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Interspecific variation of tree root architecture in a temperate agroforestry system
characterized using ground-penetrating radar

Running Title: Tree root distributions in agroecosystems

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Keywords

Alley cropping; coarse roots; fine root density; root distribution; rooting depth; tree-based intercropping

Abstract

Background and Aims: Root system architecture regulates belowground access to soil resources. Variation in root architecture is important in agroforestry systems given management objectives to optimize resource acquisition between trees and crops.

However, the distributions of live tree roots in agroforestry systems remain understudied due to methodological constraints. In this study, we used ground-penetrating radar (GPR) to describe variation in whole-plant root architecture among tree species at the same agricultural site, with a specific focus on vertical coarse and fine root distributions within the zone of competition with neighbouring crops.

Methods: Using GPR, we detected coarse roots of five trees species (*Quercus rubra* L., *Juglans nigra* L., *Populus deltoides* × *nigra* DN177, *Picea abies* (L.) Karst, and *Thuja occidentalis* L.) at a tree-based intercropping system in southern Ontario, Canada. A subset of soil profiles were assessed for GPR accuracy. A cumulative root distribution function was used to estimate the rooting depth (D₉₅) of coarse roots. We also measured tree coarse root distributions and fine root density distributions 2 m into the crop rows, in the zone of competition.

Results: GPR accurately detected approximately 58 % of coarse roots for each study tree. Coarse root architecture varied among species, with differences in D₉₅ and rooting patterns. Fine root length density distribution also varied among species, but was consistently high at 0.10 and 0.20 m depths regardless of species. Conclusions: Our results suggest differential tree suitability for minimizing belowground competition with crops. Additionally, we illustrate the viability of GPR to characterize vertical profiles of live tree root systems, which is critical for improving our understanding of whole-plant functional traits and belowground plant interactions.

Introduction

Tree root traits influence ecosystem function (Pérez-Harguindeguy et al. 2013; Bardgett et al. 2014; Prieto et al. 2015). Tree root vertical distributions indicate the zone of belowground biophysical processes, while the density of fine roots is closely related to soil resource acquisition (Livesley et al. 2000; Bardgett et al. 2014). These architectural roots traits are increasingly incorporated in both ecosystem and agronomic models. For instance, rooting depth (e.g. D₉₅; the depth to which 95 % of the root system is located) is commonly used in biogeochemical models that describe hydrologic fluxes and carbon budgets at the whole-plant and landscape scales (Warren et al. 2015). Vertical root distributions are uniquely important to tree-based intercropping (TBI), or alley cropping, systems. The presence and function of trees in TBI systems can modify temperature and soil moisture regimes (Clinch et al. 2009), nitrogen (N) fluxes (Isaac et al. 2014) and

biological N fixation (Nasielski et al. 2015), thus improving nutrient cycles and resource-use efficiency (Thevathasan and Gordon 2004).

These regulating effects and efficiencies are commonly ascribed to complementary soil resource use and more complete soil resource exploitation via niche separation through root stratification of tree and crop root systems (Cannell et al. 1996). The vertical distribution of roots is related to depth-dependent processes occurring in the soil profile. Variation in root system structure as a response to resource availability and/or the presence of competing plants is a dominant mechanism for minimizing competition (Casper and Jackson 1997; Malamy 2005). In this regard, tree root architecture is a key determinant of complementary resource use with adjacent crops (Ong et al. 1991; Schroth 1999; Schwendenmann et al. 2010). As an added benefit, tree roots that are vertically stratified with crop roots can access nutrients leached below the crop roots, thereby reducing nutrient run-off (Van Noordwijk and Purnomosidhi 1995; Dougherty et al. 2009; Bergeron et al. 2011), and can input organic matter deeper in soil, sustaining soil carbon pools (Bambrick et al. 2010; Upson and Burgess 2013). To optimize the benefits from TBI systems, it is generally desirable that tree species should feature deep tree root systems that are vertically stratified with neighbouring crops.

Despite the need to quantify tree root architecture in TBI systems, only a few studies have examined live tree roots in situ. In these instances, researchers generally employ destructive or semi-destructive root study methods such as measuring roots that are exposed in a trench wall (e.g. Upson and Burgess 2013; Cardinael et al. 2015), visualized

91 using minirhizotons (e.g. Jose et al. 2001), extracted from soil cores (e.g. Upson and
92 Burgess 2013), and/or, less commonly, excavated (e.g. Jose et al. 2001; Das and
93 Chaturvedi 2008). These studies generally differentiate between structural coarse roots
94 (typically > 2 mm in diameter) and absorptive fine roots (typically < 2 mm) and often
95 describe the root system architecture in terms of relative depth in the soil profile. Since
96 roots are generally concentrated near the surface and their prevalence decreases with
97 depth, empirical models that capture this trend are useful for comparative purposes and
98 for calculating the proportion of roots at given depths (Gale and Grigal 1987; Jackson et
99 al. 1996; Gwenzi et al. 2011). However, destructive sampling methods are not repeatable
100 at the same location, only a portion of the root system is measured, and large amounts of
101 root data are challenging to collect. Therefore, alternative approaches to destructive
102 sampling are appealing (Jayawickreme et al. 2013).

