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Comparison of wood density in roots and stems of black spruce before and after commercial thinning

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ABSTRACT

Roots play an important physiological and mechanical role in the survival and growth of a tree, but also in the success of silvicultural treatments. Studies comparing the xylem in roots and stems have shown that conifer tracheids tend to be wider and longer in roots, which renders root wood less dense and more susceptible to cavitation and embolism. The increased radial growth often observed after thinning may induce changes in wood anatomy that could alter wood properties, such as wood density, in the stem and roots. The aim of this study was to compare growth, wood density and tracheid dimensions between the stem and roots of black spruce trees growing in the boreal forest. We also evaluated whether these wood properties were altered by the application of a commercial thinning treatment. Six black spruce trees were harvested in four commercially thinned stands. Samples were collected from the stem and two locations of each root. Radial growth, wood density and tracheid dimensions were measured on each sample. Results show that all wood density components, especially earlywood density, were higher in the roots than in the stem in black spruce. This denser wood in roots might provide increased safety against cavitation in a part of the xylem where hydraulic stresses are higher. After thinning, growth was increased in the stem and particularly in roots, resulting in slight wood density decreases, which should not influence the vulnerability of roots to cavitation or wood quality in the stem. These results lead us to suppose that the hydraulic network of the black spruce root system may not be so vulnerable to cavitation.

1. Introduction

The stem and roots of trees are both physiologically and mechanically important, but survival and growth are to a great extent determined by the root system. Roots provide anchorage and stability (Danjon and Reubens, 2008), as well as the water and nutrients needed for growth and development, and are important for storage of reserves and synthesis of certain growth hormones (Pallardy, 2008). Despite its importance, the root system of mature trees receives less scientific attention than the stem because of the difficulty in accessing the roots and the lack of commercial interest in this part of the tree (Fayle, 1968; Marcati et al., 2014).

Most of the water taken up and transported by the root system is returned to the atmosphere via transpiration (Jackson et al., 2000). This long-distance water transport in the soil-plant-atmosphere continuum requires an efficient conduit network (Holbrook and Zwieniecki, 2005) that is also resistant to cavitation and embolism. Cavitation, which refers to the formation of water vapor bubbles in columns of water subjected to tensile stresses that exceed the tensile strength of water, results in the formation of an embolism that breaks the continuity of the water column, preventing water transport in this part of the xylem (Tyree and Sperry, 1989; Hacke et al., 2001; Niklas and Spatz, 2012).

Vulnerability to cavitation is known to be influenced by the structure of the xylem (Hacke et al., 2001). Strong conduits with a high proportion of wall material per unit volume will be resistant to implosion and provide protection against cavitation (Sperry, 2003). The amount of cell wall material is a strong determinant of wood density because the density of the cell wall material itself is rather constant in wood (Panshin and De Zeeuw, 1970; Saranpää, 2003). Denser wood is thus considered to be more resistant to xylem cavitation and confers a greater hydraulic safety (Meinzer et al., 2003; Jacobsen et al., 2005). However, density is also determined by the dimensions of the cells (Butterfield, 2003), and in turn their length, diameter, and wall thickness can all influence xylem flow resistance, protection against cavitation and risk of wall collapse (Sperry et al., 2006).

Studies comparing the vulnerability of root and stem xylem have shown that roots are more vulnerable to cavitation (Alder et al., 1996; Hacke and Sauter, 1996), suggesting that they might be the weakest

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point along the hydraulic network from soil to atmosphere (Jackson et al., 2000). Conduits tend to be wider and longer in roots than in stems (Bannan, 1965; Fayle, 1968; Patel, 1971), which presumably renders root wood less dense and more susceptible to cavitation and embolism. The earlywood part of the growth ring, which is where the lowest wood density values are generally found, presents the highest vulnerability to cavitation in the xylem of roots and stems (Dalla-Salda et al., 2009). On the contrary, maximum wood density values are normally obtained in the latewood, which gives the mechanical resistance (Stokes and Mattheck, 1996).

Roots also play an important role in the success of silvicultural treatments. For instance, the canopy opening following commercial thinning makes forest stands more susceptible to windthrow (Cucchi and Bert, 2003; Riopel et al., 2010; Lavoie et al., 2012), due to the greater wind penetration into the residual stand (Achim et al., 2005). Tree stability, which depends greatly on the development of the root system, must be maintained or increased in order to withstand wind-induced loading and support the enhanced growth that is expected after thinning (Vincent et al., 2009; Krause et al., 2014). Thinning is also associated with higher transpiration at tree level, and thus a greater need for water uptake from the roots (Gebhardt et al., 2014; Boczoń et al., 2016). In parallel, the increased radial growth often observed after thinning may induce changes in the wood anatomy that could alter wood properties of the stem and roots, especially wood density and tracheid dimensions (Lemay et al., 2016; Pamerleau-Couture, 2016). Such changes could have an impact on water transport and vulnerability to cavitation. Stem and root wood anatomy have been reported to vary in similar ways, but to a greater extent in the roots (Cutler, 1976). Roots could thus be more affected by thinning, which could increase their vulnerability to cavitation.

