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Original article

Fine root dynamics of trembling aspen in boreal forest and aspen parkland in central Canada

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Abstract

- Fine root responses to potential climate change are relatively unknown in spite of their central role in ecosystem functioning.
- We quantified fine root length, production, and turnover in boreal forest and aspen parkland of central Canada because the future climate of the boreal site is expected to be similar to the current climate of the parkland site.
- Root depth distribution and turnover were similar between sites. Fine root mass was 4× greater at the parkland site and root length was 10× greater. Accordingly, the ecosystem level fine root: leaf mass ratio was 1.6 in the boreal site compared to 4.3 in the parkland site. On a per tree basis, however, fine root biomass was similar between sites due to the higher stem density of the parkland site.
- The parkland site had a greater proportion of very fine roots (62% of the fine roots were < 0.1 mm in diameter) compared with the boreal site (82% of the fine roots were between 0.1–0.5 mm in diameter).
- These differences indicate a large-scale shift towards increased root allocation at the parkland site associated with decreasing water availability and earlier successional stage.

1. INTRODUCTION

Fine roots are central to carbon and nutrient cycles because of their role in water and nutrient uptake, and high turnover rates (Block et al., 2006; Pregitzer, 2002; Steinaker and Wilson, 2005). The response of fine roots to changing environmental conditions has received a great deal of attention recently, in particular the impact of changing CO_2 concentrations, temperature, and precipitation in controlled experiments (Milchunas et al., 2005; Pregitzer et al., 2000). In general, with rising temperatures and the associated drier soil conditions, plants are expected to allocate relatively more resources to root production (Barton and Montagu, 2006; Tilman, 1988). For example, in a long-term water manipulation experiment in a mature hardwood forest, the drier treatment had significantly greater root production than the ambient or wet treatment (Joslin and Wolfe, 1998). However, in a review of fine root dynamics of *Populus* plantations, Block et al. (2006) found that root production increased with increasing soil moisture.

Other components of fine root dynamics besides biomass allocation and production may also be impacted by a changing environment. Root turnover is expected to increase with increasing temperature (Gill and Jackson, 2000) and drought (Meier and Leuschner, 2008) due to higher respiration rates and root mortality. Average root diameter is expected to be smaller on drier sites (West et al., 2004) since the greater absorbing surface area results in a greater ability to take up water and nutrients. Rooting depth has been shown to be shallower in water limited plants in a greenhouse study of *Populus* (Snyder and Williams, 2007) but the opposite trend has been found in field grown legume crops with water deficits resulting in a deeper rooting depth (Benjamin and Nielsen, 2006).

In western Canada, the future climate of the southern boreal forest is thought to be similar to the current climate further south in the aspen parkland where potential evapotranspiration exceeds precipitation (Hogg and Hurdle, 1995). Trembling aspen (*Populus tremuloides* Michx.) is the dominant tree species in aspen parkland, which is a transitional zone between prairie to the south and forest to the north, where trembling aspen occurs interspersed with grasses. In the southern boreal forest, trembling aspen is an important ecological and commercial tree species. Previous studies in both areas have examined root biomass using soil cores but the methods and results are not readily comparable. Wilson and Kleb (1996) found 19.8 kg m^{-3} soil of roots in aspen parkland using 1.9 cm

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diameter cores to a depth of 45 cm, while Steele et al. (1997) found 657 g m^{-2} of roots in boreal forest using a 4.5 cm diameter core to a depth of 30 cm. The minirhizotron methodology used in our current study allows for a consistent comparison between sites of fine root biomass and productivity along with other important attributes of fine root dynamics.

This study is unique in that we examined natural stands of trees in different climatic regions with the parkland site serving as a proxy for the future climate of the boreal site. Our goal was to determine if the fine root dynamics of trembling aspen ecosystems, specifically rooting depth, size class distribution, standing crop, productivity and turnover, were the same between the sites in the parkland and boreal ecoregions. Significant differences in fine root dynamics and root system characteristics between the sites may indicate potential future management concerns for the boreal site.

