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Growth and root development of black and white spruce planted after deep planting

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ABSTRACT

The capacity of trees to produce new roots is essential for rapid early growth of planted seedlings. Black and white spruce trees (*Picea mariana* and *Picea glauca*) are widely planted in the eastern boreal forest of Canada and are known to develop substantial adventitious root systems. In this study, we compared root development and growth of 17-year-old trees that had been planted at two different depths (ground level vs 10–12 cm) to see if partial stem burial would hasten adventitious root development, and in turn, growth. Root number (total and adventitious), root total area, rooting depth, year of root formation, tree height and basal diameter were measured in black and white spruce trees. Both species developed adventitious root systems, and adventitious roots size and area were greater for deeply planted trees than for trees planted at ground level. The number of adventitious roots and the speed of adventitious root development were greater for deeply planted black spruce but not for deeply planted white spruce, compared with trees planted at ground level. For the latter, site conditions could explain the absence of a planting depth response. Deep planting increased tree height and basal diameter of white spruce, but only height for black spruce trees. However, tree growth was related to total root cross-sectional area (not just adventitious roots), underscoring the importance of both types of roots for tree growth.

1. Introduction

Rapid establishment and early growth of trees is crucial for maximising plantation productivity and avoiding seedlings being quickly overtopped by competing vegetation (Ritchie and Dunlap, 1980; Trottier, 1998; Prévost and Dumais, 2003; Johansson et al., 2007; Thiffault et al., 2012). The capacity of trees to absorb water is one of the most important factors that affect the speed of establishment of planted seedlings, and drought stress is often the main reason for mortality or growth stagnation of conifer seedlings (Burdett, 1990). Planted trees access water by producing new roots (Carlson, 1986; Johnsen et al., 1988; Grossnickle, 2005). Therefore, the capacity to produce new roots is a selection criterion in nurseries and also has been suggested as a predicted relative measure of performance in plantations (Ritchie and Dunlap, 1980; Sutton, 1980; Burdett et al., 1983; Feret and Kreh, 1985; Johansson et al., 2007). The initial period of stagnant growth in planted seedlings, which is called plantation shock, corresponds to the length of time that is required for seedlings to produce new roots to comprise an adequate root system (Rietveld, 1989). Plantation shock is especially damaging for forest productivity when its effects are still noticeable long after seedlings have developed good root systems (Grossnickle, 2005). Consequently, plantation productivity can suffer from plantation shock over multiple years.

Each year, about 100–150 million seedlings are planted in Quebec (Parent et al., 2012). The most frequently planted species is black spruce (*Picea mariana* (Miller) BSP) with 60 million seedlings per year (58%), but white spruce (*Picea glauca* (Moench) Voss; 11% of planted trees) and jack pine (*Pinus banksiana* Lambert; 23%) are also commonly used (Parent, 2010). The root system of mature black spruce trees is almost exclusively adventitious, i.e., the majority of roots have developed directly on the stem (DesRochers and Gagnon, 1997; Krause and Morin, 2005). White spruce is also known to develop adventitious roots (Peters et al., 2002), but does so to a lesser extent than black spruce. This indicates that the primary root system does not develop for these two species, even for mesic sites, without large surface accumulations of organic matter (DesRochers and Gagnon, 1997). For the successful development of adventitious roots, the base of the stem must experience humid conditions (Aubin, 1996). This condition might explain, at least for black spruce, why seedlings tend to bend at the base when they are produced in nurseries (Béland and Lapierre, 1992), thereby placing their stems in contact with the soil and promoting the formation of adventitious roots.

Preliminary studies have shown that burying the bases of the seedling stems, either in the greenhouse or in the field, allowed

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for faster development of adventitious roots compared to seedlings planted at the root collar (Aubin, 1996; Gagnon, 2002). Sutton (1991) also recommended deeper nursery planting of black spruce seedlings, i.e., below root-collar level, to accelerate the development of adventitious roots. Whether faster development of adventitious roots would accelerate establishment and early growth of white and black spruce seedlings is unclear (Schwan, 1994; Whaley et al., 1995; Beyeler, 1996; Gagnon, 2002). Most studies on burial of trees took place on coastal or desert sand dunes, and these studies show generally a positive effects of partial sand burial on tree height, biomass (shoot and root), and photosynthetic rate (Zhang and Maun, 1992; Brown, 1997; Shi et al., 2004; Dech and Maun, 2006). However, a recent study in the boreal forest of Canada showed no effect of deep planting on growth or survival of black and white spruce seedlings (Paquette et al., 2011), but any differences in root development were not addressed. As stem burial in sand dunes or in the boreal forest offer very different conditions (e.g. soil type, water availability and soil temperature), tree responses to burial may vary. The lack of an overall consensus emphasises the need for further studies of tree response to partial stem burial under boreal conditions.

The goals of this study were (1) to evaluate the effects of planting depth on adventitious root production and (2) to examine the relationship between adventitious root development and tree growth. Overall, we hypothesised that burial would increase both the quantity of adventitious roots and their speed of formation, and in turn increase growth of deeply planted trees. As black spruce generally produce more adventitious roots than white spruce trees (Schwan, 1994), we assumed that black spruce would better respond to deep planting.