103
104 Ground-penetrating radar (GPR) is a geo-imaging technology that can rapidly collect
105 subsurface data while largely avoiding disturbance to root systems (Stokes et al. 2002;
106 Guo et al. 2013; Jayawickreme et al. 2013). In-field experiments have used GPR to
107 describe the vertical distribution of coarse root systems in terms of biomass with depth of
108 *Quercus douglasii* (Raz-Yaseef et al. 2013), and rooting density with depth in studies of
109 *Castanopsis eyrei* and *Schima superb* (Yan et al. 2013) and *Theobroma cacao* and
110 *Terminalia ivorensis* (Isaac and Anglaere 2013; Isaac et al. 2014). Radar signals emitted
111 from GPR can be reflected at the root-soil interface due to a difference in dielectric
112 permittivity caused by higher water content within the coarse root compared to the soil
113 (Barton and Montagu 2004; Dannoura et al. 2008; Hirano et al. 2009). As the GPR device

is moved on the surface, sequential emissions and their resulting reflected radar signals are compiled into an interpretation of the subsurface (geo-image). Generally, coarse roots greater than 0.5 cm in diameter and orientated between 45° and 135° from the plane of the GPR path can be detected and will induce a hyperbolic reflection visualized in the geo-image (Barton and Montagu 2004; Guo et al. 2013; Guo et al. 2015). These root reflections are identified across multiple geo-images to identify coarse root distribution (Isaac and Anglaere 2013; Isaac et al. 2014; Wu et al. 2014).

The objective of the present study was to describe and compare architectural roots traits that underlie ecosystem function and complementary interactions in an agroforestry system. To do this, we examined the root systems of five temperate tree species in a TBI system in southern Ontario, Canada, using GPR and a commonly used empirical distribution function to describe the vertical distribution of coarse roots to a depth of 1 m. We paid special attention to tree root distributions in the crop row to assess the zone of competition with neighbouring crops. In this zone of competition, we supplemented the structural root data (coarse roots detected by GPR) with measurements of fine root distributions (undetectable by GPR) based on soil cores. We hypothesized that given suitable soil and root conditions, GPR would provide an accurate detection of coarse root vertical distributions among tree species. We also hypothesized that detected vertical root distributions will vary among the tree species at the same agricultural site due to intrinsic growth characteristics of the species in question, and that coarse root distributions correlate with fine root density. These differences in architectural traits could be used to inform species selection and management strategies in temperate TBI systems.

Materials and Methods

Study site

Ground-penetrating radar geo-imagery and physical soil and root samples were collected at the University of Guelph Agroforestry Research Station (44°32'28" N, 80°12'32" W) between April and July, 2012. Elevation at the site is 325 m and the mean annual precipitation is 830 mm (Oelbermann and Voroney 2007). The research plot was established in 1987 as a TBI experimental site with tree species planted in a randomized block design. Our study examined root systems of 13 individual trees representative of 5 tree species: *Juglans nigra* L. (black walnut; DBH = 24.4 ± 1.2 cm (mean $\pm$ S.E.); $n = 3$), *Picea abies* (L.) Karst (Norway spruce; DBH = 21.45 ± 3.5 cm; $n = 2$), *Populus deltoides* $\times$ *nigra* DN177 (hybrid poplar; DBH = 33.5 ± 0.6 cm; $n = 2$), *Quercus rubra* L. (red oak; DBH = 21.8 ± 0.3 cm; $n = 3$) and *Thuja occidentalis* L. (eastern white cedar; DBH = 7.5 ± 0.5 cm; $n = 3$). Species selection was based on trees common in agroforestry systems in southern Ontario. Study trees were chosen from randomly selected blocks and with the requirement that the tree was located on flat soil, had neighbouring trees of the same species, and was assessed to be of representative size for that species at the site. The 25-year-old study trees were planted 6 m apart in the tree rows (except *T. occidentalis* with 1-m spacing), and intercropped with crop rows 15 m wide. *Zea mays* L. (maize), *Glycine max* L. Merr (soybean), *Triticum aestivum* L. (winter wheat) were grown in crop rows following conventional crop rotations of the region and under no-till cultivation since

160 1996 (Wotherspoon et al. 2014). The soil is Grey-Brown Luvisol with a sandy-loam
161 texture (65 % sand, 25 % silt, and 10 % clay) (Oelbermann & Voroney 2007). A moraine
162 horizon occurs approximately 1 m below the surface.

