Changes in Tree Root Architecture Resulting from Field Nursery Production Practices[1]

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Abstract

Nursery production practices subject tree root systems to mechanical and environmental factors that are not imposed on plants regenerated naturally from seed. Architecture of undisturbed root systems of nine trees species commonly planted in urban landscapes was compared to root architecture of these tree species produced using common field nursery production practices. When young nursery production seedlings are root-pruned prior to replanting, the loss of the lower portion of the main root and lateral roots emerging from it, and initiation of adventitious roots from the cut end, alter the root system architecture. Nursery production plants have 7 to 48 percent fewer natural lateral roots that could develop into flare roots than undisturbed plants. New roots initiated from the cut end of the main root on nursery production plants can substitute for the loss of lateral roots, if accepted practices are followed. Root architecture of trees is established early. With minor exceptions attributed to the loss of small roots less than 1 mm diameter, there were no significant changes in the number of lateral roots over the 4 year period in both nursery production and undisturbed plants. This consistent number of roots also suggests that pruning the main root did not stimulate additional lateral roots above the pruning cut. Root architecture of liner stock produced in nurseries can be equivalent to undisturbed root systems.

Index words: Structural roots, root pruning, bare root, root depth, taproot, root flare.

Species used in this study: Norway maple (*Acer platanoides* L.), green ash (*Fraxinus pennsylvanica* Marsh.), littleleaf linden (*Tilia cordata* L.), red maple (*Acer rubrum* L.), European white birch (*Betula pendula* Roth.), Kentucky coffee tree (*Gymnocladus dioicus* L.), domestic apple (*Malus spp.*), red oak (*Quercus rubra* L.), Siberian elm (*Ulmus pumila* Jacq.).

Significance to the Horticulture Industry

Field-grown bare-root trees used as liner stock in landscape nurseries, and also for urban landscape plantings, are transplanted as seedlings as the first step in nursery production. Before replanting, the main root is pruned, eliminating lateral roots below the pruning cut as well. New roots regenerated from the cut end can effectively replace the main root and lateral roots that were removed. These natural lateral roots and regenerated roots present on young seedlings form the architectural structure of the woody root system that persists after the trees are harvested and planted in the landscape.

This root architecture alteration does not lead to inferior root systems if care is taken to follow good practices in all stages of production. Pruning the main root at 10 cm (4 in) below the soil line initiates new roots from the cut end that will be shallower than the lateral roots they are replacing, and may be better suited to grow well in heavy, poorly drained urban soils. Conversely, if the main root is pruned at deeper depths, the regenerated roots from the cut end will be located deeper in the soil profile and these deep structural roots may not be well-positioned to grow well in urban soils. Recognizing the importance of good root structure at such an early age could have implications on other aspects of tree propagation and production, as well.

Introduction

Root systems of trees produced in nurseries are subjected to exposure, root pruning, and root regeneration during transplanting that do not occur in nature. Some of these procedures have a horticultural purpose, such as when trying to minimize the taproot development for more successful transplanting. Others are merely performed to facilitate production.

Standard nursery practices of seedling transplanting and root pruning can permanently alter the woody root architecture, and may influence the ultimate depth of structural roots in the landscape. A large portion of the natural lateral roots emerging from the main root, the principle vertical woody root (Sutton and Tinus 1983), can be lost from handling and desiccation. Adventitious roots taking their place from the cut end of the main root can form a substitute adventitious root flare that can be deeper in the soil than a natural root flare (Hewitt and Watson 2009). The depth of the adventitious root flare is dependent on where the main root was pruned (Harris et al. 2001).

The depth of the roots of young trees planted in the landscape has become a concern (Watson 2005, Watson and Hewitt 2012) and alteration of root structure during nursery production has been recognized as a potential contributing factor (Hewitt and Watson 2009). Deep root systems can lead to poor establishment or eventual decline and death of trees (Arnold et al. 2007, Day and Harris 2008, Wells et al. 2006), especially in poor quality urban soils (Watson and Hewitt 2012).

