

Deep-Rooted Trees for Urban Environments: Selection and Propagation

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Abstract. Seedling liners of three tree species (*Fraxinus uhdei*, *Pistacia chinensis*, and *Zelkova serrata*) were planted in the field and grown for 18 months. Pneumatic air excavation followed by digital photography, three-dimensional modeling, and root analysis showed there were significant differences in root architecture among the three species and within each species' population. Among the three species, *Pistacia chinensis* had, on average, the deepest, most vertically oriented root systems and *Fraxinus uhdei* and *Zelkova serrata* the shallowest; however, there were shallow-rooted and deep-rooted genotypes in each species. Shallow-rooted and deep-rooted genotypes of *Fraxinus* and *Zelkova* selected from the seedling populations were propagated vegetatively by cuttings, planted in the field, and grown for 5 to 6 years. On excavation and three-dimensional model creation, the root architecture of the cutting-propagated clones was assessed using liminal angles and individual root angles. Cutting-propagated clones of shallow-rooted parents were shallow-rooted; thus, they maintained the parents' root architecture. Cutting-propagated clones of deep-rooted parents were also shallow-rooted; they did not maintain their parents' root architecture. Results are discussed in terms of genetic, physiological (e.g., auxin treatment, adventitious root formation), and environmental (e.g., soil moisture) factors that can affect tree root growth and development.

Key Words. Arboriculture; gravitropism; infrastructure damage; liminal angle; root architecture, root growth; root system genetics; street tree; urban forestry.

Trees in urban environments provide many biologic, environmental, economic, and social benefits. These benefits come with some cost, however. Some trees have root systems that cause substantial damage to sidewalks, curbs, and gutters. Damage results from a number of factors: small planting areas, restrictive soils, and use of large-stature trees in confined areas (Costello and Jones 2003). In some cases, the trees' inherent tendency to have shallow roots is thought to be a key factor (Hamilton 1984a). As these shallow roots produce secondary thickening, they tend to lift and crack pavements. Several tree species commonly planted in northern California, U.S., have been associated with sidewalk and curb displacement: *Liquidambar styraciflua* (sweetgum), *Morus alba* (white mulberry), *Fraxinus* spp. (ash), *Ulmus* spp. (elm), *Magnolia grandiflora* (Southern magnolia), *Prunus* spp., *Pinus radiata* (Monterey pine), *Eucalyptus globulus* (blue gum eucalyptus), and *Cinnamomum camphora* (camphor) (Hamilton 1984a; Costello and Jones 2003).

This problem is of major proportions in many cities. In a 1984 survey of cities in the Bay Area of California, 60% of the street trees were estimated to have caused some or severe damage to the urban infrastructure (Hamilton 1984a). A subsequent survey of sidewalks in San Jose, California, found the estimated repair cost for tree-related damage to be \$14.3 million and annual concrete repair costs attributed to tree damage ranged from \$0.18 to \$13.65 per tree (Peper and McPherson 1995). Most recently, McPherson and Peper (2000) found in California that approximately \$70.7 million was spent annually statewide as a result of conflicts between tree roots and urban infrastructure (e.g., sidewalks, street pavement, curbs, and gutters). It is quite apparent that even a partial solution to this problem would result in substantial savings for city residents and governments.

Various strategies such as engineering, design and improved materials, and biologic/genetic approaches have been suggested

in hopes of solving this problem (Hamilton 1984b; Costello and Jones 2003). Engineering solutions include the use of steel plates bolted directly to exposed roots to prevent or minimize future damage and the use of root barriers in an attempt to force roots down below sidewalks and curbs. Design solutions include providing adequate planting strip space for tree trunk diameter increases and root crown flare. Newer paving materials may provide the necessary flexibility to prevent cracking and complete disruption of the pavement. Another strategy is the biologic/genetic approach: to identify, select, and vegetatively propagate trees that are genetically "programmed" to be deep-rooted. The basic premise behind this approach is that it is reasonable to expect as much variability in belowground architecture for trees as is found aboveground (Barker 1987; Bowman 1941). Two questions are addressed in this study: 1) are there genetic differences in root depth and orientation between and within tree species; and 2) if root architecture is under genetic control, can it be maintained through vegetative propagation techniques?

MATERIALS AND METHODS

Survey

A survey of six northern California cities (Modesto, Redwood City, Palo Alto, Berkeley, Sacramento, Sunnyvale) was conducted to identify species observed to cause infrastructure damage. More than 20 species were identified and three were selected for the research project: *Fraxinus uhdei* (Wenzig) Lingelsh. (green ash), *Pistacia chinensis* Bunge (Chinese pistache), and *Zelkova serrata* (Thunb.) Makino (zelkova).