163

adar study of coarse roots

165

166 Geo-images were collected in a grid (4.5×4.5 m) centred on the base of the tree stem
167 and aligned orthogonally with the tree and crop rows (Fig. 1). Rope attached to opposing
168 sides of frame guided the GPR unit in straight and square transects that were spaced 10
169 cm apart, which equated to 92 GPR transects within each survey area. Geo-images were
170 collected between April and July 2012 using a GPR unit with a centre frequency of 1000
171 MHz (NogginPlus; Sensors and Software Inc., Mississauga, ON, Canada), which was
172 selected to maximize both the resolution of coarse roots (to diameters of 0.5 cm) and the
173 depth of signal penetration (to depths of 50 to 100 cm) (Guo et al. 2013). The average
174 signal velocities were calculated from signal travel time to metal rods at known depths.
175 These were measured on the same day of data collection and signal velocity ranged
176 between 0.08 and 0.1 m ns⁻¹. Volumetric root water concentration was 76 % and
177 volumetric soil water concentration was 12 % (Borden et al. 2014) meeting a contrast
178 requirement for radar signal reflection (Hirano et al. 2009).

179

180 Prior to geo-image analysis, non-root anomalies (e.g. horizontal reflections and signal
181 noise) were minimized by applying a sequence of processing steps (DC shift, dewow,
182 background removal). A spreading and exponential gain filter (SEC2) was applied to

enhance delineation of reflection patterns with depth (EKKO_View Deluxe; Sensors & Software). We maximized the distance between individual trees of the same species at the site, though it is possible a nominal amount of roots from neighbouring trees were measured. Root reflections were visually identified in all geo-images and reflection locations recorded using EKKO_Interp (Sensors & Software).

To assess the level of accuracy of GPR coarse root detection, root locations were compared to identified root reflections in the geo-images. These comparisons were made from a subset of soil profiles (1.0 m wide $\times$ 0.7 m deep) exposed near each tree and matched to GPR transect locations and randomly located at 1, 1.5, or 2.0 m from the tree (Fig. 1). A positive detection was confirmed when a coarse root was found within 0.10 m of detection location, the approximate resolution of the study, and within the detectable angle range of 45° and 135° from the soil profile. We measured the diameter of each root and the depth of the root to the soil surface. When one detected coarse root matched with multiple roots, the largest diameter root was assumed as the positive detection and the smaller diameter root(s) as missed detection(s). When no root was found where an identified reflection was observed in the geo-image, a false detection was recorded.

Root distributions

GPR signal attenuation depends upon the frequency of the GPR unit and the soil conditions. During our study, radar signal attenuation occurred approximately 0.70 m below the surface. On sandy soils co-dominated by *Quercus myrtifolia* and *Quercus*

geminata, Day et al. (2013) applied GPR detected coarse root biomass estimates to a site- and species-specific cumulative curve to account for the relatively small portion of root biomass located between 60 and 100 cm, which was beyond the detectable range of GPR at that site. Similarly, we apply a commonly used root distribution model to extrapolate a fraction of roots to depths beyond that of the maximum detectable roots. The model used was described by Gale and Grigal (1987) and Jackson et al. (1996):

$$Y = 1 - \beta^D \quad (1)$$

where Y is the cumulative proportion of roots at depth (D) and β is the fitted extinction coefficient. Equation 1 assumes there is an asymptotic increase of roots cumulatively with depth and was fitted to detected coarse root data that were pooled in 0.10 m depth intervals. The depth to which 95 % of the roots are located (D_{95}), used as a measure of rooting depth but is not the maximum rooting depth, was calculated using equation 1.

We assumed that roots growing into the crop rows would have the greatest effect on crop root access to soil resources. Therefore, coarse root detections that occurred within the crop rows were separately analyzed for their distribution. Within this zone of competition (Fig. 1), root length per unit soil volume was measured as the architectural trait of the fine, absorptive roots, providing an indicator of soil exploration by fine roots with depth (Pérez-Harguindeguy et al. 2013). Fine roots were collected using soil cores (5 cm diameter) sampled at four depths, 0.10, 0.20, 0.40, and 0.60 m, from exposed soil profiles in the zone of competition (1.0, 1.5, and 2.0 m from the tree stem) (Fig. 1). Fine roots were extracted following Livesley et al. (1999). Dead roots were omitted, characterized by a loss of plasticity and change in colour (dead roots were often very dark). Soil

229 samples were collected prior to the germination of soybean crops, to limit sampling to
 230 tree fine roots in the crop rows. The exception was for *T. occidentalis* which was sampled
 231 last; in this case soybean roots were differentiated as very light in colour and with
 232 distinctive morphology (e.g. with nodules) from the fine roots of *T. occidentalis*. Fine
 233 roots were placed in deionized water and scanned using a flatbed scanner at 600 dpi and
 234 measured for length (WinRHIZO; Regents Instruments, Montreal, Canada). Fine root
 235 length density (FRLD; cm cm^{-3}) was calculated as the ratio of the length of fine roots to
 236 the volume of soil (soil core volume of 100 cm^3). Additionally, a morphological trait,
 237 specific root length (SRL; m g^{-1}), was also calculated as the ratio of total root length by
 238 the dry weight mass of roots, which were measured after being dried in an oven at 65°C
 239 for 48 hours. To also evaluate the potential of using GPR for indirectly describing fine
 240 root distribution by proxy of coarse root detections, the number of coarse roots detected
 241 by GPR were compared to the FRLD at matched depths and study trees.

