Relationships between microsite type and the growth and nutrition of young black spruce on post-disturbed lowland black spruce sites in eastern Canada

Martin Lavoie, David Paré, and Yves Bergeron

Abstract: The surface of the soil in recently harvested or burned lowland black spruce (*Picea mariana* (Mill.) BSP) sites is composed of a fine mosaic of different bryophytes (mostly *Sphagnum* spp. and feathermosses), disturbed organic material originating mostly from mosses at different stages of decay, and exposed mineral soil. Growth substrates were compared in lowland black spruce stands regenerating after either careful logging or wildfire. The 3-year annual increment for black spruce seedlings was greatest with substrates of feathermosses, mainly *Pleurozium schreberi* (Brid.) Mitt., fibric material of *P. schreberi* origin, and a mixture of fibric *P. schreberi* and humic materials; it was least with fibric *Sphagnum* spp., mineral soil, and decaying wood substrates. The most favourable substrates for growth were characterized by better black spruce N and P foliar status. Our results also suggest that categories of growth substrates in the rooting zone reflect nutritional quality better than categories of growth substrates on the soil surface. To maintain or increase black spruce growth following careful logging of sites prone to paludification, we recommend fill-planting of seedlings in substrates originating from *P. schreberi*; management techniques that favour *P. schreberi* over *Sphagnum* mosses should also be developed.

Résumé : La surface du sol de sites récemment récoltés ou brûlés dans des peuplements d'épinettes noires (*Picea mariana* (Mill.) BSP) de basses terres est composée d'une fine mosaïque de différents types de bryophytes, principalement les sphaignes et les mousses hypnacées, de matière organique perturbée composée de différents types de mousses à différents degrés de décomposition et de sol minéral exposé. Les substrats de croissance qu'on retrouve dans des peuplements d'épinettes noires de basses terres provenant de sites régénérés suite à la coupe avec protection de la régénération et des sols ou suite à un feu ont été comparés. Les résultats suggèrent que la croissance en hauteur des semis d'épinette noire sur 3 ans est plus élevée avec les substrats de *Pleurozium schreberi* (Brid.) Mitt., de matériel fibrique composé de *P. schreberi* et d'un mélange de matériels fibrique (composé de *P. schreberi*) et humique qu'avec la sphaigne fibrique, le sol minéral et le bois mort. Les substrats de croissance les plus favorables à la croissance sont caractérisés par une meilleure nutrition en azote et phosphore. Nos résultats suggèrent également que la classification des substrats de croissance au niveau des racines est plus indicative de leur valeur nutritive que la classification des substrats de croissance localisés en surface. En se basant sur ces résultats, pour maintenir ou augmenter la croissance en hauteur de l'épinette noire après coupe sur des sites susceptibles à la paludification, nous recommandons que la plantation dans des substrats formés de *P. schreberi* et qu'un aménagement qui favorise la présence de *P. schreberi* au détriment des sphaignes soient favorisés.

Introduction

In Canada, the Clay Belt region of Quebec and Ontario supports a large forest resource that is important to the forest industry. Because of the strong demand for wood products as well as increasing pressure to set land aside for conservation purposes, forestry operations in this area are being pushed towards the northern limit of the commercial forest. In lowland James Bay in Quebec and northeastern Ontario, most of the harvesting volumes allotted to forest companies are located in low-productivity peatlands (Prévost et al. 2001). These stands originate from stand-replacing wildfire (Bergeron et al. 2004), but in the absence of subsequent fires, they have developed an irregular structure (Lecomte et al. 2006*b*). Wildfire severity and time since fire have been identified as important factors contributing to forest-floor thickness, moss cover type, and stand structure and productivity (Lecomte et al. 2006*a*).

In Quebec the boreal forest is generally harvested using the "cutting with protection of regeneration and soils" (coupe avec protection de la régénération et des sols (CPRS)) system (Messier et al. 2004). CPRS is used in all conifer stands irrespective of stand characteristics (organic-matter thickness, topography, etc.) or soil properties (e.g., drainage, nutrient pools). In Ontario this harvesting system

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is called careful logging around advanced growth (CLAAG) and is applied to specific ecosites. In the Clay Belt, CLAAG is mostly used in lowland stands (i.e., ecosites 11 and 12; Kim Taylor, Northeast Science and Technology, Terrestrial Ecologist, and Dean Cedarwall, Northeast Region FMP Specialist, personal communication, 3 February 2006).

As the aim of careful-logging systems such as CPRS and CLAAG is to minimize soil disturbance and protect advanced regeneration, harvesting in forested peatlands is often carried out during winter for added protection. Currently, when the stocking and density of advanced regeneration are good before harvesting, careful-logging systems are regarded as effective harvesting methods, given that regeneration density and stocking after logging are high (Harvey and Brais 2002). Nevertheless, in spite of its general application, careful logging may not be the best harvesting method in certain areas, notably in northern black spruce (*Picea mariana* (Mill.) BSP) forests located on the Till of Cochrane in the Clay Belt (Lecomte and Bergeron 2005). In this area the mineral soil is generally heavily compacted, which facilitates paludification, and growth problems in postharvest stands have been observed (see review in Lavoie et al. 2005).

The soil surface in black spruce lowlands is composed of a large number of microsite types that vary over short distances; a single type does not usually cover more than a few square metres, and often less than 1 m^2. These microsites are the product of site drainage, disturbance history, and especially the type and severity of the last disturbance. They are mainly composed of disturbed and undisturbed layers of mosses at different stages of humification. Exposed mineral soil can also be found, as well as organic debris.

Black spruce seedbeds are relatively well understood, and differences between the effects of fire and logging on spruce germination are described in the literature (Pothier 2000; Greene et al. 2004; Jayen et al. 2006). Very little information that is currently available, however, includes the best substrates (i.e., microsites) for black spruce growth in lowland stands once seedlings are established through either natural or artificial means. To our knowledge, only two studies have been conducted on the quality of *Sphagnum* spp. vs. *Pleurozium* spp. for black spruce seedling growth, and these mostly pertain to advanced regeneration in mature forests (Arnott 1968; Jeglum 1981). However, the quality of the great variety of substrates that are found after disturbance (including mineral soil, burned substrates, other living bryophytes (e.g., *Polytrichum* spp.), exposed organic substrates at different stages of decomposition, and woody debris) has not been evaluated under field conditions. It is important that this be done because as the use of emulation silviculture (i.e., inspired by the effect of natural disturbances) increases in Canada (McRae et al. 2001), soil conditions following forestry operations are being compared with those found following wildfire (Keenan and Kimmins 1993). Information on substrate quality will also be valuable in forestry operations because it will help to evaluate the relevance of exposing soil layers during harvest or site preparation operations, or to determine what substrates should be favoured during planting.

The objective of this study was to identify and characterize the soil substrates that are found in postdisturbed sites of the Clay Belt region and to determine how black spruce growth and nutrition are related to soil substrate (microsite) type.

