Assessment of Root System Development among Four Ornamental Tree Species through Time via X-ray Computed Tomography

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Abstract. Tree root systems are inherently dynamic in their distribution within a soil volume. Analysis of tree root system space occupation through time can improve not only our implicit understanding of a virtually hidden portion of a plant, but influence future management decisions through a more thorough understanding of root placement within a soil volume. We compared root standing crop populations of four ornamental tree species including *Acer rubrum* L. ‘Franksred’ (*Acer*), *Carpinus betula* L. ‘Columnaris’ (*Carpinus*), *Gleditsia tricanthos* L. var. *inermis* ‘Skycole’ (*Gleditsia*), and *Quercus rubra* L. ‘Rubrum’ (*Quercus*) grown in a nursery mix substrate within large 57-L containers using an X-ray computed tomography (CT) approach through time. Individual root identification was performed manually on two-dimensional slices of CT scans. Our data show high variation in species total root number through time with *Carpinus* exhibiting the largest root population throughout the study period. However, species exhibited differences in root distribution patterns as exemplified by the shallow and horizontally more uniform rooting pattern of *Acer* in comparison with the highly plastic root distribution in space through time in *Gleditsia*. Root frequencies within 1-mm root diameter class distributions shifted by species with the most drastic differences found between high frequencies of relatively small diameter roots in *Acer* vs. pronounced shifts in dominate root diameter size class as found in *Gleditsia* and lesser so in *Carpinus* during a growing season. Our findings demonstrate differences in whole tree root systems space occupation non-destructively through time and highlight a disparity in how species fill a container volume during growth.

The spatial arrangement of tree roots within the soil volume remains largely obscure despite the critical roles that roots play in both tree stability and resource uptake. Countless studies have focused on a plant’s (Doussan et al., 2003; Fitter, 1987; Guo et al., 2011; Pierret et al., 2007) and in some cases on a tree’s root architectural or morphological factors in response to the soil environment (Comas and Eissenstat, 2004; Pregitzer, 2002). Rightly so, root system morphology

and spatial distribution influence a tree’s ability to forage for resources and are essential to a tree’s stability, an important factor in landscape management (Richardson-Calfee et al., 2010; Struve, 2009), agroforestry, and silvicultural practices (Coutts, 1983; Danjon et al., 1999).

Variation naturally occurs in closely related species and can be observed in the intrinsic structural development of a species’ root system (Malamy, 2005). Root exploration and space occupation within the soil volume are largely dictated by the root system’s architecture and morphology. These indices include variables such as root length and diameter, vertical and lateral root expansion, and branching structure (Hodge et al., 2009). Within a woody perennial root system, both the coarse woody roots and fine “feeder” root fractions contribute to these indices. Spatial allocation of a tree’s coarse woody roots is widely accepted as a centrally located root mass (Millikin and Bledsoe, 1999; Ouimet et al., 2008) or a shallow plate extending beyond the canopy dripline (Thomas, 2000) despite a lack of observation for most species (Yanai et al., 2008). However, reports on non-woody and fine root placement is highly variable within a three-dimensional soil volume and has resulted in less than consistent

results with studies indicating fine root distribution as centrally concentrated (Leuschner et al., 2001; Yanai et al., 2006) or horizontally even (Millikin and Bledsoe, 1999).

A tree’s root system can be classified a number of ways depending on the level of detail required for study. Experiments range from whole root system biomass to anatomical analysis of individual root segments (Guo et al., 2008; Valenzuela-Estrada et al., 2008). Variations in root function are tightly linked to coarse vs. fine root proportions in the simple sense in that coarse roots of larger diameter and higher order provide structural support, whereas finest roots, primarily of first and second order (usually classified as less than 2 mm), function in water and nutrient uptake. Root diameter classification by class is often an approximation (Pregitzer et al., 2002; Valenzuela-Estrada et al., 2008) and does not represent precise root function as once thought (Guo et al., 2008). Nonetheless, root diameter serves as a means to quantify root distribution through space and time (Danjon and Reubens, 2008) and allows for a whole root system analysis that would be time-prohibitive with an anatomical or root order analysis.

