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Soil organic layer thickness influences the establishment and growth of trembling aspen (*Populus tremuloides*) in boreal forests

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ABSTRACT

In the North American boreal forest, the presence of aspen (*Populus tremuloides* Michx.) is thought to be constrained on sites where thick (>25 cm) soil organic layers (SOL) prevail. Aspen can reproduce both by seeds and suckers, but it is still unknown how SOL thickness influences both modes of reproduction. In this study, we sought to determine how SOL thickness and chemistry in black spruce dominated stands influences aspen regeneration and growth. Aspen abundance was negatively related to SOL thickness and logistic regression indicated that the probability to detect an aspen declined from 30% at SOL = 0 cm to 10% at 30 cm. Our results also indicated that aspen diameter at breast height was significantly negatively correlated with SOL thickness and black spruce abundance, and positively correlated with soil N_{tot}, Ca, CEC and pH. Finally, we failed to detect any significant effect of SOL on aspen mode of regeneration (i.e. seeds or suckers). Our study shows that through changes in physical and chemical soil properties, SOL accumulation equally hinders both aspen seedling germination and growth, and sucker development.

1. Introduction

Along with black spruce (*Picea mariana* [Mill.] BSP), aspen (*Populus tremuloides* Michx.) is the most widely distributed tree in North America (Burns and Honkala, 1990). From east to west, its distribution range (ca. 7×10^6 km^2) stretches from Newfoundland to Alaska and, from north to south, from the Beaufort Sea to northern Mexico. It grows on a wide variety of soils ranging from shallow to deep loamy sands and heavy clay, and occasionally occurs on organic soils (Burns and Honkala, 1990). In North America, the boreal zone covers approximately 6.3×10^6 km^2 (Brandt, 2009), and almost entirely overlaps the distribution range of both black spruce and aspen. Approximately 10% (i.e. 650000 km^2) of the North American boreal zone is covered with forests growing on organic deposits (Lavoie et al., 2005). These so-called forested peatlands are mainly located in Alaska, Minnesota and the Clay Belt region of eastern Canada.

In the Clay Belt region (which covers approximately 125000 km^2 and is entirely located within the distribution range of aspen), aspen and black spruce often grow in association, and the thickness of the soil organic layer (SOL) is thought to be an important determinant of the relative importance of the two species on a given site, especially if the organic layer is mainly comprised of *Sphagnum* spp. While black spruce can grow over a broad gradient of SOL thickness, the presence of aspen is thought to be limited on sites with a thin (<30 cm) SOL (Gewehr et al., 2014). Black spruce is a low nutrient-demanding species and tends to dominate low-fertility sites (Laflèche, 2013). It produces a litter that decomposes slowly (Laganière et al., 2010) and that contributes to the accumulation of organic matter and SOL thickening (Laganière et al., 2011). In contrast, aspen is a high nutrient-demanding species which thrives on high-fertility sites (Alban, 1982; Paré et al., 2001; Grigal, 2009; Pinno et al., 2010). It is known to produce a litter that decomposes rapidly, thereby accelerating nutrient cycling, and increasing soil nutrient availability (Paré and Bergeron, 1996; Légaré et al., 2005) and stand productivity Légaré et al. (2004). As such, the presence of aspen slows the accumulation of organic matter and constrains SOL development (Légaré et al., 2005). The establishment of aspen on a given site may therefore help control SOL thickness and create soil conditions that favor its establishment, growth, reproduction and, thereby, promote its presence in the long-term.

Furthermore, aspen reproduces both sexually (seeds) and asexually (suckers). Despite high seed production and high germinative capacity (>95%; McDonough, 1985; Burns and Honkala, 1990), aspen reproduction by seeds is known to be limited by short period

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of seed viability, unfavorable moisture during seed dispersal, high soil surface temperatures and fungi (Meyer and Fechner, 1980; Côté et Blanchette, 2013). Suckering, which is stimulated by stem and root disturbance, for instance by harvest or fire (Burns and Honkala, 1990; Lavertu et al., 1994), is mainly limited by low temperature, excess moisture and severe drought (Burns and Honkala, 1990; Frey et al., 2003). Throughout the range of the species, suckering is much more frequent than reproduction by seed (Côté and Blanchette, 2013). Although much information is available on the conditions favoring aspen reproduction both by seeds and suckers, to our knowledge there is no such information on how SOL thickness influences both modes of reproduction.

