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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

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It has been suggested that without sufficient soil disturbance, harvest in boreal forested peatlands may accelerate paludification and reduce forest productivity. The objectives of this study were to compare the effects of harvest methods (clearcutting vs. careful logging) and season (summer vs. winter harvest) on black spruce regeneration and growth in boreal forested peatlands of eastern Canada, and to identify the soil variables that favour tree growth following harvest. Moreover, we sought to determine how stand growth following harvest compared with that observed following fire. The average tree height of summer clearcuts was greater than that of summer carefully logged stands and that of all winter harvested sites. Summer clearcutting also resulted in a higher density of trees > 3 m and > 4 m tall and in a 50% reduction in *Rhododendron groenlandicum* cover, a species associated with reduced black spruce growth. Height growth of sample trees was related to foliar N and P concentrations, and to soil total N, pH and available Ca and Mg but not to harvest method or season. Our results also indicate that summer clearcutting could produce stand productivity levels comparable to those observed after high-severity soil burns. These results suggest that summer clearcutting could be used to restore forest productivity following harvest in forested peatlands, and offer further support to the idea that sufficient levels of soil disturbance may be required to restore productivity in ecosystems undergoing paludification.

Keywords careful logging, clearcutting, paludification, peatland, *Picea mariana*, soil disturbance, forest productivity
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1 Introduction

Black spruce (*Picea mariana* [Mill.] BSP) is the dominant tree species in much of the boreal forest in eastern Canada. Successional paludification (i.e. a dynamic process during which well-drained forests transform into peatlands due to succession) is a dominant process in some region of eastern Canada because of a combination of cold, humid climate, flat topography, and clay surficial deposits (Simard et al. 2007, Fenton et al. 2009). It has been shown in black spruce stands undergoing paludification that at canopy breakup (i.e. approximately 100 years post-fire), *Sphagnum* spp. mosses start expanding to the detriment of feathermosses (e.g. *Pleurozium schreberi*) (Fenton and Bergeron 2006), which induces changes in forest floor processes. Compared with feathermosses, *Sphagnum* spp. mosses have a higher carbon fixation rate (Swanson and Flanagan 2001), a higher soil temperature buffering capacity (Dioumaeva et al. 2003), and a slower decomposition rate (Turetsky 2003). As a result, thick organic layers develop over the mineral soil and change the conditions in the tree's rooting zone, which becomes colder, wetter, and oxygen-poor. In the prolonged absence of fire disturbance, these changes are accompanied by an autogenic reduction in productivity (Wardle et al. 2004) that involves reduced tree growth and stand productivity (Simard et al. 2007).

Forest fires are spatially variable, and soil burn severity varies greatly within and among fires (Miyanishi and Johnson 2002, Johnstone and Chapin 2006). In boreal ecosystems where thick organic layers are the norm, soil burn severity has significant consequences for tree regeneration (Johnstone and Chapin 2006, Greene et al. 2007) and growth (Johnstone and Chapin 2006, Simard et al. 2007), and for the structure, composition and productivity of forest (Viereck 1983, Lecomte et al. 2006a, 2006b, Simard et al. 2007). 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, Simard et al. 2007, Shetler et al. 2008).

Over the past decades, because of an increasing demand for wood products, most of the harvest volumes allotted to forest companies in eastern Canada were located in low-productivity peatlands (Prévost et al. 2001). In the meantime, research and public pressure led governments and timber companies to adopt forest practices that protect the soil and advance tree regeneration. As a result, low-impact practices such as careful logging and winter harvest are now required practices in eastern Canada. However, concerns have been raised that these silvicultural practices may in some regions increase the rate of paludification because they do not sufficiently disturb the organic soil layers (Fenton et al. 2005, Lavoie et al. 2005). Ultimately, these silvicultural practices may produce growth conditions that are more similar to those associated with low-severity soil burns, leading to the establishment of low-density or patchy stands with widely variable productivity, rather than reproducing growth conditions prevailing after high-severity soil burns, which usually result in dense, productive stands (Lussier et al. 1992, Ruel et al. 2004). Consequently, the potential productivity of much of this landscape may be underestimated.

In a previous study conducted at the landscape level (Lafleur et al. 2010), we showed, 8 years after harvest, that regenerating black spruce stands were taller after clearcutting than after careful logging, regardless of soil type and drainage, and that the cover of *Sphagnum* spp. and ericaceous shrubs was also reduced by clearcutting. Together, these results suggest that soil disturbance was more severe during clearcutting than during careful logging. Since severe soil disturbance appears to be a key driver of ecosystem processes in a paludified landscape, in this study we sought to determine, 10–30 years after harvest, how soil disturbance created during different harvest operations and seasons could affect the productivity of paludified stands. The specific objectives of this study were i) to compare the effects of different harvest methods (i.e. clearcutting vs. careful logging) and season (summer vs. winter) on black spruce regeneration and growth, ii) to identify the soil variables that favour tree growth following harvest, and iii) to determine how stand growth following forest harvest compares with that observed following fire. Because machinery traffic is restricted to specific skid trails during careful logging, this harvest method protects advanced regeneration and has a lower impact on soils compared with clearcutting (CC), where machinery traffic is not restricted, consequently reducing problems related to soil rutting and decreasing the need for tree planting. Likewise, in winter, snow cover and frozen ground protect soils against rutting and compaction during harvest operations, whereas in summer this protection is lacking. Consequently, soils are disturbed over a larger area during CC as compared with careful logging, and the disturbance is expected to be more severe during summer harvest than during winter harvest. Therefore, our hypotheses are: i) clearcuts conducted during summer favour black spruce regeneration and promote tree growth compared to winter clearcuts and summer and winter careful logging; ii) at the tree level, differences in tree growth are explained by local soil nutrient concentrations; iii) clearcuts conducted during summer promote stand regeneration and growth at a level comparable to that of high severity soil burns. These results could help identify the harvest treatment most likely to reproduce the regeneration and growth patterns observed after high-severity soil burns and to help maintain or restore forest productivity in paludified black spruce stands.