Materials and methods

Study area

The study area was situated in northwestern Quebec (49°48′N, 79°01′W) and northeastern Ontario (49°45′N, 80°40′W). The fieldwork was conducted in two areas that both included sites affected by large wildfires that occurred in June 1997. The study area in Quebec included a 540 km^2 wildfire and adjacent logged sites (CPRS) and that in Ontario included a 24.5 km^2 wildfire site and adjacent cutblocks (CLAAG). The study area in Quebec is part of the ecological area on the plain of the Lake Matagami bioclimatic domain, which is part of the western black spruce – feathermoss community (Bergeron et al. 1999). According to Quebec's classification system, stands within this study belong to two ecological types: (1) black spruce stand with *Sphagnum* on mineral deposit, and (2) black spruce stand with *Sphagnum* on thick organic deposit with very poor drainage (i.e., forested peatland) (Bergeron et al. 1999). In Ontario the study sites are located in the Lake Abitibi Model Forest, which belongs to site region 3e (Jones et al. 1983). According to Ontario's classification system, the study sites are located in ecosites ES 11 (*Ledum*) and ES 8 (Feathermoss–*Sphagnum*) (Taylor et al. 2000). These sites are dominated by black spruce accompanied by balsam fir (*Abies balsamea* (L.) Mill.) and tamarack (*Larix laricina* (Du Roi) K. Koch). Bog Labrador tea (*Ledum groenlandicum* Oeder) dominates the shrub cover, with blueberries (*Vaccinium* spp.) and sheep laurel (*Kalmia angustifolia* L.) also present. *Sphagnum angustifolium* (C. Jens. ex Russ.) C. Jens. intolf, *S. capillifolium* (Ehrh.) Hedw., *S. rubellum* Wils., *S. russowii* Warnst., *S. fuscum* (Schimp.) Klinggr., *S. magellanicum* Brid., and feathermosses (mainly *Pleurozium schreberi* (Brid.) Mitt.) cover the forest floor across a landscape of hummocks and hollows. The study area is typical of the Clay Belt, a territory characterized by important glacial lacustrine deposits left by the glacial lakes Barlow and Ojibway (Vincent and Hardy 1977).

According to nearby weather stations, the mean annual temperature is 0.1–0.9 °C, annual precipitation is 776–892 mm, and there are 64–90 frost-free days (according to weather stations at Joutel, Quebec, and Iroquois Falls, Ontario, respectively) (Environment Canada 2004).

Plot layout

Two plots were established in the Ontario postwildfire site and two others in the adjacent cut; in Quebec, three plots were established on each disturbance type (wildfire and careful logging), for a total of 10 plots. Plots were at least 500 m apart and each plot was composed of four 400 m^2 subplots, for a total of 40 subplots. All plots were located in sites with relatively flat topography, clay deposits, and poor drainage. Based on forest and fire maps, all sites were older than 120 years before disturbance, with a maximum tree height below 17 m and canopy cover of less than 60% (Ministry of Natural Resources of Ontario 1993; Ministère des

Table 1. Description and abbreviation for each growth substrate, with the frequency distribution of regenerating trees for each disturbance, regeneration, and substrate type.

		Careful logging			Wildfire		
Description	Abbreviation	Seed	Planted	Layer	Seed	Planted	Layer
Soil surface							
Polytrichum spp.	Poc	5.3	4.0	0.0	38.9	14.9	—
Pleurozium schreberi	Ple	10.5	12.0	28.7	0.0	0.0	—
Fibric *Pleurozium*	FPle	15.8	20.0	4.5	0.0	0.0	—
Burned *Pleurozium*	BuPle	—	—	—	22.2	51.6	—
Sphagnum mosses	Sph	52.6	64.0	63.5	11.1	4.0	—
Fibric *Sphagnum*	FSp	15.8	0.0	2.1	11.1	2.1	—
Burned *Sphagnum*	BuS	—	—	—	16.7	26.6	—
Mixture of organic and mineral soils	MO	0.0	0.0	0.0	0.0	0.8	—
Rooting zone							
Fibric *Sphagnum*	FSp	77.6	70.8	71.9	78.3	52.1	—
Fibric *Pleurozium*	FPle	12.2	29.2	28.1	21.7	44.6	—
Mixture of fibric *Pleurozium* and humic materials	FH	0.0	0.0	0.0	0.0	1.9	—
Mineral soil	Min	10.2	0.0	0.0	0.0	1.4	—

Note: Decaying wood (soil surface and rooting zone), mixture of fibric *Pleurozium* and humic materials (soil surface) and mineral soil (soil surface) were present but were not retained when substrate classes were created.

Ressources naturelles du Québec 1999; Bergeron et al. 2004).

Regeneration survey

Microsite sampling was completed during summer 2003. Thirty regenerating trees, regardless of their origin, were studied in each of the 40 subplots. Regenerating trees are defined by height rather than by age. The great majority of trees in this site were short (<1.3 m in height). The site also contained taller trees that were presumably all remnants. Those trees were not considered because we wanted to limit the study to trees that had achieved most of their growth following the disturbance. The microsite around each regenerating black spruce tree was defined by a radius equivalent to the total height of the plant. For each tree (<1.30 m in height) we determined the type of regeneration (layer origin, planted seedlings, or seed origin), total height, the last 3-year annual increment (AI) (i.e., 2000, 2001, and 2002), root-collar diameter, mean length of three side branches, and position of regeneration (microtopography: hummock, slope, depression, or flat). Percent cover of ericaceous shrubs (mainly *L. groenlandicum*) was also visually evaluated for each regenerating tree. Growth substrates were sampled at the soil surface and in the rooting zone. To evaluate the appropriate root depth in each subplot, 30 regenerating black spruce trees were dug out randomly from different substrates to measure root depth. The results showed that the average root depth was 9.8 cm (SD = 4.38 cm; *n* = 356). Therefore, the rooting zone was determined to be 10–15 cm deep, on average. We distinguished 16 growth substrates, 11 at the surface and 5 in the rooting zone (see Table 1). We separated the decomposed material originating from mosses into two major classes: (1) *P. schreberi* as fibric *Pleurozium* after harvesting and burned *Pleurozium* after wildfire; and (2) *Sphagnum* spp. as fibric *Sphagnum* after harvesting and burned *Sphagnum* after wildfire. This classification was based on the assumption that feathermoss-based substrates (mainly *P. schreberi* in our sites) were more favourable than *Sphagnum* to black spruce growth (Arnott 1968; Jeglum 1981; Klenk 2001).