In a recent paper, Gewehr et al. (2014) suggested that at the landscape level aspen distribution was limited on sites where SOL thickness was <30 cm due to changes in soil properties associated with water table located above the mineral soil surface. However, these authors also acknowledged that the observed relationship between SOL thickness and aspen distribution might have also reflected the negative effect of aspen litter on the accumulation of organic matter. In this context, the objective of this study was to determine at the tree level how aspen regeneration and growth is related to SOL thickness. First, we sought to (i) determine if aspen establishment was impeded by the thickness of SOL and (ii) and how SOL thickness influenced aspen growth. More specifically, we sought to identify a threshold SOL thickness above which aspen establishment and growth would be drastically reduced. Then, because the presence of black spruce may have both direct (by increasing SOL thickness) and indirect (by favoring the presence of *Sphagnum* which creates soil conditions detrimental to aspen) effects on aspen, we sought to established relationships between aspen growth and black spruce abundance and soil chemistry. Finally, we sought to determine if SOL thickness had an effect on the mode of reproduction (seeds vs. suckers) of aspen.

2. Methods

2.1. Study area

This study was conducted in three black spruce stands initiated in 1997 following fire. The study area is located north of the Clay Belt region of northwestern Quebec (49°46′30″N, 79°01′40″W), and is part of the western black spruce–feathermoss bioclimatic domain (Bergeron et al., 1999). More specifically, the stands were located on the Cochrane till, a compact till made up of a mixture of clay and gravel, created by a southward ice flow approximately 8000 years BP (Veillette, 1994). Prior to fire, the tree layer of the sampling sites was dominated by black spruce and established on thick organic deposits (>30 cm) with hydrous drainage (Bergeron et al., 1999). Labrador tea (*Rhododendron groenlandicum* Oeder) and sheep laurel (*Kalmia angustifolia* L.) dominated the shrub cover, whereas *Sphagnum* spp. and feathermosses (mainly *Pleurozium Schreberi* [Brid] Mitt.) dominated the forest floor.

From 1981 to 2010, average annual temperature was 0.0 °C and average annual precipitation was 909 mm, with 30% falling during the growing season (Joutel weather station; Environment Canada, 2014). The average number of degree-days (>5 °C) was 1240, and the frost-free season was about 80 days, with frost occasionally occurring during the growing season.

2.2. Experimental design and sampling

Data collection was initiated in September 2012 with the establishment of 20 50-m long and 4-m wide transects evenly distributed across the three stands. Stand were at least 2 km apart, and, within stands, transects were located at a minimum distance of 100 m from each other. Along these transects, we measured the thickness of the soil organic layer (SOL) every 2 m for a total of 25 locations along each transect (total of 500 sampling points). Centered on these sampling points, we installed a circular sampling plot (2 m radius; 12.5 m^2) in which we tallied aspen and black spruce. On each tallied aspen, we measured diameter at breast height (DBH). Then, along each transect we collected the organic layer (at a depth of 10–30 cm, i.e. where the bulk of the roots were located) at three randomly chosen locations for nutrient analysis.

In October 2012, we excavated the stump and root system of 7 randomly chosen aspens along nine randomly (three in each stand) chosen transects (total of 63 root systems). The collected stumps and root systems were used to determine whether the trees originated from seeds or suckers. More precisely, the stem was first cut at the level of the root collar. Then, the roots of each sampled tree were exposed to a depth of about 30 cm below the root collar. Roots were then cut off, leaving 2 cm of roots attached to the stump. Stumps were transported to the laboratory where they were air dried for 2 months. Cross sections of the root collar and the larger root were then sanded with progressively finer grades of sandpaper, ending with 600 grit, so rings could be seen clearly. Ring width and number were recorded along two radii, both at the root collar and the larger root, using a Velmex micrometer to a precision of 0.0001 mm. Since parent roots are older than trees of sucker origin, trees with roots older than the root collar were considered suckers; otherwise they were considered to originate from seeds. On the sampled trees, we measured DBH, tallied black spruce in a 2 m-radius, and measured the thickness of the organic layer at the base of the tree.

Browsing is known to influence the growth performance of aspen (Kaye et al., 2005). In our study area, the moose (*Alces alces*) and the woodland caribou (*Rangifer tarandus caribou*) are the two most important browsers of aspen. The most recent aerial surveys conducted in our study area established that moose density was 1.67 moose 10 km^{-2} (Lamontagne et Lefort, 2004) and woodland caribou density was 2.0 caribous 100 km^{-2} (Rudolph et al., 2012). Therefore, we considered that the influence of browsing on aspen growth was negligible in our study area and did not take its effect in the analyses.

2.3. Soil analyses

Following sampling, organic soil samples were air-dried for 48 h, returned to the laboratory and frozen. Immediately prior to analysis, all samples were air-dried at 30 °C for 48 h, pooled among transects and ground to pass through 6-mm sieves. Substrate pH was analyzed in distilled water (Carter, 1993). Total C and N were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation, St. Joseph, MI). Extractable inorganic P was determined by the Bray II method (Bray and Kurtz, 1945), and exchangeable Ca and other cations were extracted using unbuffered 0.1 M $BaCl_2$ and determined by atomic absorption (Hendershot and Duquette, 1986).