2. Materials and methods

2.1. Study sites

In June 1993, 26,000 bare-root seedlings of black (BS) and white spruce (WS) were planted by Quebec's Ministry of Natural Resources at eight study sites that were between 49°12′N and 49°14′N, and between 72°38′W and 72°40′W. The sites were located in boreal forest of the Lac-Saint-Jean region (Quebec, Canada), within the western balsam fir-paper birch (*Abies balsamea* (L.) Mill. – *Betula papyrifera* Marsh.) bioclimatic domain (Grondin, 1996). The provincial nursery at Normandin supplied two-year-old (2 + 0) bare-root stock. Soil scarification was done prior to planting using a Wadell disk-trencher. The field trial design was simple, with 4 sites per species (Fig. 1). For each species, two sites (replicates) were planted at ground level and the other two at 10–12 cm deep (deep planting, Fig. 1). Spacing in plantation was around 2 × 2 m (2200 trees per hectare) and between 2900 and 3400 trees were planted per site. Minister of natural resources recorded tree mortality during the two years following plantation, and no differences were recorded between planted sites. From 1971 to 2000, precipitation was recorded at the closest Environment Canada weather station (Albanel), averaging 887 mm annually (639 mm as rainfall, 248 mm as snowfall). Average annual temperature (±standard deviation, SD) was 1.7 ± 4.9 °C (Environnement Canada, 2011). Slope was generally low (4–8%). Soils were constituted with glacial deposits of undifferentiated till with moderate drainage (mesic). The ground cover included ericaceous shrubs and a dense mat of fruticose lichen, feather moss, or sphagnum (Table 1).

2.2. Field measurements

Sampling was done in September 2010. Height (m), basal diameter (cm, at soil level) and diameter at breast height (cm; DBH, 1.3 m, when possible) were measured for 30–50 trees that were located in a randomly established 20 × 20 m quadrat within each site (Table 2). Tree height was measured using a measuring pole and basal diameter with a digital calliper. Average tree height and basal diameter was first calculated for each site, and 5 trees that were close to these averages or higher (codominant or dominant trees) were then selected for excavation. Soil level was identified on each tree using tape. The five selected trees were cut and their root system excavated by hand with shovels. In the field, soil was removed from around the root mass by shaking the trees and the remaining soil was removed in laboratory by washing roots under water. Tree boles, stumps and all roots within a 50–60 cm radius of the stem were brought to the laboratory for further analysis. For each tree, we estimated mean crown radius (by measuring the length of three largest branches) to determine competition radius. Competition radius is the estimated crown radius of canopy trees multiplied by 3.5 (Hegyi, 1974). If a tree was located in the competition radius, it was recorded as a competitor. However, we found that only one black spruce tree had competition, thus this variable was dropped from further analysis.

2.3. Dendrochronological analysis

Each root was identified and cross-sectional area of the root was measured at the stump. To minimise bias due to root eccentricity, average root diameter was determined as the average between the longest and a second measurement made at about 90° from the first. Root cross-sectional area at the stump was calculated, as π multiplied by the longest and radius at 90°. A cross-section of about 1 cm thick was cut at the base of the stump for each root with a diameter greater than 2 mm. The cross-sections were air-dried for several months and then sanded with coarse to fine papers (up to 600 grit). Where necessary, the visibility of very narrow rings was increased by using a razor blade and white chalk. The ages of trees and roots were determined by counting the number of annual growth rings under a binocular microscope. To avoid mistakes related to missing or partial rings, cross-dating was done using skeleton plots and pointer years such as frost marks, light rings, compression wood, and narrow or wide rings (Schweingruber, 1988). For the 17 years, we found 7 pointer years (essentially frost marks).

To determine the location of the root collar (root/shoot interface), stumps were cut into very thin cross-sections (2–3 mm thick), using a band saw. The root collar was identified as the shift from the presence of a pith to a central vascular cylinder (DesRochers and Gagnon, 1997). The distance between the root collar and soil level (identified in the field with tape) was defined as organic matter accumulation since the year of planting, 1993. For deeply planted trees, this value thus also included 10–12 cm of mineral soil. Roots that were located above the root collar were labelled as adventitious roots, while roots that were located below the root collar were labelled as initial roots. Some of the trees that were excavated were older or younger than the plantation age; these individuals were probably of natural origin and were thus excluded from the analysis. A total of 16 black (9 planted at ground level and 7 deeply planted) and 19 white (10 planted at ground level and 9 deeply planted) spruces were used for statistical analysis.

2.4. Statistical analysis

Statistical analyses were performed in R v. 2.7.2 (R Development Core Team, 2008), and a significance level of $\alpha = 0.05$ was chosen for all response variables. Data from excavated trees ($N = 35$) were first used to determine the effects of planting depth

