Development of Root Architecture in Thirty-seven Tree Species of Field Grown Nursery Stock[1]

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Abstract

The number and size of lateral roots of a tree seedling can be evaluated visually, and could potentially be used to select plants with better root systems early in nursery production. To evaluate how root architecture develops in young trees, root architecture of 37 species of trees was compared at two stages of development: as harvested seedlings, and then one year after replanting. The total number of lateral roots and the number of roots >2mm (0.08 in) diameter that were present on the portion of the taproot remaining on seedlings after standard root pruning were recorded. Neither could consistently predict the number of lateral roots on the root system one year after replanting. Development of roots (sum of diameters) regenerated from the cut end of the seedling taproot was equal or greater than lateral root development in 84 percent of evaluated species. Even when regenerated root development was significantly less than lateral root development, the regenerated roots still comprised up to 44 percent of the root system. Regenerated roots from the cut end of the taproot can become a major component of the architecture of the structural root system in nursery stock.

Index words: structural roots, nursery production, root regeneration.

Species used in this study: European black alder (*Alnus glutinosa* Gaertn.), green ash (*Fraxinus pennsylvanica* Marshall), quaking aspen (*Populus tremuloides* Michx.), European white birch. (*Betula pendula* Roth), river birch (*Betula nigra* L.), black locust (*Robinia pseudoacacia L.*), northern catalpa (*Catalpa speciosa* (Warder) Warder ex Engelm.), Mazzard cherry [*Prunus avium* [L.) L.], chokecherry (*Prunus virginiana* L.), American elm (*Ulmus americana* L.), Siberian elm (*Ulmus pumilia* L.), goldenchain tree (*Laburnum anagyroides* Medik.), northern hackberry (*Celtis occidentalis* L.), Cockspur hawthorn (*Crateagus crus-galli L.*), single seed hawthorn (*Crateagus monogyna* Jacq.), honeylocust (*Gleditsia tricanthos* L.), Japanese pagodatree [*Sophora japonica* (L.) Schott], Katsura tree (*Cercidiphyllum japonicum* Siebold & Zucc.), Kentucky coffee tree [*Gymnocladus dioicus (L.) K. Koch*], littleleaf linden (*Tilia cordata* Mill.), boxelder (*Acer negundo* L.), hedge maple (*Acer campestre* L.), Norway maple (*Acer platanoides* L.), red maple (*Acer rubrum* L.), silver maple (*Acer saccharinum* L.), sugar maple (*Acer saccharum* Marshall), sycamore maple (*Acer pseudoplatanus* L.), English Oak (*Quercus robur* L.), northern red oak (*Quercus rubra* L.), Siberian peashrub (*Caragana arborescens* Lam.), American plum (*Prunus Americana* Marshall), Myrobalan plum (*Prunus cerasifera* Ehrh.), redbud (*Cercis Canadensis* L.), Russian olive (*Elaeagnus angustifoliaI L.*), tuliptree (*Liriodendron tulipifera* L.), black walnut (*Juglans nigra* L.), Japanese zelkova (*Zelkova serrata* (Thunb.) Makino).

Significance to the Horticulture Industry

The nursery industry strives to produce quality plants. Considerable attention is given to developing quality root systems. Devising methods of evaluating root system architecture when transplanting seedlings early in production could result in trees with better root systems and greater vigor, both in the nursery and in the landscape. It could also reduce the number of plants with a poor root system that need to be culled later after additional expenses have been incurred. Though number and size of lateral roots as a seedling can be easily evaluated visually, these characteristics did not prove to be useful for predicting development of the architecture of the structural root system of most species. Other characteristics need to be investigated. This study did confirm that roots regenerated from the cut end of the seedling taproot do become a major component of the architecture of the structural root system in all 37 species tested. Most species had equal or greater regenerated root development than lateral root development one year after replanting the seedlings. Even when regenerated root development was significantly lower than lateral root development, the regenerated roots still comprised up to nearly half of the root system. Since these regenerated roots become a major component of the root system, this emphasizes the need to prune the taproot as short as possible so that the regenerated roots are shallow enough to survive and grow vigorously when they are later planted in shallow urban soils.

Introduction

Root architecture refers to the structural organization or spatial arrangement of a plant's root system (Lynch 1995). In nature, root architecture development begins as the primary root emerges from the seed and grows downward into the soil, followed by the development of lateral roots just below the junction of the primary root and the hypocotyl (Coutts et al 1999). As the taproot develops, the growth rate eventually slows as the tip encounters less favorable soil conditions in deeper soils, resource allocation is shifted, and the growth rate of lateral roots increases (Coutts 1987, Drexhage et al. 1999, Lyford and Wilson 1964).

The taproot root is a component of all seedling root systems, and can persist longer in some species. Since the soil environment becomes less suitable for root growth with depth, the taproot seldom persists as a major component of mature tree root architecture (Cutler et al 1990). Urban sites frequently restrict rooting depth even more than undisturbed natural sites (Day et al 2010).

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Although urban soils are heterogeneous, it is common to find impenetrable horizons relatively near the surface. Examples include subsoils compacted by construction activity and poorly drained horizons (Alberty et al. 1984, Day et al. 2000, Lyford and Wilson 1964, Stone and Kalisz 1991). Shallow, horizontal roots are typically the most dominant aspect of root architecture in shallow urban soils.

Field nursery production systems can alter the natural structural root architecture of trees (Day et al. 2009, Hewitt and Watson 2009). Seedlings are transplanted after one, or sometimes two, years in a seedling bed. In this process, the taproot is pruned before replanting. Loss of the taproot itself may not be important on trees destined for urban sites.