Earlier work established the loss of lateral roots and creation of the adventitious root flare by analyzing plants at various stages of commercial propagation and liner production (Hewitt and Watson 2009). A direct comparison of plants grown from seed and never transplanted, to plants

subjected to standard nursery production practices, was needed.

Materials and Methods

Plants were grown at J. Frank Schmidt & Son Co., Boring, Oregon, USA, to subject them to the same cultural conditions as standard production. The soil was a Bornstedt silt loam (Soil survey staff). Nine species of trees were grown from seed sown by nursery staff. Logistical concerns prevented sowing the seed of all 9 species in a single year. Norway maple (*Acer platanoides* L.), green ash (*Fraxinus pennsylvanica* Marsh.) and littleleaf linden (*Tilia cordata* L.) were planted the first year, red maple (*Acer rubrum* L.), European white birch (*Betula pendula* Roth.), Kentucky coffee tree (*Gymnocladus dioicus* L.), domestic apple (*Malus spp.*), red oak (*Quercus rubra* L.), and Siberian elm (*Ulmus pumila* Jacq.) were planted the following year.

Seedlings transplanted according to standard nursery procedures were compared to seedlings never moved. Species were planted in separate adjacent areas. Within species, trees of each treatment and harvest year were planted together in a group to make harvesting large plants over a 4 year period in tightly spaced nursery rows possible. For both treatments, seeds were planted directly in the soil and grown for one year. At that time, seedlings to be subjected to standard nursery production practices were dug. Forty 6 mm (0.25 in) caliper seedlings were selected and pruned as they would normally be during production. Main roots were pruned to 10 cm (4 in) below the soil line. Any woody lateral roots were pruned to 2.5 cm (1 in), and stems were pruned at 30 cm (12 in). The seedlings were replanted on the same site in two rows, 76 cm (30 in) apart with 30 cm (12 in) between plants in each row (designated the nursery production method). Other undisturbed seedlings, similar in grade size to those that were transplanted, were left to grow without transplanting at the same spacing (designated the undisturbed method). The planting was weeded, fertilized, and irrigated according to standard nursery practice throughout the experiment.

The first 10 plants each of transplanted and non-transplanted treatments were harvested at the end of the first season after transplanting (year 1, the second season after seed planting). At this time, the remaining transplanted seedlings were cut back to just above soil level and a bud was trained to become a straight, vertical stem (referred to as stub and grow straight) as is standard in nursery production of liner stock. Those that were not transplanted, were not cut back. The second harvest took place at the end of this second season after transplanting (year 2). The remaining plants were harvested the following two years (years 3 and 4). Data from years 2 and 3 are not shown for clarity.

Lateral root diameter and depth relative to the soil surface were recorded. Lateral roots were measured along the full length of the main root on undisturbed plants, and above the adventitious roots initiated from the cut end of the main root on nursery production plants. Diameter of regenerated roots from the cut end was recorded as well. Roots with a diameter of less than 1 mm could not be measured accurately and were recorded as 1 mm. The sum of root diameters was used to estimate the overall development of the lateral and regenerated roots. Main root diameter was measured at the soil surface.

Statistical analysis was performed with the R statistical software [version 3.5.3, R Core Team (2019)]. Analysis of variance and post-hoc Tukey's Honestly Significant Difference ($p < .05$) pair-wise comparisons were used to assess differences between years within undisturbed and nursery production treatments and t-tests were performed to compare undisturbed to nursery production treatments.

Results and Discussion

Transplanting young seedlings during production of field-grown tree liner stock introduces opportunity for changes in the root system (Fig. 1). Root pruning removes the lower portion of the main root and the lateral roots growing from it, and laterals above it can be lost from handling or desiccation. One year after the seedlings were transplanted, estimated development (sum of diameters) of all lateral and regenerated roots on the nursery production (pruned) plants were smaller than on undisturbed plants in six of the nine species (Table 1). Differences in these six species in year 1 persisted to year 4, when the trees would be harvested as branched liners, in four of the six species. Main root diameter differences between nursery production and undisturbed seedlings in year 1 persisted to year 4 in only three of the six species (Table 1). These differences in root system development may reflect changes in architecture of the main and lateral roots.