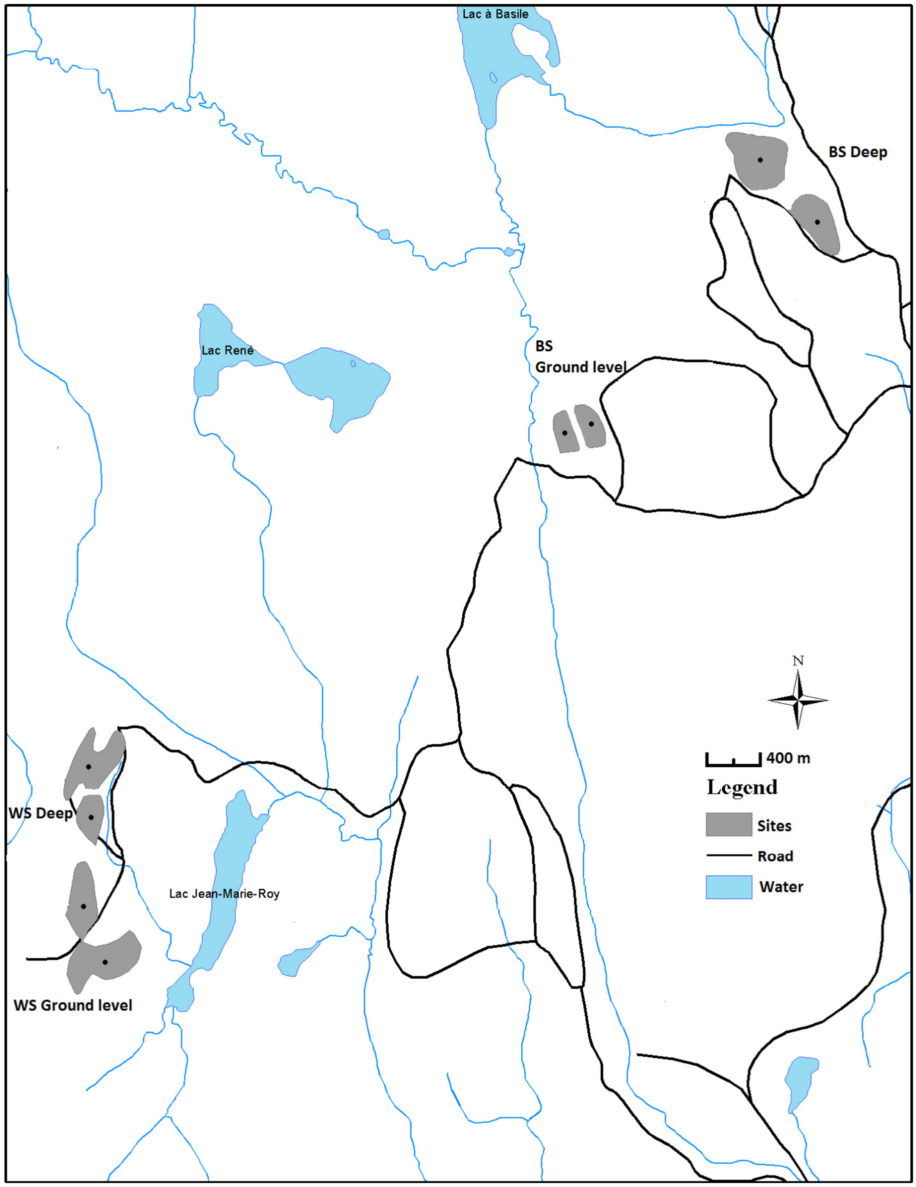

Fig. 1. Map of excavated sites. Four sites were planted with black spruce (BS) and 4 sites with white spruce trees (WS). For each species, two sites were planted at ground level and the other two at 10–12 cm deep.

Table 1
Ground cover of the 8 excavated sites planted at ground level and deeply planted (10–12 cm).

	White spruce		Black spruce	
	Ground level	Deep	Ground level	Deep
Replicate 1	Lichen/mosses	Lichen	Mosses/small patch of lichen	Mosses
Replicate 2	Lichen/mosses	Lichen/small patch of mosses	Mosses/small patch of lichen	Mosses

Table 2
Average tree height and basal diameter of trees planted at ground level and at 10–12 cm (deep). Standard errors of the mean are in parentheses.

	White spruce		Black spruce	
	Ground	Deep	Ground	Deep
All trees (N = 333)				
Tree height (m)	0.79 (0.05)	1.07 (0.12)	1.63 (0.12)	1.62 (0.10)
Diameter at base (mm)	17.36 (0.50)	22.73 (1.17)	28.96 (1.25)	30.68 (2.89)

on root number, root cross-sectional area at the stump, rooting depth, timing of adventitious root formation and organic matter accumulation. We also separated roots in two size classes: lower or greater than 2 mm in diameter. Data from excavated trees ($N = 35$) were then used to determine the effects of root characteristics (number and root cross-sectional area at the stump) on tree height (m) and basal diameter (mm). To focus on the effect of planting depth and given the low number of excavated trees per replicate (i.e., 3–5), separate models were created for black spruce ($N = 16$) and white spruce ($N = 19$). When response variables were: (1) discrete (root number, root cross-sectional area and timing of adventitious root formation), we applied Poisson regression using the *glmer* function of the *lme4* library (Bates and Maechler, 2009); (2) continuous (rooting distance, tree height and basal diameter), we used the *lme* function of the *nlme* library (Pinheiro et al., 2008). Unlike traditional analysis of variance (ANOVA), *glmer* and *lme* function (linear mixed models) incorporate both fixed and random effects parameters (West et al., 2007). It allows for testing the response variables by incorporating tree- and site-level variability as random effects (Hurlbert, 1984). Sites were considered as random effects in all statistical models. Depth of planting was used as categorical factor (A = ground level; B = 10–12 cm). When explanatory variables were highly correlated, several global models were done and compared based on the second-order Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002) using the *aictab* function of the *AICcmodavg* library (Mazerolle, 2006). Models with low ΔAICc and high Akaike weights (ωi, interpreted as probabilities) were considered to have the greatest statistical support (Lynch and Ritland, 1999). Multimodel inference that was based on AICc was performed using the *modavg.mer* function and predictions were obtained with the *modavgpred.mer* function of the *AICcmodavg* library (Mazerolle, 2006). A log-transformation (base 10) was applied to tree height and basal diameter.

In parallel with linear mixed models, we created distance (0_30 mm, 31_60 mm, 61_90 mm, 91_120 mm, > 120 mm) and age (0_3 years, 4_7 years, 8_11 years, >11 years) classes for adventitious rooting distance and time needed for adventitious root production. To determine if observed frequencies within each class were affected by planting depth, we tested sampling distribution using χ^2 analyses.

3. Results

3.1. Number of roots and root surface area

The nineteen excavated white spruce trees produced on average 19.69 roots per tree (SE = 1.44) of which 11.08 (SE = 1.08) were adventitious. Average proportion of adventitious roots per white spruce tree was 53.7%. All white spruce produced adventitious roots. Black spruce trees produced on average 18.65 roots per tree (SE = 2.57) of which 12.01 (SE = 2.14) were adventitious. Average proportion of adventitious roots per black spruce tree was 56.8%. Only one black spruce did not produce adventitious roots.

