

Growth of planted black spruce seedlings following mechanical site preparation in boreal forested peatlands with variable organic layer thickness: 5-year results

Benoit Lafleur · David Paré · Nicole J. Fenton · Yves Bergeron

Received: 20 April 2011 / Accepted: 7 September 2011
© INRA and Springer-Verlag, France 2011

Abstract

• **Context** Following forest harvest, mechanical site preparation (MSP) is commonly used to regenerate harvested sites. In boreal forested peatlands, however, the effectiveness of MSP to regenerate harvested sites is likely to be hampered by thick organic layers.

• **Aim** We sought to determine the capability of different MSP techniques to improve growth conditions of planted black spruce seedlings in boreal forested peatlands where closed-crown productive forests could revert to unproductive forested peatlands in the absence of severe soil disturbance.

• **Methods** The effects of disc scarification, mounding and patch scarification on soil chemistry and seedling growth were contrasted.

• **Results** Seedlings of site-prepared plots were 15% taller than those of untreated ones, irrespective of the MSP technique used, likely owing to the greater abundance of exposed mineral soil and mesic substrates created. Mounding and patch scarification were able to expose mineral soil over a greater proportion (>25% vs. <10%) of the treated area compared with disc scarification and control, whereas the combined surface area of exposed mineral soil and mesic

substrates was higher in every MSP treatments relative to the control (>57% vs. 41%, respectively). Individual seedling growth was influenced by substrate type and drainage. Seedlings planted in moderately and well-drained mesic substrates and mineral soil were 25% taller than those planted in poorly drained fibric substrates.

• **Conclusion** All three MSP techniques were effective because they succeeded in creating high-quality microsites despite thick organic layers.

Keywords Black spruce · Forest floor disturbance · Mechanical site preparation · Organic layer · Seedling growth

1 Introduction

The variation in forest floor thickness commonly observed in forest ecosystems (Qian and Klinka 1995; Šamonil et al. 2008; Schöning et al. 2006) influences the vertical distribution of soil physico-chemical properties (Bringmark 1989; Jobbágy and Jackson 2001; Legout et al. 2008) and tree growth (Geyer et al. 1980; Meredieu et al. 1996). In boreal forests, forest floor thickness has been related to post-disturbance regeneration success (Greene et al. 2005; Jayen et al. 2006; Meunier et al. 2007), stand spatial structure (Lavoie et al. 2007a) and stand growth (Johnstone and Chapin 2006), as well as to soil nutrient and understory vegetation spatial variability (Lecomte et al. 2005; Laiho et al. 2008). Likewise, the regeneration of boreal tree species has been related to habitat factors such as water availability and paludification process (Simard et al. 2007; Yarie 2008).

Following forest harvest, mechanical site preparation (MSP) is commonly used to improve survival and growth of planted tree seedlings, and to ensure successful regen-

Handling Editor: Douglas Jacobs

B. Lafleur (✉) · N. J. Fenton · Y. Bergeron
NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest
Management, Université du Québec en Abitibi-Témiscamingue,
445 boul. de l'Université,
Rouyn-Noranda, Québec J9X 5E4, Canada
e-mail: benoit.lafleur@uqat.ca

D. Paré
Natural Resources Canada, Canadian Forest Service,
Laurentian Forestry Centre,
1055 du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy,
Québec QC G1V 4 C7, Canada

eration in harvested sites (Sutherland and Foreman 1995). Common MSP treatments aim to remove the overlying organic layer and to expose mineral soil. In boreal forests, soil disturbances such as those created by MSP have been shown to increase growth of planted spruce seedlings by (1) increasing nutrient availability by reducing the cover of competing vegetation (Staples et al. 1999; Sutherland and Foreman 2000), (2) enhancing root growth via reduced soil bulk density and increased soil temperatures (Burdett et al. 1983; Örlander et al. 1990) and (3) increasing N mineralization and uptake due to warmer soil and improved soil moisture (Johansson 1994; Nordborg et al. 2003). In boreal forested peatlands, i.e. closed-crown forest growing on a thick (>30 cm) organic layer, however, MSP, with the exception of drainage, is not a common practice. Indeed, the removal of organic layers and exposition of mineral soil by MSP is not a recommended practice as these ecosystems have been identified as being vulnerable to rutting (Groot 1998) as well as to frost heaving and flooding (Sutherland and Foreman 1995). However, Morris et al. (2009) showed in a peatland dominated by black spruce (*Picea mariana* [Mill.] BSP) that moderate levels of rutting or forest floor disturbance may enhance conifer recruitment as well as seedling survival and growth. Likewise, in a series of studies conducted in recently harvested black spruce stands growing on thick (>30 cm) organic deposits, we found that disruption (i.e. the mechanical breakdown) of the surficial organic layers was sufficient to promote growth of natural and planted black spruce seedlings (Lafleur et al. 2010, 2011). However, as it has been shown in several experiments, the exposition of mineral soil or its mixing with organic substrate could have an even greater effect on seedling growth (Prévost and Dumais 2003; Thiffault et al. 2010). Still, in boreal forested peatlands, thick (>30 cm) organic deposits may preclude the exposure of mineral soil or its mixture with organic soil during MSP; in these sites, MSP is more likely to disturb the organic layer. As these sites are likely to undergo paludification (Simard et al. 2007), MSP techniques are seen as an alternative to drainage to maintain forest productivity. Soil drainage in these low conductivity soils resulted in limited success and high costs (Jutras et al. 2002). Furthermore, in regions dominated by forested peatlands, inherent low forest productivity, sparse population base and underdeveloped road network, low cost methods to restore productivity are required.

In this context, we sought to determine in boreal forested peatlands how effective MSP techniques are at exposing mineral soil and creating microsites (i.e. the local features of the soil surface that characterize a seedling's growing environment, such as physico-chemistry or microclimate; Whittaker and Levin 1977) that are favourable to black spruce seedling growth despite large variations in organic

layer thickness. In order to create adequate planting microsites, different MSP techniques use different soil disturbance strategies. For instance, some techniques aim to break up and mix the forest floor (with or without the underlying mineral soil), whereas other techniques specifically aim to expose the mineral soil. Here, we contrasted three MSP techniques: disc scarification + crushing (SC), which aimed to break up and mix the forest floor, as well as patch scarification (PS) and mounding (MD), both of which contributed in exposing the mineral soil. These MSP treatments were chosen not only because of the different strategies used to disturb the forest floor, but also because of the probable differences in their capacity to expose mineral soil over a large area (SC < MD < PS). Specifically, we wanted to determine (1) the effects of MSP treatments on stand height, (2) the relative abundance of potential planting microsites, as influenced by the thickness of the organic layer and (3) the effects of the different types of microsites created by MSP on the growth of individual black spruce seedlings. First, we hypothesized that MSP, regardless of the soil disturbance strategy, would produce taller stands relative to the control. Then, we hypothesized that MSP treatments, despite the overall thickness of the organic layer, would be able to increase the frequency of mesic organic matter and mineral substrates at the soil surface and at rooting depth (i.e. 5–15 cm) relative to the control, and that this frequency would be modulated by the thickness of the organic layer. In a study conducted in the same region, Lavoie et al. (2007b) showed that mesic organic matter and mineral soil were more favourable to black spruce growth than fibric organic matter. Consequently, we postulated that stand height would be related to the capability of MSP techniques to increase the frequency of exposed mineral soil and mesic organic matter at the soil surface and at rooting depth compared with the control. Considering the large landbase occupied by boreal forested peatlands (North America, ~59 Mha; Sweden and Finland, ~6.2 Mha; Lavoie et al. 2005a), the restoration of these forests may contribute significantly to maintaining productive forests.