Seed-Propagated Trees in the Field

Fifty seed-propagated individuals (liners) of each of the selected tree species were purchased and planted in a field plot in July

1997. The trees were planted in rows of 15 and spaced 3.05 m (10.1 ft) apart. There were three rows of each species making a total of 45 seed-propagated genotypes for each species. Each tree was given an identification that reflected its species, row number, and tree number. For example, the fifth *Fraxinus* tree in row two would be 2Frax5. The field plot was chosen for its consistent soil texture (Yolo Loam with 43% sand, 32% silt, and 25% clay) and soil depth (more than 2 m [6.6 ft]). From mid-March to late November each year, all trees were irrigated weekly with a sub-surface irrigation system using a 0.28 cm (0.1 in) OD soaker hose (Teknor Apex Co., Pawtucket, RI). During each irrigation event, the soil within an approximately 1 m (3.3 ft) radius of the tree was brought to field capacity (approximately 22% moisture content) to a depth of at least 1 m (3.3 ft). Irrigation frequency and timing necessary to reach field capacity were determined early on in the project by taking soil cores down to an approximately 0.9 m (2.97 ft) depth followed by soil moisture content determinations. Deep irrigation was practiced to reduce the potential influence of shallow irrigation on root growth and development. Periodic herbicide applications of XL 2G (Dow Agro-Sciences, Indianapolis, IN), glyphosate (Roundup; Monsanto, St. Louis, MO), and Rout (The Scotts Company, Marysville, OH) were used to control weeds. In December 1998, 15 trees of each species were randomly selected and excavated using a pneumatic technique (Air-Spade®; Concept Engineering Group, Inc., Verona, PA) (Nathenson and Jarabak 2001; Smiley 2001) that removed the soil without observable damage to roots larger than approximately 5 mm (approximately 0.2 in) in diameter. At this time, the selected trees ranged in height from 2.5 m (8.25 ft) to 3.5 m (11.55 ft) tall with trunk calipers at ground level of between 5.1 cm (2.04 in) and 10.8 cm (4.32 in).

After soil excavation, each root system was marked with brightly colored push pins as photograph reference markers. The push pins were inserted into major structural roots (larger than 2 cm [0.8 in]) at locations where the root changed direction or where there were large gaps (more than 20 cm [approximately 8 in]) between push pins. Root segments between push pins were deemed to be straight lines. Digital photographs were taken from four vantage points roughly 90° apart around the root system (Figure 1). Photograph files were imported into modeling software (PhotoModeler Pro 5.0; Eos Systems, Vancouver, BC, Canada) and marked to label specific root locations on each photograph using the colored push pins. The base of each push pin was used in this process to mark the uppermost surface of each root. Once marked, PhotoModeler software created three-dimensional models with accompanying X, Y, and Z coordinates for each push pin over the entire root system (Figure 2).

X and Y coordinates from the three-dimensional models were used to calculate the linear distance (LD) of each push pin location from the origin in the X–Y plane (soil surface). Linear regressions of LD versus depth (Z coordinate) for each tree were conducted using the SAS PROC REG (SAS Institute, Inc., Cary, NC) (Figures 2 and 3). This was followed by an analysis of covariance using PROC GLM to determine significant differences among the calculated slopes. We arbitrarily defined shallow-rooted trees to have slopes between 0 and –1.0 and deep-rooted trees to have slopes less than –1.5. A tree that had a root distribution slope of –1.0 meant the average angle from the soil surface was –45° (see Figures 2 and 3).

The X, Y, and Z coordinates were used to calculate the individual root angle (IRA) and the liminal angle (LA) (Johnson and

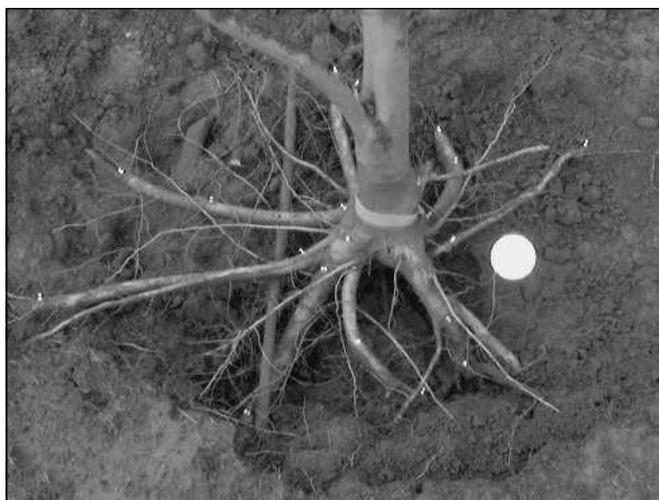


Figure 1. Example of one of four photographs taken of a root system that had been exposed using an Air-Spade®. Push pin locations are shown on the root system. White, spherical ball (10.16 cm (4.1 in) in diameter) was used for dimensional calibration.

Tibbitts 1968; Coutts and Nicoll 1991) (Figure 4). The IRA was defined as the angle (relative to the soil surface) for each root segment between adjacent push pins. A horizontal root segment had an IRA = 0 and a vertical root segment had an IRA = –90. The angle from the vertical Z axis (plumb line through trunk origin) to each push pin was defined as the LA. The tree's origin was defined as that point in the center of the main trunk where the X and Y coordinates were both 0; therefore, the origin was defined as 0, 0, 0. A vertical root had an LA = 0 and a horizontal root had an LA = 90. IRA and LA were calculated for each root segment (IRA) and for each push pin (LA) for 15 trees of each species. The IRA was determined by: 1) calculating the differences (dx, dy, dz) between adjacent pushpin X, Y, and Z coordinates; 2) calculating the length of the root segment by taking the square root of the summed squares of the dx, dy, and dz values; and 3) taking the arcsine of dz divided by the length of the root segment. The LA for each push pin was determined by: 1) calculating the distance of each push pin from the X–Y origin (square root of $x^2 + y^2$); 2) calculating the distance of the pushpin from the X–Y–Z origin by taking the square root of ($x^2 + y^2 + z^2$); and 3) taking the arcsine of (distance from X–Y origin/distance from X–Y–Z origin). The end result of these calculations provided angles (relative to the soil surface) of each root segment (IRA) and LAs of each push pin relative to the plumb line or Z axis through the trunk center (LA). These data were analyzed using PROC GLM (SAS Institute, Inc.).