Soil and foliar analyses

The nutritional value of all microsites was evaluated in three ways: (1) substrate analysis (C and total N, cation exchange capacity (CEC), and pH), (2) seedling foliar analysis (N, P, K, Ca, and Mg), and (3) seedling growth. Growth substrates and needles were sampled in such a way that all types of substrates found at the subplot level were included. Owing to limitations of logistics and budget, and also because regenerating trees were often in more than one type of substrate (soil surface and rooting zone), substrate sampling was reduced to 658 samples. Our objective was to obtain a minimum of 50 samples of each dominant substrate type, but we were unable to achieve this for substrates that were less abundant. Substrate samples were immediately placed in coolers, 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 mesh sieves. Substrate pH was determined in distilled water and $CaCl_2$ (Carter 1993). Total C and N were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation). Exchangeable cations were extracted using unbuffered 0.1 mol/L $BaCl_2$ and determined by atomic absorption (Hendershot et al. 1993). CEC was defined as the sum of exchangeable cations (Na_e, K_e, Mg_e, Ca_e, Mn_e, Fe_e, and Al_e). Mineral soil texture was determined by granulometric analysis (Carter 1993).

Needle samples were collected in late September 2003, when the growing season had ended. Needle samples were collected from seven randomly selected regenerating trees per subplot, thus yielding a total of 280 samples of which 265 were kept for the analysis (134 samples in the harvest plots and 131 samples in the wildfire plots), as the discarded ones were found on multiple substrate types. 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. For the same reasons as mentioned above, needle sampling was restricted. We also randomly selected all needle samples in each plot and for each type of disturbance. Samples for needle and substrate analysis were not necessarily taken at the same tree locations. These samples were oven-dried at 70 °C for 48 h. After drying, needles were separated from twigs and ground. Total C and N were determined as for the substrates on a CNS analyzer, while total cations and P were determined following calcination at 500 °C and dilution with hydrochloric acid (Miller 1988). Cations were analyzed by atomic absorption and P by colorimetry (Lachat Instruments, Milwaukee, Wisconsin).

Data analysis

The preliminary redundancy analysis (RDA) (ter Braak and Smilauer 1998) explained very little (<26%) of the variation in black spruce growth rates. The RDA also showed that the type of regeneration greatly contributed to the variability in black spruce growth rates, and that there was a close relationship between the type of regeneration and substrate availability. For example, we found more planted trees and *Polytrichum* spp. after wildfire, while layers and *Pleurozium* categories were more abundant after harvesting. Therefore, to control the effect of regeneration type and substrate availability, subsequent analyses were performed only with planted seedlings because they were the only type of regeneration that was found on all the substrates. Moreover, to test the effect of the type of substrate on black spruce growth more effectively, we decided to use only planted trees with pure substrates (i.e., substrates dominated (>70%) by a single substrate type) for subsequent analyses. This step was necessary because trees were often growing in more than one type of substrate. This therefore reduced the initial database of 1200 regenerating trees down to 454/401 (rooting zone/soil surface) planted seedlings, and several substrate types (decaying wood, mixture of fibric *Pleurozium* and humic material, and mineral soil) could not be considered anymore and were discarded from further analysis.

Box plots were used to compare the properties of substrates as well as foliar nutrient concentrations of regenerating black spruce trees growing on different substrates. The relationships between 3-year AI, foliar nutrient concentration, and needle mass were determined using stepwise regression (holding p to enter = 0.1 and p to remove = 0.05) with a subset of 265 regenerating trees (i.e., each regenerating tree used for needle sampling).

Canonical discriminant analysis can be used to classify a category-dependent variable that has more than two categories, based on a number of interval-independent variables. We used it to investigate the differences between growth substrates (testing rooting zone and soil surface separately) and to find both the combination of substrate nutrient concentrations and the combination of foliar nutrient concentrations that best distinguish these substrates.

A mixed linear model was used to assess the effect on black spruce growth (3-year AI) of the two most abundant substrates that were present in all plots (*Pleurozium* and *Sphagnum*, which covered over 90% of the soil surface), the type of disturbance (wildfire and careful logging), and the interaction of these two factors while taking randomization restrictions into account. The use of a mixed linear model was possible only with *Pleurozium* and *Sphagnum* categories, owing to the low number of samples and the poor distribution of the other growth substrates. Inverse transformation was used to correct non-normally distributed data. Two outliers (the highest one and the lowest one) also had to be taken out of the database to correct for normality. A second mixed linear model was used to control the effect of the type of regeneration on black spruce growth, with growth substrate as the fixed effect. Square-root transformation was used to achieve normality. All statistics were conducted with SAS® version 8.02 (SAS Institute Inc. 2001).

Results

Growth substrates

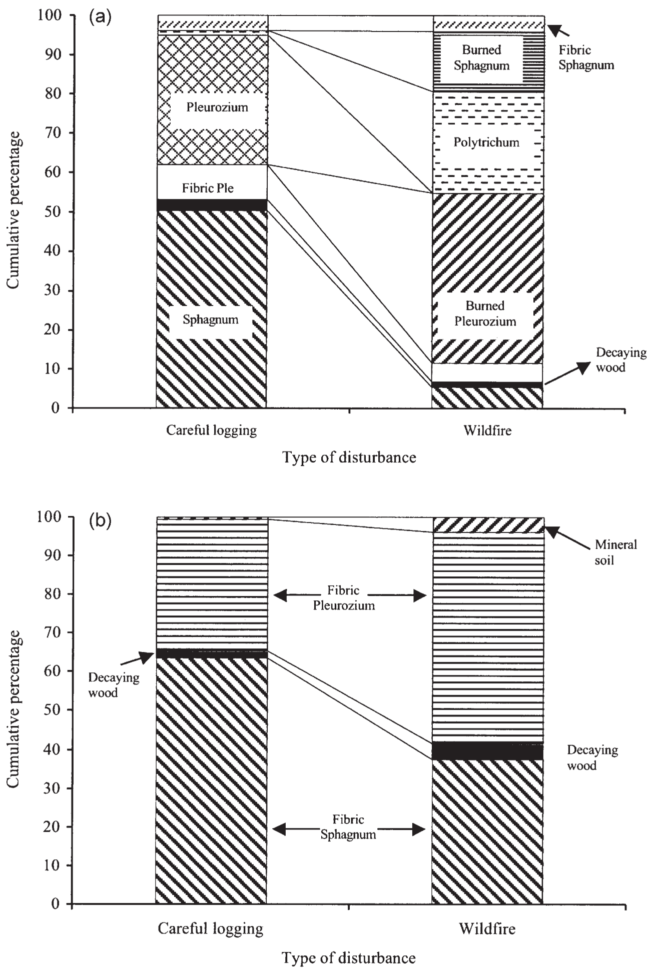
Overall, *Sphagnum* followed by *P. schreberi* and burned *Pleurozium* constituted the most abundant soil surface substrates, while fibric *Sphagnum* followed by fibric *Pleurozium* were the most abundant in the rooting zone. In wildfire plots, burned substrates (*Pleurozium* 43%, *Sphagnum* 16%) and *Polytrichum* spp. (26%) were the most abundant substrates at the soil surface, while fibric *Pleurozium* (55%) and fibric *Sphagnum* (38%) were the most important substrates in the rooting zone (Fig. 1). Following careful logging, *Sphagnum* spp. (50%) and *P. schreberi* (33%) were the most abundant substrates at the soil surface, while fibric *Sphagnum* (64%) and fibric *Pleurozium* (34%) were the most abundant substrates available in the rooting zone (Fig. 1). A χ^2 test showed that at both depths (soil surface and rooting zone) the distribution of substrates differed significantly (p = 0.001) between wildfire and careful logging.