On average, white spruce planted at ground level formed the same proportion of adventitious roots and a similar number of roots (total and adventitious) as did deeply planted trees ($P > 0.05$; Table 3 and Fig. 2a). Further, planting depth had no effect on the number of roots when they were separated into size classes (large or small; $P > 0.05$; Table 3 and Fig. 2b). Black spruce trees also developed the same proportion of adventitious roots and the same number of roots (total and adventitious) for both planting depths ($P > 0.05$; Table 3 and Fig. 2d). When considering large roots only (>2 mm diameter), the proportion of large adventitious roots

Table 3
Results of mixed-models testing the effect of planting depth on the number of roots and root area (total and adventitious), on adventitious rooting distance from the root collar (maximum and mean), and on the year of adventitious root formation. Statistically significant values ($P < 0.05$) are given in bold.

Model	Factors White spruce	Estimate	Standard error	*P*-value	Estimate Black spruce	Standard error	*P*-value
Total root number	Intercept	2.92	0.07	<0.001	2.77	0.17	<0.001
	epthB	0.10	0.10	0.336	0.29	0.22	0.181
Number of adv roots	Intercept	2.36	0.10	<0.001	2.26	0.21	<0.001
	DepthB	0.11	0.14	0.443	0.04	0.26	0.175
Proportion of adventitious roots	Intercept	−0.56	0.10	<0.001	−0.50	0.11	<0.001
	DepthB	0.01	0.14	0.969	0.07	0.15	0.631
Total large root number	Intercept	2.28	0.10	<0.001	2.46	0.10	<0.001
	DepthB	0.21	0.14	0.128	0.39	0.13	**0.003**
Number of large adv roots	Intercept	1.76	0.13	<0.001	1.86	0.13	<0.001
	DepthB	0.20	0.18	0.261	0.61	0.17	**<0.001**
Proportion of large adv roots	Intercept	−1.17	0.15	<0.001	−0.91	0.13	<0.001
	DepthB	0.10	0.21	0.622	0.33	0.17	0.053
Total small root number	Intercept	2.17	0.12	<0.001	1.45	1.05	0.168
	DepthB	−0.04	0.18	0.834	−0.61	1.32	0.641
Number of small adv roots	Intercept	1.57	0.14	<0.001	1.15	0.89	0.194
	DepthB	−0.03	0.21	0.894	−0.89	1.14	0.434
Proportion of small adv roots	Intercept	−1.35	0.14	<0.001	−1.62	0.57	0.004
	DepthB	−0.13	0.21	0.544	−1.05	0.75	0.163
Adv root area	Intercept	5.51	0.14	<0.001	6.26	0.33	<0.001
	DepthB	0.40	0.20	**0.050**	0.79	0.41	0.053
Total root area	Intercept	6.05	0.06	<0.001	6.64	0.30	<0.001
	DepthB	0.48	0.09	**<0.001**	0.65	0.37	0.084
Maximum rooting distance	Intercept	96.26	11.54	<0.001	66.85	15.33	<0.001
	DepthB	36.06	16.50	0.161	103.53	23.17	0.140
Rooting distance	Intercept	51.68	5.52	<0.001	48.15	9.16	<0.001
	DepthB	12.27	8.11	0.270	59.68	13.11	**0.045**
Year of root formation	Intercept	1.71	0.10	<0.001	1.70	0.17	<0.001
	DepthB	−0.04	0.08	0.573	−0.15	0.08	**0.042**
Organic matter accumulation	Intercept	171.32	15.33	<0.001	130.81	14.34	<0.001
	DepthB	44.98	21.86	0.176	139.11	21.68	0.098

Note: DepthB is planting between 10 and 12 cm.