2 Materials and methods

2.1 Study area

The study area is located in the Clay Belt region of northwestern Quebec (49°52' N; 78°46' W; 275 ma.s.l.) and is part of the western black spruce–feathermoss bioclimatic domain (Bergeron et al. 1999). Prior to harvest, the stands sampled were classified as black spruce stands with *Sphagnum* on thick organic deposits (>30 cm) with hydrous drainage (i.e. forested peatlands) (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). Because of this combination of a cold, humid climate with flat topography and clay surficial deposits, stands in this region are prone to paludification.

Prior to harvest, the tree layer of the sampled stands was dominated by black spruce. Labrador tea (*Rhododendron groenlandicum* Oeder) and sheep laurel (*Kalmia angustifolia* L.) dominated the shrub cover, while *Sphagnum angustifolium*, *Sphagnum capillifolium*, *Sphagnum rubellum*, *Sphagnum russowii*, *Sphagnum fuscum*, *Sphagnum magellanicum* and feathermosses (mainly *Pleurozium schreberi*) dominated the forest floor. Furthermore, surveys conducted prior to harvest indicated that tree density and diameter at breast height averaged 1,330 stems ha^{-1} (SD=550 stem ha^{-1}) and 17.4 cm (SD=6.1 cm), respectively. According to the Soil Classification Working Group (1998), the soils were classified as organic soils (i.e. >40 cm thick). Yet, although surface topography appeared relatively flat the thickness of the organic layer was highly variable (i.e. from 30 to >120 cm thick) due to the undulating nature of the underlying mineral deposit.

According to the nearest weather station (Joutel, Quebec; 49°27' N; 78°18' W; ~50 km), the average annual temperature for the 1971–2000 period was 0.1°C, and average annual precipitation was 892 mm, with 35% falling during the growing season (Environment Canada 2010). The average number of degree-days (>5°C) is 1,249, and the frost-free season lasts approximately 60 days; frost can occasionally occur during the growing season.

2.2 Site selection and site preparation

The selected area was harvested by careful logging (in Quebec, cut with protection of regeneration and soils) during the winter of 2002; MSP was carried out in June 2003 and the area was planted in September 2003. Prior to the MSP treatment, the selected area was divided into 15 plots (0.5 to 2.1 ha), each of which was randomly assigned to one of four MSP treatments, i.e. (1) disc scarification + crushing (four replicates), (2) patch scarification (four replicates), (3) mounding (four replicates) and (4) control (three replicates).

Disc scarification + crushing aimed first to loosen and break up the forest floor, and second to knock down residual standing stems and break slash using machinery. The treatment was completed using a Komatsu D65PX tractor dozer equipped with a crushing roll and a disc scarifier. According to Cormier (2004), SC made it possible to expose mineral soil in areas where the organic layer was relatively thin (i.e. ~30 cm thick) and woody debris scarce.

Patch scarification consisted in removing the organic layer and exposing the mineral soil over a surface of approximately 15 m^2 . Patches were created by pushing the slash and the organic layer during the extension movement of the articulated arm. The treatment was done using a Komatsu PC250LC excavator. The machinery operator had instructions to work from the skid trails and to create patches approximately 3 m apart. Patch scarification created on average 230 patches ha^{-1} (Cormier 2004). This treatment exposed the mineral soil in all site conditions (Cormier 2004).

Mounding was done using the same excavator used for patch scarification. In this case, however, the machinery operator had instructions to create patches of exposed mineral soil approximately 4 m^2 in size. The slash and organic layers were first removed from the surface by the extension movement of the articulated arm, and pushed away a few metres from their original location. Then, the exposed mineral soil was dug to a depth of approximately 20 cm, and a mound of about 2 m^2 , 20 cm high and made exclusively of mineral soil was created next to the hole. Compared with patch scarification, this technique created smaller but more abundant patches of exposed mineral soil. On average, mounding created 370 mounds ha^{-1} (Cormier 2004). As it was the case for PS, this treatment exposed the mineral soil in all site conditions (Cormier 2004).

Finally, controls (CT) consisted of plots harvested by careful logging that had not been subjected to any of the above-mentioned MSP techniques.

Both for the PS and MD treatments, depressions and holes were at times filled with water.

Following site preparation, plots were planted with 2-year-old containerized black spruce seedlings following Quebec's provincial norms for planting. These norms state that in the boreal forest a minimum of 1,500 seedlings ha^{-1} should be planted and that these should be planted at 2-m intervals (Ministère des Ressources Naturelles et de la Faune 2010). At the time of planting, seedlings were on average 24.8 cm tall (SE=0.46).

2.3 Subplot layout and survey

Subplot layout and survey were carried out in August 2008, 5 years after planting. By that date, stocking varied between 58% and 68% and did not significantly differ among treatment ($p=0.4161$). In each replicate, we first installed three 120 m^2 quadrats. Stand height was determined by averaging the total height of each planted seedling located within the plots. Current year increment was also determined on each stem located within the quadrats.

Then, in each plot we used the point intercept method to identify the type of substrate found at the soil surface every 5 m along two 50-m linear transects. At each

sampling spot, we also estimated the thickness of the organic layer (OL) prior to MSP by measuring the thickness of the OL at the nearest adjacent location positioned between skid trails, i.e. where the forest floor had not been disturbed by harvest or MSP operations. It is likely that OL thickness changed where MSP operations disturbed the soil, and therefore these transects allowed us to determine how OL thickness prior to MSP influenced the frequency of potential planting microsites created by the different MSP treatments.