2 Methods

2.1 Study Area

The study area is located in the Clay Belt region of northwestern Quebec (49°48´N; 79°01´W) and is part of the western black spruce-feathermoss bioclimatic domain (Bergeron et al. 1999). According to Quebec's classification system (Robitaille and Saucier 1998), stands sampled in this study were black spruce stands with a ground cover dominated by *Sphagnum* spp. on thick organic deposits (>25 cm) with hydric drainage (i.e. forested peatland) (Bergeron et al. 1999). In this region, the last glacial advance during the Wisconsin glaciation (ca. 8000 before present) flattened the topography and compacted the lacustrine clays that had been laid down by glacial lakes Barlow and Ojibway (Vincent and Hardy 1977).

From 1971 to 2000 the average annual temperature was 0.1 °C, and average annual precipitation was 892 mm, with 35% falling during the growing season (Joutel weather station; Environment Canada 2009). The average number of degree-days (>5 °C) is 1249, and the frost-free season is about 60 days, with frost occasionally occurring during the growing season.

2.2 Site Selection

This study took advantage of stands that had been harvested under different forest management regimes to examine the long-term effects of different silvicultural practices on soil disturbance and black spruce growth. Forest maps produced by Tembec, the major forest company in the region, were used to identify 28 paludified stands (open multi-layer canopy with soil organic layer >25 cm thick) that had been harvested by careful logging (in Quebec, cut with protection of regeneration and soils [CPRS]) in winter (WCPRS, 5 replicates) or in summer (SCPRS, 5 replicates), and stands that had been clearcut in winter (WCC, 8 replicates) or in summer (SCC, 10 replicates). Because forest regulations and practices changed over time, and sites were harvested over a period of ca. 20 years, there was some overlap between management practices (Table 1). Only sites with a slight slope (<4%) and a clay mineral soil covered with a thick (>25 cm) organic layer were selected.

Prior to and after harvest, the tree layer of the sampling sites was dominated by black spruce, while Labrador tea (*Rhododendron groenlandicum*) and sheep laurel (*Kalmia angustifolia*) dominated the shrub cover. *Sphagnum fallax sensu lato, S. capillifolium, S. rubellum, S. russowii, S. fuscum, S. magellanicum* and feathermosses (mainly *Pleurozium schreberi*) dominated the forest floor.

2.3 Plot Layout and Survey

At each site, the direct results of harvest at the stand and tree levels were assessed through a

Table 1. Characteristics of the 28 paludified black spruce stands of the Clay Belt used in this study.

Harvest method	Site No.	Harvest year	Sampling year	TSH[a] (yr)	OL[b] thickness (cm ± 1 SD)
Summer clearcut (SCC)	CN-23	1975	2007	32	74.1 (26.3)
	CN-71	1975	2008	33	77.5 (38.2)
	CN-69	1980	2007	27	106.3 (19.0)
	MI-54	1982	2008	26	39.6 (27.9)
	MI-55	1982	2008	26	58.3 (35.3)
	CN-68	1984	2006	22	47.2 (17.2)
	MI-66	1986	2006	20	80.0 (22.8)
	MS-63	1986	2007	21	78.8 (26.7)
	VP-32	1990	2006	16	63.6 (37.8)
	WA-45	1993	2007	14	25.3 (11.7)
Winter clearcut (WCC)	WA-43	1982	2006	24	73.5 (29.8)
	MI-64	1982	2006	24	37.8 (31.3)
	MI-53	1986	2007	21	36.9 (22.4)
	MI-52	1987	2006	19	41.1 (21.3)
	VP-39	1989	2006	17	51.1 (10.2)
	VP-40	1989	2006	17	51.7 (17.3)
	MI-62	1991	2006	15	77.2 (26.4)
	VP-33	1993	2006	13	40.6 (11.8)
Summer CPRS[c] (SCPRS)	VP-35	1989	2007	18	121.1 (2.3)
	VP-36	1989	2007	18	41.3 (13.1)
	VP-37	1989	2007	18	58.2 (20.7)
	CS-11	1990	2006	16	37.2 (16.4)
	WA-44	1994	2006	17	57.8 (23.5)
Winter CPRS (WCPRS)	WA-42	1989	2007	18	32.7 (16.1)
	MI-56	1989	2007	18	121.2 (1.7)
	MI-58	1991	2007	16	105.3 (19.7)
	CN-24	1994	2007	13	46.1 (12.9)
	CN-70	1996	2007	11	77.0 (11.3)