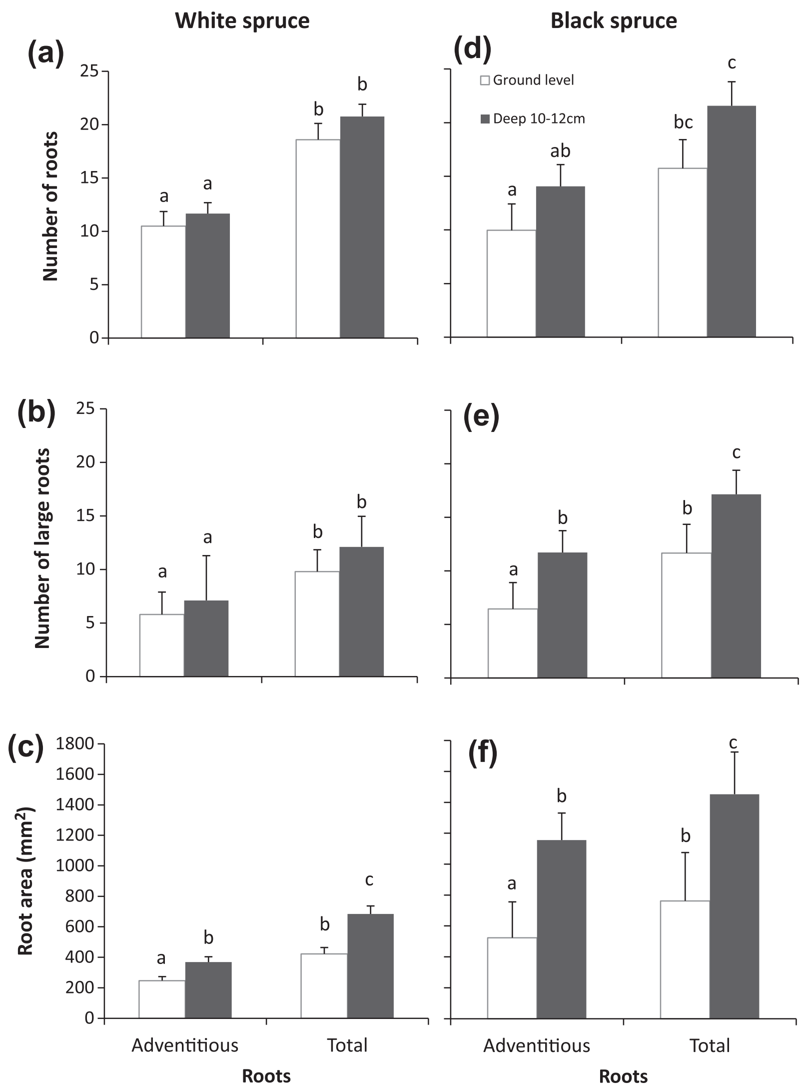

Fig. 2. Mean root cross-sectional area and number of total and adventitious roots of excavated (a–c) white spruce and (d–f) black spruce trees. Within a graph, bars with the same letter indicate a non-significant difference (Tukey's test at $P \leqslant 0.05$). Large roots have diameters >2 mm.

per tree ($P = 0.053$; Table 3 and Fig. 2e) and the number of total and adventitious roots increased with planting depth ($P < 0.05$; Table 3 and Fig. 2e). The number and proportion of small-diameter roots (<2 mm) did not change with planting depth ($P > 0.05$; Table 3).

Total root cross-sectional area at the stump in white spruce trees ranged from 267 to 1156 mm^2 (mean ± SE: 553.27 mm^2 ± 33.92), while from adventitious roots ranged from 214 to 342 mm^2 (mean ± SE: 307.73 mm^2 ± 44.12). Both total root cross-sectional area and the area of adventitious roots were smaller for ground level-planted white spruce trees than for deeply planted white spruce trees ($P \leqslant 0.05$, Table 3 and Fig. 2c). Total root cross-sectional area for black spruce trees ranged from 230 to 2892 mm^2 (mean ± SE: 1107.55 mm^2 ± 272.42), while the area of adventitious roots ranged 119–2640 mm^2 (mean ± SE: 839.90 mm^2 ± 224.01). Root cross-sectional area (total and adventitious) was marginally greater in deeply planted black spruce trees compared to ground level-planted trees ($P = 0.053$ for area of adventitious roots, and $P = 0.084$ for total root cross-sectional area; Table 3 and Fig. 2f).

3.2. Organic matter accumulation, rooting depth and timing of adventitious root development

When using the distance between the root collar and the current level of organic matter, organic matter accumulation averaged 17.13 cm (SE = 0.74) for white spruce and 13.08 cm (SE = 1.71) for black spruce sites planted at ground level. In deep plantations, organic matter accumulation averaged 21.46 cm (SE = 1.10) for white spruce and 26.99 cm (SE = 1.08) for black spruce sites. In white spruce sites, organic matter accumulation was not influenced by planting depth ($P = 0.176$; Table 3) while deeply planted black spruce, sites showed marginally higher organic matter accumulation ($P = 0.098$; Table 3). Maximum distance of adventitious roots above the root collar was 12.16 and 14.54 cm, respectively, for white and black spruce trees that had been planted at ground level, and 14.00 and 21.60 cm for deeply planted white and black spruce trees, respectively. Maximum rooting depth of adventitious roots above the root collar was not influenced by planting depth for either species ($P > 0.05$; Table 3). For trees planted at ground level, mean adventitious rooting distance above the root collar was 4.98 cm in white spruce and 5.18 cm in black spruce. For deeply planted trees, mean distance of adventitious roots above the root collar was 6.71 cm in white spruce and 11.17 cm in black spruce. Planting depth did not affect mean rooting distance above the root collar of adventitious roots in white spruce ($P > 0.05$; Table 3), while adventitious roots of black spruce trees that had been planted at ground level were produced closer to the root collar (smaller rooting distance) compared to trees that were planted deeply ($P = 0.045$; Table 3). For both species, χ^2 tests showed that root distribution along base of the stem was influenced by planting depth ($P < 0.001$ for both species; Fig. 3a and b); When trees were planted at ground level, the majority of adventitious roots (32% and 44% for white and black spruce, respectively) formed just above (0–3 cm) the root collar, with the number of adventitious roots then decreasing with distance from the root collar (Fig. 3a and b). For deeply planted white spruce, most of adventitious roots were found between 3 and 6 cm (Fig. 3a), while the majority of adventitious roots were located more than 12 cm above the root collar in black spruce (Fig. 3b).

In black spruce trees, adventitious root formation occurred 6.21 years after planting (SE = 0.44) for trees planted at ground level and 5.61 years after planting (SE = 0.46) for deeply planted trees. In white spruce trees, adventitious root formation occurred 5.45 and 5.54 years after planting (SE = 0.43 and 0.39) for trees planted at ground level and at 10–12 cm, respectively. Linear mixed models showed that there was no effect of planting depth on year of adventitious formation for white spruce trees ($P > 0.05$; Table 3) but black spruce trees planted at ground level formed adventitious roots later than deeply planted black spruce ($P = 0.04$; Table 3). The χ^2 analyses also found an effect in black ($P < 0.001$) but not in white ($P = 0.21$) spruce. The χ^2 analysis revealed differences between the timing of adventitious root formation, which began just after planting in white and black spruce (0–3 years after planting; Fig. 3c and d). In white spruce, adventitious root formation decreased with time (Fig. 3c). Although adventitious root formation also decreased with time in black spruce that had been planted at ground level, there were still adventitious roots forming at the time of excavation (Fig. 3d). For deeply planted black spruce trees, most adventitious roots formed during the first few years (Fig. 3d).