Vegetatively Propagated Clones

Genotype Selection

Based on the root architecture analysis from the seed-propagated trees, two shallow-rooted genotypes (i.e., those having a slope greater than –1.0) and two deep-rooted genotypes (i.e., those having a slope less than –1.5) from each species were selected for vegetative propagation. The shallow-rooted genotypes included 3Pist14 (slope = –0.49) and 3Pist15 (slope = –0.92) for *Pistacia*, 2Zelk4 (slope = –0.57) and 2Zelk6 (slope = –0.75) for *Zelkova*, and 2Frax9 (slope = –0.61) and 2Frax10 (slope = –0.82) for *Fraxinus*. The deep-rooted genotypes included 3Pist7

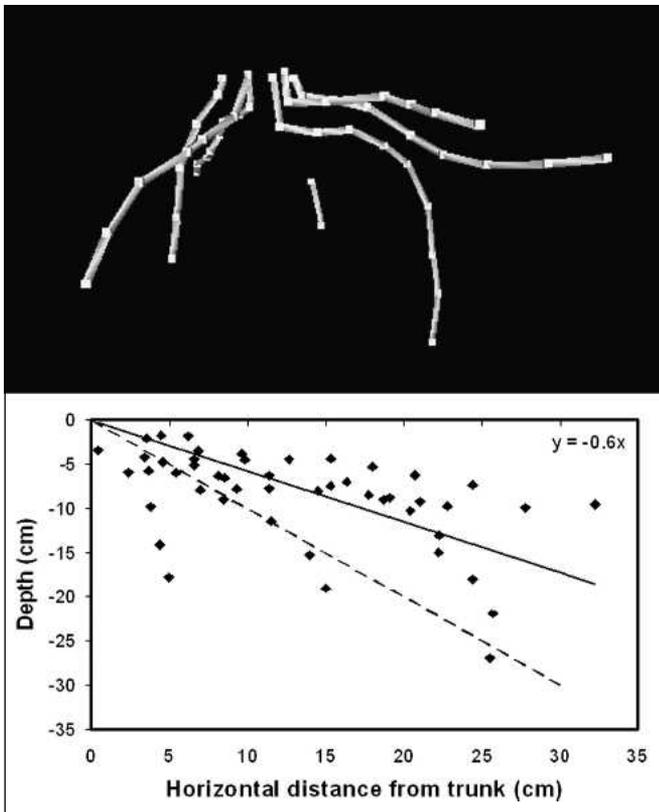


Figure 2. Three-dimensional model (top) and two-dimensional root distribution projection (bottom) for 2Frax9, a shallow-rooted individual with a root distribution slope of -0.6 . The dashed line in the graph shows a slope of -1.0 = a 45° angle from the soil surface.

(slope = -2.95) and 3Pist10 (slope = -3.31) for *Pistacia*, 2Zelk2 (slope = -1.85) and 2Zelk9 (slope = -1.69) for *Zelkova*, and 2Frax8 (slope = -1.75) and 3Frax13 (slope = -2.28) for *Fraxinus*.

Genotype Cutting Propagation

Pistacia chinensis: The protocol established by Lee et al. (1976) was followed. Terminal stem cuttings, 10.2 to 15.2 cm (4.1 to 6.1 in), were taken in August 2000. The base of each cutting was treated for 15 sec in 2 N H_2SO_4 followed by a 30 sec dip in 12.4 mM (3,000 ppm) KIBA (potassium salt of indolebutanoic acid). The cuttings were immediately placed in a 30.5 cm \times 50.8 cm \times 6.3 cm (12.2 \times 20.3 \times 2.5 in) plastic flat containing a 1:1 (v:v) mixture of perlite and vermiculite. The flats were placed under intermittent mist (5 sec every 5 min, dawn to dusk) with no bottom heat.

Zelkova serrata: The protocol established by Dirr and Frett (1983) was followed. Terminal stem cuttings, 10.2 to 15.2 cm (4.1 to 6.1 in), were taken in August 2000. The base of each cutting was treated for approximately 30 sec in an 80 mM (16,000 ppm) IBA, 50% ethanol solution. The cuttings were immediately placed in a 30.5 cm \times 50.8 cm \times 6.3 cm (12.2 \times 20.3 \times 2.5 in) plastic flat containing a 1:1 (v:v) mixture of peat moss and perlite. The flats were placed under intermittent mist (5 sec every 5 min, dawn to dusk) with no bottom heat.