2.4. Data analysis

The effect of SOL thickness and black spruce abundance on aspen abundance and growth (DBH) were explored by using various linear regression models. Identification of SOL thickness threshold was facilitated by segmented regression. The distribution of aspen occurrence (presence/absence data) was analyzed by logistic regression.

Then, we performed principal components analysis (PCA) in order to explore the relationships among soil physico-chemical properties, black spruce abundance, and aspen DBH. To support

PCA, Pearson correlations were used to determine the strength of the relationships between aspen DBH, black spruce abundance and soil variables.

Finally, we used logistic regression to quantify the relationship between SOL thickness and aspen origin, i.e. seed or sucker. We also used one-way mixed-effect ANOVAs to test for the statistical significance of stem origin (i.e. seed vs. sucker) on aspen DBH and age, SOL thickness, and black spruce abundance. Stem origin was introduced into the models as a fixed effect, and transect and stand as random effects.

Regression analyses, Pearson correlations, and one-way ANOVA were performed using JMP 11 (SAS, 2012), and PCA was performed using Canoco v4.5 (ter Braak and Smilauer, 2002).

3. Results

3.1. Study sites characteristics

The twenty transects were relatively similar with respect to soil chemistry as revealed by overall narrow CVs (<25%, with the exception of Ca [CV = 45%] and P [CV = 34%]) (Table 1). Typical of peatland soils, mean total N, extractable P, exchangeable Ca, and pH were relatively low, whereas mean C:N was relatively high.

The thickness of the organic layer varied moderately (CV = 60%) among transects (Table 2), but its variability was larger within transect as revealed by wide CVs (mean CV = 70%, min. = 21%, max. = 122%).

Similarly, the number of aspen and black spruce varied widely both among transects (CV = 79% and 96%, respectively) (Table 2), whereas aspen DBH had narrower CV (65%).

3.2. Aspen establishment and SOL thickness

As revealed by Fig. 1, aspen abundance was negatively related to SOL thickness. Fig. 1a shows that >90% of the aspen sampled ($n = 300$) were established in microsites where SOL thickness was <20 cm. Similarly, using aspen number and mean SOL thickness for the twenty transects, Fig. 1b shows that at the site level aspen abundance was linearly negatively related to SOL thickness (red dashed line, $r^2 = 0.51$, $p = 0.0005$). A segmented regression (gray dashed line, $r^2 = 0.54$, $p = 0.0005$) performed on the same data set revealed a cut-off point near 25 cm, indicating that beyond this point the abundance of aspen decreases rapidly.

Table 2
Mean number of aspen and black spruce per sampling point, aspen diameter at breast height (DBH), and soil organic layer (SOL) thickness along the 20 transects.

Transect	Aspen		Number of black spruce[a]	SOL thickness (cm)
	Number[a]	DBH (cm)		
1	2.0 (1.0)	1.2 (0.3)	16.0 (0.0)	51.0 (10.7)
2	2.5 (1.3)	5.6 (1.5)	8.3 (5.2)	41.2 (18.6)
3	10.0 (5.6)	3.1 (2.7)	1.6 (0.9)	7.4 (9.1)
4	10.5 (5.9)	2.6 (3.2)	1.3 (0.9)	12.5 (13.3)
5	10.5 (5.9)	2.6 (1.6)	1.2 (1.5)	14.4 (11.5)
6	8.0 (4.5)	1.7 (1.5)	3.1 (1.7)	18.5 (13.7)
7	7.0 (3.9)	2.1 (2.8)	3.8 (1.9)	14.0 (9.7)
8	5.0 (2.7)	1.5 (0.6)	2.8 (2.0)	8.5 (6.0)
9	3.0 (1.6)	1.4 (1.0)	6.2 (5.7)	30.4 (28.7)
10	13.0 (7.4)	1.5 (1.7)	1.5 (1.1)	7.4 (6.5)
11	4.0 (2.2)	5.0 (4.1)	1.7 (0.7)	20.2 (16.9)
12	1.5 (0.7)	1.0 (0.0)	0.0 (0.0)	42.2 (30.4)
13	2.0 (1.0)	1.0 (0.0)	6.0 (6.0)	43.4 (28.5)
14	15.5 (8.8)	1.3 (1.3)	4.4 (2.8)	15.0 (7.2)
15	2.5 (1.3)	3.5 (2.8)	3.8 (2.4)	28.9 (12.8)
16	1.5 (0.7)	1.4 (0.6)	2.0 (0.0)	33.4 (30.5)
17	19.5 (11.1)	1.0 (0.0)	2.1 (0.8)	13.2 (9.2)
18	14.0 (7.9)	1.0 (0.0)	1.8 (0.7)	12.8 (7.4)
19	24.5 (14.0)	1.0 (0.0)	2.3 (0.6)	9.3 (2.3)
20	6.5 (3.6)	1.0 (0.0)	1.8 (0.4)	30.8 (30.8)
Mean	*13.4*	*2.0*	*2.6*	*22.7*
SD	*10.6*	*1.3*	*2.5*	*13.8*
CV (%)	*79.1*	*65.0*	*96.1*	*60.8*

[a] Number of aspen and spruce in a 2 m-diameter circular plot centered on SOL thickness sampling point ($n = 25$ per transect).