3.3. Effect of species, planting depth, and root system on tree growth

Height of trees that were planted at ground level averaged 1.02 and 1.52 m for white and black spruce, respectively. Basal diameter for trees planted at ground level was 23.44 mm for white spruce and 33.51 for black spruce. For deeply planted trees, mean tree height was 1.31 m for white spruce and 2.09 m for black spruce trees, while basal diameter averaged 28.04 and 33.36 for white and black spruce, respectively. AICc analyses revealed that only two models explained white spruce height: the model including planting depth ($\Delta AIC = 0$ and $\omega i = 0.51$; Table 4), and the model including total root cross-sectional area ($\Delta AIC = 0.75$ and $\omega i = 0.35$; Table 4). According to multimodel inference, white spruce height increased with total root cross-sectional area and planting depth (Table 5 and Fig. 4a). Three models explained white spruce basal diameter (Table 4), but the best supported model only contained total root cross-sectional area ($\Delta AIC = 0$ and $\omega i = 0.64$; Table 4). Even if the model with planting depth was not amongst the three models showing support, multimodel inference showed that white spruce diameter increased not only with total root cross-sectional area, but also with planting depth (Table 5 and Fig. 4b).

There were three models explaining black spruce height, but the model including depth of planting had the most support ($\Delta AIC = 0$ and $\omega i = 0.6$; Table 4). Multimodel inference revealed that black spruce height significantly increased with planting depth and was marginally affected by the total number of roots (Table 5 and Fig. 5). AIC and multimodel inference showed that black spruce basal diameter was not influenced by any factor that was tested (Tables 4 and 5). Further, trees planted at ground level had the same diameter as those that were deeply planted (Table 5).

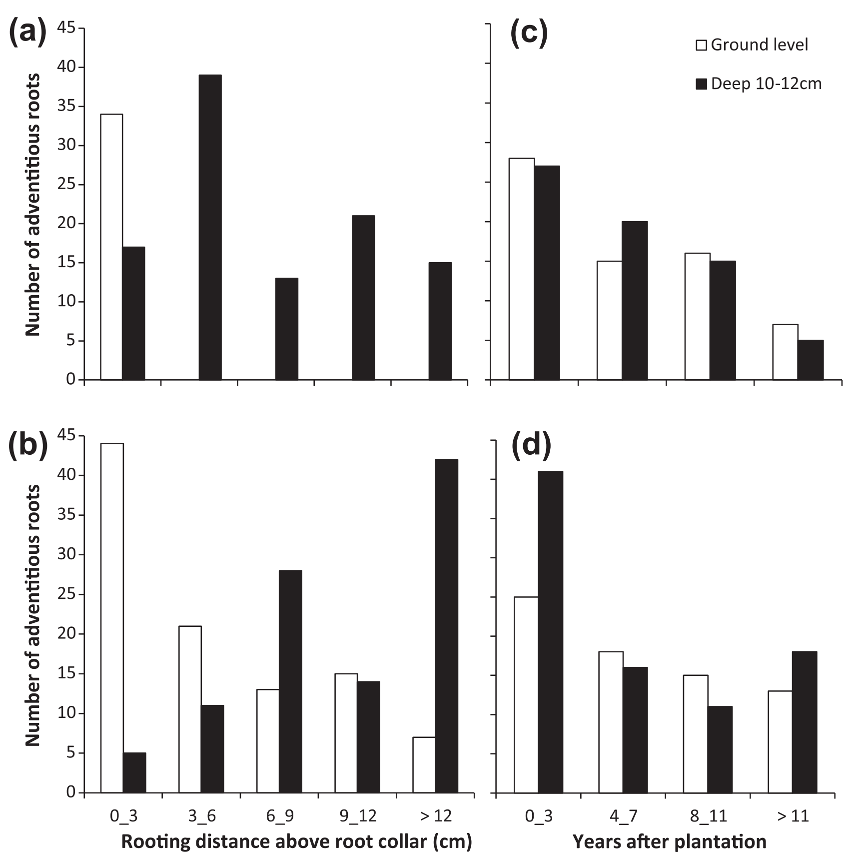

Fig. 3. Total number of adventitious roots formed per tree in each distance class from the root collar and according to time since planting for (a and c) white spruce and (b and d) black spruce trees.

Table 4
Model selection according to results of the Akaike Information Criterion (AICc). HEIGHT and DIAMETER models (lme) were respectively the models relating tree height and diameter at base to depth of planting, root area (total and adventitious), and number of roots (total and adventitious). Model selection was done separately for white spruce and black spruce.

Factors tested	ΔAIC	ωi
White spruce		
HEIGHT		
Depth	0	0.51
tot_root_area	0.75	0.35
tot_root_numb + tot_root_area	4.47	0.05
adv_root_numb + tot_root_area	4.49	0.05
adv_root_numb	7.79	0.01
tot_root_numb	8.50	0.01
tot_root_numb + tot_root_area + tot_root_numb:tot_root_area	8.86	0.01
adv_root_numb + tot_root_area + adv_root_numb:tot_root_area	8.88	0.01
adv_root_area	9.34	0
DIAMETER		
tot_root_area	0	0.64
tot_root_numb + tot_root_area	3.11	0.14
adv_root_numb + tot_root_area	3.70	0.10
adv_root_numb + tot_root_area + adv_root_numb:tot_root_area	5.13	0.05
Depth	5.2	0.05
tot_root_numb + tot_root_area + tot_root_numb:tot_root_area	6.38	0.03
adv_root_numb	12.55	0
tot_root_numb	13.52	0
adv_root_area	13.59	0
Black spruce		
HEIGHT		
Depth	0	0.6
tot_root_numb	2.30	0.19
adv_root_numb	3.57	0.10
tot_root_area	5.01	0.05
adv_root_area	5.46	0.04
adv_root_numb + adv_root_area	7.66	0.01
adv_root_numb + adv_root_area + adv_root_numb : adv_root_area	12.42	0
DIAMETER		
adv_root_numb	0	0.26
tot_root_area	0.60	0.20
Depth	0.78	0.18
tot_root_numb	0.96	0.16
adv_root_area	1.26	0.14
adv_root_numb + adv_root_area + adv_root_numb : adv_root_area	4.27	0.03
adv_root_numb + adv_root_area	4.28	0.03

Notes: tot_root_area is total root cross-sectional area; adv_root_area is the adventitious root cross-sectional area of; tot_root_numb is the total root number and adv_root_numb is the number of adventitious roots.