Undisturbed root system development. An understanding of root development of undisturbed plants is necessary to evaluate changes in architecture introduced by nursery production. In undisturbed plants, the number of natural lateral roots along the main root in year 1 varied by species from 14.9 to 79.6 (Table 2). The root architecture of these young root systems did not always conform to accepted perceptions of mature root systems of the species. Red oak, a species considered to have a strong taproot and weak lateral roots, as young plants had approximately twice as many lateral roots as red maple, Norway maple, and littleleaf linden, which are usually considered species with strong lateral root systems. European white birch, which is not considered to be a taprooted species, had the fewest lateral roots at this stage of development.

The number of lateral roots in year 4 was not significantly different than in year 1 for any species, with the exception of red oak (Fig. 2). This suggests that lateral roots that will persist for years, and perhaps permanently, are present in year 1. Red oak had significantly fewer lateral roots in year 4 than in year 1, 23 less per tree (Fig. 2). In the 1-year-old oak seedlings, 37 of the 53 lateral roots each plant averaged were less than 2 mm diameter, which would be considered fine roots. Eighty percent of those were less than 1 mm diameter (data not shown). Fine roots are known to be short lived (McCormack 2012). It is likely that the reduction in lateral roots by year 4 reflects the loss of many of these small lateral roots. If these small roots had survived to grow into a larger size class, there

Fig. 1. Examples of typical root architecture of 4-year-old green ash undisturbed (left) and nursery production (right) root systems. Root pruning during nursery production results in multiple roots being initiated from the cut end of the main root and loss of many, sometimes all, lateral roots above the cut.

Table 1. Main root diameter and estimated development (sum of root diameters) of all lateral and regenerated roots of nursery production and undisturbed root systems one and four years after transplanting nursery production seedlings. Differences in main root diameter between root treatments in year 1 did not persist to year 4 in most species. Differences in estimated root development in year 1 did persist in the majority of species.

Species	Growing method	Main root diameter (mm)[z]				Estimated development of all lateral and regenerated roots (mm)[z]			
		Year 1		Year 4		Year 1		Year 4	
Norway maple	Nursery production	1.5	a	5.7	a	58.3	a	241.1	a
	Undisturbed	2.0	b	5.8	a	66.8	a	278.1	a
Green ash	Nursery production	1.4	a	3.9	a	54.3	a	152.3	a
	Undisturbed	1.7	b	5.0	a	75.2	b	235.3	b
Littleleaf linden	Nursery production	1.3	a	5.5	a	42.6	a	171.1	a
	Undisturbed	2.1	b	7.4	b	79.3	b	243.6	b
Red maple	Nursery production	1.3	a	5.7	a	55.4	a	222.0	a
	Undisturbed	1.9	a	5.7	a	86.8	b	265.8	a
European white birch	Nursery production	1.2	a	8.0	a	41.3	a	233.9	a
	Undisturbed	1.7	a	7.3	a	47.7	a	187.7	a
Kentucky coffee tree	Nursery production	0.8	a	4.0	a	25.2	a	143.0	a
	Undisturbed	1.0	b	4.7	a	49.3	b	230.2	b
Domestic apple	Nursery production	1.4	a	4.5	b	67.6	a	192.8	b
	Undisturbed	1.0	a	3.0	a	68.4	a	102.9	a
Red oak	Nursery production	0.8	a	4.6	a	25.3	a	146.3	a
	Undisturbed	1.9	b	6.0	b	83.0	b	251.8	b
Siberian elm	Nursery production	1.8	a	7.6	a	64.2	a	252.3	a
	Undisturbed	2.3	b	6.8	a	104.1	b	296.2	a

[z]Means within a species, growing method and year followed by different letters are statically different from each other at $P<0.05$ level of significance.