[a] TSH = time since harvest
[b] OL = organic layer
[c] CPRS = cut with protection of regeneration and soils

series of nested plots. Specifically, three 400 m^2 circular plots were randomly installed at each site, each placed 50 m apart to ensure independence of the sampling points. The effects of harvest method and season at the stand level were assessed in two ways. First, black spruce stand height was estimated by measuring and averaging the total height of all black spruce stems taller than 1.3 m located in each circular plot. Second, stem density was assessed by determining the number of stems (> 1.3 m tall) ha^{-1} in each circular plot (total area sampled = 1200 m^2). Then, three sample trees were randomly selected in each circular plot. On these trees, we determined the total increment of the last 3 years (i.e. 3-year annual increment; 3YAI) and sampled foliage for nutrition analyses. Furthermore, these same trees were sampled for stem analysis, which enabled us to compare tree growth during the first 10 years following harvest (hereafter referred to as "height at age 10"). Cross-sections were taken at ground level, 0.3 m, 1 m, 1.3 m, 2 m, and every meter thereafter, and were then polished (400 grit) and cross-dated using standard dendrochronological techniques (Stockes and Smiley 1968). For trees established before harvest, we used the inflection in the age-height growth curve (indicating growth release following harvest) as age 0 (Curtis 1964). Because the degree of decomposition of the soil organic layers is known to influence the growth of black spruce seedlings (Lavoie et al. 2007), we characterized the microsite of each sample tree by determining the proportion of their root system present in the fibric (von

Post scale = 0–4; Damman and French 1987) and mesic (von Post scale = 5–8; Damman and French 1987) organic layers. Then, the organic layer (at a depth of 10–20 cm, i.e. where the bulk of the roots were located) was sampled for nutrient analysis. Finally, in order to assess the effect of harvest on *Sphagnum* and ericaceous shrub cover (i.e. *K. angustifolia* and *R. groenlandicum*), visual estimates were made in four 4-m^2 sub-plots established in each 400-m^2 circular plot; species were evaluated individually so that total cover can exceed 100%. Surveys were conducted during the summers of 2006, 2007, and 2008.

2.4 Soil and Foliar Analyses

Chemical properties of all microsites were evaluated using substrate analysis (C:N, N_{tot}, P, Ca, Mg and pH) of the organic layer samples, and foliar nutrition was determined using foliar N and P concentrations.

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), and exchangeable Ca and Mg were extracted using unbuffered 0.1 M $BaCl_2$ and determined by atomic absorption (Hendershot and Duquette 1986).

Needle samples were collected in mid-September 2007 and 2008 when the growing season had ended. Needle samples were collected on the three sample trees selected for stem analysis, thus yielding a total of 252 samples. Needle samples were selected from the current year's growth and were sampled from various positions in the crown (mid, top 1/3, and leader) and all needles from an individual tree were mixed. These samples were oven-dried at 70 °C for 48 h. After drying, needles were separated from twigs and ground. 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 Statistical Analyses

The effects of harvest method and season on stand-level parameters (i.e. black spruce stand height, density of stems taller than 2, 3, and 4 m, and cover of *Sphagnum* spp. and ericaceous shrubs) were determined using two-way mixed-effect ANOVAs. Harvest method and season were introduced into these models as fixed effects, plot and site as random effects, and time since harvest as a covariate. Then, two-way mixed-effect ANOVAs were used to analyze the effects of harvest method and season on the growth parameters (i.e. 3YAI and height at age 10) of sample trees, using harvest method and season as fixed effects, plot and site as random effects, and sample tree total height as a covariate. Next, two-way mixed-effect ANOVAs were used to analyze the effects of harvest method and season on soil physico-chemistry and foliar nutrition. In these models, harvest method and season were introduced as fixed effects, and plot, site and tree as random effects. Finally, we used Pearson correlations to determine the strength of the relationships between 3YAI and height at age 10, and soil physico-chemical variables, foliar nutrition, and tree rooting location (i.e. % of the root system in the fibric and mesic layers).

Prior to analysis, residuals were tested for normality and homogeneity of variances, and were log- or square root-transformed when necessary. For the covariance analyses, we also tested for interactions between fixed effects and covariates. Mixed-effects analyses were done using the MIXED procedure in SAS (SAS Institute Inc. 2004). Post-hoc comparisons (Tukey HSD) were made to contrast the levels of the fixed variables, and differences were deemed significant when $p \leq 0.05$, except for interactions that were considered significant when $p \leq 0.10$.