Table 5
Multimodel inference based on AIC for models testing the effect of planting depth, root area (total and adventitious), and number of roots (total and adventitious) on tree height (HEIGHT) and basal diameter (DIAMETER). Estimated values, standard errors, and 95% confidence interval are given for each factor tested. Statistically significant values (when 0 was excluded from the confidence interval) are given in bold.

Factors tested	Model average estimate		Standard error		95% confidence interval	
	HEIGHT	DIAMETER	HEIGHT	DIAMETER	HEIGHT	DIAMETER
White spruce						
DepthB	0.28	0.22	0.05	0.06	**0.18/0.37**	**0.11/0.33**
Adv_root_numb	−0.01	0.01	0.04	0.04	−0.09/0.07	−0.07/0.09
Tot_root_numb	−0.02	0.06	0.07	0.07	−0.15/0.11	−0.08/0.19
Adv_root_area	−0.01	0.003	0.06	0.07	−0.13/0.11	−0.14/0.14
Tot_root_area	0.24	0.33	0.07	0.07	**0.1/0.39**	**0.2/0.46**
Black spruce						
DepthB	0.26	0.05	0.06	0.06	**0.15/0.37**	−0.08/0.17
Adv_root_numb	0.05	−0.05	0.04	0.04	−0.02/0.12	−0.12/0.03
Tot_root_numb	0.12	−0.04	0.06	0.07	0/0.25*	−0.19/0.1
Adv_root_area	0.01	0.01	0.05	0.04	−0.09/0.09	−0.08/0.09
Tot_root_area	−0.04	0.04	0.05	0.05	−0.15/0.06	−0.05/0.13

Note: DepthB is planting between 10 and 12 cm.
* Means statistically significant at 90% confidence interval.

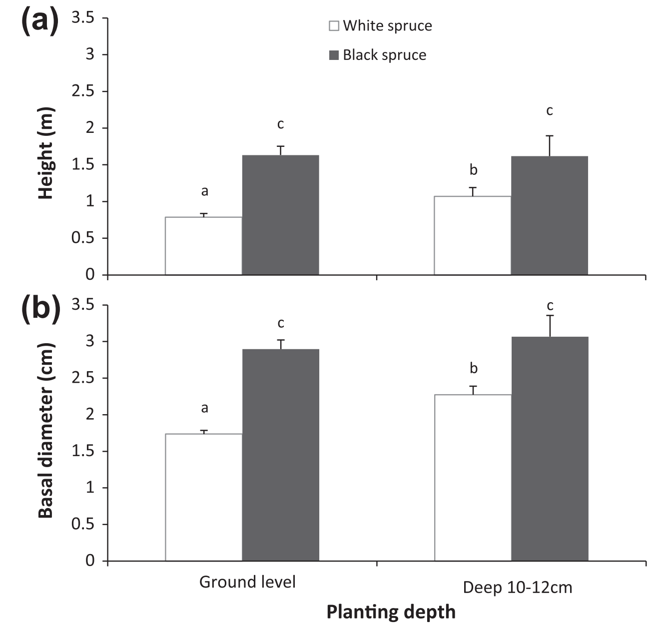

Fig. 4. Relationships between white spruce (a) tree height and (b) basal diameter and total root area and planting depth (ground level and 10–12 cm).

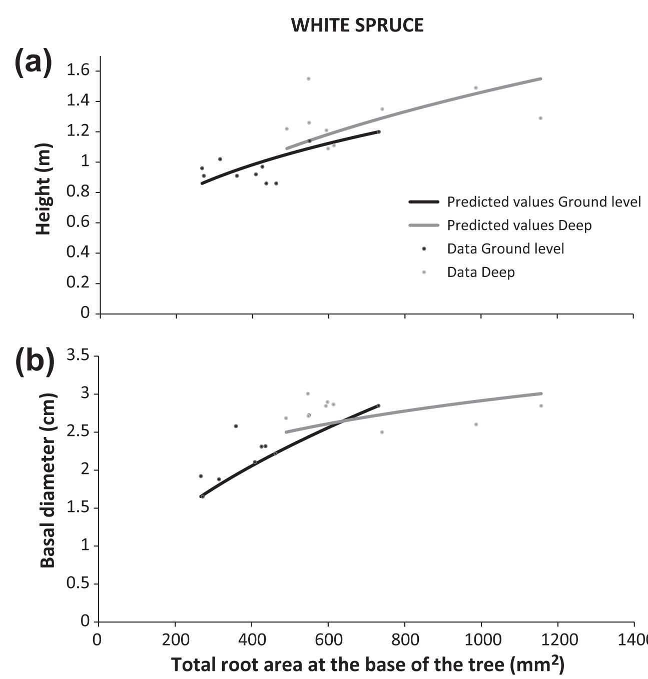

Fig. 5. Black spruce tree height according to total number of roots for ground level and deeply (10–12 cm) planted trees.