Finally, the effects of substrate type and drainage on individual seedling growth were assessed through a series of nested subplots. Specifically, three 300 m² (i.e. 10 × 30 m) subplots were installed in each plot. In these subplots, we searched for black spruce seedlings planted in microsites consisting of the combination of the three most frequent substrates found at 5–15 cm depth (i.e. fibric and mesic organic material (von Post scale = 0–4 and 5–8, respectively; Damman and French 1987), and mineral soil) and three drainage classes (i.e. well, moderate and poor). Growth substrate was determined by the position of the root plug at planting. Drainage classes were determined following Brais and Camiré (1992). For each substrate/drainage combination, we intended to sample two seedlings, for a total of 810 seedlings. However, due to the uneven distribution of the substrates and drainage classes across the study area, it was not possible to achieve this goal. We sampled 494 seedlings. Table 1 shows the distribution of the sampled seedlings according to MSP treatment, substrate type and drainage. Seedling total height and current year increment were measured. Soils (at root depth, i.e. 5–15 cm), whether mineral or organic, and foliage were sampled for nutrient analyses, and seedlings were harvested for biomass measurements. In the laboratory, seedlings were oven-dried at 70°C for 48 h. The foliage and root system dry mass were measured separately on an analytical balance (precision 0.01 g). This survey allowed us to identify the type of growth substrate (in terms of substrate type and drainage) most conducive to individual seedling growth.

2.4 Soil and foliar analyses

Following sampling, soil samples were air-dried for 48 h, returned to the laboratory and frozen. Immediately prior to analysis, all substrate samples were air-dried at 30°C for 48 h and ground to pass through 6-mm sieves. Total C and N concentrations were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation), and extractable inorganic P concentration was determined by the Bray II method (Bray and Kurtz 1945).

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 mixed. These samples

were oven-dried at 70°C for 48 h. After drying, needles were separated from twigs and ground. Total N concentration was determined as for the substrates on a CNS analyzer. Phosphorus concentration was determined following calcination at 500°C and dilution with hydrochloric acid (Miller 1998), and analyzed by colorimetry (Lachat Instruments, Milwaukee, WI).

2.5 Statistical analyses

First, one-way mixed-effect ANOVAs were used to contrast the effects of MSP treatments on stand height. MSP treatment was introduced into the model as a fixed effect, whereas the grid and quadrat were used as random effects. Then, because substrate type could prove important to explain seedling growth, the effect of MSP treatments on the frequency of surface substrate type was determined using a chi-squared test. Finally, the effects of MSP treatment, substrate type and drainage on individual black spruce seedling growth (i.e. total height, current year increment and foliage and root system dry mass), foliar nutrition and soil chemistry were contrasted using three-way mixed-effect ANOVAs. MSP treatment, substrate type and drainage were introduced into the models as fixed effects, whereas subplots and plots were used as random effects. Owing to the absence of samples for certain levels of some fixed effects (e.g. moderately well- and poorly drained mineral soil in the control treatment; Table 1), we constructed a priori contrasts to answer the following questions: (1) Regardless of drainage, as compared with CT, does MSP increase total height, current year increment and root and foliage biomass of seedlings planted in fibric and mesic organic matter (SC + MD + PS vs. CT)? (2) Regardless of drainage, and for the CS, MD and PS treatments only, are seedlings planted in mesic organic matter (Mes) and mineral soil (Min) larger than those planted in fibric organic matter (Fib) (Mes + Min vs. Fib)? (3) Regardless of MSP treatment, and for fibric and mesic organic matter only, are seedlings planted in well- (W) and moderately well- (MW) drained substrates larger than those planted in poorly drained (P) substrates (W + MW vs. P)? The same questions were also applied to determine the effects of MSP treatment, substrate type and drainage on foliar nutrition and soil chemistry.

Variable residuals were tested for normality and homogeneity of variances, and the data were log or square root transformed when necessary. In the case of the covariance analyses, we also tested for interactions between fixed effects and the covariate. Mixed-effect analyses were done using the *Mixed* procedure in SAS, and a priori contrasts were constructed using the CONTRAST statement (SAS Institute Inc. 2004). Differences were deemed significant when $\alpha \leq 0.05$.

Table 1 Number of seedlings sampled by mechanical site preparation treatment, rooting substrate and substrate drainage

Drainage	Mechanical site preparation treatment											
	Crushing (SC)			Mounding (MD)			Patch scar. (PS)			Control (CT)		
	Fib	Mes	Min	Fib	Mes	Min	Fib	Mes	Min	Fib	Mes	Min
Good	24	24	24	21	21	24	19	17	24	15	12	0
Moderate	19	22	0	16	23	0	20	16	0	13	15	0
Poor	17	11	0	19	19	0	19	16	0	11	13	0

Fib fibric organic matter, *Mes* mesic organic matter, *Min* mineral soil

3 Results

3.1 Stand height

MSP had an effect on stand growth parameters. Stands were significantly ($p < 0.0001$) taller in SC, MD and PS sites as compared with CT sites (Fig. 1a), whereas current year increment was significantly ($p = 0.0110$) higher in MD and PS sites as compared with CT sites (Fig. 1b).

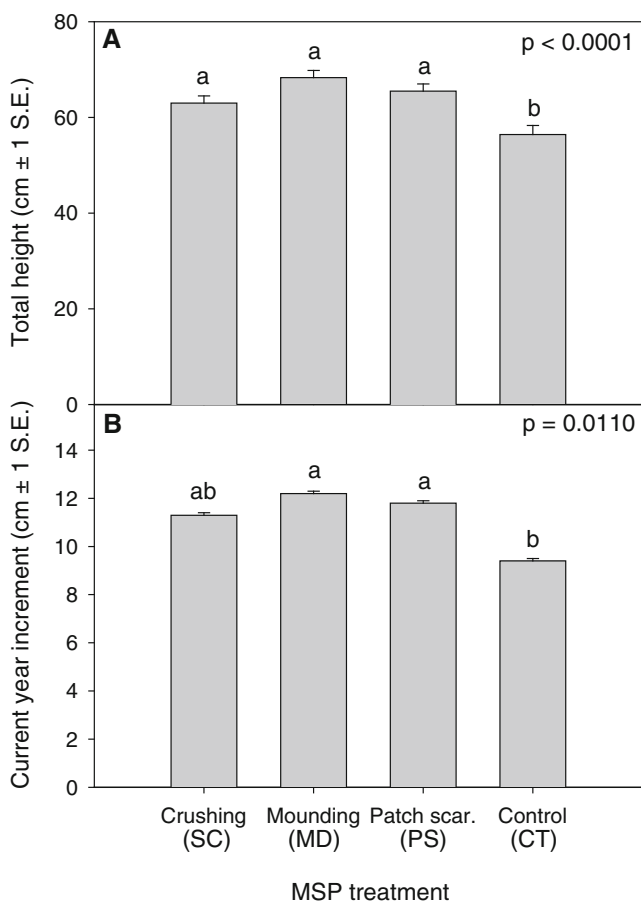


Fig. 1 Total height (a) and current year increment (b) of planted black spruce seedlings by MSP treatment, substrate type and drainage

3.2 Frequency of potential growth microsites

The MSP treatments considered in this study were able to produce a wide variety of potential planting microsites at the soil surface (Table 2). After adjusting for OL thickness prior to MSP (see Table 3 for information regarding average OL thickness according to treatment and plot), the significant chi-square test ($\chi^2 = 92.448$, $df = 24$, $p < 0.0001$) revealed that mineral soil was overrepresented in SC, MD and PS sites, whereas it was underrepresented in CT sites, and that *Sphagnum* spp. were overrepresented in CT sites (Table 2).