2.6 Comparing Harvest Methods with Wildfires

Because one of the general objectives of this study was to compare the effects of wildfires with those of harvest practices, we compared our results on stand height with a dataset from a previous study conducted in the same study area that compared the effects of low- and high-severity soil burns on forest productivity (Simard et al. 2007). In this study, all black spruce stems in 10 m × 10 m plots were sampled for stem analyses. Cross-sections were taken at ground level, 0.4 m, 1 m, 4 m, and every 4 m thereafter, and were then polished (400 grit) and cross-dated using standard dendrochronological techniques (Stockes and Smiley 1968). All stands were dominated by black spruce and located on clay soils. We used a subset of Simard et al.'s (2007) data, i.e., three paired low- and high-severity fires that occurred around 1907, 1916 and 1948 (Simard et al. 2007). To compare the results of the two studies, we compared the effects of the type of disturbance (i.e. harvest treatments [SCC, WCC, SCPRS and WCPRS] and soil burn severity [low- and high-severity soil burns]) on stand height and density of stems taller than 2, 3, and 4 m using one-way mixed-effect ANOVAs. The type of disturbance was introduced into these models as a fixed effect, plot as random effects, and time since disturbance as a covariate. Due to the large difference in stand age between stands originating from harvest (mean = 19.9 yrs, S.D. = 5.2) and those originating from fire (mean = 77.3 yrs, S.D. = 21.5), we used the stem analysis data from Simard et al. (2007) to reconstruct tree height at age 20. Therefore, time since disturbance was set at 20 years for the sites originating from fire.

Although we recognize that climate was likely different during the first 10 years of growth between the forest stands originating from wildfires (which occurred in the early and mid-20th century) and those originating from forest harvest (which occurred in the late 20th century), we nonetheless believe that these comparisons could reveal important similarities in terms of growth between stands originating from wildfires or from forest harvest of varying soil disturbance severities. These preliminary results could help identify the harvest method most likely to reproduce the effects of high-severity soil burns in terms of stand growth rate and productivity, and therefore adjust forest harvest practices to maintain or restore forest productivity in paludified black spruce stands.

3 Results

3.1 Effects of Harvest Method and Season on Stand-Level Parameters

3.1.1 Stand Development

Both harvest method and season had a significant effect on stand growth parameters. Season of harvest had a significant effect on mean stand height, with taller stands after summer than after winter harvest (Fig. 1a), while the effect of harvest method was marginally significant (CC > CPRS; $p = 0.0730$). More importantly, however, the significant interaction between harvest method and season reveals that stands were approximately 35% taller after SCC than after WCC ($p = 0.0007$), SCPRS ($p = 0.0148$) and WCPRS ($p = 0.0046$; Fig. 1a).

Furthermore, summer harvest produced a significantly greater number of stems >3 m and >4 m ha^{-1} (respectively 2.5 times and 4 times more stems per hectare), and a marginally significantly greater number of stems >2 m ha^{-1} than winter harvest (Fig. 1b). The significant interaction between harvest method and season reveals that SCC produced 6 times more stems >4 m per hectare than the three other harvest method/season combinations (Fig. 1b). These last results, together with those for stand height, suggest that SCC disturbed the forest floor more intensively and over a larger area than any of the three other harvest method/season combinations.

3.1.2 Sphagnum and Ericaceous Shrub Cover

Neither harvest method nor season or their interaction had a significant effect on *Sphagnum* spp. or *K. angustifolia* (Fig. 2) percent cover. Harvest method, however, had a significant effect on *R.*

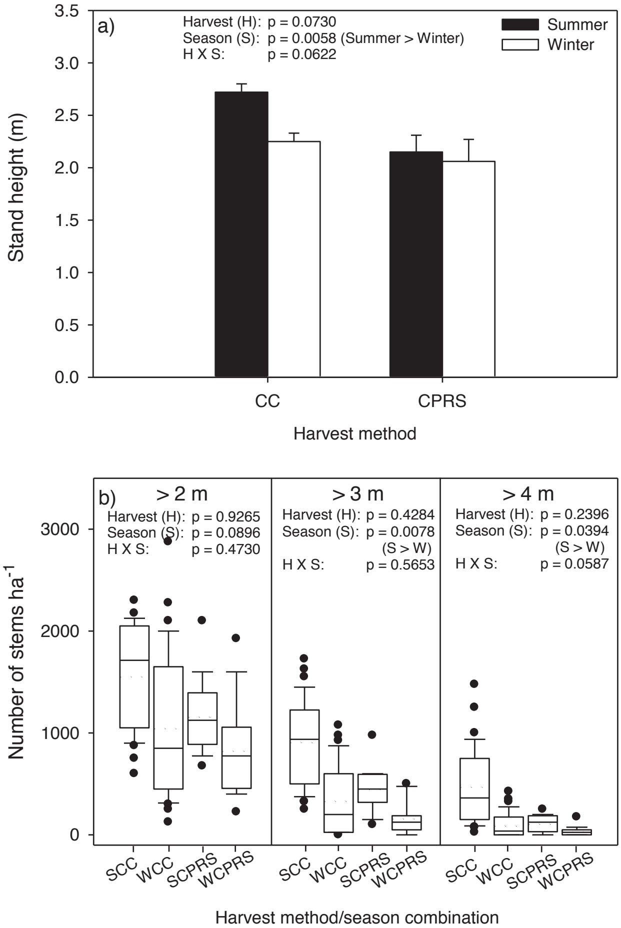

Fig. 1. a) Black spruce mean stand height (m ± 1 S.E) according to harvest method and season. Values are adjusted means after controlling for time since harvest. CC = clearcut, CPRS = cut with protection of regeneration and soils. b) Box plots showing stem density of black spruce taller than 2 m, 3 m and 4 m according to harvest method and season. Values are adjusted means after controlling for time since harvest. The solid black lines represent the median; the dotted line, the mean; the vertical boxes, the 25th and 75th percentiles; the upper and lower bars, the 10th and 90th percentiles; black dots show outliers outside the 10th and 90th percentiles. SCC = summer clearcut, WCC = winter clearcut, SCPRS = summer cut with protection of regeneration and soils, WCPRS = winter cut with protection of regeneration and soils.