2. MATERIALS AND METHODS

Trembling aspen stands at two sites in different ecological regions were used in this study. The boreal site is located at the Boreal Forest Research and Monitoring Site (BERMS) old aspen stand (53° 38′ N, 106° 12′ W). This site is 50 km northwest of Prince Albert, Saskatchewan in the mid-boreal lowland ecoregion. The vegetation consists of a pure trembling aspen overstory with a nearly continuous understory of mainly beaked hazel (*Corylus cornuta*) along with wild rose (*Rosa woodsii*) and green alder (*Alnus crispa*). This is a single aged stand with 85-year-old trees about 24 m tall, average diameter at breast height of 20 cm, and 830 stems per hectare. The mean annual precipitation for the site based on climate records from nearby Waskesiu Lake for the years 1971–2000 is 467 mm with precipitation exceeding potential evapotranspiration. Average January temperature is –18 °C and average July temperature is 16 °C. The soil is an Orthic Gray Luvisol with a loam to clay loam texture. More detailed information on this site can be found in Kalyn and Van Rees (2006). The parkland site, approximately 370 km south of the boreal site, was located at the White Butte Recreation Area (50° 28′ N, 104° 22′ W), 20 km east of Regina, Saskatchewan in the aspen parkland ecoregion. The vegetation consists of a mixture of natural grasslands and trembling aspen stands. Most of the trembling aspen are 22 years old with approximately one quarter of the trees being 46 years old (Pinno, unpublished data). The average canopy height is 12 m, average diameter at breast height is 9 cm, and tree density is 3000 stems per hectare. The understory consists of shrubs (mainly *Symphoricarpos occidentalis* and *Rosa acicularis*) and grasses (*Bromus inermis* and *Poa pratensis*). The mean annual precipitation for the site based on the nearby Regina climate records is 388 mm with potential evapotranspiration exceeding precipitation. Average January temperature is –16 °C and the average July temperature is 19 °C. The soil is a Regosol on silty sand which has lower fertility than the clay loam soil at the boreal site. More detailed information on this site can be found in Steinaker and Wilson (2005).

Nine minirhizotron tubes were installed at each site. At the parkland site, the tubes were distributed along a 500 m transect and were installed in 2000 at 45° angle to the soil surface. At the boreal site, the tubes were distributed in three groups of three tubes with 8 m between groups and were installed in 2002 at 38° angle to the soil surface. Images were not taken until the 2004 growing season to allow at least two years for fine roots to colonize disturbed soil around the tubes. For the parkland site, images were taken bi-weekly resulting in 13 measurement dates from March to November while for the boreal site monthly images were taken from May to September for five measurement dates. These measurement dates represent the approximate growing season for the two sites and significant root growth is not expected outside of this window. The maximum depth of tube installation was 40 cm for the boreal site so this was the maximum depth studied at the parkland site as well. Root length was determined for five diameter classes (< 0.1, 0.1–0.2, 0.2–0.5, 0.5–1.0, and 1.0–2.0 mm) and averaged for each tube at each sampling date. For rooting depth comparisons, depth classes of 0–20 cm and 20–40 cm were used. Fine root biomass values were calculated for both sites using specific root length values for the individual diameter classes (300, 60, 15, 3, 1 m root/g root respectively) using a standard depth of field of 1.54 mm for the minirhizotron images (Steinaker, 2006). Comparisons of fine root mass and length between sites were made from the final measurement period in 2004. Fine root production and mortality by size class was calculated for each image for each sampling interval and then summed to determine total annual productivity. Fine root turnover was calculated as annual production divided by maximum standing crop (Gill and Jackson, 2000). Distinguishing between the roots of trembling aspen trees and understory vegetation was not possible so the values presented represent the fine root dynamics of these trembling aspen dominated ecosystems as a whole.