Belowground approaches and protocols for studying root development and architecture are confined by methodological challenges of studying tissues embedded in an opaque substrate matrix. Techniques such as rhizotrons, minirhizotrons, root-exclusion tubes, and ground-penetrating radar have dramatically improved our understanding of root growth (Fang et al., 2012). However, improvement in root sampling methodology must bypass the limitation of highly disruptive root excavation, viewing roots on planar surfaces, and resolution restrictions of bulk-imaging techniques. Recent non-destructive in situ methodologies for studying roots and root systems embedded within a medium currently include magnetic resonance imaging, laser, and ultrasound options (see Fang et al., 2012 for a comprehensive review).

High-resolution X-ray CT scanning offers spatiotemporal imaging of root development (Lontoc-Roy et al., 2006; Tracy et al., 2010). Primary complexities with this method include root organ (root branch) visualization resulting from similarities between the attenuation coefficient of root tissue and organic matter (Fang et al., 2012). Studies to date use large-particle substrate types comprised largely of sand (Kaestner et al., 2006; Perret et al., 2007) and small sampling volumes (Flavel et al., 2012; Pierret et al., 2002; Tracy et al., 2010) as a means to optimize root system visualization. Root visualization through X-ray CT has undergone a number of advances since its first inception by Watanabe et al. (1992) including improvements in pixel resolution, signal noise ratios, and programs available for image slice stacking to produce a three-dimensional sample segmentation (Dhont et al., 2010; Perret et al., 2007) and root tracking (Mairhofer et al., 2012). Although these improvements to the field of CT technology are necessary to advance the field, there remains a lack of replicated studies on the

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development of tree root systems and the use of growing medium that more closely resembles a “natural” soil. Moreover, we are only aware of two studies that used CT technology to examine the change in root systems through time. Tracy et al. (2012) observed tomato (*Solanum lycopersicum* L.) and Gregory et al. (2003) observed wheat (*Triticum aestivum* L. cv. Charger). However, both experiments used extremely young plant material on the scale of a few days old, and the experiments also were relatively short-lived (maximum of 10 d).

Our main aim was to use a non-destructive method to visualize and quantify perennial woody root systems in a growing medium. Specifically, we wanted to shed light on species differences in root system development and production through time and space among economically important shade tree species of a caliper that is common within nursery production and typical for planting in landscapes and urban environments (Watson, 2005). Root growth and developmental patterns have clear implications on how we water, fertilize (Danjon et al., 2007), and manage trees in containers and potentially influence on urban and forest tree stability and performance.

Materials and Methods

Plant material and growing conditions.

Four nursery tree species with varying root system morphologies were selected for this study: *Acer rubrum* L. ‘Franksred’ (*Acer*), *Carpinus betula* L. ‘Columnaris’ (*Carpinus*), *Gleditsia tricanthos* L. var. *inermis* ‘Skycole’ (*Gleditsia*), and *Quercus rubra* L. ‘Rubrum’ (*Quercus*). Three 2-year-old liner replicate trees ($n = 3$) were transplanted in April of 2010 into 57-L pots (44 cm wide $\times$ 38 cm deep) containing a mixture of 71% pine bark, 21% peatmoss, 7% sterilized regrid potting soil, and 1% 12N–0P–34.9K slow-release fertilizer (Agrozz Inc., Wooster, OH). Substrate physical properties were 56.3% water-holding capacity, 10.7% air space, 67% total porosity, and a bulk density of $0.35 \text{ g}\cdot\text{cm}^{-3}$. Before the experiment initiation, trees were grown in the same growing medium to prevent large shifts in the rooting environment. Mean caliper and height for each species at the end of the experiment were: *Acer*, 2.3 cm, 1.97 m;

Carpinus 2.5 cm, 1.32 m; *Gleditsia* 2.7 cm, 2.12 m; and *Quercus* 2.8 cm, 2.22 m. Trees were arranged in a completely randomized block design and placed 1.6 m on center apart in in-ground socket containers lined with gravel for drainage, i.e., a pot-in-pot system at the Blue Grass Lane field experimental site, Ithaca, NY. Weather conditions were typical for the northeast United States (Fig. 1). Fertilizer was top-dressed one time at the beginning of the growing season (18N–2.2P–7.5K, Osmocote Classic; Scotts, Marysville, OH). Tree containers were irrigated using one 360° spray stake per pot (Netafilm Inc., Israel) positioned ≈ 5 cm from the outer edge of the container. Trees were irrigated twice a day at 600 and 1800 HR for a total of 4 L of water per container per day. Volumetric water content (VWC) was checked weekly with a handheld Theta Probe (Dynamax Inc., Houston, TX) and remained between 35% and 42%.