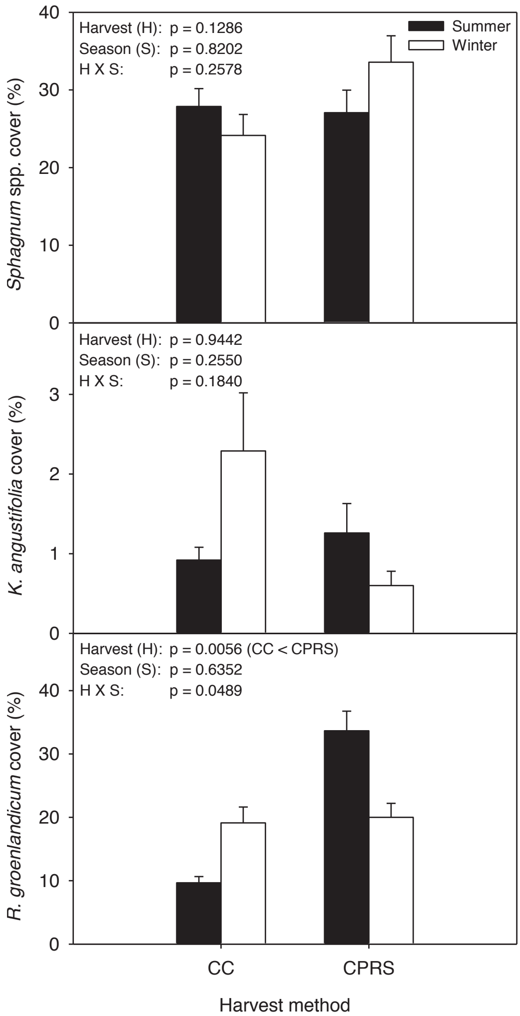

Fig. 2. *Sphagnum* spp. and ericaceous shrub cover (% ± 1 S.E.) according to harvest method and season. Values are adjusted means after controlling for time since harvest. CC = clearcut, CPRS = cut with protection of regeneration and soils.

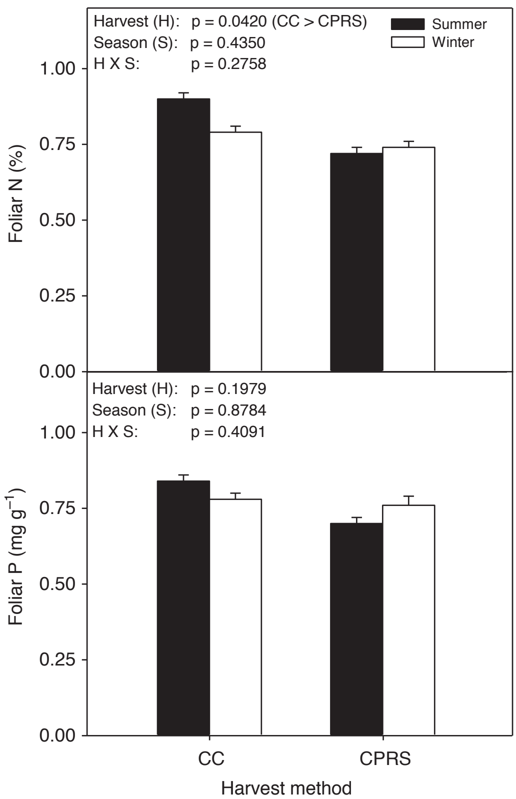

Fig. 3. Black spruce foliar N (% ± 1 S.E.) and P (mg g^{-1} ± 1 S.E.) according to harvest method and season. CC = clearcut, CPRS = cut with protection of regeneration and soils.

groenlandicum cover (Fig. 2), which was approximately 2 times higher after CPRS than after CC. The significant interaction between harvest method and season indicates that *R. groenlandicum* cover was lower after SCC than after both WCPRS (p = 0.0899) and SCPRS (p = 0.0016), and that it was also lower after WCC as compared with after SCPRS (p = 0.0087; Fig. 2).

3.2 Effects of Harvest Method and Season on Sample Trees and Soil Variables

Harvest method (p = 0.5772), season (p = 0.2901) or their interaction (p = 0.8437) had no effect on sample tree height at age 10 (across all harvest method/season combinations, $\bar{\chi}$ = 100 cm, S.E. = 3.6 cm). Likewise, harvest method (p = 0.8267), season (p = 0.3992) or their interaction (p = 0.5010) did not have an effect on sample tree 3YAI (across all harvest method/season combinations, $\bar{\chi}$ = 48 cm, S.E. 1.4 cm).

Similarly, harvest method and season had no significant effect on soil C/N, N_{tot}, P_{avail}, Ca, Mg or pH, nor was the interaction between them significant, except for a significant interaction for C/N (Table 2). Post-hoc contrasts indicated that

Table 2. Means (± S.E.) of soil properties under black spruce trees after summer and winter clearcut and summer and winter cut with protection of regeneration and soils (CPRS) in paludified black spruce stands.