3.3 Soil chemistry

MSP treatment and drainage had no significant effect on soil chemistry (Tables 4 and 5). Substrate type, however, had significant effects on soil N_{tot} and P (Tables 4 and 5). The CONTRAST statements allowed us to identify significant differences among MSP treatment, substrate type and drainage despite the incompleteness of our database. First, regardless of drainage, both for fibric and mesic organic matter, soil N_{tot} was higher ($p = 0.0400$) in CT than in the other MSP treatments. Second, in SC, MD and PS, and considering well-drained microsites only, both fibric and mesic organic matter soil had higher soil N_{tot} ($p < 0.0001$) and P ($p < 0.05$) than mineral soil. Third, in SC, MD and PS, and considering well-drained microsites only, mesic organic matter soil had higher soil N_{tot} ($p < 0.0001$) and P ($p = 0.0189$) than mineral soil. Finally, regardless of drainage, mesic organic matter had higher soil N_{tot} ($p = 0.0525$) and P ($p = 0.0014$) than fibric organic matter. Two- and three-way interactions were scarce, indicating that the effects of substrate type and drainage on soil chemistry and foliar nutrition were independent of each other and independent of MSP treatment.

3.4 Seedling growth and nutrition

According to our three-way mixed-effect model, MSP had no effect on individual seedling growth parameters, while

Table 2 Frequency (%) of potential growth substrates found at the soil surface by MSP treatment, after adjusting for organic layer thickness

Substrate	Mechanical site preparation treatment			
	SC	MD	PS	CT
CWD	8.7	3.7	1.3	8.3
Lichen	0.0	0.0	3.7	5.0
Fibric	6.3	11.1	2.5	1.7
Mesic	47.5	32.5	37.5	41.7
Humic	3.7	6.3	5.0	0.0
Mineral	10.0	31.3	25.0	<u>5.0</u>
<i>P. schreberi</i>	3.8	0.0	7.5	13.3
<i>Polytrichum</i> spp.	10.0	5.0	13.7	0.0
<i>Sphagnum</i> spp.	10.0	10.0	3.8	25.0

Values in bold indicate that the substrate is overrepresented for a given treatment, whereas underlined values indicate that the substrate is underrepresented for a given treatment ($\chi^2=92.448$, $df=24$, $p<0.0001$)

SC disc scarification + crushing, MD mounding, PS patch scarification, CT control, CWD coarse woody debris

both substrate type and drainage significantly influenced individual seedling growth (Table 6, Figs. 2 and 3). First, seedlings planted in mesic organic matter and mineral soil grew taller and were heavier than those planted in fibric organic matter. Second, seedlings planted in well- and moderately well-drained substrates grew taller and were heavier than those planted in poorly drained substrates. In addition, both for total height and current year increment, the significant interaction between substrate type and drainage (Table 6, Fig. 2) indicated that globally, total height and current year increment were higher in moderately well- and well-drained mesic and mineral substrates as compared with a poorly drained fibric substrate. Otherwise, the absence of two- and three-way interactions between substrate type, drainage and MSP treatment indicated that the effects of these fixed variables on growth parameters were independent of each other.

Furthermore, despite the incompleteness of our database, pre-planned contrasts allowed us to identify significant differences among MSP treatments and to detail the significant differences found by our general model for substrate type and drainage. First, regardless of drainage, black spruce seedlings planted in either fibric or mesic organic matter had greater total height, current year increment and root and foliar dry mass in SC, MD and PS sites as compared with CT sites (Table 7, Figs. 2 and 3). Second, black spruce seedlings planted in mesic organic matter and mineral soil had significantly greater total height, current year increment as well as root and foliar dry mass than those planted in fibric organic matter (Table 7, Figs. 2 and 3). Third, for both fibric and mesic organic matter, seedlings planted in well-drained or moderately well-drained microsites had greater total height, current year increment as well as root and foliar dry mass than those planted in poorly drained microsites (Table 7, Figs. 2 and 3). Finally, while seedling growth did not differ between well-drained and moderately well-drained substrates, seedlings planted in mineral soil had higher root and foliar dry mass than those planted in mesic organic matter (Table 7, Figs. 2 and 3).

Moreover, neither MSP treatment nor substrate type or drainage had a significant effect on foliar N concentration (Tables 4 and 8). Likewise, neither MSP treatment nor substrate type had a significant effect on foliar P concentration. Drainage, however, had a significant effect on foliar P concentration (Tables 4 and 8). Again, the CONTRAST statements allowed us to identify significant differences among MSP treatment, substrate type and drainage despite the incompleteness of our database. First, regardless of drainage, both for fibric and mesic organic matter, foliar P was lower ($p=0.0088$) in CT than in the other MSP treatments. Second, for both fibric and mesic organic matter, foliar P was higher in well-drained and moderately well-drained ($p=0.0033$) microsites compared with poorly drained microsites. Two-way and three-way interactions were non-existent, indicating that the effects of substrate type and drainage on soil chemistry and foliar nutrition were independent of each other and independent of MSP treatment.

Table 3 Mean organic layer thickness (cm±SE) prior to MSP by treatment and plot

Plot no.	Treatment			
	Crushing (SC)	Mounding (MD)	Patch scar. (PS)	Control (CT)
1	31.1 (12.4)	44.9 (12.4)	46.3 (14.1)	51.9 (28.8)
2	45.7 (17.6)	56.2 (26.2)	48.2 (28.5)	59.7 (38.5)
3	55.2 (25.2)	94.1 (25.2)	94.5 (29.3)	97.2 (39.2)
4	85.7 (18.6)	129.4 (27.8)	114.3 (19.7)	–
Mean	54.4 (13.6)	80.7 (20.3)	77.3 (19.8)	74.6 (24.0)

Treatments did not differ significantly; $p=0.242$ ($F=1.43$)

Table 4 Means (± 1 SE) of soil properties and foliar nutrition for planted black spruce seedlings according to MSP treatment, rooting substrate and substrate drainage in paludified black spruce stands