Above-ground tree total biomass and foliar biomass values for the parkland site were determined from measurements of tree height and diameter at each root sampling location (Lambert et al., 2005). Understory foliar biomass was obtained by clipping, drying, and weighing vegetation in a 10 × 100 cm quadrat at each root sampling location. Above-ground biomass values for the boreal site are taken from Gower et al. (1997) and Kalyn and Van Rees (2006) while understory foliar values are from Barr et al. (2004). Statistical analysis was completed using JMP software (SAS Institute, Cary, NC) and consisted of one-way ANOVAs to compare root characteristics between the sites with individual tubes considered replicates for each site. Data were log-transformed to improve normality. Untransformed means and standard deviations are presented.

3. RESULTS

Biomass of fine roots was significantly higher at the parkland site (23.2 Mg ha^{-1}) than the boreal site (5.4 Mg ha^{-1}) (Tab. I). Relative to the above-ground tree biomass on site, fine roots make up a larger percentage of total biomass at the parkland site than boreal (30.5% vs. 2.8%) but on a per tree basis the fine root biomass values are quite similar at 7.7 kg $tree^{-1}$ for the parkland site compared to 6.5 kg $tree^{-1}$ for the boreal site. On an ecosystem scale, including both over and understory foliage, the parkland site had a larger fine root: leaf mass ratio (4.3 vs. 1.6). Rooting depth distribution was similar between sites with 61 and 56% of the fine root length in the upper 20 cm at the parkland and boreal sites respectively ($P = 0.840$) although at both depths the parkland site had significantly greater fine root length (Fig. 1). Therefore, for all other analyses, all fine roots to a depth of 40 cm will be considered together.

Length of fine roots was significantly greater at the parkland site (540.8 m m^{-2} image) than at the boreal site (58.0 m m^{-2} image, Tab. II). Diameter class distribution was also different

Table I. Above-ground and fine root biomass and biomass production for trembling aspen in boreal and parkland sites. Values in parentheses are standard deviations between tubes ($n = 9$).

Ecosystem component	Boreal	Parkland	P
Above-ground standin tree biomass (Mg ha^{-1})	195.0	76.0	–
Aspen leaf mass (Mg ha^{-1})	1.8	3.2	–
Understory leaf mass (Mg ha^{-1})	1.5	2.2	–
Fine root biomass (Mg ha^{-1})	5.4 (5.0)	23.2 (18.0)	0.011
Fine root biomass production (Mg ha^{-1} y^{-1})	3.4 (3.2)	5.2 (5.2)	0.377

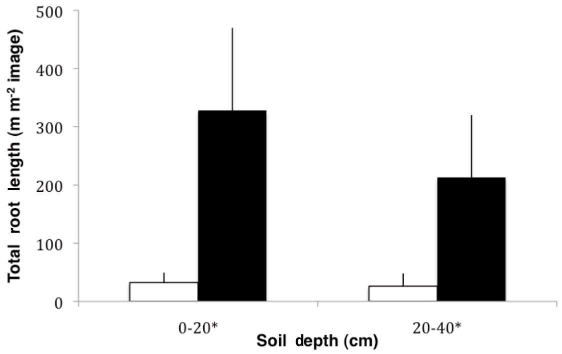

Figure 1. Total fine root length of trembling aspen by soil depth. The error bars are equal to 1 standard deviation. The open bars represent the boreal site while the black bars represent the parkland site. * Indicates significant difference between the boreal and parkland sites at $P < 0.05$.

Table II. Trembling aspen fine root length by size class for the boreal and parkland sites. Values in parentheses are standard deviations between tubes ($n = 9$).