Treatment	C/N	N_{tot} (%)	P_{avail} (mg g^{-1})	Ca (cmol(+) kg^{-1})	Mg (cmol(+) kg^{-1})	pH
Clearcut						
Summer	42.1 (2.3)	1.27 (0.05)	0.029 (0.001)	27.7 (3.1)	5.1 (0.3)	4.11 (0.05)
Winter	44.1 (1.9)	1.20 (0.05)	0.032 (0.002)	35.9 (4.5)	6.5 (0.4)	4.25 (0.09)
CPRS						
Summer	55.1 (2.2)	0.92 (0.04)	0.029 (0.001)	21.2 (1.9)	4.7 (0.4)	3.92 (0.07)
Winter	41.6 (3.1)	1.22 (0.06)	0.030 (0.003)	26.0 (2.7)	6.0 (0.7)	4.28 (0.09)
p-value						
Harvest (H)	0.2190	0.1566	0.9405	0.3272	0.7008	0.6256
Season (S)	0.2003	0.2801	0.8587	0.3476	0.2443	0.1666
H X S	0.0547	0.1002	0.2065	0.9816	0.5875	0.3589

SCPRS had a significantly ($p = 0.0459$) higher C/N than WCPRS.

Foliar N concentration was significantly higher after clearcutting (CC) than after CPRS (Fig. 3). However, neither season nor the interaction between harvest method and season had an effect on foliar N concentration. Foliar P concentration did not significantly differ between harvest methods and seasons, nor was their interaction significant (Fig. 3).

3.2.1 *Linking Organic Layer Physico-Chemical Properties and Foliar Nutrition to Tree Growth Parameters*

Table 3 shows the correlations between soil physico-chemical properties with sample tree height at age 10 and 3YAI. While tree height at age 10 was significantly negatively correlated to C/N, it showed significant positive correlations with organic layer N_{tot}, Ca and Mg and pH. P_{avail} showed no correlation with tree height at age 10. Contrary to height at age 10, 3YAI was not significantly correlated to any soil variables.

Although N and P foliar nutrition was positively correlated to 3YAI, these correlations were not significant. However, both N and P foliar nutrition showed significant positive correlations with tree height at age 10 (Table 3).

Finally, both 3YAI and height at age 10 were correlated to the proportion of the tree's root system growing in the fibric (negative correlation) and mesic (positive correlation) layers (Table 3).

Table 3. Correlations between 3-year annual height increment and height at age 10, and soil variables, foliar nutrition and proportion (%) of the root system located in fibric and mesic organic layers.

Variable	3-year annual increment		Height at age 10	
	r	p-value	r	p-value
Soil variable				
C/N	–0.102	0.133	–0.243	**<0.001**
N_{tot}	0.106	0.120	0.270	**<0.001**
P_{avail}	0.001	0.994	0.083	0.222
Ca	0.020	0.780	0.229	**<0.001**
Mg	0.120	0.086	0.262	**<0.001**
pH	0.023	0.738	0.270	**<0.001**
Foliar nutrition				
N	0.100	0.127	0.215	**<0.001**
P	0.116	0.077	0.148	**0.022**
Root system				
Fibric	–0.208	**0.002**	–0.241	**<0.001**
Mesic	0.145	**0.029**	0.183	**0.004**

Appendix 1 shows the average proportion of the tree's root system growing in fibric, mesic and humic organic matter, and in mineral soil according to harvest method and season of harvest.

3.3 Comparisons between Wildfires and Harvested Stands

Disturbance type had a significant effect on stand height. Stands originating from SCC and high-severity soil burns were significantly taller than

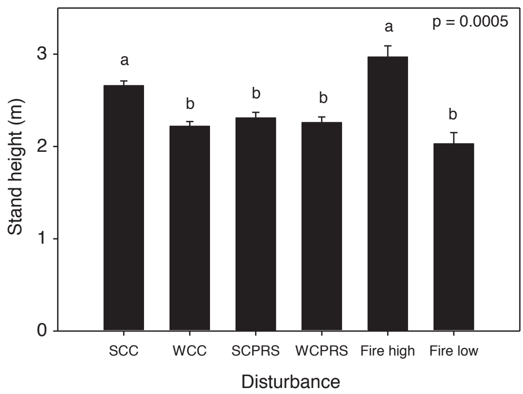

Fig. 4. Black spruce mean stand height (m ± 1 S.E) according to harvest treatment and soil burn severity. Values are adjusted means after controlling for time since disturbance. SCC = summer clearcut, WCC = winter clearcut, SCPRS = summer cut with protection of regeneration and soils, WCPRS = winter cut with protection of regeneration and soils; Fire high = high-severity soil burn; Fire low = low-severity soil burn. Disturbances identified by different letters are significantly different. Data for Fire high and Fire low from Simard et al. (2007).

those originating from the other types of disturbance (Fig. 4).

Disturbance type also had a significant effect on stem density. High-severity soil burns produced a significantly greater number of stems > 2 m and > 3 m than any other types of disturbance (Fig. 5). In addition, SCC produced a significantly greater number of stems > 3 m than both WCC and WCPRS, and both for stems > 2 m and > 3 m, SCC produced an average number of stems equivalent to low-severity soil burns (Fig. 5). Finally, both SCC and high-severity soil burns produced a significantly greater number of stems > 4 m than any other types of disturbance (Fig. 5).