X-ray computed tomography. All tree replicates were transported to the Cornell Veterinary Hospital three times (May, July, and September) during the 2010 growing season where they were scanned using X-ray CT (Toshiba Aquilion 16-slice large-bore CT scanner, Tustin, CA) with a 16 mm $\times$ 0.5-mm quantum detector. Containers and thus the trees were carefully placed horizontally on the scanner bench, secured with foam cubes, and aligned with pre-placed markings to ensure consistent and repeatable container image positioning before moving through the X-ray plane. Each tree was scanned for ≈ 5 min at a voxel (volumetric pixel) size of 1 mm $\times$ 1 mm $\times$ 1 mm at 120 kVp and 100 mA. The field of view was filled with the sample to eliminate differences in beam intensity. Soft tissue settings were selected from the pre-installed Toshiba Aquilion software to provide the highest level of root detection from the surrounding substrate. One full 360° scan with 1-mm slices in both the horizontal and vertical directions per tree replicate was imaged during each scanning session and saved as a raw volume.

Raw two-dimensional reconstructed CT slice images (DICOM) of scans were loaded into Carestream Vue solutions software Version 11.3.2.0220 (Carestream Health Inc., Rochester, NY) to normalize viewing

areas. Three concentric rings resulting in four areas of 63.6 cm², 190.9 cm², 318.1 cm², and 445.3 cm² were superimposed onto the projection images to provide user orientation (Photoshop Version CS6; Adobe Systems Inc., San Jose, CA) (Fig. 2). Ring 1 refers to the innermost location within the container and Ring 4 to the outermost location within the container. For every 25 image slices from the stack of CT scans (≈ 2.5 -cm depth increments), we selected a CT slice to count total number of roots present and to measure root diameter (Image J; National Institutes of Health, Bethesda, MD; <http://rsb.info.nih.gov/ij/>) (Fig. 3). As a result of the large amount of time needed to manually measure root diameter, if more than 20 roots were present within the slice, then a subsample of 20 random roots was selected for diameter measurements. Root material was visually resolved from the soil matrix by three classifications: 1) root tissues resulted in a higher attenuation (i.e., lighter gray) pixel classification compared with the growing medium or air; 2) the area of interest “root” was continuous through several image slices and circuitous in its orientation, unlike the determinate pine bark material, for example; and 3) the object of interest followed a cylindrical shape through multiple CT slices. Final data output was standardized by area to allow for comparison across concentric rings.

Statistical analysis. To account for differences in vertical sampling area, concentric ring areas were standardized to the largest area (445.3 cm²). Root standing crop (no. of roots per sampling time) met the assumptions of normality and were analyzed using analysis of variance (ANOVA) with the three depth increments (0 to 12 cm, 12 to 24 cm, and 24 to 38 cm) analyzed as a fixed factor and month as a covariate in the model (SPSS Inc. Version 12.0, Chicago, IL). Subsequent least significant difference post hoc tests were used to

Fig. 1. Biweekly means of meteorological data over the course of the study (May to September 2010). Mean air temperature (°C) is represented by the black circles, and mean precipitation (mm) is represented by the gray bars.

Fig. 2. Schematic diagram representing four concentric rings (1 to 4) and three depth intervals (1 to 3) [Depth 1 (0 to 12 cm), depth 2 (12 to 24 cm), and depth 3 (25–38 cm) used for root distribution assessment of computed tomography (CT) scans]. Root number and diameter were measured every 25 image slices, ≈ 2.5 cm.

Fig. 3. Representative two-dimensional (2D) slices of projection images of roots within a 57-L container for the 3 months of the study period (May, July, September) (example taken from *Gleditsia* at 20-cm depth). Three concentric rings resulting in four areas of 63.6 cm², 190.9 cm², 318.1 cm², and 445.3 cm² were superimposed onto the projection images. Image slices were used to count total number of roots present and to measure root diameter as indicated by the hatch marks present on counted roots.

determine differences between species. Root diameter classes were analyzed by comparing root diameter class distributions in 1-mm intervals (0 to 0.99 mm, 1 to 1.99 mm, 2 to 2.99 mm, 3 to 3.99 mm, and 4 mm or greater) among species and by depth (vertical) and ring (horizontal) space for our three sampling times (May, July, and September) using PROC FREQ (SAS Institute Inc., Cary, NC). In the event that more than two variables were examined, a Cochran-Mantel-Haenszel statistic was used to adjust for the effect of the third variable. More detailed analysis on the distribution of “fine” roots 2 mm or less in diameter were performed in a four-factor ANOVA with month, depth, ring, and species analyzed as fixed factors. Before analysis, data were log-transformed to meet the assumptions of equal variance.