Size class	Fine root length (mm^{-2} image)		P
	Boreal	Parkland	
< 0.1 mm	7.0 (8.6)	333.7 (12.1)	< 0.001
0.1–0.2 mm	30.3 (13.9)	121.2 (61.6)	0.001
0.2–0.5 mm	15.4 (11.7)	63.3 (60.7)	0.034
0.5–1.0 mm	3.6 (5.4)	15.0 (12.7)	0.025
1.0–2.0 mm	1.6 (2.4)	7.5 (10.6)	0.126
Total	58.0 (25.1)	540.8 (185.7)	< 00.1

with the parkland site having 62% of the total root length in the smallest diameter size class (< 0.1 mm) compared to 11% for the boreal site. Accordingly, the boreal site had a larger percentage (82% boreal vs. 33% parkland) of the total root length in the 0.1–0.2 mm and 0.2–0.5 mm size classes (Fig. 2). Total root length was greater for each individual size class at the parkland site compared to the boreal site although for the largest size class the difference was not statistically significant (Tab. II).

Production of fine roots was greater at the parkland site for roots less than 0.2 mm in diameter and for the total length of all fine roots (Fig. 3a). For roots greater than 1.0 mm, the boreal site tended to have greater production although this was not statistically significant. Relative to the total fine root length production at each site, the parkland site allocated most root production to the smallest diameter size class while the boreal site allocated more root production to the 0.1–0.2 mm and 0.2–0.5 mm diameter classes (Fig. 3b). Finally, fine root length turnover was similar between sites for all size classes with a total turnover rate of 41% per year at the parkland site and 49% at the boreal site (Tab. III). However, fine root total biomass turnover was significantly greater at the boreal site (57% vs. 27%, $P = 0.012$).

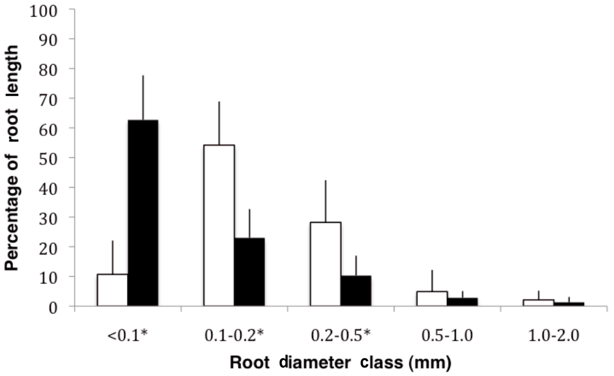

Figure 2. Percentage of total fine root length for each diameter class. The error bars are equal to 1 standard deviation. Open bars represent the boreal site while the black bars represent the parkland site. * Indicates significant difference between the boreal and parkland sites at $P < 0.05$.

4. DISCUSSION

Fine root mass was over four times higher in parkland than boreal forest. When comparing fine root length this difference was even greater, with the parkland site having ten times the root length of the boreal site. These results obtained from standardized minirhizotron methodology, confirm the scale and direction of differences found using root cores (Steele et al., 1997; Wilson and Kleb, 1996). Greater root biomass and root: leaf mass ratio were expected at the parkland site due to the drier climate, younger stand age, and higher stem density. The impact of moisture availability has been shown with a long-term water manipulation study in a mature hardwood forest