Then, using the 500 sampling points, we performed a logistic regression which determined the probability to detect an aspen in relation to SOL thickness (Fig. 2). The model was significant ($Chi^2 = 44.4$, $p < 0.0001$) and indicated that the probability to detect an aspen was 30% at SOL = 0 cm, 20% at 10 cm, 15% at 20 cm, 10% at 30 cm, and 6% at 40 cm.

3.3. Aspen growth, SOL thickness and black spruce abundance

Segmented regressions using the 300 sampled aspens showed that across our data set aspen DBH was significantly negatively

Table 1
Soil chemical properties (mean, standard deviation [SD] and coefficient of variation [CV] of the 20 transects.

Transect	N_{tot} (%)	C:N	P (mg k^{-1}g)	Ca (cmol(+) kg^{-1})	CEC (cmol(+) kg^{-1})	pH
1	1.08	46.1	35.8	37.1	65.2	3.85
2	0.99	37.9	34.7	23.8	58.6	3.72
3	0.86	36.2	58.3	13.4	43.5	3.12
4	0.70	62.9	33.2	23.7	58.0	3.79
5	0.88	43.6	36.5	18.8	43.6	3.97
6	0.71	34.3	33.4	16.2	60.0	3.80
7	1.00	44.0	62.8	43.3	66.3	4.46
8	0.54	51.7	44.0	11.6	38.0	3.49
9	0.90	45.3	33.7	51.8	88.3	4.37
10	0.75	60.8	35.6	15.7	36.5	3.08
11	0.85	55.8	41.4	9.2	32.2	2.81
12	0.76	65.1	57.3	16.8	49.1	3.18
13	0.96	46.8	60.9	12.3	50.3	3.23
14	0.83	51.3	71.6	27.6	60.2	3.97
15	0.72	65.7	50.8	21.2	47.4	3.32
16	0.73	68.6	43.5	7.6	28.0	2.78
17	0.85	58.4	52.0	16.7	34.2	3.06
18	0.87	56.4	53.4	12.7	35.5	2.97
19	0.90	55.5	86.0	13.1	41.5	3.09
20	1.08	43.6	91.4	14.7	36.2	3.13
Mean	*0.84*	*52.1*	*56.2*	*18.7*	*45.6*	*3.41*
SD	*0.10*	*8.6*	*19.2*	*8.6*	*11.9*	*0.46*
CV (%)	*11.9*	*16.5*	*34.2*	*45.9*	*26.1*	*13.5*

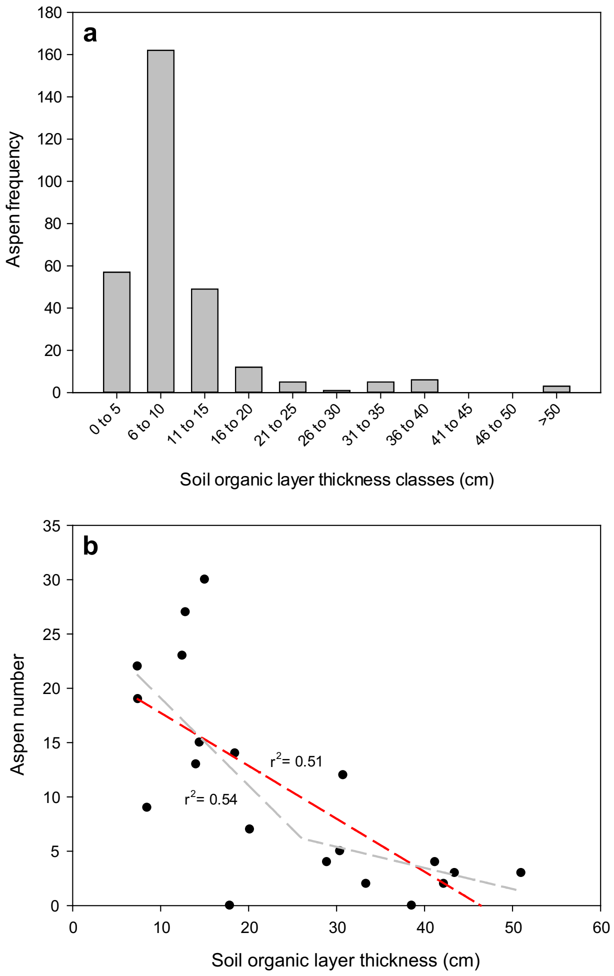

Fig. 1. Aspen frequency (a, $n = 300$, tree-level relationship) and number (b, $n = 20$, site-level relationship) in relation to SOL thickness 15 years after stand initiation by fire. Red dashed line = linear regression; gray dashed line = segmented regression. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