Results

Total root standing crop. Total root standing crop differed among tree species ($P = 0.003$) with *Carpinus* having 2- to 4-fold more roots than other species (Fig. 4). Depth ($P < 0.001$), month ($P < 0.001$), species $\times$ depth interaction ($P < 0.001$), and species $\times$ depth $\times$ month ($P = 0.014$) were also significant within the model. Root diameter class distribution analysis revealed species differences within each of the three months of this study, May ($P < 0.001$), July ($P < 0.001$), and September ($P < 0.001$) (Fig. 5). Relatively few roots were located in the first diameter class (less than 1 mm), a direct result of the resolution capacity of the CT scanner.

Vertical distribution of root standing crop. Species differed in the depth distribution of their roots ($P < 0.001$) with a significant interaction between species $\times$ month $\times$ depth ($P = 0.017$). Sites of greatest root production depended on species ($P < 0.001$) with *Acer* and *Carpinus* having the greatest proportion of total root standing crop in the top substrate layer (0 to 12 cm) and *Gleditsia* and *Quercus* produced the greatest total root

Fig. 4. Total root standing crop for four ornamental tree species *Acer*, *Carpinus*, *Gleditsia*, and *Quercus* for three sampling points through the growing season (May, black bars; July, striped bars; and September, hatched bars) in 2010 (± 1 SE). Differences in total root standing crop across the four tree species was significant ($P = 0.003$).

standing crop in the 12- to 24-cm substrate zone (Fig. 6). *Quercus* had the greatest total root standing crop within the central substrate depth (depth interval 2, Fig. 2) in May, likely a result of the large woody root mass associated with this species. Across all species, very few fine roots grew in the deepest substrate layer. However, by the end of the experiment (September), *Acer* and *Carpinus* maintained a greater proportion of total root standing crop in the top 12 cm of the substrate profile. *Quercus*, on the other hand, produced the most roots in the middle substrate layer (12 to 24 cm), and *Gleditsia* shifted its root production the deepest substrate layer (24 to 38 cm).

Vertical and temporal root distribution of diameter classes. Within the entire root population, the distribution of roots within the five root diameter classes varied greatly among species for May ($P < 0.001$), July ($P < 0.001$), and September ($P < 0.001$). In May, *Gleditsia* and *Acer* exhibited the two extremes in their diameter class distribution

with *Gleditsia* having the majority of its roots in the largest diameter classification (4 mm or greater) and *Acer* in the 1- to 2-mm diameter range (Fig. 5). *Carpinus* grew the majority of its roots in the 2- to 3-mm diameter class with an almost bell-shaped curve distribution within other diameter classifications. *Quercus* on the other hand had a bimodal root diameter distribution with large fractions of its roots falling into either 1 to 2 mm or 4 mm or greater classifications. By July all species, except *Gleditsia*, maintained similar patterns of root diameter class distributions. Root diameter class distribution in *Gleditsia* shifted toward a much more even distribution of roots within all diameter classes except the finest root fraction (less than 1 mm). In September, again, similar patterns were found among species with the exception of *Gleditsia*. *Gleditsia* produced two times more roots in the 1- to 2-mm diameter class fraction compared with the three other species.

Closer examination of differences in diameter class vertical distribution among

Fig. 5. Percentage of roots present in May, July, and September for four ornamental tree species (*Acer*, *Carpinus*, *Gleditsia*, and *Quercus*). Diameter classes are in 1-mm intervals (i.e., diameter class one represents roots from 0 to 0.99 mm) with the exception of diameter class five, which represents all roots 4 mm or greater.