Fraxinus uhdei: The protocol established by Evans (1971) was followed. Terminal stem cuttings, 10.2 to 15.2 cm (4.1 to 6.1 in),

were taken in August 2000. The base of each cutting was dipped in a powder formulation of IBA, 40 mM (0.8%) (Hormodin #3), and placed in a 30.5 cm \times 50.8 cm \times 6.3 cm (12.2 \times 20.3 \times 2.5 in) plastic flat containing a 1:1 (v:v) mixture of peat moss and perlite. The flats were placed under intermittent mist (5 sec every 5 min, dawn to dusk) with no bottom heat. After 9 weeks, all the cuttings were removed from the mist bench, transplanted into 15.2 cm (6.1 in) pots containing UC Mix (1:1:1, by volume of peat moss, redwood sawdust, and sand), and grown in a greenhouse ($24^\circ C$ to $27^\circ C$ [$75.2^\circ F$ to $80.6^\circ F$]) for 4 weeks.

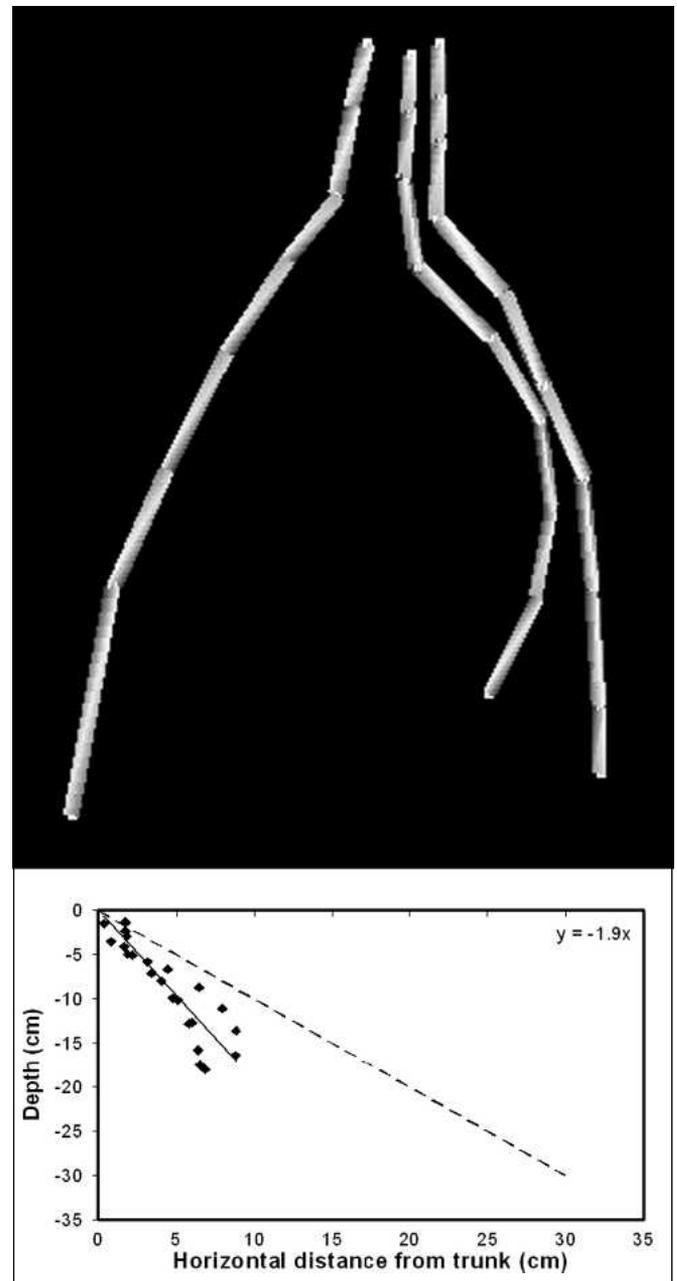


Figure 3. Three-dimensional model (top) and two-dimensional root distribution projection (bottom) for 3Frax13, a deep-rooted individual with a root distribution slope of -1.9 . The dashed line in the graph shows a slope of -1.0 = a 45° angle from the soil surface.

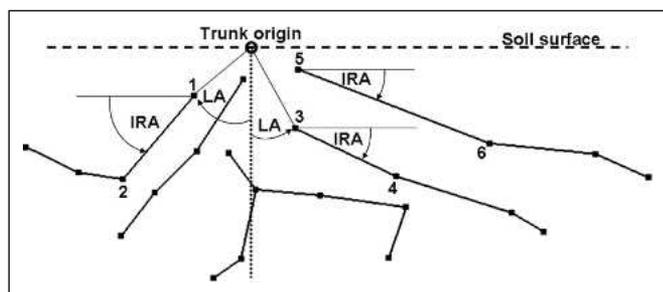


Figure 4. Diagram showing how the liminal angle (LA) and individual root angle (IRA) were determined. LA, the angle from the vertical Z axis (plumb line through trunk origin) to each push pin (examples numbered 1 and 3 in the diagram), was calculated using X, Y, and Z coordinates provided by the three-dimensional software (PhotoModeler). IRA was determined by calculating the angle, relative to the soil surface, of the root segment between adjacent push pins (example segments numbered 1-2, 3-4, and 5-6 in the diagram).