4 Discussion

This study supports our first hypothesis that clearcuts conducted during summer favour the growth of black spruce stands over winter clearcuts and summer and winter CPRS. In addition, in agree-

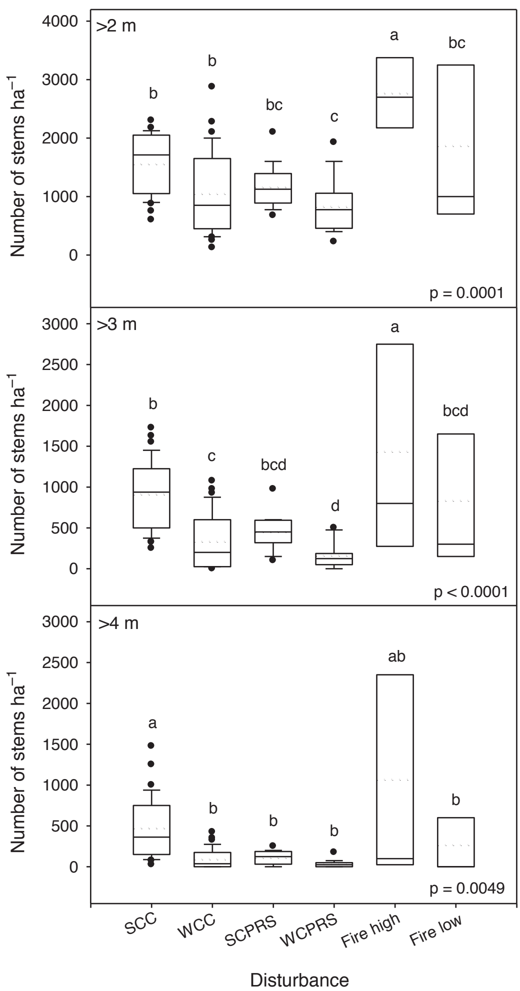

Fig. 5. Box plots showing stem density of black spruce taller than 2 m, 3 m and 4 m according to harvest treatment and soil burn severity. Values are adjusted means after controlling for time since harvest. The solid black lines represent the median; the dotted line, the mean; the vertical boxes, the 25th and 75th percentiles; the upper and lower bars, the 10th and 90th percentiles; black dots show outliers outside the 10th and 90th percentiles. SCC = summer clearcut, WCC = winter clearcut, SCPRS = summer cut with protection of regeneration and soils, WCPRS = winter cut with protection of regeneration and soils; Fire high = high-severity soil burn; Fire low = low-severity soil burn. Disturbances identified by different letters are significantly different. Data for Fire high and Fire low from Simard et al. (2007).

ment with our second hypothesis, our results show that following harvest individual tree growth is related to microsite chemical properties, in particular soil N_{tot} and C/N as well as pH and exchangeable Ca and Mg. Finally, the growth of black spruce stands that have been clearcut during summer was similar to that of post-fire stands, which supports our third hypothesis that in forested peatlands, summer clearcuts promote the growth of black spruce stand at a level comparable to high-severity fire.

4.1 Effects of Harvest Method and Season on Stand- and Tree-Level Parameters

Both mean stand height and the abundance of trees > 4 m were greater in SCC sites as compared to the other harvest method/season combinations, suggesting that SCC generates a greater proportion of the area that is conducive to rapid growth. The observation of more rapid stand growth with CC as compared to CPRS was confirmed by a parallel landscape study conducted on a combination of soil types and soil drainage conditions on the Clay Belt (Lafleur et al. 2010).

At the stand level, levels of soil disturbance were also reflected in differences in percent cover of *R. groenlandicum*. Harvest methods had an effect on *R. groenlandicum* cover, which was 50% lower following CC than after CPRS, while the significant interaction between harvest method and season indicated that *R. groenlandicum* cover was higher in SCPRS sites as compared to SCC and WCC sites. Reduced *R. groenlandicum* cover after CC may have had important consequences for tree growth as this species is known to interfere with black spruce growth (Inderjit and Mallik 1996, 1997). These authors suggested that the production of water-soluble phenolic compounds by *R. groenlandicum* and changes in nutrient availability were possible sources of the interference of *R. groenlandicum* with black spruce growth.

At the individual tree level, differences in the level of soil disturbance could be reflected in the soil physico-chemical properties of microsites. Our results showed that height at age 10 was both positively correlated to soil N_{tot} and negatively correlated to soil C/N. In black spruce stands, soil disturbance, such as may occur during logging activities, is known to accelerate organic matter mineralization and to increase nutrient availability (Keenan and Kimmins 1993, Simard et al. 2001, Locky and Bayley 2007). In forested peatlands, where black spruce seedling growth is N-limited (Munson and Timmer 1989, Timmer and Munson 1991), any soil disturbance that increases N availability is likely to favour their growth.