242

statistical analysis

244

245 Statistical analysis was completed in R version 3.2.4 (R Foundation for Statistical
 246 Computing, Vienna, Austria) and the level of significance was set at $p < 0.05$. GPR
 247 accuracy was calculated as the proportion of correctly identified coarse roots relative to
 248 the total number of exposed coarse roots. Logistic regression tested for the effects of root
 249 diameter, root depth, and species on GPR detection accuracy (1 = detected, 0 = not
 250 detected). For the correlation between GPR-detected coarse roots and FRLD, the inherent
 251 variability of different sampling depths on FRLD was assessed using linear regressions

which tested for main and interactive effects. Analysis of variance (ANOVA) was completed for each summary statistic (mean depth and skewness of the detected coarse roots) across the five species and, when significant, this analysis was followed by Tukey's HSD for pairwise comparisons. Larger positive skewness describes a higher concentration of detected roots nearer the surface and a tail of detected roots with increasing depth, while a skewness value closer to 0 indicates symmetrical distribution of root depths. Parametric assumptions of normality and equal variance were met, based on graphical analyses and the Shapiro-Wilk test. When data did not meet parametric assumptions, Kruskal-Wallis test and post hoc test from the *agricolae* package was used to test for variation among groups, specifically for differences among species or sampling distances and depths for FRLD and GPR accuracy data.

Results

PR root detection accuracy

The locations of 89 coarse roots were correctly identified in the subset of GPR geo-images of a total of 160 actual coarse root locations (true positives) in matched soil profiles. The level of accuracy per study tree was 57.9 ± 3.7 % (mean $\pm$ S.E.; $n = 13$) and when false positives were included was 48.1 ± 3.6 % ($n = 13$). The number of false positives occurred relatively evenly through the soil profile and did not vary significantly among depth intervals determined from the non-parametric Kruskal-Wallis test ($p = 0.69$), and were thus assumed to have a marginal effect on estimates of relative coarse

275 root distributions. Logistic regression of GPR detections and missed detections indicated
 276 significant differences in detection accuracy related to root depth ($p = 0.012$) and root
 277 diameter ($p < 0.001$). To illustrate, in the top 0.50 m of soil the accuracy of coarse root
 278 detection was $60.3 \pm 3.6 \%$ ($n = 13$) opposed to an accuracy of $35.2 \pm 14.8 \%$ ($n=9$) for
 279 coarse roots between 0.50 and 0.70 m depths. Larger coarse roots (≥ 1 cm) were more
 280 successfully detected by GPR with an accuracy of $83.5 \pm 5.8 \%$ ($n = 12$), opposed to an
 281 accuracy of $49.8 \pm 4.8 \%$ ($n = 13$) for small coarse roots (< 1 cm). Once root size and
 282 depth effects were accounted for, there were no significant effects of tree species in
 283 logistic regression analyses.

284

285 Fine roots are assumed to be undetectable by GPR. As an indirect method of detecting
 286 fine roots, we found that the number of coarse roots detected by GPR explained only 11%
 287 of the variation of FRLD ($n = 52$; $p = 0.02$). However, root distribution is a highly depth-
 288 dependent process and sampling depth was found to be a strong predictor of FRLD ($r^2 =$
 289 0.55 ; $p < 0.001$). Furthermore, including both depth and coarse root quantity as predictors
 290 revealed a significant main effect of depth only ($p < 0.001$), with no significant
 291 interaction effect (depth $\times$ coarse roots) ($p > 0.05$).

292

Whole plant coarse root architecture

294

295 The vertical distribution of coarse roots showed significant variation among species in
 296 terms of the mean depth of detected coarse roots ($p = 0.009$; Table 1). Skewness
 297 measures showed no significant differences among species, but ranged from 0.21 ± 0.16