Mean 3-year AI

Planted seedlings exhibited considerable variation in growth response depending on growth substrates (Fig. 2). At the soil surface, all substrates except the mixture of organic and mineral soils and burned *Sphagnum* had a normal distribution (data not shown). Three-year AI was significantly less for black spruce growing on burned *Sphagnum* (only 23 cm) than on any other surface substrate ($p < 0.0001$). For the rooting zone, only mineral soil and the mixture of fibric *Pleurozium* and humic materials resulted in a normal distribution. Box-plot results showed that the last 3-year AI was significantly ($p < 0.0001$) higher with the mixture of fibric *Pleurozium* and humic materials (46 cm) than with fibric *Pleurozium* (36 cm), mineral soil (28 cm), and fibric *Sphagnum* (25 cm); however, all substrates exhibited a wide range of values.

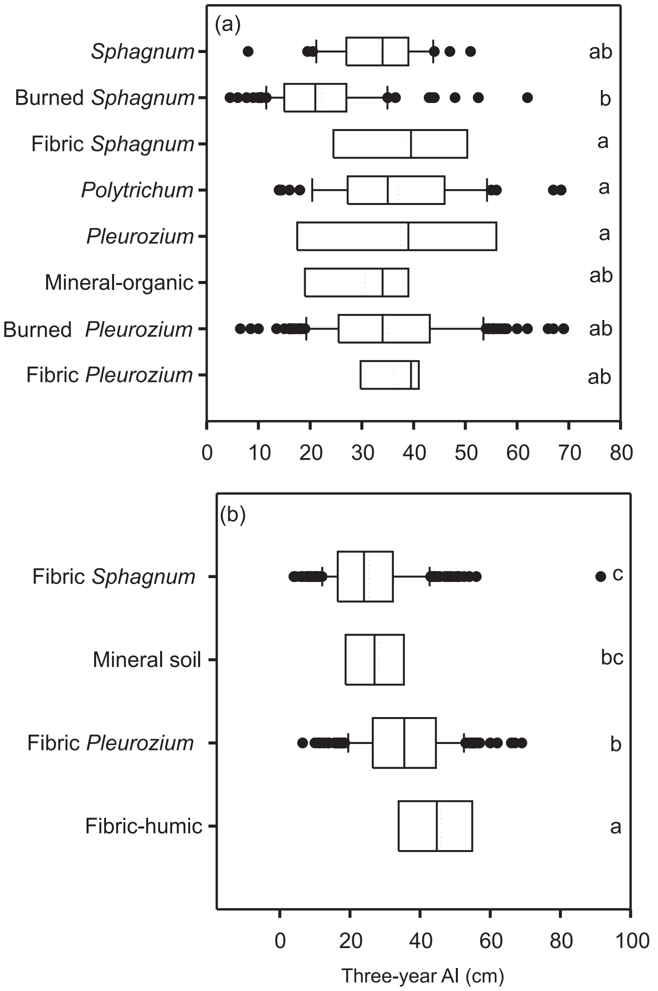
The properties of each substrate are presented in Fig. 3. At the soil surface, pH values in water and $CaCl_2$ were significantly lower in decaying wood. CEC was similar in all substrates except for significantly lower values in mineral soil ($p < 0.0001$). For soil surface substrates, the C/N ratio was significantly higher in decaying wood and lower in mineral soil ($p < 0.0001$). For the rooting zone, soil pH was significantly higher in mineral soil (in water and $CaCl_2$) and lower in decaying wood (in water and $CaCl_2$) ($p < 0.0001$).

Fig. 1. Distribution of growth substrates at the soil surface (*a*) and in the rooting zone (*b*) after careful logging and wildfire.



For CEC, decaying wood and mineral soil showed significantly lower average concentrations than the other substrates. C/N ratios were significantly higher in decaying wood followed by fibric *Sphagnum*, fibric *Pleurozium*, mixtures of fibric *Pleurozium* and humic materials, and mineral soil ($p < 0.0001$) (Fig. 3).

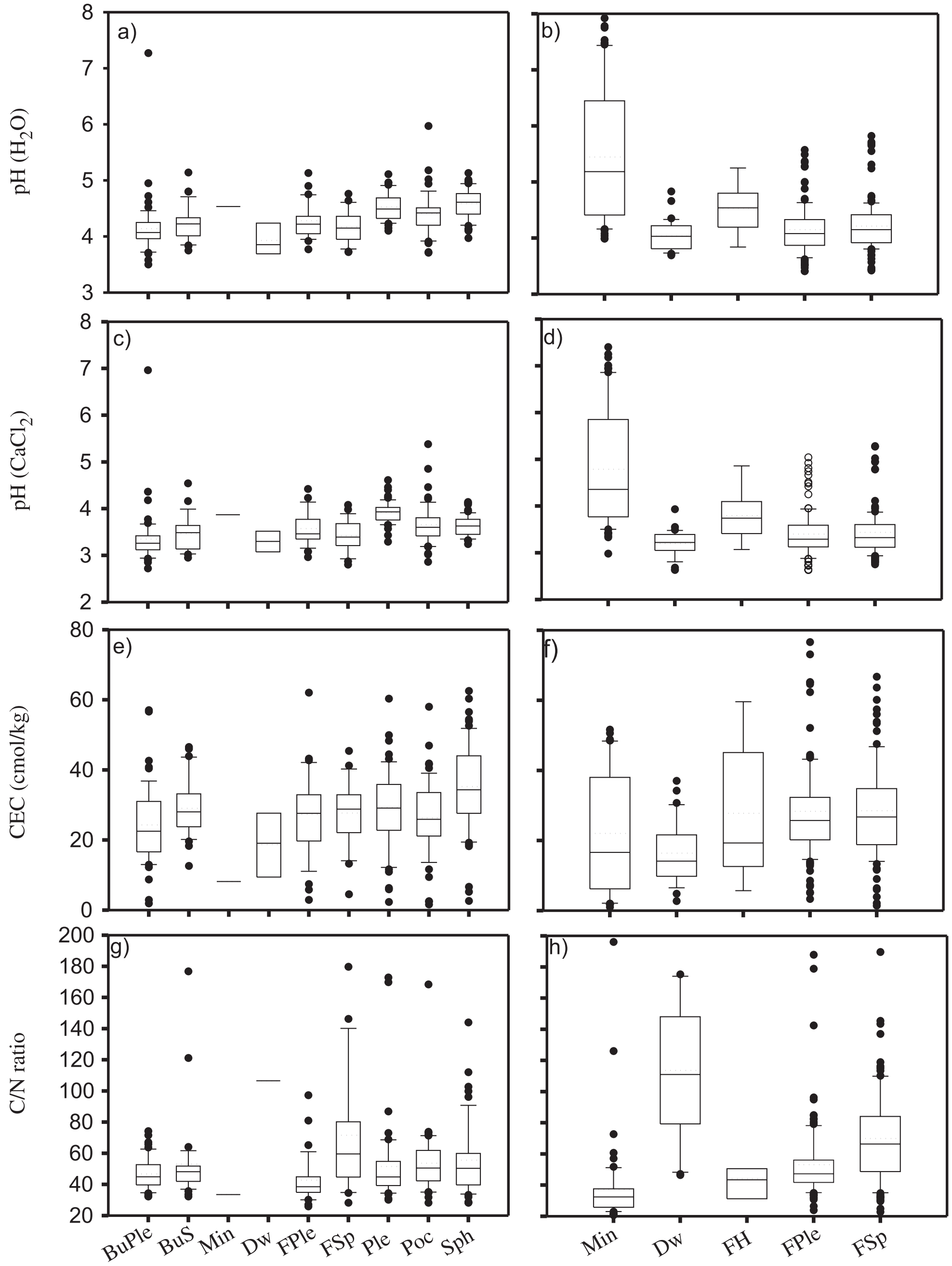
Fig. 2. Box plots showing the 3-year annual increment (AI) for different substrates at the soil surface ($n = 401$) (*a*) and in the rooting zone ($n = 454$) (*b*) for planted seedlings. The central vertical bar denotes the median, the vertical dotted line denotes the mean, the horizontal boxes denote the 25th and 75th percentiles, and the left- and right-hand bars denote the 10th and 90th percentiles. The large solid dots represent outliers outside the 10th and 90th percentiles. Different letters designate significant differences between growth substrates.



