
Simard, M., Lecomte, N., Bergeron, Y., Bernier, P., Paré, D., 2009. Ecosystem management of Québec's northern Clay Belt spruce forest: managing the forest. and especially the soils. In: Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, Bergeron, Y. (Eds.), Ecosystem Management in the Boreal Forest. Presses de l'Université du Québec, Québec, QC, Canada, pp. 229–256.
Siren, G., 1955. The development of spruce forest on raw hummus sites in northern Finalnd and its ecology. Acta For. Fenn. 62, 408.
Soil Classification Working Group, 1998. The Canadian System of Soil Classification, third ed. Research Branch, Agricultural and Agri-Food Canada, Publication, NRC Research Press, Ottawa, ON, Canada, 1646.
Taylor, K.C., Arnup, R.W., Merchant, B.G., Parton, W.J., Nieppola, J., 2000. A Field Guide to Forest Ecosystems of Northeastern Ontario, second ed. Queen's Printer for Ontario, Canada.
Thiffault, E., Bélanger, N., Paré, D., Munson, A.D., 2007. How do forest harvesting methods compare with wildfire? A case study of soil chemistry and tree nutrition in the boreal forest. Can. J. For. Res. 37, 1658–1668.
Thiffault, E., Hannam, K.D., Quideau, S.A., Pare, D., Belanger, N., Oh, S.-W., Munson, A.D., 2008. Chemical composition of forest floor and consequences for nutrient availability after wildfire and harvesting in the boreal forest. Plant Soil 308, 37–53.

Thiffault, N., Jobidon, R., 2006. How to shift unproductive *Kalmia angustifolia* – *Rhododendron groenlandicum* heath to productive conifer plantation. Can. J. For. Res. 36, 2364–2376.

Thiffault, N., Cyr, G., Prégent, G., Jobidon, R., Charette, L., 2004a. Régénération artificielle des pessières noires à éricacées: effets du scarifiage, de la fertilisation et du type de plants après 10 ans. For. Chron. 80, 141–149.

Thiffault, N., Titus, B.D., Munson, A.D., 2004b. Black spruce seedlings in a *Kalmia-Vaccinium* association: microsite manipulation to explore interactions in the field. Can. J. For. Res. 34, 1657–1668.

Thiffault, N., Fenton, N., Munson, A.D., Hébert, F., Fournier, R.A., Valeria, O., Bradley, R.L., Bergeron, Y., Grondin, P., Paré, D., Joanisse, G., 2013. Managing understory vegetation for maintaining productivity in black spruce forests: a synthesis within a multi-scale research model. Forests 4, 613–631.

Veillette, J.J., 1994. Evolution and paleohydrology of glacial Lakes Barlow and Ojibway. Quat. Sci. Rev. 13, 945–971.

Viereck, L.A., 1983. The effects of fire in black spruce ecosystems of Alaska and Northern Canada. In: MacLean, D.A., Wein, R.W. (Eds.), The Role of Fire in Northern Circumpolar Ecosystems. John Wiley & Sons, pp. 201–220.

Viereck, L.A., Dyrness, C.T., Foote, M.J., 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. Can. J. For. Res. 23, 889–898.

Vincent, J., Hardy, L., 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Géogr. Phys. Quat. 31, 357–372.

Walbridge, M.R., Navaratnam, J.A., 2006. Phosphorus in boreal peatlands. In: Wieder, R.K., Vitt, D.H. (Eds.), Boreal Peatland Ecosystems. Springer, New York, pp. 231–258.

Walker, T.W., Syers, J.K., 1976. The fate of phosphorus during pedogenesis. Geoderma 15, 1–19.

Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11, 1349–1365.

Wardle, D.A., Zackrisson, O., Nilsson, M.-C., 1998. The charcoal effect in Boreal forests: mechanisms and ecological consequences. Oecologia 115, 419–426.

Wiensczyk, A., Swift, K., Morneault, A.E., Thiffault, N., Szuba, K., Bell, F.W., 2011. An overview of the efficacy of vegetation management alternatives for conifer regeneration in boreal forests. For. Chron. 87, 175–200.

Zhu, H., Mallik, A.U., 1994. Interactions between Kalmia and black spruce: isolation and identification of allelopathic compounds. J. Chem. Ecol. 20, 407–421.