298 for *J. nigra* and 0.68 ± 0.19 for *Populus* sp. (Table 1). Fitted β values were calculated
 299 from equation 1 using species' means of pooled detected coarse roots in 0.10 m depth
 300 increments. The rooting depth at which 95 % of roots are located (i.e. D_{95}) of all species
 301 ranged between 0.52 and 0.95 m (Table 1).
 302
 303 Of the deciduous species, *Populus* sp. had a shallower coarse root distribution with a
 304 mean detected coarse root depth of 0.22 ± 0.01 m and a lower β (0.958) leading to a D_{95}
 305 of 0.70 m (Table 1). The coarse roots of *P. abies* followed a similar vertical distribution
 306 pattern to *Populus* sp. in terms of mean detected coarse root depths (0.21 ± 0.02 m) and
 307 D_{95} (0.70 m) (Table 1). However, *P. abies* had a slightly more symmetric distribution,
 308 indicated by a lower skewness (0.43 ± 0.08) (Table 1). There was a prominence of coarse
 309 roots (approximately 67 %) between 0.10 and 0.30 m for both *P. abies* and *Populus* sp.
 310 (Fig. 2). *Q. rubra* and *J. nigra* had a lower dominant zone of coarse roots which was less
 311 pronounced, with 53 and 55 %, respectively, of coarse roots located between 0.20 and
 312 0.40 m (Fig. 2). *J. nigra* and *Q. rubra* had the deepest root systems with mean detected
 313 root depths of 0.29 ± 0.01 and 0.29 ± 0.02 m and D_{95} of 0.95 m (Table 1). *T. occidentalis*
 314 was distinctly the most shallow-rooted tree species with a mean detected coarse root
 315 depth of 0.17 ± 0.02 m and a D_{95} of 0.52 m (Table 1). Its high skewness (0.65 ± 0.15 ;
 316 Table 1) indicates a high concentration of roots near the soil surface, specifically there
 317 was a high proportion of coarse roots (45 %) detected between 0.10 and 0.20 m (Fig. 2).
 318

coarse and fine root distribution in the zone of competition

320

In the crop rows, the mean depth of detected coarse roots varied among tree species, but only the mean depths of detected coarse roots of *T. occidentalis* and *J. nigra* were significantly ($p = 0.031$) different at 0.18 ± 0.03 and 0.30 ± 0.02 m respectively (Table 2). *J. nigra* and *Q. rubra* had the deepest detected coarse roots in the zone of competition with a mean depth of detected coarse roots of 0.30 ± 0.02 and 0.27 ± 0.03 m, respectively (Table 2). The deeper root profiles for these two species led to a higher β (0.969 and 0.963, respectively) and deeper D_{95} (0.95 and 0.80 m, respectively) (Table 2). The coarse roots of *Populus* sp. and *P. abies* were moderately deep in the crop rows, with a D_{95} of 0.74 and 0.66 m, respectively (Table 2). D_{95} of coarse roots in the zone of competition (Table 2) closely matched D_{95} values for the entire tree (Table 1), with less than 10 cm differences. *Q. rubra* showed the largest divergence in these values; a D_{95} of 0.82 m in the zone of competition (Table 2), compared to a D_{95} of 0.95 m for the entire coarse root system (Table 1).

Fine root densities varied significantly among species at each sampling depth ($p < 0.01$; Fig. 3). There was no significant variation of FRLD among sampling distances following a Kruskal-Wallis test ($p > 0.05$). Generally, the highest concentrations of fine roots were found at the 0.10 m and 0.20 m sampling depths. *P. abies* and *Populus* sp. had the highest FRLD (2.99 ± 0.57 and 2.75 ± 0.35 (mean $\pm$ S.E.) cm cm^{-3} , respectively) at 0.10 m depth (Fig. 3). FRLD consistently declined with sampling depth for all species. The largest decline in FRLD with increasing depth occurred for *P. abies* with a reduction of FRLD between the 0.20 and 0.40 m sampling depths of 84 % (Fig. 3). At 0.60 m depth, *Populus* sp., *Q. rubra*, and *P. abies* had the highest FRLD of 0.56 ± 0.13 , 0.33 ± 0.07 , and $0.24 \pm$

0.06 cm cm⁻³, respectively (Fig. 3). *T. occidentalis* had significantly less FRLD than the other species at all sampling depths, except at 0.10 m (Fig. 3). *T. occidentalis* also showed significantly lower SRL (21.4 ± 3.4 m g⁻¹; mean $\pm$ S.E.) than the other tree species following significant ANOVA ($p < 0.001$) and Tukey's honest significance test. There were no significant differences of SRL among the other tree species, although *J. nigra* had the highest SRL (69.7 ± 7.4 m g⁻¹) followed by *Q. rubra*, *Populus* sp., and *P. abies* (55.1 ± 5.0 , 51.0 ± 4.7 , and 46.0 ± 7.7 m g⁻¹, respectively).