Tree nutrition

All needle nutrient concentrations (except Mg) showed a significant positive correlation with 3-year AI (Fig. 4), with N and P having the highest level of correlation with 3-year AI. However, *r* values were low (<0.37). Needle samples were randomly collected on each regenerating tree growing in all microsites. Some trees were growing in microsites composed of pure substrate (i.e., >70% cover of one substrate) and others were growing in microsites composed of several substrates. To retain the greatest number of samples in the analysis, we created substrate classes that were either pure or a mixture of two substrates in relatively equivalent proportions (ranging from 40% to 60%). At the soil surface (i.e., 10 substrate classes) and for the rooting zone (i.e., 6 substrate classes), foliar nutrient concentrations were very variable within each substrate (Table 2). Stewart and Swan (1970) and Lowry (1975) also found high variability in foliar concentrations within substrate types, with values ranging from deficiency to optimal levels. Although average nutrient concentrations were at a sufficiency level for N, P, and K, they expressed a deficiency of Mg and exceeded consumption levels for Ca. Standard foliar concentrations for black spruce suggested by Stewart and Swan (1970) for the range “transition zone from deficiency to sufficiency” are 1.20%–1.50% for N; 1.4–1.8 mg·g^{-1} for P; 3.0–4.0 mg·g^{-1} for K; 0.9–1.2 mg·g^{-1} for Mg; and 1.0–1.5 mg·g^{-1} for Ca. The statistics for multiple linear regression models are shown in Table 3. The variables that performed the best in predicting 3-year AI for black spruce were developed from needle P concentrations ($R^2 = 0.171$). Adding needle N concentration and needle mass increased the fit between the

Fig. 3. Box plots showing pH (in H_2O, $CaCl_2$), cation exchange capacity (CEC), and C/N ratio for different substrates at the soil surface (*a*, *c*, *e*, *g*) and in the rooting zone (*b*, *d*, *f*, *h*). Abbreviations are as follows: BuPle, burned *Pleurozium*; BuS, burned *Sphagnum*; Min, mineral soil; Dw, decaying wood; FPle, fibric *Pleurozium*; FSp, fibric *Sphagnum*; Ple, *Pleurozium schreberi*; Poc, *Polytrichum* spp.; Sph, *Sphagnum* spp.; FH, mixture of fibric *Pleurozium* and humic materials. The central horizontal bar represents the median, the horizontal dotted line the mean, the vertical boxes the 25th and 75th percentiles, and the lower and upper bars the 10th and 90th percentiles. The large solid dots show outliers outside the 10th and 90th percentiles.



measured and predicted 3-year AIs for regenerating black spruce trees (R^2 = 0.227).

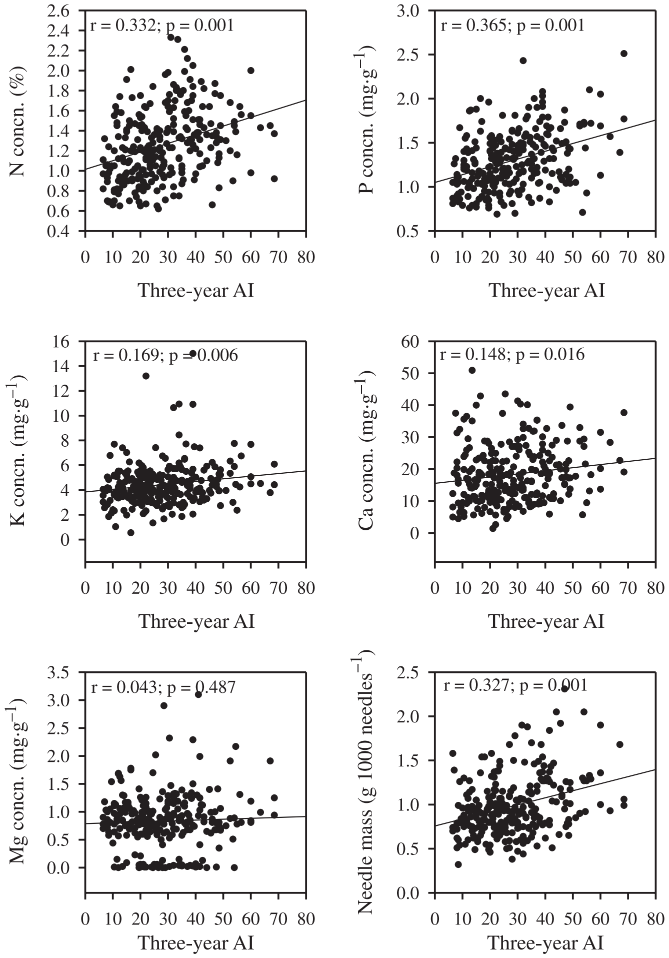
Discriminant analysis indicated that the seven main growth substrates at the soil surface were significantly separated by the first four of the six canonical functions. Of the nine variables included in the canonical discriminant analysis to evaluate differences among growth substrates at the surface, Na_e, K_e, and pH had the greatest discriminatory importance for the first two canonical functions (Table 4) and explained 73% of the total variance. The first canonical axis represents the direction of the greatest variance (58%) between growth substrates at the soil surface. Na_e, K_e, and pH were the variables with the highest correlation with the first axis. The second canonical axis represents 15% of the variance between growth substrates for the soil surface. An overall classification accuracy of 50% was obtained for growth substrates at the soil surface (Table 5). Classification accuracy (i.e., the analysis evaluates the performance of a

Table 2. Foliar nutrient concentrations and needle mass for growth substrates at the soil surface and in the rooting zone.