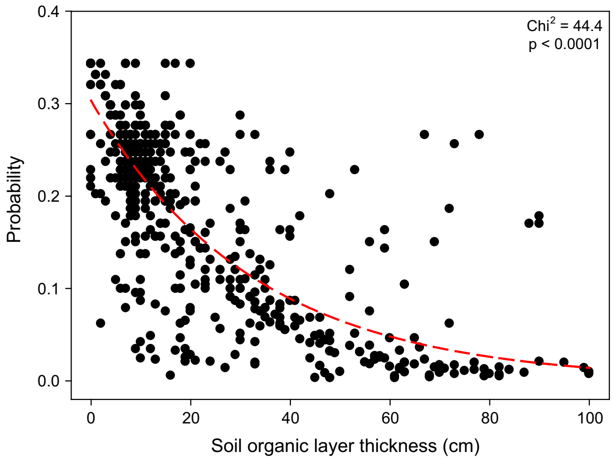

Fig. 2. Scatter plot showing the probability to detect an aspen 15 years after stand initiation by fire vs SOL thickness ($n = 500$). The red dashed line indicates the fit between SOL thickness and the probability to detect an aspen. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

correlated to both SOL thickness ($r = 0.297$, $p < 0.0001$) and black spruce abundance ($r = 0.173$, $p = 0.03$) (Fig. 3). The segmented regression using SOL thickness revealed a cut-off point *circa* 6 cm and suggests that growth is severely impeded when SOL thickness >20 cm (Fig. 3a), whereas that using black spruce abundance revealed cut-off a point *ca.* 5, suggesting that aspen growth is severely impeded when the number of black spruce established in a 2-m radius around an aspen tree is greater than 5 (Fig. 3b).

3.4. Relationships between aspen growth and habitat factors

As illustrated by PCA (Fig. 4) and confirmed by Pearson correlations (Table 3), aspen diameter was positively correlated to soil N_{tot}, Ca, CEC and pH, and negatively to black spruce abundance, SOL thickness and soil C:N. Moreover, the number of black spruce was positively correlated to SOL thickness and C:N.

3.5. Mode of reproduction: seeds vs suckers

The study of the root systems revealed that 26 (41%) aspens stems originated from suckers and 37 from seed (59%). Only 3 out of 63 (5%) aspen stems were established prior to fire (1 sucker and 2 originating from seeds); out of the remaining 60 stems, 48 (80%) established in the first 5 years following fire. Furthermore, one-way ANOVAs failed to detect any significant differences between aspen originating from seeds and suckers with regards

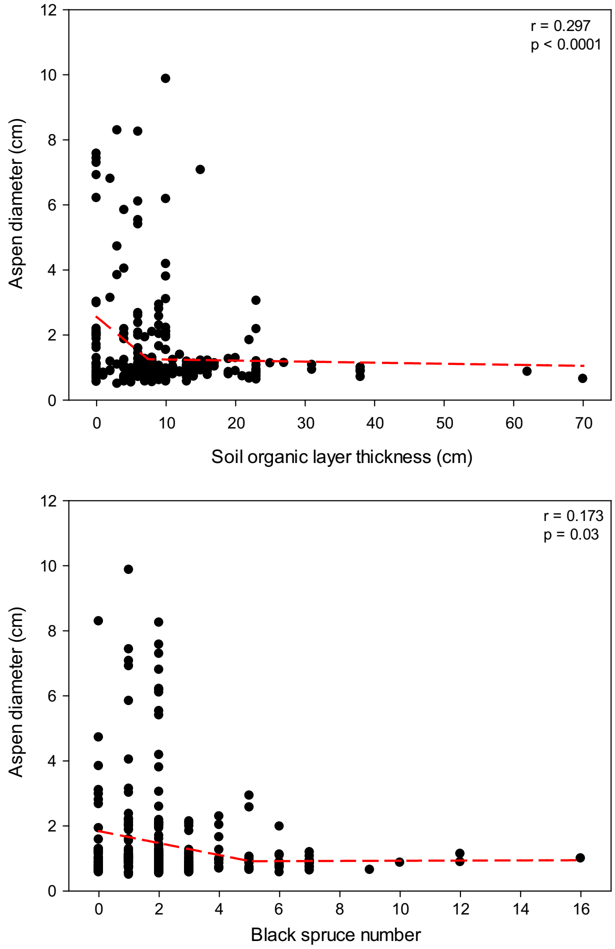

Fig. 3. Aspen diameter 15 years after stand initiation by fire in relation to SOL thickness (a) and black spruce abundance (b).