Table 2. Comparison of lateral root development nursery production trees and undisturbed plants, and between nursery production trees and on the upper 10 cm (4 in) of undisturbed plants (Undisturbed-10).

| | | Lateral roots | | | | | | | |
| | | Number | | | | Diameter (mm) | | | |
Species	Growing method	Year 1		Year 4		Year 1		Year 4	
Norway maple	Nursery production	7.6	a	9.5	a	3.0	a	16.9	a
	Undisturbed	26.0	b	26.4	b	2.8	a	11.7	a
	Undisturbed-10	14.9	b	8.1	a	2.7	a	15.6	a
Green ash	Nursery production	4.6	a	5.8	a	2.0	a	7.4	a
	Undisturbed	40.6	b	35.4	b	2.1	a	8.0	a
	Undisturbed-10	15.0	b	10.7	b	2.0	a	12.2	a
Littleleaf linen	Nursery production	12.1	a	9.6	a	2.6	a	10.6	a
	Undisturbed	27.1	b	35.8	b	3.1	a	8.1	a
	Undisturbed-10	16.8	a	13.4	a	3.7	a	13.3	a
Red maple	Nursery production	10.0	a	9.2	a	3.6	a	12.9	a
	Undisturbed	30.3	b	26.1	b	3.5	a	11.0	a
	Undisturbed-10	17.6	b	14.0	a	3.9	a	11.6	a
European white birch	Nursery production	6.9	a	9.4	a	3.2	a	16.2	a
	Undisturbed	14.5	a	22.5	b	3.3	a	9.4	a
	Undisturbed-10	10.0	a	10.8	a	3.4	a	11.4	a
Kentucky coffee tree	Nursery production	18.1	a	10.0	a	1.2	a	6.2	a
	Undisturbed	41.4	b	41.1	b	1.2	a	6.0	a
	Undisturbed-10	23.9	a	16.6	b	1.3	a	5.9	a
Domestic apple	Nursery production	26.6	a	49.5	a	2.0	a	4.7	a
	Undisturbed	79.6	a	55.0	a	1.2	a	1.9	b
	Undisturbed-10	48.3	a	32.0	a	1.2	a	2.2	b
Red oak	Nursery production	3.8	a	5.0	a	1.5	a	7.1	a
	Undisturbed	53.3	b	29.5	b	1.6	a	8.6	a
	Undisturbed-10	23.3	b	9.2	b	1.1	a	8.8	a
Siberian elm	Nursery production	16.4	a	18.9	a	2.5	a	6.6	a
	Undisturbed	37.0	b	50.6	b	3.2	a	6.0	a
	Undisturbed-10	16.4	a	24.6	b	3.2	a	6.0	a

[z]Means within a species, and year followed by different letters between nursery production and either undisturbed or undisturbed-10 growing method are statically different from each other at P<0.05 level of significance.

would likely have been an increase in the number of 2-5 mm diameter roots. The number of roots 2-5 mm diameter was 3 per tree less in year 4 than in year 1 (data not shown), supporting the likelihood that most of the lateral roots less
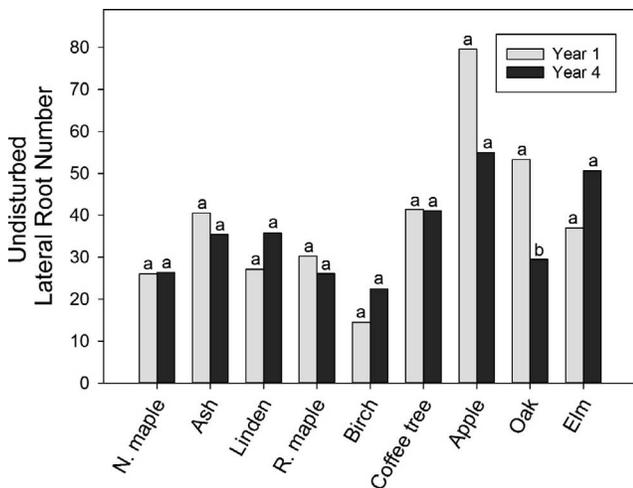

Fig. 2. Number of lateral roots on undisturbed main roots did not change significantly between year 1 and 4 for most species. Species code: N. maple = Norway maple, Ash = green ash, Linden = littleleaf linden, R. maple = red maple, Birch = European white birch, Coffee tree = Kentucky coffee tree, Apple = domestic apple, Oak = red oak, Elm = Siberian elm. Within a species, different letters indicate significant differences between years (P<0.05).

than 2 mm diameter never increased in size and ultimately died.