Variable	Mechanical site preparation treatment												
	Drainage	Crushing (SC)			Mounding (MD)			Patch scarification (PS)			Control (CT)		
		Fibric	Mesic	Mineral	Fibric	Mesic	Mineral	Fibric	Mesic	Mineral	Fibric	Mesic	Mineral
Soil properties													
C/N	Good	48.0 (5.3)	40.5 (5.4)	33.7 (3.0)	40.8 (4.1)	36.2 (7.2)	39.1 (3.8)	46.5 (4.1)	37.8 (2.5)	42.6 (0.00)	39.3 (2.75)	46.8 (2.0)	NIL
	Moderate	43.8 (3.6)	46.2 (3.1)	NIL	43.3 (6.2)	38.6 (6.9)	NIL	48.1 (2.6)	38.5 (2.3)	NIL	53.7 (2.4)	33.3 (4.5)	NIL
	Poor	51.3 (8.3)	53.6 (3.0)	NIL	33.4 (9.7)	34.2 (4.7)	NIL	44.8 (2.2)	46.4 (2.6)	NIL	42.4 (-)	33.9 (3.3)	NIL
N (%)	Good	0.97 (0.11)	1.15 (0.10)	1.33 (0.04)	1.20 (0.15)	1.15 (0.21)	1.13 (0.09)	0.97 (0.03)	1.09 (0.08)	1.08 (0.07)	1.27 (0.09)	1.08 (0.06)	NIL
	Moderate	0.97 (0.03)	1.11 (0.08)	NIL	0.95 (0.05)	1.14 (0.11)	NIL	0.82 (0.06)	1.19 (0.04)	NIL	0.88 (0.01)	1.34 (0.23)	NIL
	Poor	0.98 (0.18)	0.89 (0.04)	NIL	1.53 (0.39)	1.26 (0.22)	NIL	1.01 (0.07)	1.07 (0.08)	NIL	1.10 (-)	0.84 (0.07)	NIL
P (g kg ⁻¹)	Good	0.06 (0.01)	0.07 (0.01)	0.05 (0.00)	0.05 (0.00)	0.06 (0.01)	0.05 (0.00)	0.07 (0.01)	0.06 (0.01)	0.04 (0.00)	0.05 (0.0)	0.06 (0.01)	NIL
	Moderate	0.07 (0.01)	0.07 (0.02)	NIL	0.06 (0.01)	0.07 (0.010)	NIL	0.10 (0.01)	0.06 (0.01)	NIL	0.07 (0.01)	0.06 (0.01)	NIL
	Poor	0.08 (0.02)	0.05 (0.00)	NIL	0.08 (0.02)	0.06 (0.01)	NIL	0.08 (0.01)	0.08 (0.01)	NIL	IL	0.07 (0.01)	NIL
Foliar nutrition													
N (%)	Good	1.13 (0.18)	1.16 (0.06)	1.26 (0.05)	1.34 (0.07)	1.24 (0.09)	1.24 (0.09)	1.39 (0.09)	1.19 (0.11)	1.11 (0.10)	1.01 (0.01)	1.18 (0.04)	NIL
	Moderate	1.18 (0.08)	1.32 (0.07)	NIL	1.26 (0.03)	1.26 (0.08)	NIL	1.19 (0.02)	1.22 (0.06)	NIL	1.29 (0.12)	1.08 (0.06)	NIL
	Poor	1.17 (0.11)	1.15 (0.12)	NIL	1.24 (0.12)	1.41 (0.20)	NIL	1.11 (0.05)	1.11 (0.04)	NIL	0.98 (0.01)	1.16 (0.13)	NIL
P (%)	Good	0.16 (0.02)	0.15 (0.02)	0.13 (0.01)	0.17 (0.01)	0.15 (0.01)	0.13 (0.01)	0.19 (0.01)	0.16 (0.01)	0.15 (0.02)	0.19 (0.01)	0.18 (0.01)	NIL
	Moderate	0.18 (0.01)	0.17 (0.01)	NIL	0.18 (0.01)	0.15 (0.02)	NIL	0.18 (0.01)	0.16 (0.02)	NIL	0.22 (0.02)	0.24 (0.03)	NIL
	Poor	0.19 (0.02)	0.15 (0.03)	NIL	0.16 (0.01)	0.11 (0.01)	NIL	0.17 (0.01)	0.15 (0.01)	NIL	0.19 (0.03)	0.19 (0.01)	NIL

Table 5 Results of three-way ANOVAs describing the statistical significance of MSP treatment, growth substrate and substrate drainage on soil chemical properties

Variable	Source	F value	Prob. > F
N _{tot} (%)	MSP (M)	0.42	0.7400
	Substrate (S)	41.69	<0.0001
	Drainage (D)	0.05	0.9505
	S × D	2.94	0.0574
	M × S	0.71	0.6144
	M × D	0.94	0.4671
	M × S × D	0.62	0.7159
P (mg kg ⁻¹)	MSP (M)	0.24	0.8679
	Substrate (S)	9.57	0.0002
	Drainage (D)	1.11	0.3334
	S × D	0.49	0.6129
	M × S	0.38	0.8616
	M × D	0.41	0.8698
	M × S × D	0.51	0.8007
C/N	MSP (M)	1.13	0.3422
	Substrate (S)	1.66	0.1960
	Drainage (D)	1.19	0.3098
	S × D	1.77	0.1763
	M × S	3.18	0.0104
	M × D	0.86	0.5305
	M × S × D	0.52	0.7919

4 Discussion

In agreement with our first hypothesis, at the stand scale, planted black spruce seedling growth was 15% greater in the three MSP treatments compared with the control. Our second hypothesis was also upheld since despite variations in OL thickness, all three MSP treatments were able to create a higher frequency of mineral microsites compared with the control. Finally, mesic organic matter and mineral soil constituted the most favourable growth microsites for planted black spruce seedlings, which is in agreement with our third hypothesis.

4.1 Stand height

Stands were approximately 15% taller in SC, MD and PS as compared with the control, and current year increment was 20% higher in MD and PS as compared with the control. These observations are likely the result of the higher frequency of mineral soil (both at the surface and at rooting depth) in MD and PS as compared with SC and CT. In addition, when combined together, the frequency of mineral soil and mesic organic matter found at the surface amounts to 63.8%, 62.5%, 57.5% and 46.7%, respectively, in MD, PS, SC and CT. Likewise, at rooting depth, the combined frequency of mineral soil and mesic organic matter amounts

Table 6 Results of three-way ANOVAs describing the statistical significance of the effect of MSP treatment, substrate type and drainage on black spruce seedling growth parameters using organic layer (OL) thickness as a covariate

Variable	Source	F value	Prob. > F	
Height	MSP (M)	0.53	0.6610	
	Substrate (S)	37.12	<0.0001	
	Drainage (D)	31.65	<0.0001	
	S × D	5.04	0.0072	
	M × S	1.62	0.1554	
	M × D	1.05	0.3822	
	M × S × D	0.78	0.5852	
	OL × M	1.88	0.1141	
	CYI	MSP (M)	1.56	0.1997
		Substrate (S)	15.07	<0.0001
Drainage (D)		11.57	<0.0001	
S × D		5.52	0.0045	
M × S		1.39	0.2305	
M × D		0.74	0.6159	
M × S × D		0.60	0.7337	
Root dry mass	OL × M	1.30	0.2681	
	MSP (M)	0.34	0.7974	
	Substrate (S)	25.11	<0.0001	
	Drainage (D)	9.09	0.0002	
	S × D	1.36	0.2599	
	M × S	2.16	0.0627	
	M × D	0.45	0.8408	
Foliage dry mass	M × S × D	0.19	0.9786	
	OL × M	1.05	0.3824	
	MSP (M)	0.61	0.6079	
	Substrate (S)	14.32	<0.0001	
	Drainage (D)	12.92	<0.0001	
	S × D	2.43	0.0920	
	M × S	1.71	0.1372	
CYI current year increment	M × D	0.73	0.6243	
	M × S × D	0.51	0.7985	
	OL × M	1.98	0.1015	

CYI current year increment

to 73.7%, 72.5%, 84.3% and 67.2%, respectively, in MD, PS, SC and CT. Together, these results confirm that in black spruce stands growing on thick (>30 cm) organic deposits, MSP is likely to increase the frequency of growth substrates conducive to better seedling growth following harvest and, consequently, to promote tree growth.