	Soil surface						
	Poc	Ple	BuPle	FPle	Ple–FPle	Ple–Sph	Sph
N (%)	1.32 (0.052)	1.11 (0.046)	1.31 (0.042)	1.37 (0.074)	1.13 (0.11)	0.97 (0.047)	1.09 (0.060)
P ($mg \cdot g^{-1}$)	1.32 (0.063)	1.17 (0.055)	1.41 (0.046)	1.19 (0.061)	1.35 (0.023)	1.03 (0.037)	1.20 (0.051)
K ($mg \cdot g^{-1}$)	4.83 (0.25)	3.96 (0.26)	4.34 (0.25)	3.92 (0.21)	4.16 (0.29)	3.74 (0.48)	4.74 (0.28)
Mg ($mg \cdot g^{-1}$)	0.74 (0.070)	0.78 (0.066)	0.88 (0.11)	0.87 (0.061)	0.80 (0.21)	0.96 (0.099)	0.72 (0.068)
Ca ($mg \cdot g^{-1}$)	20.11 (1.53)	16.44 (1.45)	18.51 (1.21)	18.30 (1.85)	19.57 (6.62)	20.29 (4.55)	16.07 (1.29)
Needle mass ($g \cdot 1000$ $needles^{-1}$)	1.04 (0.059)	1.09 (0.065)	0.94 (0.044)	1.01 (0.051)	1.10 (0.19)	0.90 (0.097)	1.01 (0.067)

Note: Values are given as the mean with the standard error in parentheses. Abbreviations are as follows: Poc, *Polytrichum* spp.; Ple, *Pleurozium* Sph, *Sphagnum* spp.; BuS, burned *Sphagnum*; FSp, fibric *Sphagnum* spp.; Mix, mix of various substrates; FPle–Min, fibric *Pleurozium* – mineral soil;

Fig. 4. Correlations (Pearson's coefficient) between foliar nutrient concentrations, needle mass, and 3-year AI (n = 265).



discriminant criterion by estimating error rates in the classification of future observations) was reduced by a high statistical misclassification (i.e., poor performance) for three substrates: fibric *Pleurozium*, burned *Sphagnum*, and fibric *Sphagnum*.

For the rooting zone, the discriminant analysis indicated that the four main growth substrates were significantly separated by the three canonical functions. Of the nine variables included in the canonical discriminant analysis to evaluate differences among growth substrates, N_t, pH, and Fe_e had the greatest discriminatory importance for the first two canonical functions (Table 4) and explained 94% of the total variance. The first canonical axis represents the direction of the greatest variance (83%) between growth substrates for the rooting zone. N_t, pH, and Fe_e were the variables with the highest correlation with the first axis. The second canonical axis represents 11% of the variance between growth substrates for the rooting zone. The variables that influenced axis 1 also had the most influence on axis 2, but the direction of the correlation differed for pH and Fe_e. The overall success of classifying samples into the four growth substrates correctly was 74%. Group membership was predicted well for three of the four growth substrates (Table 5).

Discriminant analysis was also used to classify growth substrates at the soil surface and for the rooting zone, this time based on the foliage nutrient concentrations (N, P, Ca, Mg, K) of trees growing in these substrates. Classification accuracy was very low (25% and 46% for the soil surface and rooting zone, respectively; results not shown). This low accuracy might be explained in part by substrate classes created from a mixture of two substrates (40%–60% of each). Three of the 10 growth substrates comprised a mixture of two substrates at the soil surface, and three of six growth substrates comprised a mixture of two growth substrates in the rooting zone.

As shown in Fig. 1, growth substrates at the soil surface are mainly *P. schreberi* and *Sphagnum* spp. after harvesting, and burned *Pleurozium* and burned *Sphagnum* after wildfire, and these types are present in almost all harvested or burned subplots, respectively. Thus, a mixed linear model was used to test the effect of the two main substrates (*P. schreberi* vs. *Sphagnum* spp.), the type of disturbance (wildfire vs. careful logging), and the interaction of these two factors on the 3-year AI. Since we used only planted seedlings for analysis, the type of disturbance and the interaction between substrate and disturbance could not be tested because many plots in harvested sites did not contain planted trees. The random effects selected in the model were zone (Quebec or Ontario), the interaction zone × type of disturbance, and subplots nested in the interaction zone × type of disturbance × plot. The decision to remove error terms was based on Akaike's information criterion. There was a significant (p = 0.0009) effect of substrate on growth, with higher growth rates observed on *Pleurozium* substrates.

Discussion

Initially we were hoping to include in our analysis all types of regeneration (i.e., seeds, planted seedlings, and lay-

			Rooting zone					
BuS	FSp	Mix	FPle	FPle–Min	FPle–Dw	FSp–FPle	FSp	Min
1.32 (0.060)	1.41 (0.095)	1.32 (0.19)	1.22 (0.033)	1.56 (0.095)	1.35 (0.11)	1.32 (0.065)	1.21 (0.034)	1.69 (0.10)
1.43 (0.054)	1.39 (0.076)	1.34 (0.12)	1.27 (0.03)	1.63 (0.076)	1.64 (0.065)	1.35 (0.077)	1.26 (0.030)	1.32 (0.13)
4.57 (0.45)	4.82 (0.39)	4.55 (0.36)	4.14 (0.16)	5.21 (0.68)	4.81 (0.31)	4.62 (0.42)	4.54 (0.16)	4.17 (0.33)
0.81 (0.087)	1.01 (0.074)	0.80 (0.17)	0.83 (0.063)	0.85 (0.22)	1.14 (0.11)	0.85 (0.063)	0.80 (0.038)	0.97 (0.12)
17.86 (1.60)	21.63 (2.23)	23.31 (4.45)	17.49 (0.89)	25.03 (2.62)	24.98 (2.92)	16.15 (1.90)	18.13 (0.82)	20.79 (2.94)
0.75 (0.030)	0.92 (0.089)	0.96 (0.092)	1.02 (0.038)	1.00 (0.06)	0.96 (0.076)	1.13 (0.049)	0.90 (0.030)	1.07 (0.11)

schreberi; BuPle, burned *Pleurozium*; FPle, fibric *Pleurozium*; Ple–FPle, *Pleurozium schreberi* – fibric *Pleurozium*; Ple–Sph, *P. schreberi* – *Sphagnum* spp.; Fple–Dw, fibric *Pleurozium* – decaying wood; FSp–FPle, fibric *Sphagnum* – fibric *Pleurozium*; Min, mineral soil.