In year 1, species mean lateral root diameters ranged from 1.2 to 3.5 mm (Fig. 3). Species with the larger numbers of lateral roots tended to have the smaller average diameters (eg. Kentucky coffee tree and domestic apple, Fig. 2 and 3). In all species, lateral root diameter was significantly larger in year 4 (Fig. 3).

Nursery production root system development. The aggressive root pruning resulted in very little mortality after replanting. No plants were lost in 6 of 9 species. Losses in littleleaf linden, domestic apple, and European white birch, were 3, 10, and 25 percent, respectively.

Since nursery production includes pruning the seedling main root approximately 10 cm (4 in) below the soil line during transplanting, natural lateral roots could exist only above the root pruning location. The mean number of lateral roots of root-pruned plants ranged widely among species in year 1, from 4 to 26 (7-48 percent of the number of lateral roots of undisturbed plants of the same species) (Table 2). At least part of the reduced number can be attributed to pruning off the lower portion of the main root and the laterals emerging from it. Exposure and handling during transplanting could also have resulted in loss of some of the lateral roots as well (Hewitt and Watson 2009).

Nursery production red oak and green ash had the fewest lateral roots in year 1, 7 and 11 percent of the undisturbed
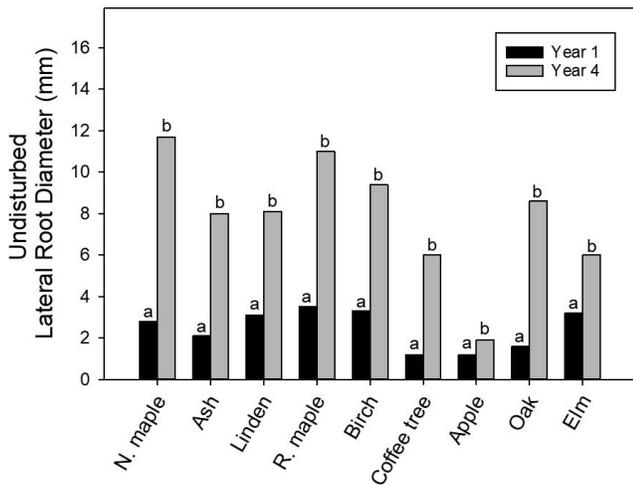
Fig. 3. Mean diameter of lateral roots on undisturbed main roots increased significantly between year 1 and year 4 for all species. Species code: N. maple = Norway maple, Ash = green ash, Linden = littleleaf linden, R. maple = red maple, Birch = European white birch, Coffee tree = Kentucky coffee tree, Apple = domestic apple, Oak = red oak, Elm = Siberian elm. Different letters indicate significant differences between years for each species (P<0.05).

Fig. 4. Mean number of lateral roots on pruned main roots of nursery production trees did not change significantly between year 1 and 4 for most species. Species code: N. maple = Norway maple, Ash = green ash, Linden = littleleaf linden, R. maple = red maple, Birch = European white birch, Coffee tree = Kentucky coffee tree, Apple = domestic apple, Oak = red oak, Elm = Siberian elm. Different letters indicate significant differences between years for each species (P<0.05).

plants, respectively (Table 2). These low values can be explained by the size of the lateral roots present on undisturbed seedlings in year 1. On undisturbed seedlings, over 60 percent of red oak roots, and 41 percent of green ash roots, were 1 mm diameter or less (data not shown). On these two species, these small roots could easily have been lost from handling and exposure during transplanting, in addition to any natural attrition of small roots as described above for undisturbed plants.