Furthermore, both foliar N and P concentrations showed positive correlations with individual tree height at age 10. These results could indicate that although nutrient availability was not different among harvest method/season combinations, nutrient uptake may have been facilitated in microsites supporting larger trees. Because high foliar N and P concentrations have been linked to faster growth and higher photosynthetic activity of conifers (Macdonald and Lieffers 1990), and because N and P uptake is influenced by soil temperature (Van Cleve et al. 1981, BassiriRad 2000, Domisch et al. 2002), any soil disturbance likely to increase soil temperature is also liable to facilitate or to increase nutrient uptake and favour tree growth.

The proportion of the root system in the fibric and mesic organic layers was correlated to tree growth and height (i.e. 3YAI and height at age 10). Because the fibric layer is considered a poor growth medium for black spruce (Greene et al. 1999, Lavoie et al. 2007), and the mesic layer a good growth medium (Lavoie et al. 2007), trees with a high proportion of their root system in the mesic layer may have had access to a larger pool of nutrients. The thickness of the fibric layer, known to be a poor growth substrate, is related to site type but may also be influenced by soil disturbance during harvest operations as it is located on the top portion of the soil.

Thus, the nutritional quality of microsites and the position of the root system (i.e. whether the roots are mainly in the fibric or mesic organic layers) are important factors explaining tree growth following harvest operations in forested peatlands. In this study, we found no significant differences in the sample tree 3YAI or height at age 10 between harvest methods or seasons, nor did we find any interactions between these variables. Therefore our results suggest that at the tree level each harvest method and season was able to create a variety of microsites in terms of nutritional conditions, including nutrient-rich microsites that favoured tree growth.

4.2 Harvest Method vs. Wildfire

Only SCC was able to produce black spruce stands with an average height that was comparable to that of stands originating from high-severity soil burns, whereas all other harvesting treatments produced stands that had a mean height similar to that of low-severity soil burns (Fig. 4 and 5). Furthermore, both SCC and high-severity soil burns resulted in a greater abundance of trees >4 m as compared with the other types of disturbance. Comparing the effects of soil burn severity on stand development in the boreal forest of northwestern Quebec, Lecomte et al. (2006a) showed that high-severity soil burns resulted in higher initial tree density as compared with low-severity soil burns, whereas Ilisson and Chen (2009) showed that black spruce recruitment after clearcutting was comparable to that of wildfire. Therefore, at the stand level, SCC could create growth responses more similar to those of high-severity soil burns than any other harvest method/season treatment combinations. This study suggests that SCC could be used in paludified black spruce stands if management objectives include restoring stand productivity and slowing paludification.

5 Conclusions

Our results showed that in paludified black spruce stands of the Clay Belt, SCC was better suited than any other harvest method/season combinations we tested to favour stand regeneration and growth. Summer clearcuts likely disturbed the soil over a greater proportion of the cutover area, which may have resulted in a greater abundance of microsites conducive to better tree growth, as shown by the greater abundance of trees >4 m in SCC sites compared with other harvest treatments. More importantly, SCC produced soil conditions favourable to tree growth in greater abundance, producing overall stand growing conditions that were comparable to high-severity soil burns. The concern that greater soil damage by rutting during summer operations (Morris et al. 2009) could decrease site productivity in organic soils was not verified one or two decades following harvest. These results therefore suggest that SCC reproduces to some extent the effects of high-severity soil burns (i.e. in terms of growth rate at the tree level, and in terms of mean stand height and density of trees taller than 4 m at the stand level). In turn, this suggests that SCC could be used in forest management strategies to help restore forest productivity when harvesting has inadvertently decreased potential stand productivity by favouring paludification. However, clearcutting may have greater impact than careful logging on several ecosystem properties and functions not evaluated in this study such as streamflow, water quality, and biodiversity and wildlife habitats (Keenan and Kimmins 1993). Hence, the simultaneous use of clearcutting and careful logging, along with the creation of conservation areas, could favour, at the landscape level, the maintenance of wood production as well as that of ecosystem properties and functions.

Finally, in agreement with other studies, we showed that soil disturbance may be required to restore productivity in ecosystems undergoing autogenic reduction in productivity (Wardle et al. 2004). In paludified forests, a thick organic layer insulates the soil, and mechanical disturbance to this layer may cause an effect similar to the assart effect (Kimmins 1997), i.e. a kick start for nutrient cycles and tree development in the early regeneration stage. However, to achieve optimal productivity following forest harvest, the appropriate level of soil disturbance to specific site and drainage conditions needs to be better defined.

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Appendix 1. Proportion (% ± S.E.) of tree's root system growing in fibric, mesic and humic organic matter, and in mineral soil according to harvest method and season of harvest.

Treatment	Fibric	Mesic	Humic	Mineral
Clearcut				
Summer	68.1 (3.1)	26.2 (2.9)	3.7 (0.9)	2.0 (0.4)
Winter	64.7 (3.1)	24.0 (2.4)	8.5 (1.4)	2.8 (0.5)
CPRS[a)]				
Summer	73.9 (3.5)	24.3 (3.5)	1.5 (0.5)	0.3 (0.1)
Winter	73.6 (4.0)	23.9 (3.6)	2.5 (1.7)	0.0 (0.0)
p-value				
Harvest (H)	0.1871	0.7352	0.1250	ND[b)]
Season (S)	0.8964	0.6618	0.3895	ND
H × S	0.6360	0.8660	0.4922	ND

[a)] CPRS = Cut with protection of regeneration and soils
[b)] ND = Not determined