Table 3. Three-year annual increment (AI) prediction models for black spruce (n = 265).

Model	R^2	Adj. R^2	p	SEE	Constant	P	N	Needle mass
Three-year AI								
1: P	0.171	0.168	<0.001	2.00	–0.436	2.791	—	—
2: P + N	0.211	0.205	<0.001	1.96	–1.123	1.837	1.530	—
3: P + N + needle mass	0.227	0.218	<0.001	1.95	–1.747	1.839	1.360	851.39

Note: Adj. R^2 is the adjusted R^2 value; SEE is the standard error of the estimate; P is the phosphorus concentration (needles); and N is the nitrogen concentration (needles).

Table 4. Discriminatory importance of the observation variables (total N, pH, and exchangeable cations in growth substrates) shown by the within-group correlation coefficient between variables and the first two canonical functions at the soil surface (n = 321) and in the rooting zone (n = 324).

	Soil surface		Rooting zone	
Observation variable*	Function 1	Function 2	Function 1	Function 2
N_t	–0.257	0.112	**0.658**	**0.581**
pH	**0.500**	–0.279	**–0.487**	**0.435**
Fe_e	0.314	**0.478**	**0.276**	**–0.377**
Ca_e	–0.131	0.041	0.179	0.316
Mn_e	0.293	**0.373**	–0.016	0.196
Mg_e	0.255	0.279	0.144	0.135
Na_e	**0.727**	**0.532**	–0.017	–0.178
Al_e	0.001	–0.051	–0.050	–0.015
K_e	**0.608**	–0.111	–0.045	0.050
Variance explained (%)	58.3	14.9	83.4	10.9

Note: For each function, values in boldface type indicate the three variables with the highest correlation coefficients.

*A subscript "t" denotes total and "e" exchangeable.

ers) to measure the effect of growth susbstrates on black spruce growth. However, our preliminary results (i.e., RDA) showed differences in growth rate between the types of regeneration, as well as a close relationship between the type of regeneration and substrate availability. Thus, to determine as clearly as possible the effect of growth substrates on black spruce growth, we retained only planted seedlings for our analysis. Therefore, the following discussion takes into account only planted and not naturally regenerated seedlings.

Our results show that black spruce height growth tends to be greater on substrates composed of feathermosses and fibric material than on any other type of substrate. This is consistent with the pioneer greenhouse work of Arnott (1968), which indicated a tendency for black spruce growing on *P. schreberi* to have a greater shoot mass and better foliar levels of P and lower levels of K than when growing on *S. capillifolium.* In a greenhouse study, Jeglum (1981) also found greater growth with *P. schreberi* than with *S. angustifolium* and *S. fuscum* substrates, but only when there was daily watering (Jeglum 1979). Our results from the field experiment were also recently confirmed by those from a greenhouse experiment (Lavoie et al. 2006). Our results also show poor growth on mineral soil, which is less consistent with the literature. In some field experiments, a tendency has been reported for black spruce to exhibit more rapid height growth on soil covered with either moss or a thin organic layer than on bare mineral soil (Linteau 1957; Fleming and Mossa 1995), while in some the opposite has been reported (Vincent 1965). Our results are nevertheless consistent with a greenhouse experiment (Lavoie et al. 2007*a*) that indicated very poor growth on mineral soil in

Table 5. Discriminant classification results for predicted group membership for growth substrates at the soil surface (n = 321) and in the rooting zone (n = 324).

(A) Soil surface.

		Predicted group membership							
Group	No. of cases	Poc	Ple	BuPle	FPle	Sph	BuS	FSp	Correctly classified (%)
Polytrichum	52	27	8	8	0	5	2	2	51.9
Pleurozium	54	13	28	4	1	7	0	1	51.9
Burned *Pleurozium*	59	2	2	45	1	2	4	3	76.3
Fibric *Pleurozium*	35	2	6	15	6	4	0	2	17.1
Sphagnum	56	9	4	4	0	37	1	1	66.1
Burned *Sphagnum*	38	1	7	15	0	3	7	5	18.4
Fibric *Sphagnum*	27	6	5	2	1	2	0	11	40.7

(B) Rooting zone.

		Predicted group membership				
Group	No. of cases	FPle	FSp	Min	Dw	Correctly classified (%)
Fibric *Pleurozium*	115	95	17	1	2	82.6
Fibric *Sphagnum*	114	34	71	4	5	62.3
Mineral soil	63	1	4	56	2	88.9
Decaying wood	32	5	9	1	17	53.1

Note: For an explanation of abbreviations see Table 1.

the same sites. The mineral soil in the Clay Belt is generally heavily compacted, owing to a high silt and clay content and, in our area, to a second glacial readvance that left a very hard argillaceous till (i.e., Till of Cochrane). Regenerating trees on bare mineral soil microsites have a tendency to suffer drought stress under dry conditions, whereas trees located in depressions can become waterlogged under prolonged wet conditions (Bergsten et al. 2001; de Chantal et al. 2003). Even though the depth of accumulated organic matter is generally important in our study area, our results suggest that mineral soil exposed by heavy disturbances such as severe wildfires or site preparation could reduce black spruce growth.

Our study also confirmed that the microsites suitable for establishment of black spruce seedlings are not necessarily the best substrates for subsequent black spruce seedling growth. It is well known that *Sphagnum* mosses and peat provide better conditions for black spruce germination and seedling survival than feathermosses, mainly because of a better moisture level and water supply (Roe 1949; Heinselman 1957; Arnott 1968; Wood and Jeglum 1984; Groot and Adams 1994). However, as the root system of seedlings becomes established, the nutrient supply may become more important to seedling growth than water availability. Seedling growth may also be affected on *Sphagnum* moss substrates because seedlings can be smothered as a result of the faster growth of these mosses (Roe 1949; Arnott 1968; Jeglum 1981; van Breemen 1995). Even though our results show that growth substrates at the soil surface generally (80% of samples) correspond to growth substrates for the rooting zone, data obtained from the rooting-zone sampling showed a better relationship between substrate type and seedling growth.