4.2 Frequency of potential growth microsites

The higher frequency of mineral soil observed at the surface (after adjusting for OL thickness) is likely due to the different soil disturbance strategy used in the MSP treatments we

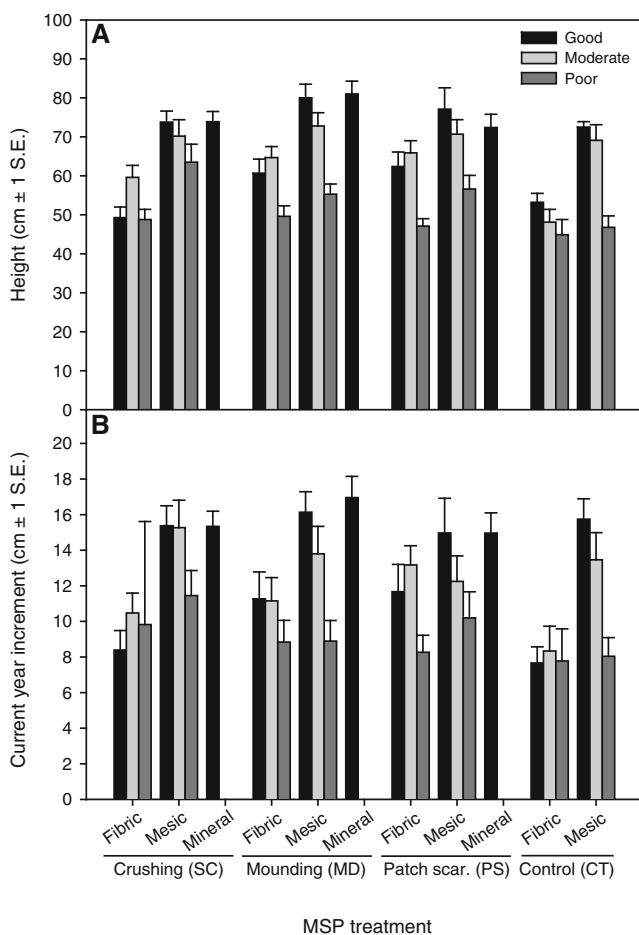


Fig. 2 Total height (a) and current year increment (b) of black spruce stands (planted seedlings only) by MSP treatment

contrasted. Indeed, while disc scarification + crushing disturbed primarily the forest floor surface (i.e. the top 30 cm; Cormier 2004; personal observation), both MD and PS were more successful at exposing the mineral soil. Nonetheless, all three MSP treatments were able to expose mineral soil more frequently than what was observed on CT sites where forest harvesting operations had exposed only some areas.

However, the quite similar frequency of mesic organic matter among MSP treatments and the control indicates that forest harvesting alone was as efficient as MSP treatments at disturbing the forest floor surface and at creating mesic microsites.

Therefore, while OL thickness had no influence on the ability of MSP treatments to create a higher frequency of mesic microsites relative to the control, it did reduce the ability of SC to expose mineral soil compared with MD and PS.

4.3 Individual seedling growth

As observed by Lavoie et al. (2007b), we detected better growth in seedlings planted in mesic organic matter and

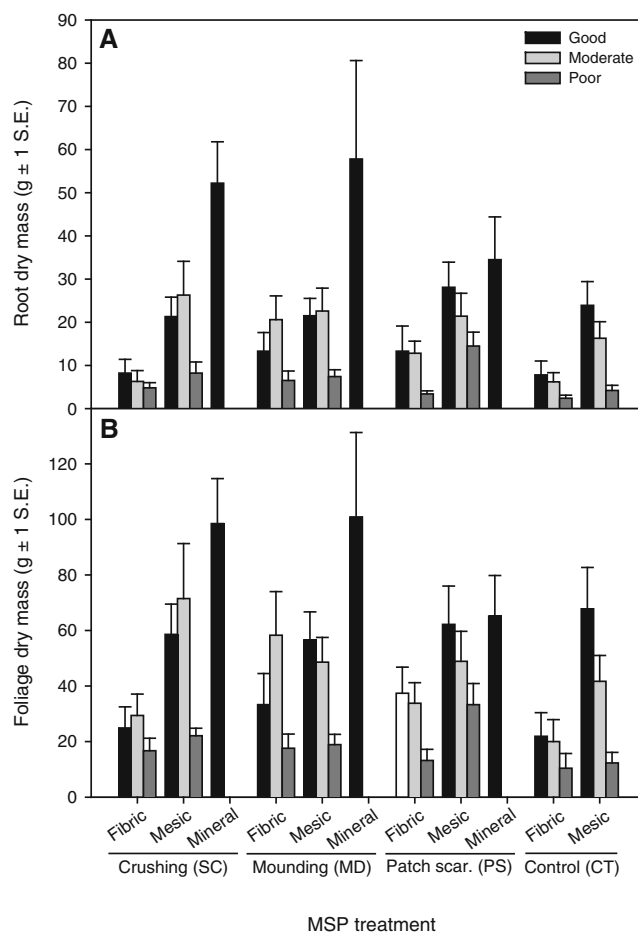


Fig. 3 Root (a) and foliage (b) dry mass of planted black spruce seedlings by MSP treatment, substrate type and drainage

mineral soil as compared with those planted in fibric organic matter. According to Lavoie et al. (2007b), these substrates constitute better microsites for growth than fibric organic matter owing to both higher nutrient availability and uptake. Our results are in agreement with Lavoie et al. (2007b), as we also found higher N and P concentrations in mesic organic matter than in fibric organic matter, although this was not the case for mineral soil. Alternatively, better root growth could also account for better height growth in mesic organic matter and mineral soil (see Fig. 3a).

In addition, substrate drainage also explained differences in growth among substrate types; seedlings in well-drained and moderately well-drained substrates were taller and heavier than seedlings in poorly drained substrates. As reviewed by Grossnickle (2000), excess soil water may limit seedling growth through reduced substrate aeration, lower net photosynthesis and lower nutrient uptake. In a parallel study, we also observed reduced growth of black spruce seedlings planted in poorly drained organic substrate (Lafleur et al. 2011).