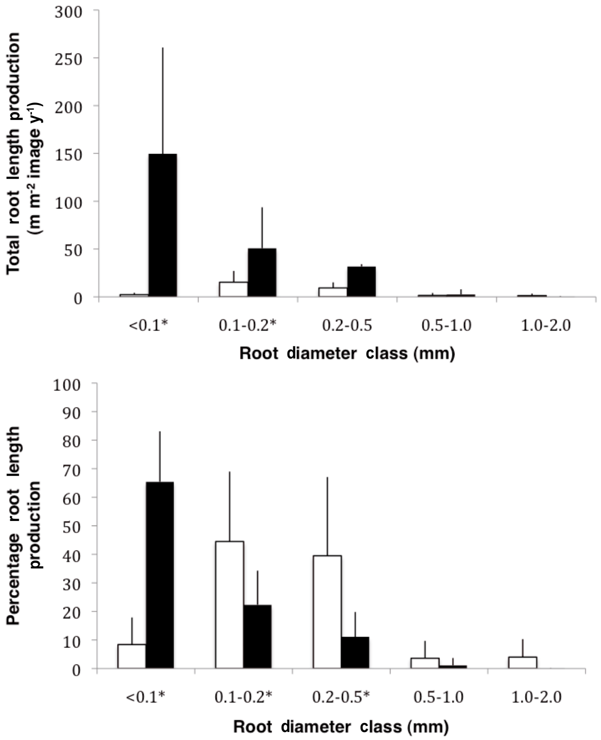

Figure 3. Summary by root diameter class of: (a) total root length production per year, and (b) percentage of root legth production in each diameter class. The error bars are equal to 1 standard deviation. Open bars represent the boreal site while the black bars represent the parkland site. Note: * indicates significant difference between the boreal and parkland sites at $P < 0.05$.

where the drier treatment had significantly greater root production (Joslin and Wolfe, 1998). This difference in available site moisture was also increased additionally due to the lower water holding capacity of the sandy soil at the parkland site compared with than the loamy soil at the boreal site (Liang et al., 1989). The difference in allocation of resources to roots means that the parkland site has a much higher root: leaf mass ratio which has been shown to be an effective drought tolerance mechanism in hybrid poplar clones (Tschaplinski et al., 1998).

The difference in stand ages may also have had an impact on fine root standing crop since relatively younger stands have been shown to have up to 175% of the fine root biomass of mature stands (Claus and George, 2005). Higher stem density was also likely responsible for some of the difference in fine root biomass between sites given the 3.5× greater number of stems per hectare at the parkland site. This is reflected in the similar fine root biomass per tree values between sites. Given the experimental design it is impossible to definitively determine the cause of the difference in fine root biomass between the boreal and parkland site. It does appear, however, that both water availability and successional stage (age and density) play a major role.

Table III. Trembling aspen yearly fine root length turnover for the boreal and parkland sites. Values in parentheses are standard deviations between tubes ($n = 9$).

Size class	Fine root length turnover ($\% \ y^{-1}$)		P
	Boreal	Parkland	
< 0.1 mm	46 (46)	43 (23)	0.896
0.1–0.2 mm	44 (25)	36 (20)	0.437
0.2–0.5 mm	65 (22)	40 (37)	0.095
0.5–1.0 mm	17 (24)	15 (24)	0.842
1.0–2.0 mm	27 (44)	11 (33)	0.387
Total	49 (16)	41 (22)	0.385

The magnitude of the difference in fine root standing crop between sites was still unexpected. Our method of using a standard depth of field for minirhizotron methods may have over-estimated standing root crop compared to other methods such as the plane-intersect (Metcalfe et al., 2007). However, the relative relationship between the two sites would still hold since the same method was used for both sites. Our fine root biomass estimates are within the range of other estimates for similar ecosystems. Root biomass at the parkland site (23.2 Mg ha^{-1}) is similar to grassland ecosystems with a similar climate. Fine root biomass was estimated at 13.5 Mg ha^{-1} for a pasture and 35 Mg ha^{-1} for shrubland in a Colorado steppe (Liang et al., 1989) and between 15–26 Mg ha^{-1} in Mongolian grassland (Gao et al., 2008). For the boreal site, which had a fine root biomass of 5.4 Mg ha^{-1}, comparable estimates include 0.8 Mg ha^{-1} for trembling aspen in northern Manitoba (Steele et al., 1997), 1.7 Mg ha^{-1} in central Saskatchewan (Kalyn and Van Rees, 2006), 3 Mg ha^{-1} for a young aspen stand in Wisconsin (King et al., 2001) and 6.5 Mg ha^{-1} for a deciduous forest in Japan (Tateno et al., 2004).