There was no change in lateral root number from year 1 to year 4, except for Kentucky coffee tree, which had fewer roots in year 4 (Fig. 4). There was a relatively high number of Kentucky coffee tree roots in year 1, and 59 percent were 1 mm diameter or less (data not shown). Natural attrition may have reduced the number by year 4 to closer to the number in most other species. The stable number of lateral roots, indicates that the persistent woody, structural lateral roots are initiated in the first year, similar to undisturbed plants (Fig. 2). The lack of an increase in number also indicates that pruning the main root did not stimulate additional lateral roots above the pruning cut.

In year 1, species mean lateral root diameters of nursery production plants ranged from 1.2 to 3.6 mm (Table 2), a nearly identical range as lateral root diameter of undisturbed plants. Lateral root diameter was significantly larger in year 4 in all species except red oak (Fig. 5). Though lateral root diameter of red oak did not differ significantly between years, the mean was over four times larger in year 4.

The number of roots regenerated from the cut end of the main root ranged from 3.4 in Kentucky coffee tree to 12.5 in Norway maple in year 1 (Table 3). The lack of significant difference between year 1 and year 4 in all species except Norway maple suggests that regenerated roots initiated in the first year persist through year 4. Norway maple mean regenerated root number was the highest in year 1, and significantly reduced by year 4,
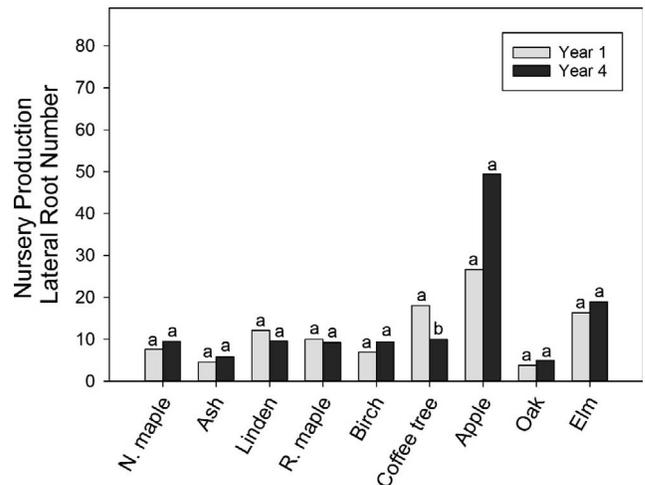
bringing it down to a value similar to all other species. This suggests that such a high number of regenerated roots initially cannot be supported sustainably over time.

In year 1, species mean regenerated root diameters ranged from 0.9 to 5.5 mm (Table 3). In all species, lateral root diameter was significantly larger in year 4 (Table 3.).

Undisturbed and nursery production comparison. There were significantly fewer lateral roots on root-pruned nursery production seedlings than on undisturbed seedlings
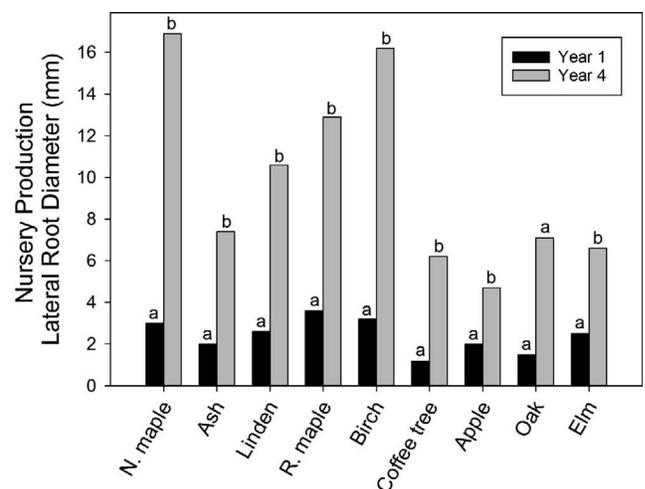

Fig. 5. Mean diameter of lateral roots on pruned main roots of nursery production trees increased significantly between year 1 and year 4 for most species. Species code: N. maple = Norway maple, Ash = green ash, Linden = littleleaf linden, R. maple = red maple, Birch = European white birch, Coffee tree = Kentucky coffee tree, Apple = domestic apple, Oak = red oak, Elm = Siberian elm. Different letters indicate significant differences between years for each species (P<0.05).