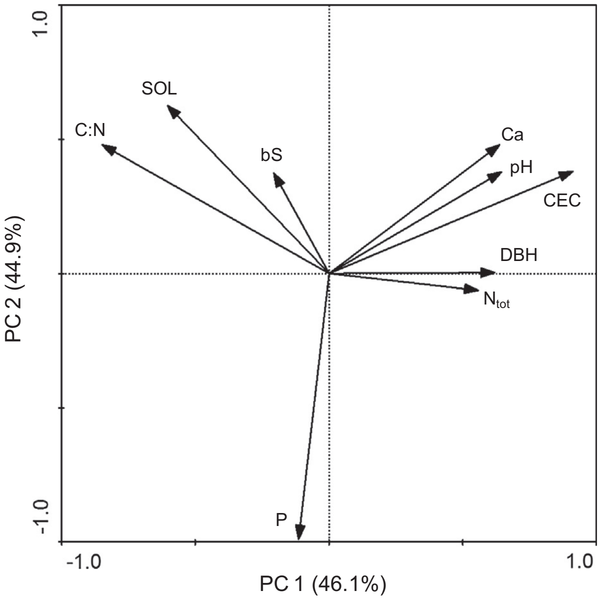

Fig. 4. PCA biplot showing the relationships between aspen diameter at breast height (DBH) and black spruce abundance (bS) and soil factors. C:N, soil C to N ratio; Ca, soil calcium concentration; CEC, soil cation exchange capacity; N_{tot}, soil total nitrogen concentration; P, soil available phosphorus concentration; pH, soil pH, SOL, soil organic layer thickness.

to DBH, age, SOL thickness and the number of black spruce established in a 2-m radius around individual stems (Table 4).

Using logistic regression we determined if SOL thickness had an effect on the mode of reproduction of aspen, i.e. seed vs sucker. Logistic regression failed to detect any effect of SOL thickness on aspen mode of reproduction ($Chi^2 = 0.41$, $p = 0.44$), suggesting that SOL had the same effect on reproduction by seeds or suckers.

Root collar annual radial growth revealed dissimilar growth patterns between stems from seed origin and suckers (Fig. 5). For the first 3 or 4 years following fire, stems originating from seeds displayed a relatively small annual radial growth rate relative to suckers (Fig. 5a). However, their annual radial growth tended to increase over time, while growth of suckers tended to decrease between 1997 and 2005, after what it started to increase (Fig. 5a). Despite this difference in annual radial growth rate during the first few years following fire, stems originating from seeds and suckers had similar root collar diameter at the time of sampling (Fig. 5b).

4. Discussion

Over all, our results suggest that following fire in boreal forests SOL thickness and the proximity and abundance of black spruce may influence both the establishment and growth of aspen, and confirm that soil chemistry, especially N, play an important role in aspen growth.

4.1. Aspen establishment in response to SOL thickness

Our results strongly suggest that aspen establishment, whether by seed or sucker, is strongly impeded by SOL thickness, especially if >25 cm thick. These results are similar to those of Gewehr et al. (2014) who suggested that at the landscape level aspen distribution was limited on sites where SOL thickness was >30 cm. Other authors, including Johnstone and Chapin (2006), Greene et al. (2007), and Shenoy et al. (2011), also pointed out that SOL thickness could be an important factor for aspen establishment following fire, and suggest that SOL as thin as 2–10 cm could limit aspen establishment. The results reported by these last authors seem to be in contradiction with the results reported in Fig. 1 which seems to suggest that SOL 2–10 cm thick does not limit aspen establishment. However, the figure rather suggests that aspen establishment is not as impeded when SOL is 2–10 cm thick as it is when SOL is >25 cm thick.

According to Burns and Honkala (1990) and Gewehr et al. (2014), the main constraint on aspen establishment can be attributed to changes in soil physical properties, especially when the water table is located above the mineral soil surface (Gewehr et al., 2014). Indeed, SOL accumulation causes the water table level to rise (Oechel and Van Cleve, 1986; Simard et al., 2007) and soil temperature to decrease (Kasischke and Johnstone, 2005; Gewehr et al., 2014). Aspen has been shown to have an optimum

Table 3
Pearson correlation coefficient among aspen diameter, black spruce abundance, and soil variables at the level of single tree. Numbers in bold are significant at $p \leqslant 0.05$.