Table 7 Results of pre-planned contrasts for seedling growth parameters

Contrasts	Total height		CYI		Root dry mass		Foliage dry mass	
	<i>F</i> value	Prob. > <i>F</i>	<i>F</i> value	Prob. > <i>F</i>	<i>F</i> value	Prob. > <i>F</i>	<i>F</i> value	Prob. > <i>F</i>
SC + MD + PS vs. CT (Fib + Mes only)	5.26	0.0225	5.96	0.0153	3.69	0.0570	4.28	0.0407
Mes + Min vs. Fib (SC, MD + PS only)	59.47	<0.0001	24.82	<0.0001	35.99	<0.0001	22.99	<0.0001
Mes vs. Min (SC, MD + PS only)	0.01	0.9262	0.24	0.6274	18.86	<0.0001	5.18	0.0246
W + MW vs. P (Fib + Mes only)	63.19	<0.0001	22.86	<0.0001	18.17	<0.0001	25.80	<0.0001
W vs. MW (Fib + Mes only)	0.15	0.6997	0.33	0.5639	0.00	0.9925	0.02	0.8888

SC crushing, MD mounding, PS patch scarification, CT control, Fib fibric organic matter, Mes mesic organic matter, Min mineral soil, W well-drained substrate, MW moderately well-drained substrate, P poorly drained substrate

These results therefore suggest that soil disturbances that promote tree establishment in mesic organic matter or mineral soil and that improve moisture conditions of growth substrates are likely to favour growth of individual black spruce seedlings.

4.4 Management considerations

Considering that (1) SC favoured seedling regeneration and growth at levels similar to MD and PS, and (2) SC is more cost efficient than both MD and PS (PS and MD are respectively two and three times more expensive than SC to treat an equivalent surface; Cormier 2004), both from economic and forest regeneration stand points and as long as it can expose mesic organic matter or mineral soil, SC seems to be a relevant MSP technique to use in order to increase the frequency of microsites conducive to better growth and to regenerate post-logged black spruce stands growing on organic deposits.

Table 8 Results of three-way ANOVAs describing the statistical significance of MSP treatment, growth substrate and substrate drainage on foliar N and P concentrations

Variable (%)	Source	<i>F</i> value	Prob. > <i>F</i>
N	MSP (M)	0.37	0.7751
	Substrate (S)	1.27	0.2844
	Drainage (D)	2.07	0.1307
	S × D	2.82	0.0630
	M × S	0.42	0.8339
	M × D	0.75	0.6105
	M × S × D	0.30	0.9373
P	MSP (M)	0.92	0.4351
	Substrate (S)	1.63	0.1998
	Drainage (D)	5.48	0.0052
	S × D	0.05	0.9557
	M × S	0.89	0.4905
	M × D	0.52	0.7944
	M × S × D	0.94	0.4717

5 Conclusions and management considerations

All MSP techniques evaluated were found to increase black spruce growth at the stand scale presumably by exposing better substrate and creating drainage for tree growth at the micro-site scale. Additionally, disturbance of the organic layer could decrease plant competition and enhance soil temperature as observed in similar site conditions (Lafleur et al. 2011).

Regardless of MSP treatment, stand growth was similar among SC, MD and PS treatments. Although black spruce is not considered very responsive to soil disturbance (Thiffault et al. 2005, 2010), these results suggest that disturbance of the organic layer should be sufficient to improve growth substrate conditions and to promote the growth of planted black spruce seedlings following MSP in forested peatlands (Lafleur et al. 2011). Although this study reports the results of the effects of MSP on seedling growth only for the first few years following treatment, it is likely that this effect may be sustained over time. Indeed, Thiffault et al. (2004) reported that scarification in a post-harvest black spruce stand had a sustainable impact on micro-site characteristics and planted seedling growth for at least 10 years. Therefore, MSP could help restore forest productivity following harvest or, at least, could delay the conversion from closed-crown, productive forests to forested peatlands.

In paludified black spruce forests of northwestern Quebec, it has been shown that high-severity soil burns (which consume most of the organic layer) promote the establishment of productive post-disturbance stands on mineral soil, whereas low-severity soil burns leave the forest floor almost intact, and promote the establishment of less productive stands on thick organic layers (Simard et al. 2007). In this study, despite thick organic layers, some MSP techniques (i.e. MD and PS) were able to expose mineral soil over approximately 30% of the site's prepared area, suggesting that MSP could to some extent reproduce the effects of high-severity fires on mineral soil exposition. However, this hypothesis remains to be tested.

Combined with other silvicultural treatments known to severely disturb soils, such as summer clearcutting and prescribed burning, MSP techniques could therefore constitute a simple cost-effective way of restoring closed-canopy productive forests that are susceptible to revert to unproductive peatlands. Over the large landbase of boreal forested peatlands, restoring these forests contributes not only to maintaining productive forests used by the forest industry, but also to maintaining diversified landscapes to meet biodiversity objectives (Lavoie et al. 2005b). Compared with other options that results in high costs and frequent re-entries, such as forest drainage, simple and one-time MSP techniques could be particularly suited for vast areas of low productivity boreal forested peatlands, where high-cost management options are prohibitive and where road accessibility is limited in space and time.

Acknowledgements We thank Julie Arsenault, Sylvie Gewehr, Élisabeth Turcotte and Christine Vigeant for technical assistance in the field; Michelle Bernier-Cardou and Stéphane Daigle for statistical advice; Martin Lavoie and Dodick Gasser for valuable comments on earlier versions of the manuscript and Pamela Cheers and Isabelle Lamarre for editing the text. We also thank Denis Cormier at FPInnovations—Feric Division for helping with site preparation as well as the staff of Tembec. The first author received a scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds québécois de la recherche sur la nature et les technologies (FQRNT), and Tembec.

Funding The first author received a scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds québécois de la recherche sur la nature et les technologies (FQRNT), and Tembec. FPInnovations—Feric Division conducted site preparation, while the staff at Tembec helped with the identification of the study site.