This study focuses on black spruce (*Picea mariana* (Mill.) B.S.P.), which is one of the most widely distributed conifer species in the North American boreal forest (Viereck and Johnston, 1990). It is a slow-growing species, and has a great economic importance due to its abundance and the quality of its wood (Zhang and Koubaa, 2008). The root system of black spruce consists of several coarse lateral roots extending from the stem near the soil surface, i.e. mostly concentrated in the top 20–30 cm of soil (Strong and LaRoi, 1983). Although water is generally not a primary limiting factor for tree growth in the eastern boreal forest of North America, the shallow depth of their roots makes black spruces somewhat more susceptible to dry spells. In drier periods, the first layer of soil can dry out rapidly, and with a plate root system that limits the ability to draw water from deeper soil layers, vulnerability to cavitation can increase (Cochard, 2006).

The aim of this study was to compare growth, wood density and tracheid dimensions between the stem and roots of black spruce trees growing in the boreal forest. We also evaluated whether these wood properties were altered by the application of a commercial thinning treatment. Our hypotheses were that (1) mean and earlywood density are lower and tracheid dimensions larger in the roots than in the stem, (2) thinning has a proportionally greater effect on radial growth in the roots than in the stem, and (3) all wood density components and tracheid dimensions are lower in both parts of the tree as a result of the increase in radial growth.

2. Materials and methods

2.1. Study sites and tree sampling

Four even-aged black spruce stands covering an east–west gradient were sampled in the Saguenay-Lac-Saint-Jean, Abitibi-Témiscamingue and Côte-Nord regions of Quebec, Canada, between 48°41′ and 50°30′N and 68°47′ and 70°22′W (Fig. 1). All stands had similar characteristics in terms of species composition, density and diameter. A commercial thinning had been conducted in each stand about ten years prior to sampling, i.e. between 1997 and 2000.

Fig. 1. Localisation of the study sites.

At each site, 6 black spruce trees were chosen randomly from the dominant or codominant stems in 400 m^2 plots. Sample trees were healthy-looking, free of visible injuries or defects and located at least 2 m away from a logging trail. For each tree, height, diameter at breast height (DBH, 1.3 m above the ground), and proportion of live crown were recorded at the time of sampling (Table 1).

Samples from the stem and roots were collected from each tree. On the stem, two adjacent discs were harvested at 1.3 m to measure radial growth and wood properties (wood density and tracheid dimensions). The root systems were excavated within a radius of 60 cm around each tree. In this way, we obtained the part of the root system responsible for tree stability and anchorage (Coutts, 1987; Danjon et al., 2005; Danquechin Dorval et al., 2016) since most soil movements induced by mechanical loads on the stem occur between 35 and 50 cm around the stem (Stokes, 1999).

Within the root system, all roots exhibiting a diameter > 2 cm were sampled at two different locations (Fig. 2A). A first 10-cm-thick section was taken close to the root-trunk interface (proximal part of the root) and a second one at a distance of 60 cm from the root–trunk interface (distal part). These were used to measure root radial growth and wood properties (density and tracheid dimensions). In the event that a root branched, we collected distal samples from all branches. A total of 615 root sections were sampled on 229 roots, from 24 harvested trees.

2.2. Radial growth

All stem and root discs were dried and sanded to increase the contrast of the tree-ring delineations. With the first disc collected at breast height, annual ring widths were measured to the nearest 0.01 mm along four radii using the WinDendro software (Regent Instruments Inc. Québec, QC, Canada). When discontinuous or very narrow growth rings were present, a LINTAB measurement table together with the TSAP-Win program (Rinntech, Heidelberg, Germany) were used instead. A similar procedure was applied to each disc from both sampling locations in the roots, but due to the eccentric growth of the roots and the sometimes large number of discontinuous rings, only one radius per root section was measured where the most growth rings were visible (Krause and Eckstein, 1993), which was generally on the upper part of the root (Fig. 2B). As black spruce is a slow-growing species, growth rings were generally narrow; in the stem, mean ring width was 0.96 mm, while in

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