Discussion

Methodological considerations to advance the study of root systems

More than half of the coarse roots in exposed soil profiles were correctly identified by GPR; with improved accuracy for larger coarse roots and roots at shallower depths. Signal resolution dictates that smaller coarse roots are less likely to be detected by GPR than larger coarse roots and radar signal attenuation limits the detection of coarse roots with increasing depth (Butnor et al. 2001; Hirano et al. 2012; Guo et al. 2015). Therefore, given consistent moisture contents and soil texture, inaccuracies in the GPR data can be largely attributed to reduced signal:noise ratio in deeper and smaller roots. In our study, the detection accuracy for coarse roots larger than 1 cm in diameter was almost twice the level of accuracy for coarse roots less than 1 cm in diameter. Hirano et al. (2012), in their study of *Pinus thunbergii* coarse roots on sandy soils in Japan (the only other in-field study to report similar accuracy data), reported a dramatic improvement in detection

accuracy from 6.6 % for coarse roots less than 1 cm in diameter to 54.4 % for roots larger than 1 cm. Differences in detection frequencies among studies can be attributed to variations in substrate and biotic conditions required for optimal GPR detection of tree roots, and to instrumentation, but also to experimenter bias, as a higher frequency of identified detections might occur simultaneously with an increase in false positives.

While advancements have been made towards developing an automated tool to describe coarse root architecture based on GPR data (e.g. Wu et al. 2014; Li et al. 2016), in-field application and root identification still requires supervised analysis steps. As emphasized in other recent studies (e.g., Guo et al. 2015), field-based accuracy assessments will better inform the experimenter of any bias and possible need to compensate during analysis.

Since tree root studies rarely sample to the maximum root depth due to methodological challenges, it is also appealing to describe less-accessible roots based on measurable root distributions (Schenk and Jackson 2002). To address the under-representation of deep roots detected by GPR (in this study, those deeper than 0.70 m), a root distribution curve was applied to extrapolate the distribution data to lower depths. D_{95} values calculated during this study were shallower than 1 m for all species, which supports the assertion that root systems are predominately located in the upper 1 m of soil (Jackson et al. 1996).

While we did not sample to the maximum rooting depth of the study trees in this study, and thus the calculated D_{95} values might be underestimated, a companion study that completely excavated the same study trees (Borden et al. 2014) observed few roots growing beyond the moraine till located approximately at 1 m depth. The restrictive subsurface could be a main determinant of rooting depth at this site (Stone and Kalisz

1991). However, when there is a high proportion of deep roots, our approach would not be appropriate for two reasons: i) GPR is limited in detecting deep coarse roots, the depth of which varies according to GPR frequency and site conditions, and ii) the proportion of roots with depth may not follow the cumulative curve (e.g. phreatophytes) (Zhang et al. 2013). Complete excavations of deep roots systems in conjunction with GPR assessments would be necessary to fully explore this issue.

coarse root architecture of trees in temperate intercropping systems

We found interspecific variation of coarse root architecture among same-aged tree species in a temperate agricultural system. Notably, there were identifiable differences in rooting depth, characterized by D_{95} , and vertical rooting pattern, characterized by relative root distribution, skewness, and the cumulative root curve (β). If roots are more evenly and deeply distributed in the profile, the cumulative proportion of roots will increase less rapidly with depth and the resultant β value will describe a more gradual asymptotic curve (i.e. higher β values) (Gale and Grigal 1987; Jackson et al. 1996; Gwenzi et al. 2011). In the present study, the shade tolerant *T. occidentalis* had the lowest β value, with many superficial coarse roots and high skewness, characteristic of its late-successional and slow-growing status. *P. abies* and *Populus* sp. had moderately deep coarse root systems. *P. abies* is known to have many lateral roots in surface soils (Puhe 2003), and is also associated with late-successional forests. While *P. abies* is reported to have roots that can grow below 2 m (Stone and Kalisz 1991; Puhe 2003), with maximum root depth variable according to soil conditions (i.e. texture and moisture levels), on sandy loam

soils it was found that this species had a majority of its roots located in the top 1 m (Puhe 2003). The fast-growing *Populus* sp. was the largest tree species (at the time of measurement) included in the present study. *Populus* hybrids generally have extensive lateral root systems, and prolific root systems are documented in agroforestry systems (Mulia and Dupraz 2006; Plante et al. 2014). *Populus* sp. in this study is a hybrid of the shade-intolerant species *Populus deltoides* and *P. nigra*; its early successional status would make rapid and deep root growth advantageous (Gale and Grigal 1987). Although *Populus* sp. at this study site had deep coarse roots, it also displayed a relatively high concentration of roots near the surface compared to the two other deciduous species.

The other deciduous species, *J. nigra* and *Q. rubra*, which are shade intolerant and mid-tolerant, respectively, had a prominence of coarse roots at lower depths (between 0.20 and 0.40 m depth). This type of root distribution might be beneficial to access soil resources from various depths earlier in forest succession. Both species are known to have pronounced taproots and had the deepest roots among the study trees. *Quercus* spp. are known to have particularly deep root systems that can access deep water in xeric environments (Canadell et al. 1996). At a TBI system in Indiana, USA, on silty loam soils, complete excavation of *J. nigra* and *Q. rubra* revealed root systems to 0.90 m (Jose et al. 2001), which is similar to the D₉₅ values reported in our study (0.95 m). Although the trees at the Indiana site were younger (10 years old), they grew in less constrained soils (silt loam subsoil to ~1.75 m) (Jose et al. 2001).