	Diameter	bS	SOL	C:N	N_{tot}	P	Ca	pH	CEC
Diameter	1								
bS	−**0.145**	1							
SOL	−**0.390**	**0.584**	1						
C:N	−**0.692**	**0.406**	**0.774**	1					
N_{tot}	**0.650**	−**0.476**	−**0.883**	−**0.915**	1				
P	−0.034	−**0.168**	−**0.245**	0.098	0.044	1			
Ca	**0.126**	0.031	−0.028	−0.081	**0.168**	−**0.124**	1		
pH	**0.149**	0.034	−**0.165**	−**0.404**	**0.274**	−**0.224**	**0.833**	1	
CEC	**0.214**	0.039	−**0.120**	−**0.315**	**0.283**	−**0.120**	**0.841**	**0.868**	1

Diameter = aspen diameter at breast height, bS = number of black spruce, SOL = soil organic layer thickness, and CEC = cation exchange capacity.

Table 4
Results of one-way mixed-effect ANOVAs testing the statistical significance of stem origin (i.e. seed vs. sucker) on aspen DBH and age, SOL thickness, and black spruce abundance. Values are mean ± standard error ($n = 9$).

Origin	Frequency	DBH (cm)	Age	SOL thickness (cm)	Black spruce abundance
Sucker	8.7 (1.2)	27.6 (3.4)	12.0 (1.1)	10.1 (5.7)	4.1 (2.7)
Seed	12.3 (1.2)	35.9 (21.0)	11.9 (0.8)	11.1 (7.9)	5.5 (3.7)
F	2.85	2.75	0.06	0.07	0.73
p-Value	0.111	0.102	0.802	0.781	0.396

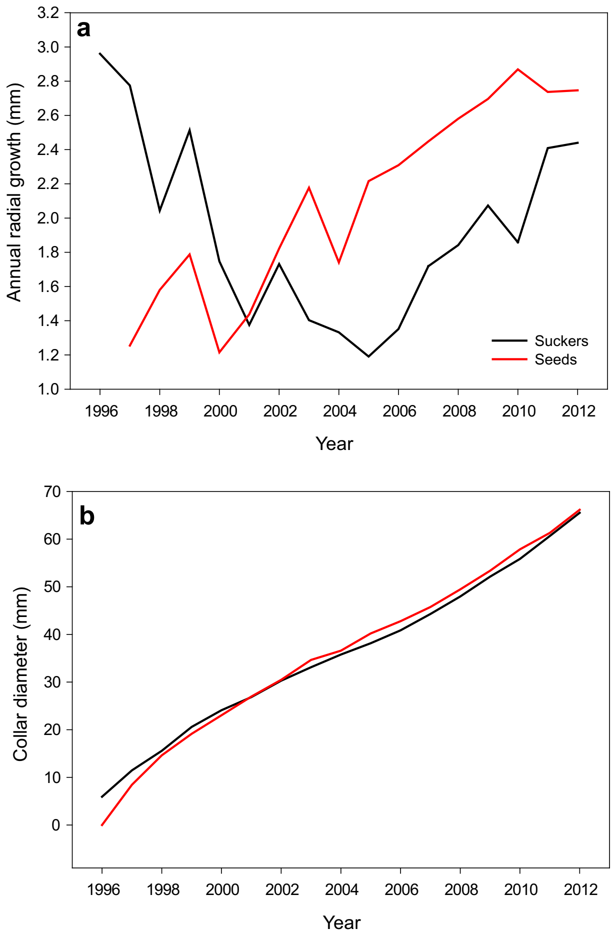

Fig. 5. Collar annual radial growth (a) and diameter (b) of aspen stems originating from seeds or suckers during the first 15 after stand initiation by fire.

temperature for root growth of 19 °C (Peng and Dang, 2003; Landhäusser et al., 2001) showed for aspen that decreased soil temperatures was responsible for lowered assimilation rates, lowered leaf and shoot growth, and cessation in root growth. In the same vein, Fraser et al. (2002) showed that sucker initiation was stimulated by warm soils. Hence, the 25 cm SOL thickness threshold affecting aspen establishment could be the result of an abrupt change in soil properties induced by the rise of the water table and by their inability to reach and grow in the mineral soil (Simard et al., 2007). The shallow water table would subsequently submerge root systems and induce anaerobic conditions that would cause the death of the roots (Kozlowski, 1997) soon after seedling establishment.

Furthermore, we did not observe any effect of SOL thickness on stem origin (i.e. seed or sucker). Similarly, while Greene et al. (2007) observed a strong negative relationship between SOL thickness and aspen survivorship, origin (i.e. seeds or suckers) of aspen regeneration did not appear to be influenced by SOL thickness. Hence, SOL accumulation in sites prone to waterlogging likely have a negative effect on aspen recruitment whether through limiting seed establishment or through reducing sucker initiation (Greene et al., 2007). While aspen seed germination requires well drained microsites (Barnes, 1966), sucker development is limited by waterlogged conditions (Fechner et al., 1981; Frey et al., 2003). Optimal sucker development requires particular soil conditions, notably soil temperature ca. 23° (Burns and Honkala, 1990). However, as stated soil temperature decreases as SOL thickens which is likely to impede sucker development. Hence, SOL accumulation may hinder both aspen seedling germination and growth (Johnstone and Chapin, 2006; Greene et al., 2007) and sucker development (Fechner et al., 1981; Frey et al., 2003).