Ten of the most vigorous, vegetatively propagated clones of each of *Zelkova serrata* genotypes (2Zelk4 and 2Zelk9) and *Fraxinus uhdei* genotypes (2Frax8, 2Frax9, 2Frax10, 3Frax13) were planted (in October 2000) 3.05 m (10.1 ft) apart in rows 3.05 m (10.1 ft) apart in the same plot of land used for the original seed-propagated trees. No cuttings of *Pistacia* rooted; therefore, this species was dropped from subsequent experimentation. The trees were irrigated weekly from early April to mid-November each year with a subsurface irrigation system using a 0.28 cm (0.7 in) OD soaker hose (Teknor Apex Co.). During each irrigation, the soil within approximately 1 m (3.3 ft) radius of the tree was brought to field capacity to a depth of approximately 0.9 m (2.97 ft). Irrigation frequency and timing necessary to reach field capacity were determined early on in the project by taking soil cores down to an approximately 0.9 m (2.97 ft) depth followed by soil moisture content determinations.

In February 2005, the root systems of the *Fraxinus* clones were excavated using the Air-Spade® marked with brightly colored push pins and photographed to facilitate the creation of three-dimensional models using PhotoModeler software as before. In February 2006, the same process was followed for the *Zelkova* clones.

RESULTS AND DISCUSSION

Survey

The three tree species selected were of interest to the city arborists who were interviewed because of their positive attributes. However, these trees were rarely recommended or planted as a result of their reputations for causing sidewalk and curb damage. All three species have appeared on previously published lists of trees commonly thought to cause infrastructure damage (Hamilton 1984a; Wager and Barker 1985; Sommer and Cecchetti 1992; Sommer and Summit 1996; Costello and Jones 2003). D'Amato et al. (2002) suggested that *Zelkova serrata* was an "aggressive" species in terms of its root spread under sidewalks in a relatively short period of time compared with *Gleditsia*, *Koelreuteria*, and *Quercus*.

Seed-Propagated Trees in the Field

Many of the roots from the three species exposed with the Air-Spade® were heart roots, originating from the buttress of the

trunk, or lateral roots. There were very few tap, sinker, or striker roots (roots growing vertically downward from shallow lateral roots). Three-dimensional models of the experimental trees showed a distribution from very shallow-rooted to very deep-rooted (Figures 2 and 3). In the figures, a slope of -1.0 indicated a mean angle of -45° from the horizontal soil surface (see Figures 2 and 3). The slope of the linear regressions provided some measure of the average rooting depth of each tree root system. The slopes ranged from -0.11 (shallow-rooted) to -1.7 (deep-rooted) for *Fraxinus*, from -0.54 to -2.47 for *Pistacia*, and from -0.51 to -2.07 for *Zelkova*. Linear equations were fitted to these data and the slopes used to compare root systems within each species. Deeper root systems had more negative slopes of the fitted lines. *Pistacia chinensis* trees had the most negative mean slope (deepest root systems) (Table 1) and also had the highest percentage of trees with slopes below -1.0 (data not shown). *Fraxinus uhdei* and *Zelkova serrata* were less negative and not significantly different from one another.

Significant differences in LA were found among the three species. *Pistacia chinensis* had the lowest LA with *Zelkova serrata* intermediate and *Fraxinus uhdei* the highest (Table 1). Deeper root systems had lower mean LA values. There was a significant difference in mean IRA between *Pistacia chinensis* and *Zelkova serrata* (Table 1) with *Fraxinus uhdei* being intermediate. Deeper root systems had more negative mean IRA values. Taken together, the slope, LA, and IRA values all indicated that *Pistacia chinensis* had, on average, the deepest roots systems for the seed-propagated genotypes. Differences between *Fraxinus uhdei* and *Zelkova serrata* genotypes were not as clear, but both had root systems that were significantly shallower than *Pistacia chinensis*.

All three methods (slope, LA, IRA) showed the same basic trends among the three tree species. Seed-propagated trees of *Pistacia chinensis* had the most negative slope, lowest LA, and more negative IRA values, all indicating deeper root systems for *Pistacia*. These results corroborate earlier work (Hamilton 1984a; Wager and Barker 1985; Sommer and Cecchetti 1992; Sommer and Summit 1996; D'Amato et al. 2002). There are genetic differences in root architecture (e.g., depth) among trees species that may or may not be altered in response to soil conditions.

Genotype Cutting Propagation

The three tree species had different capacities for forming adventitious roots in response to the treatments imposed. No roots were formed on any of the *Pistacia chinensis* cuttings; therefore, it was not possible to continue the research with that species. There were also dramatic differences in the abilities of the four genotypes of *Zelkova serrata* to form adventitious roots. No cuttings from genotypes 2Zelk2 and 2Zelk6 formed adventitious

Table 1. Mean slope, liminal angle (LA), and individual root angle (IRA) of seed-propagated trees (22 months old) of three tree species.

Genus	Slope	LA (°)	IRA (°)
<i>Fraxinus uhdei</i>	-1.1 a	47.8 a	-39.5 ab
<i>Zelkova serrata</i>	-1.2 a	39.4 b	-35.8 a
<i>Pistacia chinensis</i>	-1.5 b	33.7 c	-41.9 b

Means followed by the same letter are not significantly different at $P = 0.01$ using Scheffe's mean separation test.

