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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