tree root distribution and potential competitiveness in a tree-based intercropping system

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438 Root studies conducted in TBI or alley cropping systems often target the tree-crop
439 interface and have typically included measures of the absorptive fine roots such as FRLD
440 (e.g. Livesley et al. 2000; Bouttier et al. 2014). In our study, to further assess tree-crop
441 interactions we sampled live tree coarse and fine roots within a 1 to 2 m zone from the
442 tree rows, an active zone of competition with crops (Thevathasan and Gordon 2004)
443 where suppression of crop yield has been reported (Gillespie et al. 2000; Miller and
444 Pallardy 2001; Thevathasan and Gordon 2004; Reynolds et al. 2007). In this zone of
445 competition, all tree species, except for *T. occidentalis*, had a D₉₅ that were below 0.60
446 m, indicating that many deeper lateral roots extended into the crop rows, which might
447 reduce belowground competitive interaction with crops.

448

449 Despite the presence of deep roots and the potential for complementary acquisition of soil
450 resources with crops, *Populus* sp. in particular demonstrated high competitive traits in the
451 crop rows: a high concentration of coarse and fine roots in shallow soils (above 0.30 m).
452 Mulia and Dupraz (2006) speculated that fast growing *Populus euramericana* cv. I214,
453 with earlier leaf phenology rapidly colonized surface soils prior to crop growth, when soil
454 moisture in topsoil is still high. In the present study, which is representative of early-
455 season conditions, there was high and relatively consistent FRLD for *Populus* sp. at 0.10
456 and 0.20 m sampling depths. At the same study site, Link et al. (2015) using stable
457 isotope analysis ($\delta^{18}\text{O}$) found this species acquired soil water predominantly from 0.20 m

in the soil profile early in the growing season. Interestingly, later in the growing season *Populus* sp. acquired more water from lower in the soil profile but overall water uptake seemed to occur throughout the soil profile (0 to 0.70 m) (Link et al. 2015). In response to crop competition, *Populus* hybrids have shown limited stratified fine root distributions with crop roots within the top 0.30 m of soil compared to *Quercus rubra* (*Populus deltoides* × *nigra* DN3333 and DN3570; Bouttier et al. 2014) and compared to *Juglans* hybrid (*Populus euramericana* cv. I214; Mulia and Dupraz 2006). More research with higher repetitions is required to assess the degree of intraspecific plasticity for *Populus* hybrids given shifting resource demands during the crop growing period.

Both of the coniferous species examined had relatively high concentration of shallow roots, which would likely increase root overlap with crop rooting zones. Similarly, Plante et al. (2014) showed that 2 m into the cropping area in a temperate windbreak system fine and coarse roots of *Picea abies* and *P. glauca* were predominately located in sandy loam topsoil (0 to 0.30 m). In a forest study on silt loam soils, *P. abies* fine roots were mainly above 0.30 m grown in either monoculture or in mixture with a potential competitor (*Fagus sylvatica*) (Bolte and Villanueva 2006). The smaller and shallow-rooted *T. occidentalis* showed a potentially similar rooting profile to that of herbaceous crops. However, we found this smaller tree species to have a low coarse and fine root density in the crop row in conjunction with low SRL, suggesting a low competitive threat to crops despite its shallow root system.

J. nigra had the deepest coarse roots in the cropping area ($D_{95} = 0.98$ m) followed by *Q. rubra* ($D_{95} = 0.80$ m). These two species also had less coarse and fine root density in shallow soils compared to *Populus* sp. and *P. abies*. However, the SRL of *J. nigra* and *Q. rubra* were higher than for the other species. Link et al. (2015) found that active early growth fine roots of *J. nigra* acquired water at 0.10 m, but that this activity was lower in the soil profile (0.40 to 0.70 m) later in the season with high crop growth. Variation in root morphological traits (e.g. SRL) can modify resource acquisition patterns in a soil profile, with competitive exclusion potentially inducing root distributions that are more complementary. In southern France on sandy and silty alluvial soils, a *Juglans* hybrid displayed deeper root systems when grown with durum wheat (*Triticum turgidum* L. subsp. *durum*) compared to tree-only stands (Mulia and Dupraz 2006; Cardinael et al. 2015). Similarly, on silt loam and clay loam soils the fine root distribution of *Q. rubra* showed a tendency to stratify with adjacent crop roots in the top 0.30 m of soil (Bouttier et al. 2014). In Indiana, USA, *Q. rubra* and *J. nigra* had a high density of roots at similar depths as the adjacent crops, specifically above 0.30 m (Jose et al. 2001); however, root distribution was not differentiated within that depth class (0 to 0.30 m), where some stratification of roots could occur. The results from our study showed differences in coarse and fine root distributions among the study species within the 0 to 0.30 m soil depth, which could correspond to important differences for shared soil resources with crops.