Table 2. Mean liminal angle (LA) and individual root angle (IRA) for seed-propagated and cutting-propagated trees of *Fraxinus* and *Zelkova*.^z

Tree genotype	Root type	LA (°)		IRA (°)	
		Seed propagated	Cutting propagated	Seed propagated	Cutting propagated
2Frax9		50.8 a	48.8 a	-28.9 a	-26.6 a
2Frax10	Shallow	52.7 a	51.4 a	-44.5 a	-25.0 b
2Frax8		48.7 a	60.8 b	-49.6 a	-20.9 b
3Frax13	Deep	38.0 a	59.7 b	-41.0 a	-17.0 b
2Zelk4	Shallow	50.2 a	56.2 b	-29.2 a	-21.3 b
2Zelk9	Deep	37.6 a	57.6 b	-39.6 a	-14.6 b

^z2Frax9 and 2Frax10 were shallow-rooted; 2Frax8 and 3Frax13 were deep-rooted. 2Zelk4 was shallow-rooted and 2Zelk9 was deep-rooted. Values followed by the same letter are not significantly different at $P = 0.01$.

roots, whereas 15% of the cuttings from 2Zelk4 and 35% of the cuttings from 2Zelk9 formed adventitious roots. The genotypes of *Fraxinus uhdei* rooted relatively well, all showing rooting percentages above 60%. The differences in rooting potential shown here among closely related genotypes are common for woody perennials and provide additional evidence of the important role genetics plays in root morphology, physiology, and development.

Vegetatively Propagated Trees: *Fraxinus* and *Zelkova*

As seen in the seed-propagated populations, most of the roots from vegetatively propagated, field-grown *Fraxinus* and *Zelkova* clones exposed with the Air-Spade® were heart or lateral roots. There were very few tap, sinker, or striker roots observed. For *Fraxinus uhdei*, trees 2Frax9 and 2Frax10 were chosen as shallow-rooted genotypes and 2Frax8 and 3Frax13 were chosen as deep-rooted genotypes based on the mean slopes of their root systems. For 2Frax9, neither the LA nor IRA values for the seed-propagated parent and its cutting-propagated progeny population differed from one another (Table 2). For 2Frax10, the LA values for seed-propagated and cutting-propagated trees were not significantly different, but the values for IRA were (-44.5 to -25.0). The IRA for the cutting-propagated progeny was less negative (signifying a shallower root system) than its seed-propagated parent (Table 2). For 2Frax8 and 3Frax13, the deep-rooted genotypes, the cutting-propagated progeny had significantly higher values for LA and significantly less negative values for IRA indicating that they had shallower roots systems than their seed-propagated parents (Table 2). Similar results were found with the two *Zelkova* genotypes. Genotype 2Zelk4 was shallow-rooted, whereas 2Zelk9 was the deep-rooted genotype. For both genotypes, the cutting-propagated progeny had significantly higher LA values and significantly less negative IRA values indicating that they had shallower roots systems than their seed-propagated parents (Table 2). For shallow-rooted *Fraxinus* and *Zelkova* genotypes, cutting-propagated progeny differed little, if at all, from their seed-propagated parents in LA (no differences for 2Frax9 and 2Frax10 and a difference of 6° for 2Zelk4), whereas for deep-rooted genotypes, cutting-propagated progeny always differed from their seed-propagated parents (12.1° for 2Frax8, 21.7° for 3Frax13, and 20° for 2Zelk9) by having shallower root systems (Table 2).

The assessments of tree root architecture used in this study (slope, LA, and IRA) clearly support the ideas that: 1) there are genetic differences among species related to root architecture (Hamilton 1984a; Oyanagi et al. 1991; Rubio et al. 2003); and 2)

root systems develop and function by responding, within a genetically predetermined range, to their environment (Clausnitzer and Hopmans 1994; Rubio et al. 2003). The research site for this study was carefully chosen and tree management, especially irrigation, was performed so as to minimize influences of soil texture and depth and water availability that can influence root development (Perry 1982; Feldman 1988; Coutts and Nicoll 1991; Nakamoto 1994; Jourdan et al. 2000; Rubio et al. 2003). However, with the present information, the relative importance of inherent, genetic versus external, environmental factors cannot be pinpointed (Jourdan et al. 2000). Firn and Digby (1997) hypothesized that roots possessed a mechanism that allows them to attain a stable, gravitropic position (gravitropic set point [GSA]) and that the GSA can be developmentally changed and/or regulated by environmental factors.

This research is the first to make direct comparisons of root systems between seed-propagated trees and their cutting-propagated progeny and may indicate that the process of vegetative propagation through adventitious root formation has profound influences over the inherent root architecture of the tree, perhaps by altering the roots' responses to gravitropic influences. Others have noted that adventitious roots tend to be more horizontal than seminal roots (Kolesnikov 1930; Serebryakov 1962; Külla and Löhms 1999; Miller et al. 2003; Tsutumi et al. 2004). In this study in which relatively high concentrations of auxin were used to enhance the formation of adventitious roots, it is not possible to determine whether it was the auxin treatment, the de novo formation of adventitious roots from stem cells, or a combination of both that led to the decreased gravitropic response. In work with tea (*Camellia sinensis* [L.] Kuntze), Masataka et al. (1997) found that adventitious roots from cuttings grew more horizontally than seedling seminal roots. Their anatomic analyses showed that adventitious root cap cells contained fewer amyloplasts than seminal roots and this was the reason for the different gravitropic responses. If cutting-propagated trees do tend to have shallower root systems than individuals propagated by seeds, one may want to seriously consider not growing trees known to be propagated by stem cuttings in close proximity to urban infrastructure such as sidewalks, curbs, and streets. With a better understanding of the genetic and environmental influences on the gravitropic responses of roots of woody perennials, improved solutions to root system-urban infrastructure conflicts may be found.