Fig. 6. Vertical distribution of the population of roots (standing crop) expressed as percent of root produced in each soil depth/total root production for that species (± 1 SE) for *Acer* (black squares), *Carpinus* (white squares), *Gleditsia* (black circles), and *Quercus* (white circles) tree species over three soil depths. Depth 1 (0 to 12 cm), depth 2 (12 to 24 cm), and depth 3 (25 to 38 cm).

species in the coarse woody root fraction (4 mm or greater) revealed significant differences in diameter class depth distributions over time (May, $P < 0.001$; July, $P < 0.001$; September, $P = 0.008$). Similar to total root standing crop results, *Acer* and *Carpinus* increased their proportion of woody roots in the shallow substrate layer, whereas *Gleditsia* and *Quercus* maintained a large woody root fraction in the mid substrate layer (Fig. 7B). Surprisingly, very few woody roots were found in the deepest substrate layer across all species. Depth distribution of the finest root fraction (2 mm or less) also differed across species for all months (May, $P = 0.001$; July, $P = 0.001$; September, $P = 0.001$) with *Acer* and *Carpinus* producing the greatest fine root fraction in shallow to mid-substrate layers, *Quercus* concentrating the majority of its fine roots in the central layer of the container, and *Gleditsia* placing the largest fraction of its fine root population in the deepest substrate layer (Fig. 7A).

Horizontal distribution of root standing crop. Our data showed an inverse relationship between root proportion and distance from the center of the container ($P < 0.001$) with a significant interaction in species root number by month ($P = 0.004$). Interestingly, the percent of total roots within Ring 1 decreased with time for most species (Fig. 8). Within species, patterns of horizontal root distribution across all rings showed *Carpinus* had the most uniform root standing crop through time with a modest to no increase in root standing crop across rings. *Acer* was most conservative in its interior number of roots compared with all other species with an average of 54 roots in Ring 1 compared with 123 in *Carpinus*, 136 in *Gleditsia*, and 155 in *Quercus*. A similar pattern in root number was found for Ring 2. However, the opposite was found in Rings 3 and 4, where *Acer* maintained among the greatest proportion of roots during May and July (Fig. 8). In general, species maintained somewhat constant root

proportions within each concentric ring over time with the exception of *Gleditsia*, which had the largest decrease in root standing crop within the central portion of the rooting volume and the greatest increase in roots within the peripheral rings. Absolute root numbers also reveal a large “flush” of roots within Rings 3 and 4 by the end of the study period.

Horizontal and temporal distribution of diameter classes. Diameter class distributions differed among species for Rings 3 and 4 (Ring 1, $P = 0.211$; Ring 2, $P = 0.318$; Ring 3, $P < 0.001$; and Ring 4, $P < 0.001$, respectively). The coarse woody root fraction (4 mm or greater) revealed species differences in horizontal frequency distribution across rings (Ring 1, $P < 0.001$; Ring 2, $P < 0.001$; Ring 3, $P < 0.001$; and Ring 4, $P = 0.011$) in all months of the study (May, $P < 0.001$; July, $P < 0.001$; and September, $P = 0.002$) largely driven by the concentration of woody roots in the central portion of the container (Fig. 9B).

Species fine root diameter fraction (2 mm or less) also differed across Ring 2 ($P < 0.001$), Ring 3 ($P < 0.001$), and Ring 4 ($P < 0.001$). Month was also significant with species naturally increasing their number of fine roots in central Rings 2 and 3 in July and Rings 3 and 4 in September, a likely result of root exploration toward the outlying unexplored substrate volume (Fig. 9A).

Discussion

Various attempts have been made to describe root growth and foraging of tree root systems (Nichols and Alm, 1982; Nielsen and Hansen, 2006; Richardson-Calfree et al., 2007). This is the first study, to our knowledge, that allowed for a direct comparison of perennial root systems' spatial development across multiple tree species through time, in a growing medium, using a purely non-destructive technique. Most CT studies to date have not considered plant specimens let alone root systems of this size. Although the large pine bark content in our medium prevented automated three-dimensional (3D) analysis with readily available 3D software, we found that working with the two-dimensional

Fig. 7. Frequency of root diameter class 2 mm or less (A) and 4 mm or greater (B) present in May, July, and September for four ornamental tree species (*Acer*, *Carpinus*, *Gleditsia*, and *Quercus*) over three soil depths. Depth 1 (0 to 12 cm), depth 2 (12 to 24 cm), and depth 3 (25 to 38 cm).

Fig. 8. Horizontal distribution of the population of roots (standing crop) expressed as percent of root produced in each concentric ring/total root production for that species (± 1 SE) for *Acer* (black squares), *Carpinus* (white squares), *Gleditsia* (black circles), and *Quercus* (white circles).