Foliar analysis provided little explanation for the differences in height growth of black spruce between the growth substrates. We also tried vector analysis but the results were not conclusive. Black spruce is a conservative species and this sometimes makes it difficult to use vector analysis (see Thiffault et al. 2006). However, the nutritional value of the growth substrates was more informative. The discriminant analysis suggests the importance of total N concentration, pH (negative with the first axis), and exchangeable Fe (negative with the second axis) in the rooting zone. This did not come as a surprise, since total soil N is usually correlated with available N (Binkley and Hart 1989; Côté et al. 2000), especially in organic soils, where it reflects the soil C/N ratio. A positive correlation between tree growth and soil pH is a general feature of mineral soils, as acidic conditions increase soluble Al availability and decrease P availability, but this relationship has also been reported for boreal peatlands (Jeglum 1981). A lower soil pH in organic soil also affects soil microorganism activities such as N and P mineralization (Persson and Wirén 1995; Davidsson and Stahl 2000). On the other hand, at the soil surface the separation between substrates was different. For the first axis, the three highest correlations (all positive) were with exchangeable Na, K, and pH, while exchangeable Na, Fe, and Mn were the three highest correlations (all positive) with the second axis. These results are more surprising, even though Na, Fe, and Mn are micronutrients. Our results may indicate that the classification of growth substrates from the soil surface is more indicative of soil physico-chemical conditions than of nutrient quality because Fe and Mn solubility is directly linked to reducing conditions. However, Mn can play an important role in lignin degradation by white rot fungi (Kirk and Farrell 1987) and by accelerating N mineralization (Berg 2000). A closer look at the nutritional value of each substrate showed that fibric material and the mixture of fibric and humic materials in the rooting zone had lower C/N ratios than fibric *Sphagnum*. Previous work has shown higher rates of decomposition of organic matter and N mineralization under feathermosses than under *Sphagnum* mosses (Klenk 2001; O'Connell et al. 2003). Finally, DeLuca et al. (2002) reported that *P. schreberi* was a host for an associative or symbiotic *Nostoc* species that has an N-fixation potential of 1.5–2.0 kg N·ha^{-1}·year^{-1}, which could partially explain the better spruce growth we observed on the *P. schreberi* substrate. N deficiencies are quite common in all types of forests in Canada, while P deficiencies also appear to be a feature of some temperate-zone forests (Gradowski and Thomas 2006), forested wetlands (Arnott 1968; Alban and Watt 1981; Roy et al. 1999; Banner et al. 2005), and boreal forests (Prévost and Dumais 2003). Our results suggest that P availability is potentially an important limiting factor for black spruce growth, and there is certainly a need for more information on P cycles in black spruce ecosystems, especially after wildfire (Dyrness and Norum 1983; Certini 2005).

In addition to the effect of substrate quality, black spruce growth could also have been influenced by the presence of ericaceous shrubs, variation in the water table, and the thickness of the organic layer. We did not observe a significant correlation between *L. groenlandicum* (the main ericaceous shrub present in these sites) cover and black spruce height growth for planted seedlings. These results contradict the literature on *L. groenlandicum* (Inderjit and Mallik 1996, 1997) but are in agreement with the detrimental effect of the mechanical removal of aboveground *L. groenlandicum* on black spruce growth observed by Lavoie et al. (2006) as well as the absence of the effect of *L. groenlandicum* on black spruce germination found by Titus et al. (1995).

High water tables can have a negative effect on tree growth (Lavoie et al. 2005), but we do not believe that this was an issue at our sites. Water table depth was only measured once in the Quebec sites (data not presented) and was not measured in Ontario. When the water table was found to be above the mineral soil surface (17% and 60% of regenerating trees in the burned and the harvested sites, respectively), its depth from the surface was, on average, 24 cm with a standard deviation of 12 cm, which is below the average rooting depth of 10–15 cm. Moreover, the low percent cover of *Sphagnum* (living, burned, or fibric) in the wildfire sites (see Fig. 1) combined with the thin organic layer (<25 cm, on average) in the wildfire sites (Lavoie et al. 2007*b*) suggests that the water table was not near the soil surface. Therefore, we are confident that most roots of planted trees were above the water table.

Lastly, we observed a negative correlation between organic-matter thickness and 3-year AI but the correlation was relatively weak (planted seedlings: $r = -0.351$, $p = 0.001$). This suggests that organic-matter thickness has a negative impact but that organic-matter composition (i.e., fibric *Pleurozium* vs. fibric *Sphagnum*) and its properties are also important. In fact, the literature generally reports good productivity on well-decomposed organic soils (see review in Lavoie et al. 2005).

Conclusion and management implications

Little information is available on the quality, for black spruce growth, of the different substrates that are found in lowland forests. Most of this information is based on studies on substrates in mature forests. Our study provides new information on the quality, for tree growth, of the substrates that are found in lowland sites after disturbance (harvest and wildfire). This study shows that black spruce height growth is highly variable (i.e., RDA) and that environmental variables such as organic-matter thickness and percent cover of *L. groenlandicum* explain very little of this variability. On the other hand, our results show that black spruce seedlings growing on soil-surface substrates composed of *P. schreberi* and fibric *Pleurozium* or rooting-zone substrates composed of either fibric *Pleurozium* or a mixture of fibric *Pleurozium* and humic materials performed better than seedlings growing on *Sphagnum* materials (fresh, decomposed, or burned), decaying wood, or mineral soil. It is noteworthy that these growth substrates were always located in the same sites, often very close to each other. Usually, most regenerating trees grew on more than one type of substrate (soil surface and rooting zone).

Our study also confirms that microsites suitable for the establishment of black spruce seedlings are not identical with those suitable for their growth. Thus, relying mainly on layers and favourable seedbeds (i.e., *Sphagnum*) to regenerate black spruce stands may not yield a tree distribution that is optimal for initial tree growth. This may partly explain the better growth of planted versus naturally regenerated black spruce in some sites (Prévost and Dumais 2003; Thiffault et al. 2004). To improve stocking and increase the number of regenerating trees on the best available growth substrates (i.e., *P. schreberi* and fibric material originating from *P. schreberi*), targeted planting (i.e., infill planting on high-quality substrates) of black spruce seedlings after harvesting should be considered.

At the young stage considered in this study, the regenerating tree roots were in the top 20 cm of the profile and did not reach the mesic (i.e., 5–6 on the Von Post decomposition scale) and humic (i.e., 7–10 on the Von Post decomposition scale) peat soil layers or the mineral soil in undisturbed substrate. As the trees grow, the root system may reach these layers. The mesic and humic peat layers and the mineral soil may also be exposed by site preparation (e.g., mounding) or intense disturbance (e.g., wildfire). Thus, the impact of the physical and chemical properties of these soil layers on black spruce growth requires further investigation. Finally, to maintain or increase black spruce growth in these low-productivity stands with regard to sustainable forest management, we recommend (*i*) planting in substrates originating from *P. schreberi* and (*ii*) the development of management techniques that favour forest mosses over *Sphagnum* mosses (Lavoie et al. 2005). For example, following harvesting, stands should be re-established at high density to limit light availability in order to restrain the growth of *Sphagnum* and *L. groenlandicum* (Fenton et al. 2005).

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