Table 3. The number of regenerated roots on nursery production trees did not change between year 1 and year 4 in all but one species, and all increased in diameter, suggesting that regenerated roots initiated in first year persist through year 4 and may become part of the permanent root architecture.

Species	Nursery production regenerated roots							
	Number[z]				Diameter (mm)[z]			
	Year 1		Year 4		Year 1		Year 4	
Norway maple	12.5	a	7.6	b	3.5	a	21.3	b
Green ash	8.7	a	7.1	a	5.5	a	15.1	b
Littleleaf linden	5.2	a	6.0	a	3.7	a	13.5	b
Red maple	4.3	a	5.1	a	4.8	a	22.4	b
European white birch	4.1	a	5.4	a	4.8	a	24.2	b
Kentucky coffee tree	3.4	a	4.9	a	0.9	a	20.4	b
Domestic apple	8.9	a	6.8	a	3.9	a	12.4	b
Red oak	6.5	a	6.9	a	3.3	a	17.6	b
Siberian elm	5.3	a	5.4	a	4.9	a	28.9	b

[z]Means for each species between years followed by different letters are statically different from each other at $P < 0.05$ level of significance.

in 7 of 9 species in year 1, the exceptions being European white birch and domestic apple (Table 2). Those two species did have two and three times more lateral roots, respectively, on undisturbed seedlings than on nursery production seedlings, but were not significantly different. Red oak and green ash showed the most extreme differences, 14 and 9 times as many lateral roots, respectively, on undisturbed seedlings. The 1-year-old oak seedlings of these species had many very small lateral roots that would have been more susceptible to loss from desiccation or mechanical injury during transplanting.

The seven significant differences in number of lateral roots between undisturbed and nursery production plants in year 1 persisted through year 4 (Table 2). The difference also became significantly different in European white birch in year 4. There was still no significant difference in domestic apple in year 4, though the difference between the nursery production and undisturbed means had been reduced from 300 percent to 12 percent. High variation in the nursery production data (coefficient of variation 67 percent) explains this lack of statistical significance.

Comparing the number of lateral roots in the same upper 10 cm (4 in) of the main root between nursery production plants and undisturbed plants (designated undisturbed-10) provides insight into losses due to transplanting the seedlings. There were significantly more lateral roots on the same 10 cm (4 in) segment of main root of undisturbed seedlings in year 1 in 4 of 9 species, green ash, red oak, red maple and Norway maple. Even when not significantly different, the trend was similar with undisturbed seedlings having at least a third more lateral roots (Table 2). This suggests that some lateral roots were lost in transplanting in all species, but not always enough to be significantly different.

By year 4, the difference in the number of lateral roots between undisturbed-10 and nursery production seedlings was no longer significant in Norway and red maple (Table 2). In both species, the number of lateral roots on undisturbed-10 was lower in year 4 than year 1, while the number on nursery production plants remained more constant. This suggests that natural attrition of the larger

number of lateral roots on undisturbed plants reduced the difference. The same trend occurred in green ash and red oak where a significant difference was maintained. The difference had become significant in Kentucky coffee tree and Siberian elm in year 4.

Though root pruning reduced the number of lateral roots in nursery production plants in most species, reducing the number of lateral roots had no effect on lateral root diameter. Lateral root diameter of nursery production plants was not different than undisturbed plants, or undisturbed-10 in any species in year 1. It would be reasonable to expect roots to grow larger if there were fewer of them in order to sustain growth of the plant, but the regenerated roots from the cut end of the main root may have been effectively replacing the lost laterals. In year 4, there was still no difference, except domestic apple where the nursery production lateral roots were larger (Table 2). The reason for this unusual vigor of lateral roots on transplanted trees in domestic apple is unclear.