Fig. 9. Frequency of root diameter class 2 mm or less (A) and 4 mm or greater (B) present in May, July, and September for four ornamental tree species, *Acer* (black squares), *Carpinus* (white squares), *Gleditsia* (black circles), and *Quercus* (white circles) across four concentric rings.

(2D) output of our data sets greatly increased the efficiency and accuracy of our ability to detect and measure tree roots.

The species *Acer* produced the largest proportion of roots less than 2 mm, but also the smallest total root standing crop throughout the study (Fig. 4). Two factors that may

have contributed to this disparity arise from the lack of roots produced in higher root diameter classes within the species and compared with other species as well as the fraction of finer roots (1 mm or less in diameter) that were not accounted for as a result of CT resolution (see discussion on scanner

resolution below). In contrast, *Carpinus* and *Quercus*, tree species with generally “finer” roots (Pregitzer et al., 2002), produced significantly larger root-standing crops compared with *Acer* and *Gleditsia*, yet notably with a large proportion of roots in higher diameter classes (Fig. 5).

There are clear implications for where a tree builds its roots and its ability to forage for resources. Several studies within forested systems have indicated fine root placement within the upper substrate profile maximizes nutrient uptake potential (Millikin and Bledsoe, 1999; Steele et al., 1997; Wang et al., 2002), whereas deeper fine root placement maximizes water capture particularly in variable environments (Hendrick and Pregitzer, 1996). Clearly, substrate physical, chemical, and biological properties can influence root placement and development (Pierret et al., 2007). Therefore, we standardized our growing medium across species as a means to compare root development and foraging strategies. Our results emphasize the shallow root foraging of *Acer* and *Carpinus* vs. the “deeper” root placement in *Quercus* and especially *Gleditsia* over time, suggesting possible differences in root foraging strategies between the species we examined. Factors controlling periods of abundant root growth (root flushes) and root placement during the growing season are not well understood. A more thorough examination of root growth periodicity among tree species would help to shed light on species-specific peak periods of root production and distribution. Although we did not manipulate water or nutrients in this study, we cannot eliminate the possibility that our fertilizer application or watering regime influenced root placement through artificial resource heterogeneity. However, the relatively constant trajectory of root production in space, with the exception of *Gleditsia*, leads us to believe this is not the case. Our study supports the widespread agreement on the centrality of the coarse root fraction within the horizontal rooting profile (Millikin and Bledsoe, 1999; Ouimet et al., 2008). However, within the fine root fraction, species exhibited greater variation in root placement with *Carpinus* exhibiting a predominantly centrally located fine root fraction compared with the more evenly dispersed root system of *Acer* (Fig. 8). Interestingly, within a single species, with the exception of *Gleditsia*, root standing crop across the growing season was relatively stable across concentric rings suggesting either long root lifespans or relatively slow turnover of the root population (Fig. 8). Among four widely used ornamental species, we found *Gleditsia* to be the most plastic in its fine root growth and allocation within the container as emphasized by its decrease in root standing crop in the center depth of the container and subsequent increase in the deepest substrate depth interval. Likewise, *Gleditsia* also had the greatest increase in root standing crop toward more peripheral concentric rings of the container.

There are inherent tradeoffs in sample volume size vs. scanner resolution. We recognize the major limitation to this study lies in the resolution threshold of the CT scanner we used. The finest tree roots, e.g., roots less than 1 mm, were difficult to detect and therefore absent from the final analysis. It is also important to recognize that although we examined root system variation across a root

diameter class continuum, we recognize the importance of root order and root anatomical analysis in defining root function by species (Guo et al., 2008; Pregitzer et al., 2002). However, when working in the 2D framework of CT scans, root order classification is unattainable and therefore not included as part of this study. Regardless of this limitation, however, the non-destructive visual spatial distribution of a large fraction of the trees' root system highlights the diversity of root placement between ornamental tree species that warrants further research on how root placement may shift with varying levels of water availability.

Conclusions

The growth and development of a tree's root system is a dynamic process with clear implications for the ability of trees to forage for resources. We conclude that not all trees build their root systems in the same manner demonstrated by both shallow and deeper-rooted species. Understanding root placement at the species level may allow us to better manage container-grown trees through more precise water and fertilizer applications. We suggest here that future studies should consider the relationship between tree root placement and soil moisture distribution within the container.

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