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LITERATURE CITED

- Barker, P.A. 1987. Proactive strategies to mediate tree-root damage to sidewalks. Combined Proceedings of the International Plant Propagators' Society 37:56–61.
- Bowman, F.T. 1941. Root types among apple seedlings—A basis for selecting rootstocks. Agricultural Gazette of New South Wales 52: 427–428, 475–477.
- Clausnitzer, V., and J.W. Hopmans. 1994. Simultaneous modeling of transient three-dimensional root growth and soil water flow. Plant and Soil 164:299–314.
- Costello, L.R., and K.S. Jones. 2003. Reducing Infrastructure Damage by Tree Roots: A Compendium of Strategies. Western Chapter-International Society of Arboriculture, Cohasset, CA.
- Coutts, M.P., and B.C. Nicoll. 1991. Orientation of lateral roots of trees. I. Upward growth of surface roots and deflection near the soil surface. The New Phytologist 119:227–234.
- D'Amato, N.E., T.D. Sydnor, R. Hunt, and B. Bishop. 2002. Root growth beneath sidewalks near trees of four genera. Journal of Arboriculture 28:283–290.
- Dirr, M.A., and J.J. Frett. 1983. Rooting chinese elm and Japanese zelkova cuttings. The Plant Propagator 29:10–11.
- Evans, G.E. 1971. Relationship of harvest date to rooting response of softwood cuttings of selected woody ornamentals. The Plant Propagator 17:3–9.
- Feldman, L.J. 1988. The habits of roots. Bioscience 38:612–618.
- Firn, R.D., and J. Digby. 1997. Solving the puzzle of gravitropism—Has a lost piece been found? Planta 203:S159–S163.
- Hamilton, W.D. 1984a. Sidewalk/curb breaking tree roots. 1. Why tree roots cause pavement problems. Arboricultural Journal 8:37–44.
- . 1984b. Sidewalk/curb-breaking tree roots. 2. Management to minimize existing pavement problems by tree roots. Arboricultural Journal 8:223–234.
- Johnson, S.P., and T.W. Tibbitts. 1968. The liminal angle of a plagiotropic organ under weightlessness. Bioscience 18:655–661.
- Jourdan, C., N. Michaux-Ferrière, and F. Perbal. 2000. Root system architecture and gravitropism in the oil palm. Annals of Botany 85: 861–868.
- Kolesnikov, V.A. 1930. The root system of fruit tree seedlings. Journal of Pomology 8:197–210.
- Küllä, T., and K. Löhmus. 1999. Influence of cultivation method on root grafting in Norway spruce [*Picea abies* (L.) Karst.]. Plant and Soil 217:91–100.
- Lee, C.I., J.L. Paul, and W.P. Hackett. 1976. Root promotion on stem cuttings of several ornamental plant species by acid or base pretreatment. Combined Proceedings of the International Plant Propagators' Society 26:95–99.
- Masataka, Y., T. Takyu, and T. Sasa. 1997. Gravitropic reaction in the growth of tea roots. Nihon Sakumotsu Gakkai Kiji 66:472–478.
- McPherson, E.G., and P.J. Peper. 2000. Costs due to conflicts between street tree root growth and hardscape, pp. 15–18. In Costello, L.R., E.G. McPherson, D.W. Burger, and L.L. Dodge (Eds.). Strategies to Reduce Infrastructure Damage by Tree Roots: Proceedings of a Symposium for Researchers and Practitioners. Western Chapter, International Society of Arboriculture, Cohasset, CA.
- Miller, C.R., I. Ochoa, K.L. Nielsen, D. Beck, and J.P. Lynch. 2003. Genetic variation for adventitious rooting in response to low phosphorus availability: Potential utility for phosphorus acquisition from stratified soils. Functional Plant Biology 30:973–998.
- Nakamoto, T. 1994. Plagiogravitropism of maize roots. Plant and Soil 165:327–332.
- Nathenson, R., and A. Jarabak. 2001. The evolution of air-tools for use in arboriculture. Tree Care Industry 13:47–48.
- Oyanagi, A., A. Sato, and M. Wada. 1991. Varietal differences in geotropic response of primary seminal roots in Japanese wheat. Nihon Sakumotsu Gakkai Kiji 60:312–319.
- Peper, P., and G. McPherson. 1995. Street trees and urban infrastructure: Getting at the root of the problem. Newsletter of the Western Center for Urban Forest Research and Education, Fall Update 1995:3.
- Perry, T.O. 1982. The ecology of tree roots and the practical significance thereof. Journal of Arboriculture 8:197–211.
- Rubio, G., H. Liao, X. Yan, and J.P. Lynch. 2003. Topsoil foraging and its role in plant competitiveness for phosphorus in common bean. Crop Science 43:598–607.
- Serebryakov, A. 1962. Ecological Morphology of Plants. Vyschaja chkola Publishers, Moscow, Russia. 72 pp.
- Smiley, E.T. 2001. Air excavation to improve tree health. Tree Care Industry 13:44–48.
- Sommer, R., and C.L. Cecchetti. 1992. Street tree location and sidewalk management preferences of urban householders. Journal of Arboriculture 18:188–191.
- Sommer, R., and J. Summit. 1996. An evaluation of tree descriptions in a popular garden guide. Journal of Arboriculture 22:155–159.
- Tsutumi, D., K. Kosugi, and T. Mizuyama. 2004. Three-dimensional modeling of hydrotropism effects on plant root architecture along a hillside. Vadose Zone Journal 3:1017–1030.
- Wagar, J.A., and P.A. Barker. 1985. Tree root damage to sidewalks and curbs. Journal of Arboriculture 9:177–181.