With regards to root collar annual radial growth, suckers may have an advantage over trees originating from seed because they already have a well-developed root system. However, parent roots will have a positive impact on sucker growth only if the respiration costs of that root biomass are balanced by increased photosynthetic capacity (DesRochers and Lieffers, 2001). Otherwise, parent roots may become a sink for resources, leading to the death of the suckers. Thus, the decreasing annual radial growth observed in suckers for the first 8 years following fire may be explained by the negative effect of their parent root, after what their photosynthetic capacity was high enough to sustain an increased growth rate. As a result, seedlings and suckers displayed similar root collar diameter at the time of sampling.

4.2. Aspen growth in relation to SOL thickness

As was the case for soil physical properties, SOL accumulation has been found to modify soil chemical properties and constrain aspen growth. More specifically, SOL accumulation has been found to lead to soil acidification and increased C:N (Gewehr et al., 2014; Lafleur et al., 2015). Soil C:N ratio is often used as a measure of soil quality and indicates the ability of a soil to provide N (Paul, 2007).

Aspen is a nutrient demanding species (Alban, 1982) and N availability has been shown to limit aspen growth in many instances (DesRochers et al., 2003; Tullus et al., 2010; Vadeboncoeur, 2010; Maynard et al., 2014). Likewise, Landhäusser et al. (2010) found that sucker initiation was stimulated by soil NO_3^-. In this context, the relationships we observed between aspen growth and N_{tot} (positive) and C:N (negative) are indications that aspen growth (and sucker initiation) was likely N-limited.

Furthermore, SOL is a key source of nutrients and a substantial proportion of a site's nutrients may be located in SOL (Prescott et al., 2000). Hence, SOL may constitute a nutrient sink that competes with trees, notably for N. Especially in the case of surface accumulations, the progressive immobilization of N into organic layers may over time deplete the supply of available nutrients and decrease tree growth (Prescott et al., 2000).

Finally, we observe positive relationships between aspen DBH and soil pH and exchangeable Ca. These results are in accordance with Paré et al. (2001) who showed that soil pH and Ca availability were correlated with aspen height growth on till and clay soils. Similarly, Toribio Fajardo (2005) found that soil pH was an important factor influencing distribution and growth of aspen, whereas Alban (1982) found that aspen has high Ca requirement. Aspen growth is known to be optimum between pH 5 and 7 (Lu and Sucoff, 2003; Tullus et al., 2012). Below pH 5, Al in the soil solution may adsorb Ca and P and reduce their availability to plants (Brady and Weil, 2004). Likewise, in a series of experiments, Lu and Sucoff (2003) showed that aspen growth was constrained by low Ca and P availability due to their adsorption to Al under low soil pH conditions.

5. Conclusion

The soil–plant system is a complex one where causal interactions between the soil compartment and the plant are bidirectional, and where the relative importance of the directional causalities may change according to site conditions (Ehrenfeld et al., 2005). In this respect, aspen and SOL display the same complex relationship in boreal forests. On the one hand, it has recently been suggested that aspen distribution is limited on sites where SOL thickness is >30 cm due to the negative effects of soil properties (Gewehr et al., 2014). On the other hand, it has been suggested that the relationship between SOL thickness and aspen distribution reflects the constraining effect of aspen litter on the accumulation of organic matter (Légaré et al., 2005). This study resolves a part of the enigma by showing that aspen regeneration and growth are limited on sites where thick SOL prevails.

Indeed, through changes in physical and chemical soil properties, SOL accumulation equally hinders both aspen seedling establishment and growth, and sucker development. Low soil temperature, waterlogged conditions and low N availability all likely concur to restrict the establishment and growth of aspen where SOL is >25–30 cm thick. In this context, only high-severity fires, i.e. fires that consume most of the SOL (Greene et al., 2005), have the potential to reduce SOL thickness, and increase soil temperature and nutrient availability, and thus create conditions that will favor aspen establishment and growth. However, as recently shown by Lafleur et al. (2015) and Terrier et al. (2014), in boreal forests where thick (>30 cm) SOL prevail, fire has low potential to significantly reduce the thickness of the SOL, even in the case of extreme drought (Terrier et al., 2014). These results suggest that aspen is likely to remain a minor component of the overstory in boreal forests prone to the development of thick SOL.

From a forest management perspective, considering the benefits of aspen for stand growth (Légaré et al., 2004, 2005) and how thickening SOL is likely to exclude aspen, this study suggest that using aspen as a companion species is possible where SOL is thin but that mechanical site preparation should be considered to decrease the thickness of the SOL if the maintenance of aspen and associated benefits on stand productivity are among management objectives.

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