Root architecture of trees is established early. With minor exceptions attributed to the loss of roots less than 1 mm diameter, there were no significant changes in the number of lateral roots over the 4 year period in both nursery production and undisturbed plants (Fig. 2 and 4). Mean lateral root diameter nearly always increased significantly over time, averaging 338 and 411 percent for undisturbed and nursery production plants, respectively (Fig. 3 and 5). The increase in size with a constant number suggests that root turnover is not likely to be keeping the number constant, as it would result in more consistent size of roots over time, as roots are continually replaced. Pruning the main root of seedlings results in new roots at the cut end in the first year after replanting. These roots persist as well as the lateral roots and become part of the woody, structural root system. This work shows that these production practices alter development of the architecture of the structural roots in the first year after replanting seedlings, and this architecture persists at least until the trees are harvested and sold.

Root architecture development of all the species used in this study was quite similar and combined data from all species (not shown) will be used to develop a general comparison of root architecture between nursery production and undisturbed trees. Five-year-old (year 4 of this study) undisturbed trees averaged 37 natural lateral roots. Thirteen of these were in the upper 10 cm (4 in), the length of main root remaining after seedling root pruning during nursery production. An average of 10 lateral roots existed 10-20 cm (4-8 in) deep on undisturbed plants. These deeper roots can become part of the root flare in natural soils (Wagg 1967), but may be less likely to in poor quality urban soils if their vigor is reduced by soil conditions (Day et al. 2010). When data from all nine species are combined, undisturbed tree root systems have an average of 23 woody roots that could become part of the root flare.

Nursery production seedlings have fewer total lateral roots than undisturbed plants, but a similar number in the upper 10 cm (4 in), averaging 14. Nursery production plants also have an average of six regenerated roots at the cut end of the main root, approximately 10 cm (4 in) deep.

Together, nursery production plants average 20 roots that could become flare roots. The total number of roots is very similar in nursery production and undisturbed root systems. However, nearly half of the undisturbed lateral roots are deeper than all of the nursery production roots and could be in soil less suitable for root growth on urban sites.

Root flares are typically composed of 3-15 roots (Coutts 1983, Perry 1981, Day et al. 2010), so it is not likely that all of the 20+ lateral and regenerated roots found on these young trees will all persist to become permanent flare roots. The lateral and regenerated roots varied in size on each plant. Averages of 43% and 57% of the lateral roots of the nursery production and undisturbed trees, respectively, were 3 mm diameter, or less, in year 4 (data not shown). These smaller, less vigorous roots may be less likely to become major flare roots. Undisturbed trees have a few more potential flare roots, but more of them are smaller, perhaps equalizing the number of flare roots over time.

While root architecture of trees propagated and grown in nurseries are altered in the early stages of production, this does not necessarily lead to inferior plants if care is taken to follow good practices in all stages of production. The regenerated roots from the cut end of the main root effectively replace the main root and lateral roots that were removed. However, if the main root is pruned too deeply, the regenerated roots from it will be located deeper. Though this may not inhibit growth in quality nursery soils (Jarecki et al. 2006), these deep structural roots may not be well-positioned to thrive in poorly drained urban soils. Deep root systems can lead to poor establishment or eventual decline and death of trees (Arnold et al. 2007, Day and Harris 2008, Wells et al. 2006), especially in poor quality urban soils (Watson and Hewitt 2012).

Though mature naturally regenerated trees in nature seem to all exhibit excellent root flares, root architecture of young plants can be quite variable. Many woodland seedlings and saplings would not pass a reasonable grading system in the nursery (Single 2009). In nature, "survival of the fittest" is the grading system, and the plants with weak root systems cannot compete as well. A direct comparison of root systems produced in nurseries with naturally regenerated trees could show that the average nursery root system architecture is as good, or better, than produced in nature.

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