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Résumé. Des lignées de semis de trois espèces d'arbres (*Fraxinus uhdei*, *Pistacia chinensis* et *Zelkova serrata*) ont été plantés en champs et laissés en croissance durant 18 mois. Une excavation hydraulique à l'air suivie de photographies digitales, d'une modélisation en trois dimensions et d'une analyse des racines a permis de déterminer qu'il n'y avait pas de différences significatives dans l'architecture des racines parmi ces trois espèces ainsi qu'au sein de chacune des populations par espèce. Parmi les espèces d'arbres, *Pistacia chinensis* avait en moyenne les systèmes racinaires les plus profonds et les plus orientés verticalement tandis que *Fraxinus uhdei* et *Zelkova serrata* avaient les plus superficiels; néanmoins, il y avait pour chaque espèce des génotypes plus superficiels et d'autres plus profonds. Les génotypes plus superficiels et plus profonds de *Fraxinus* et de *Zelkova* sélectionnés à partir de populations de semis ont été propagés végétativement à partir de boutures, plantés en champs et laissés en croissance durant 5 à 6 ans. Suite à l'excavation et la création d'un modèle 3-D, l'architecture des racines des clones propagés végétativement avait des angles très faibles. Les clones propagés végétativement de parents à racines superficielles étaient eux aussi superficiels, maintenant de ce fait l'architecture racinaire des parents. Les clones propagés végétativement de parents à racines profondes avaient des racines superficielles; ils n'avaient donc pas maintenu l'architecture racinaire des parents. Les résultats sont discutés en termes de facteurs génétique, physiologique (traitement d'auxine et formation de racines adventives) et environnemental (humidité du sol) qui peuvent affecter la croissance et le développement racinaire.

Zusammenfassung. Von drei Baumarten wurden Sämlinge ausgepflanzt und 18 Monate lang gezogen. Nach einer pneumatischen Ausgrabung, gefolgt durch digitale Fotografie, 3D-Modellierung und Wurzelanalyse zeigte sich, dass es signifikante Unterschiede in der Wurzelarchitektur bei den drei Spezies und innerhalb der Spezies gibt. Von allen drei Arten hat *Pistacia chinensis* durchschnittlich die längsten, überwiegend vertikal orientierten Wurzelsysteme, während *Fraxinus uhdei* und *Zelkova serrata* überwiegend flache Systeme haben. Dennoch gab es in jeder Art flach wurzelnde und tief wurzelnde Genotypen. Aus der Sämlingspopulation von *Fraxinus* und *Zelkova* wurden flach wurzelnde und tief wurzelnde Genotypen ausgewählt, Stecklinge gewonnen und im Feldversuch 5–6 Jahre gezogen. Nach der Ausgrabung und einer 3D-Modellierung wurde die Wurzelarchitektur anhand liminaler und individueller Wurzelwinkel untersucht. Die geklonten Stecklinge flach wurzelnder Eltern hatten flache Wurzelsysteme und wiederholten die Architektur der Mutterpflanzen. Die geklonten Stecklinge tief wurzelnder Eltern waren ebenfalls Flachwurzler, d. h. sie wiederholten nicht das Muster der Mutterpflanzen. Die Ergebnisse wurden in Bezug auf genetische, physiologische (z.B. Auxin-Behandlung, Formation von Adventivwurzeln) und umweltbedingte (z.B. Bodenfeuchtigkeit) Faktoren diskutiert, die das Baumwurzelsystem und Entwicklung beeinflussen.

Resumen. Se plantaron en el campo tres especies de árboles (*Fraxinus uhdei*, *Pistacia chinensis* y *Zelkova serrata*) y se observó su crecimiento por 18 meses. La excavación neumática de aire seguida de fotografía digital, modelamiento tridimensional y análisis de raíces mostraron diferencias significativas en la arquitectura de las raíces entre las tres especies y dentro de cada población de especies. Entre las tres especies, *Pistacia chinensis* tuvo en promedio el sistema de raíces más profundo, más verticalmente orientado y *Fraxinus uhdei* y *Zelkova serrata* los más someros; sin embargo, hubo genotipos con sistemas de raíces profundos y someros en cada especie. Los genotipos de raíces profundas y someras de *Fraxinus* y *Zelkova*, seleccionados de las poblaciones de brinzales, fueron propagados vegetativamente, plantados en el campo y crecidos por 5–6 años. Con la excavación y creación del modelo tridimensional, la arquitectura de raíces de los clones propagados fue evaluada usando ángulos de raíces individuales. Las raíces de los clones propagados por cortes de raíces someras fueron podadas y mantuvieron esta arquitectura. Las de las raíces profundas también fueron podadas pero no mantuvieron su arquitectura. Los resultados son discutidos en términos de genética, fisiología (por ejemplo, tratamientos con auxinas, formación de raíces adventicias) y ambientales (por ejemplo, humedad del suelo) factores que pueden afectar el crecimiento y desarrollo de la raíz del árbol.