4. Discussion

Our study showed that more than half of the roots produced in white and black spruce trees were adventitious, 17 years after planting. The proportion of adventitious roots increased with burial of the stem at planting for black spruce trees but not necessarily for white spruce trees. In the two species, adventitious root production began the same year that the trees were planted, demonstrating the high capacity of both species for producing adventitious roots, regardless of planting depth. Johnston (1970) suggested that the success of black spruce establishment required the development of an adventitious root system within the ground surface carpet of living mosses. With time, boreal forests tend to develop thick forest floors that are composed of poorly decomposed and accumulating litter (Fenton et al., 2005). Adventitious root production is thus a key process for tree survival in the face of increasing organic matter accumulation and high water contents (LeBarron, 1945). Because of their position in the uppermost part of the soil profile, adventitious roots have a better access to oxygen (LeBarron, 1945; Maun, 1998; Dech and Maun, 2006) and generally grow larger with tree development than do the initial roots (Coutts et al., 1990). In black spruce, the initial root system (below the root collar) can even be atrophied and largely abandoned to the benefit of adventitious roots as the trees mature (DesRochers and Gagnon, 1997; Krause and Morin, 2005). We also found that root cross-sectional area at the stump, together with the number of large roots, increased with planting depth. Deeper planting should thus increase tree resistance to windthrow (Coder, 2010), especially for these species, which are characterised by shallow, spreading root systems with no definite tap roots (LeBarron, 1945; Farrar, 1995).

For white spruce, adventitious root formation was not related to planting depth. Our results showed that the distance between the root collar and the actual ground level was the same for trees planted at ground (12 cm) and deeply planted trees (14 cm; $P = 0.05$). While the other sites were dominated by mosses, these sites were mostly covered by lichen, which is known for its lower rate of organic matter accumulation (Sedia and Ehrenfeld, 2005). Compared to white spruce, deeply planted black spruce exhibited a much greater distance between the root collar and the appearance of upper adventitious roots (12 cm vs 3–6 cm for black and white spruce, respectively). Deeply planted white spruce sites appeared to have had much less organic matter accumulation over time, complicating the results.

Planting depth positively influenced the growth of planted trees, especially for white spruce, which attained greater height and basal diameter when deeply planted compared to ground-level planting. In black spruce, only tree height was positively affected by planting depth. These results contrast with studies on boreal forest (Whaley et al., 1995; Beyeler, 1996; Paquette et al., 2011) who found negative or no effect of planting depth on tree growth. In costal dunes, Dech and Maun (2006) even concluded that white spruce was not tolerant of burial since they found a decrease in white spruce biomass with burial and no adventitious root production. Perhaps their study was done too soon after planting (one year after planting), considering that we found that adventitious roots developed on average 6 years after planting. Furthermore, the base of the stem must experience humid conditions to develop adventitious roots (Aubin, 1996). In consequence, it is not surprising that we found more adventitious roots than studies in coastal or dune environments. Interestingly, while white spruce is known to grow faster than black spruce, black spruce trees always had larger diameters and heights than white spruce trees in our study. We think this is probably an artefact attributable to the fact that white spruce sites were placed on poorer sites (i.e., lichen-dominated). In comparing several species, Dech and Maun (2006) suggested that differences in species responses to burial were determined by two adaptive traits: the ability to form adventitious roots, and plasticity of biomass allocation. Buried trees usually shift resources from roots to shoots in order to maintain viable source/sink ratios (Brown, 1997; Burylo et al., 2012). Both studied species were able to produce adventitious roots and increase vertical growth in response to burial. As we did not excavate the entire root systems of the individual trees, it was not possible to study root and shoot biomass allocation. However, our results suggest greater allocation by black spruce to its root system, given that its adventitious roots were larger and more numerous than those of white spruce, perhaps to the detriment of stem diameter growth. Black spruce is generally more shallowly rooted than white spruce (Farrar, 1995) and, consequently, the development of a solid adventitious root system would be more important in the former compared to the latter species.

In white spruce, tree height and basal diameter were not influenced by the mean root cross-sectional area of adventitious roots, but rather by the total root cross-sectional area (adventitious and initial roots). Similarly, black spruce height increased with the total number of roots, and not only with the number of adventitious roots, showing that both adventitious and initial roots are important for initial growth of black spruce, and white spruce, as well. In the soils that we studied, with thick mats of mosses or lichen, nutrients concentrations are usually greater in lower parts of the soil profile, which are more decomposed (Fenton et al., 2005) and occupied by initial roots.

5. Conclusions

Deep planting was beneficial to both species, and both species demonstrated the ability to produce adventitious roots quickly after planting. The size of adventitious roots increased in response to burial of the stem, but planting depth influenced the rooting responses of black spruce more strongly than those of white spruce seedlings. The number of adventitious roots increased in deeply planted black spruce but not in white spruce trees, possibly because site conditions for the latter were less conducive to adventitious root formation. Even if rooting responses of white spruce were similar at both planting depths, growth of deeply planted black and white spruce trees was greater to growth of trees planted at ground level. Effects of planting depth on tree growth were stronger in white spruce than in black spruce, since both tree height and basal diameter increased following planting. Only tree height was improved by burial in black spruce plantations. For species producing adventitious roots such as *Taxus canadensis*, *Thuja occidentalis*, *Juniperus virginiana*, *Juniperus horizontalis*, *Abies balsamea*, *Picea sitchensis*, *Picea abies*, *Larix laricina*, *Pinus strobus*, *Tsuga mertensiana and Tsuga heterophylla* (Bannan, 1942) burying the stem base could be a silvicultural practice that should be encouraged. It may help us better understand the development of adventitious roots and their influence on tree growth and establishment success in artificially regenerated stands.

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