Conclusions

We used a combination of physical and non-destructive sampling to describe tree root architectural traits. We found interspecific variation of temperate tree root depth and distribution under herbaceous crop cultivation on sandy loam soils. A *Populus* hybrid and *Picea abies* showed more competitive architectural root traits, while *Juglans nigra* and *Quercus rubra* showed more complementary root distribution patterns in association with crops. Quantifying tree rooting patterns of relevance to management objectives can be useful in species selection for TBI systems. More research is required to discern intraspecific plasticity of belowground tree root traits over time and to determine the effect of cultivation practices on tree root system architecture. Describing belowground architecture in species- and context-specific terms can better capture functional differences associated with vegetative structure in TBI systems.

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Figure captions

Figure 1: Study design for tree root study in a TBI system at the University of Guelph Agroforestry Research Station, Canada. The survey area (4.5×4.5 m) was centered on each study tree and subsurface data were collected using ground penetrating radar, pictured here for *Quercus rubra* (a). Ninety-two GPR transects were collected within each survey area, outlined in black, and accuracy of root detection was assessed at exposed 1 m wide soil profiles, indicated by the solid double line (b). To assess the zone of competition with crops, coarse roots detected by GPR were isolated for those only under the crop rows and fine roots were collected at multiple depths distances, indicated by solid black circles (b)

Figure 2: Mean GPR-detected coarse roots by 0.10 m depth intervals for each species ($n=3$, except *Populus* sp. and *Picea abies* $n=2$). Bars represent standard error of the mean

Figure 3: Fine root length density (FRLD; cm cm^{-3} ; mean $\pm$ S.E.) at four sampling depths in crop rows ($n = 18$ except $n = 12$ for *Populus* sp. and *P. abies*). Comparisons are made across five tree species in a temperate TBI system. Same letters represent non-significant

723 differences among species at each sampling depth using non-parametric multiple
724 comparisons with Kruskal-Wallis test ($p < 0.05$)

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745 **Table 1:** Distribution of coarse roots of five temperate tree species in a TBI system. Summary statistics (mean $\pm$ S.E.) of coarse roots
 746 detected by GPR followed by the cumulative root distribution coefficient (β) from the equation $Y = 1 - \beta^D$ and resulting projected
 747 depth of 95% of roots (D_{95}) are shown

Species	Depth of coarse roots detected by GPR		Modelled root distribution	
	Mean (m)	Skewness	β	D_{95} (m)
<i>Thuja occidentalis</i>	0.17 $\pm$ 0.02 a	0.65 $\pm$ 0.15	0.944	0.52
<i>Picea abies</i>	0.21 $\pm$ 0.02 a	0.43 $\pm$ 0.08	0.958	0.70
<i>Populus deltoides</i> $\times$ <i>nigra</i> DN177	0.22 $\pm$ 0.01 ab	0.68 $\pm$ 0.19	0.958	0.70
<i>Quercus rubra</i>	0.29 $\pm$ 0.02 b	0.44 $\pm$ 0.04	0.969	0.95
<i>Juglans nigra</i>	0.29 $\pm$ 0.01 b	0.21 $\pm$ 0.16	0.969	0.95

748 Letters following values within parameter sections represent statistically significant differences in the same column among the tree
 749 species (Tukey's test, $p < 0.05$, $n=3$, except $n=2$ for *Populus* sp. and *P. abies*)

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754 **Table 2:** Distribution of coarse roots detected within the zone of competition (2 m into crop row). Summary statistics (mean $\pm$ S.E.) of
755 coarse roots detected by GPR followed by the cumulative root distribution coefficient (β) from the equation $Y = 1 - \beta^D$ and resulting
756 projected depth of 95% of roots (D_{95}) are shown. These data represent of subset of total tree root system data presented in Table 1 but
757 are isolated for their location in the crop rows

Species	Depth of coarse roots detected by GPR in crop row		Modelled root distribution in crop row	
	Mean (m)	Skewness	β	D_{95} (m)
<i>Thuja occidentalis</i>	0.18 $\pm$ 0.03 a	0.26 $\pm$ 0.55	0.946	0.54
<i>Picea abies</i>	0.20 $\pm$ 0.01 ab	0.60 $\pm$ 0.49	0.956	0.66
<i>Populus deltoides</i> $\times$ <i>nigra</i> DN177	0.22 $\pm$ 0.03 ab	0.58 $\pm$ 0.00	0.961	0.74
<i>Quercus rubra</i>	0.27 $\pm$ 0.03 ab	0.49 $\pm$ 0.22	0.964	0.82
<i>Juglans nigra</i>	0.30 $\pm$ 0.02 b	0.21 $\pm$ 0.16	0.970	0.98

758 Letters following values within parameter sections represent statistically significant differences in the same column among the tree
759 species (Tukey's test, $p < 0.05$, $n=3$, except $n=2$ for *Populus* sp. and *P. abies*

760