References

- Bergeron J-F, Grondin P, Blouin J (1999) Rapport de classification écologique du sous-domaine bioclimatique de la pessière à mousses de l'ouest. Ministère des Ressources naturelles du Québec, Québec
- Brais S, Camiré C (1992) Keys for soil moisture regime evaluation for northwestern Quebec. *Can J For Res* 22:718–724
- Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. *Soil Sci* 59:39–46
- Bringmark E (1989) Spatial variation in soil pH of beech forests in relation to buffering properties and soil depths. *Oikos* 54:165–177
- Burdett AN, Simpson DG, Thompson CF (1983) Root development and plantation establishment success. *Plant Soil* 71:103–110
- Cormier D (2004) Essais comparés de diverses techniques de scarifiage dans des sites susceptibles à la paludification. Rapport d'étape. Forest Engineering Research Institute of Canada, Pointe Claire
- Damman AWH, French TW (1987) The ecology of peat bogs of the glaciated northeastern United States, Biological Report 85(7.16). U.S. Fish and Wildlife Service, Washington, DC
- Environment Canada (2010) Canadian climate normals 1971–2000. http://climate.weatheroffice.gc.ca/climate_normals/index_e.html. Accessed 28 July 2010
- Geyer WA, Marquard RD, Barber JF (1980) Black walnut site quality in relation to soil and topographic characteristics in northeastern Kansas. *J Soil Water Conserv* 35:135–137
- Greene DF, Macdonald SE, 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
- Groot A (1998) Physical effects of site disturbance on peatlands. *Can J Soil Sci* 78:45–50
- Grossnickle SC (2000) Ecophysiology of northern spruce species: the performance of planted seedlings. NRC Research Press, Ottawa
- Jayen K, Leduc A, Bergeron Y (2006) Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. *Ecoscience* 13:143–151
- Jobbágy EG, Jackson RB (2001) The distribution of soil nutrients with depth: global patterns and the imprint of plants. *Biogeochemistry* 53:51–77
- Johansson M-B (1994) The influence of soil scarification on the turnover rate of slash needles and nutrient release. *Scand J For Res* 9:170–179
- Johnstone JF, Chapin FS III (2006) Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems* 9:14–31
- Jutras S, Bégin J, Plamondon AP (2002) Impact du drainage forestier sur la croissance de l'épinette noire en forêt boréale. *Can J For Res* 32:1585–1596
- Lafleur B, Fenton NJ, 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 NJ, Bergeron Y (2011) Growth and nutrition of black spruce seedlings in response to disruption of *Pleurozium* and *Sphagnum* moss carpets. *Plant Soil* 345:141–153
- Laiho R, Sarkkola S, Kaunisto S, Laine J, Minkkinen K (2008) Macroscale variation in peat elemental concentrations in drained boreal peatland forests. *Silva Fenn* 42:555–570
- Lavoie M, Paré D, Bergeron Y (2005a) Impacts of global change and forest management on carbon sequestration in northern forested peatlands. *Environ Rev* 13:199–240
- Lavoie M, Paré D, Fenton N, Groot A, Taylor K (2005b) Paludification and management of forested peatlands in Canada: a literature review. *Environ Rev* 13:21–50
- Lavoie M, Harper K, Paré D, Bergeron Y (2007a) Spatial pattern in the organic layer and tree growth: a case study from regenerating *Picea mariana* stands prone to paludification. *J Veg Sci* 18:213–222
- Lavoie M, Paré D, Bergeron Y (2007b) Relationships between microsite type and the growth and nutrition of young black spruce on post-disturbed lowland black spruce sites in eastern Canada. *Can J For Res* 37:62–73
- Lecomte N, Simard M, Bergeron Y, Larouche A, Asnong H, Richard PJH (2005) Effects of fire severity and initial tree composition on understory vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. *J Veg Sci* 16:665–674
- Legout A, Walter C, Nys C (2008) Spatial variability of nutrient stocks in the humus and soils of a forest massif (Fougères, France). *Ann For Sci* 65:108p1–108p10
- Meredieu C, Arrouays D, Goulard M, Auclair D (1996) Short range soil variability and its effect on red oak growth (*Quercus rubra* L.). *Soil Sci* 161:29–38
- Meunier C, Sirois L, Bégin Y (2007) Climate and *Picea mariana* seed maturation relationships: a multi-scale perspective. *Ecol Monogr* 77:361–376
- Miller RO (1998) High-temperature oxidation: dry ashing. In: Kalra YP (ed) Handbook of reference methods for plant analysis. CRC, Boca Raton, pp 53–56
- Ministère des Ressources Naturelles et de la Faune (2010) Instructions relatives à l'application de l'arrêté ministériel sur la valeur des

- traitements sylvicoles admissibles en paiement des droits—exercices 2010–2013. Direction de l'aménagement des forêts publiques et privées, Québec
- Morris DM, Mackereth RW, Duckert DR, Hoepting MK (2009) The influence of soil rutting severity on regeneration potential and seedling performance for black spruce-dominated peatlands. *Can J Soil Sci* 89:57–66
- Nordborg F, Nilsson U, Örlander G (2003) Effects of different soil treatments on growth and net nitrogen uptake of newly planted *Picea abies* (L.) Karst. seedlings. *For Ecol Manage* 180:517–582
- Örlander G, Gemmel P, Hunt J (1990) Site preparation: a Swedish overview, FRDA Rep. 105. Forestry Canada and B.C. Ministry of Forests, Victoria
- Prévost M, Dumais D (2003) Croissance et statut nutritif de marcottes, de semis naturels et de plants d'épinette noire à la suite du scarifiage: résultats de 10 ans. *Can J For Res* 33:2097–2107
- Qian H, Klinka K (1995) Spatial variability of humus forms in some coastal forest ecosystems of British Columbia. *Ann For Sci* 52:653–666
- Šamonil P, Král K, Douda J, Šebková B (2008) Variability in forest floor at different spatial scales in a natural forest in the Carpathians: effect of windthrows and mesorelief. *Can J For Res* 38:2596–2606
- SAS Institute Inc (2004) SAS/STAT 9.1 User's Guide. SAS, Cary
- Schöning I, Totsche KU, Kögel-Knabner I (2006) Small scale spatial variability of organic carbon stocks in litter and solum of a forested Luvisol. *Geoderma* 136:631–642
- Simard M, Lecomte N, Bergeron Y, Bernier PY, Paré D (2007) Forest productivity decline caused by successional paludification of boreal soils. *Ecol Appl* 17:1619–1637
- Soil Classification Working Group (1998) The Canadian System of Soil Classification. Agric. and Agri-Food Can., Ottawa, Ont. Publ. No. 1646
- Staples TE, Van Rees KCJ, van Kessel C (1999) Nitrogen competition using ^{15}N between early successional plants and planted white spruce seedlings. *Can J For Res* 29:1282–1289
- Sutherland BJ, Foreman FF (1995) Guide to the use of mechanical site preparation equipment in Northwestern Ontario. Canadian Forest Service, Sault Ste. Marie
- Sutherland B, Foreman FF (2000) Black spruce and vegetation response to chemical and mechanical site preparation on a boreal mixedwood site. *Can J For Res* 30:1561–1570
- Thiffault N, Cyr G, Prigent G, Jobidon R, Charette L (2004) 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 BD, Munson AD (2005) Silvicultural options to promote seedling establishment on *Kalmia-Vaccinium*-dominated sites. *Scand J For Res* 20:110–121
- Thiffault N, Titus BD, Moroni MT (2010) Silviculture and planted species interact to influence reforestation success on a *Kalmia*-dominated site—a 15-year study. *For Chron* 86:234–242
- Vincent JS, Hardy L (1977) L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. *Géogr Phys Quat* 31:357–372
- Whittaker RH, Levin SA (1977) The role of mosaic phenomena in natural communities. *Theor Popul Biol* 12:117–139
- Yarie J (2008) Effects of moisture limitation on tree growth in upland and floodplain forest ecosystems in interior Alaska. *For Ecol Manage* 256:1055–1063