Fine root length turnover was similar between sites while the boreal site had greater fine root biomass turnover. However, it was expected that fine root turnover would be greater at the parkland site due to the greater average temperature which causes increased root respiration and shortens the optimal lifespan of fine roots (Gill and Jackson, 2000). The drier environment of the parkland site may potentially offset the greater turnover due to increased temperature by requiring the trembling aspen trees to have a longer fine root lifespan to enable the trees to take up water whenever it is available, such as immediately after rain events.

The parkland site had more fine roots than the boreal site, which had thicker roots on average. This is evident in both the fine root mass and the root length production. Finer roots are better at nutrient uptake than thicker roots although they are more expensive to the tree with faster turnover rates and higher N requirements (Pregitzer, 2002; Pregitzer et al., 2002). The thicker roots of the boreal site may be a more conservative approach in an ecosystem with fewer extremes in soil water availability throughout the year enabling the trees to allocate fewer resources to very fine roots (Bauhus and Messier, 1999). In the parkland environment, on the other hand, belowground competition for water and nutrients is more intense than in forested area (Peltzer and Wilson, 2001). The development of more of the smallest fine root classes may allow the trees to successfully compete in this environment which is consistent with West et al. (2004) who found that drier ecosites had thinner fine root systems, thereby enhancing the water absorbing surface area. The age of the stands can have an effect on fine root size distribution with younger stands having relatively thinner fine roots than mature stands (Claus and George, 2005).

Other site factors may have also played a role in fine root dynamics at these sites. The clay loam soil of the boreal site is considered to have higher fertility due to the greater cation exchange capacity as compared to the coarse textured soil at the parkland site. Previous studies have shown that increased nutrient availability, in particular nitrogen, are related to greater root biomass and root growth in poplars (Block et al., 2006; Pregitzer, 2002). However, in our study the more fertile boreal site had significantly lower fine root biomass than the parkland site indicating that the biggest impact of soil properties on fine roots was related to water holding capacity with the coarse textured parkland soil exacerbating the climate moisture differences between the sites. Another potential site factor is the differences in understory vegetation with the parkland site having greater understory biomass and likely a larger contribution to fine root biomass. The understory species composition was also different with the boreal understory being mainly shrubs while the parkland understory is a combination of shrubs and grasses. Shrubby species are known to have larger average root diameter than grasses (Pinno, unpublished data) and this may have contributed to the root distribution at the boreal site having relatively more fine roots in the larger size classes. This combination of differences in understory biomass and rooting habit between sites likely added to the differences in ecosystem fine root characteristics since it was impossible to distinguish between aspen and understory roots.

Climate warming scenarios for western Canada predict that the future climate of the boreal site will be similar to the current climate of the parkland site (Hogg and Hurdle, 1995). One of the interesting features of this study was the ability to compare fine root dynamics between ecosystems dominated by the same species, trembling aspen. A number of studies have examined the response of *Populus* spp. fine roots to simulated greenhouse effects, in particular increased CO_2 concentration, soil N and soil temperature. Root growth of trembling aspen increases with temperature (Landhäusser et al., 2001; Steinaker and Wilson, 2008) indicating a potential benefit of warming effects if sufficient soil moisture is available. With increasing atmospheric CO_2 concentration, fine root productivity of trembling aspen also increased but only if available N was also high (Landhäusser et al., 2001; Pregitzer et al., 2000). This raises the question of whether the boreal site will be able to respond to increasing CO_2 concentrations if the coarser root system is not able to access adequate soil N with increasing competitive pressures from expanding grasslands. However, other root system characteristics such as specific root length and root: shoot ratio have strong genetic control in trembling aspen clones (King et al., 1999) indicating that trees may not be able to adjust their root system to changing climatic conditions. This suggests that the difference in fine root size distribution between the boreal and parkland sites may have a significant impact on future tree growth. For example, the existing fine root system of the boreal trees may not be optimal for the drier and warmer environment of the future resulting in poorer water and nutrient uptake. This could lead to reduced trembling aspen growth and survival, potentially changing the species composition, economic value of timber produced, and ecosystem carbon and nutrient balances in the future forest.

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