Each species has a characteristic shoot-root ratio. When the root-shoot ratio is disturbed, plants respond by redirecting assimilates to replace, or substitute for, the removed parts (Kramer and Kozlowski 1979). Root pruning stimulates root growth as the plant attempts to restore the pre-pruning shoot-root ratio (Maggs 1964, Richards and Rowe 1977). Vigorously growing roots are initiated from the cut end of the seedling taproot (Harris et al. 2001, Hewitt and Watson 2009)

Lateral roots can be affected by production practices as well. Small lateral roots can be lost through exposure and mechanical injury during seedling transplanting. Drying of exposed surface soils after replanting may also hinder shallow lateral root development. Up to 60% of the natural lateral roots that could normally develop into the 5 to 15 structural roots that typically form the root flare (Day et al. 2010, Coutts 1983, Perry 1981) can be lost. By the time five species of rootstocks were harvested as branched liners three years after transplanting as seedlings, there were fewer than three lateral roots larger than 3 mm (0.12 in) per tree. Given the small number, and slow growth, of these remaining lateral roots (Hewitt and Watson 2009), there appears to be little chance they alone could support the plant and develop into a normal root flare.

Such a loss of lateral roots can reduce the health and vigor of the tree. Seedlings with fewer lateral roots consistently showed less growth in the initial years after planting (Kormanik 1986, Ruehle and Kormanik 1986, Kormanik et al. 1989, Schultz and Thompson 1997, Kormanik et al. 1998, Ponder 2000). The fate of these lateral roots was not tracked, but plants that grew better likely had roots that persisted and contributed to root architecture.

The vigorously growing adventitious roots initiated from cut end of the seedling taproot can at least partially replace the natural lateral roots and form an adventitious root flare (Hewitt and Watson 2009). However, if the remaining portion of the seedling taproot is too long, new adventitious roots will develop further below the soil surface, and the adventitious root flare will be deeper in the soil than a natural root flare. This may make the trees less able to survive on urban sites.

Each of the many species produced in nurseries for urban landscapes use may potentially differ in their root response to the nursery practices described. Understanding how root systems respond to these practices may be important to understanding how to produce quality root systems with architecture suitable for urban sites. The objectives of this study were to understand how nursery field production practices affect the root architecture of species of trees commonly planted in urban landscapes, and identify ways to use that information to select for better root systems.

Table 1. Species used in this experiment and a listing of the native range for each species (Anonymous, Missouri Botanical Garden Plant Finder)[z].

Species		Native to:
Alder, European black	*Alnus glutinosa*	Europe, Asia
Ash, green*	*Fraxinus pennsylvanica*	Eastern USA
Aspen, quaking	*Populus tremuloides*	North America
Birch, European white	*Betula pendula*	Europe, Asia
Birch, river	*Betula nigra*	Eastern USA
Black locust	*Robinia pseudoacacia*	Eastern USA
Catalpa, northern	*Catalpa speciosa*	Eastern USA
Cherry, Mazzard	*Prunus avium*	Europe, Asia
Chokecherry	*Prunus virginiana*	North America
Elm, American*	*Ulmus americana*	Eastern USA
Elm, Siberian*	*Ulmus pumilia*	Asia
Goldenchain tree*	*Laburnum anagyroides*	Europe
Hackberry, northern	*Celtis occidentalis*	Eastern USA
Hawthorn, cockspur	*Crateagus crus-galli*	Eastern USA
Hawthorn, single seed	*Crateagus monogyna*	Europe
Honeylocust*	*Gleditsia tricanthos*	Eastern USA
Japanese pagodatree*	*Sophora japonica*	Asia
Katsura tree*	*Cercidiphyllum japonicum*	Asia
Kentucky coffee tree*	*Gymnocladus dioicus*	Eastern USA
Linden, littleleaf	*Tilia cordata*	Europe, Asia
Maple, box elder	*Acer negundo*	Eastern USA
Maple, hedge	*Acer campestre*	Europe, Asia
Maple, Norway*	*Acer platanoides*	Europe
Maple, red*	*Acer rubrum*	Eastern USA
Maple, silver*	*Acer saccharinum*	Eastern USA
Maple, sugar*	*Acer saccharum*	Eastern USA
Maple, sycamore	*Acer pseudoplatanus*	Europe, Asia
Oak, English*	*Quercus robur*	Europe
Oak, northern red*	*Quercus rubra*	Eastern USA
Peashrub, Siberian*	*Caragana arborescens*	Asia
Plum, American	*Prunus americana*	Eastern USA
Plum, Myrobalan	*Prunus cerasifera*	Europe, Asia
Redbud	*Cercis canadensis*	Eastern USA
Russian olive	*Elaeagnus angustifolia*	Asia
Tuliptree	*Liriodendron tulipifera*	Eastern USA
Walnut, black	*Juglans nigra*	Eastern USA
Zelkova, Japanese*	*Zelkova serrata*	Asia

[z]* denotes that roots were undercut in the seedling bed. Those without an * were not root pruned in the seedling bed.

Materials and Methods

Ten each of 37 species used as landscape tree root stocks were selected from regular production seedling stock of J. Frank Schmidt and Sons Co., Boring, Oregon. Seeds had been germinated and grown in densely planted seedbeds for one year, or undercut in the first year and left in the seedbed for a second year (Table 1). The undercutting process was performed by drawing a blade through the soil in the raised bed approximately 10 cm (4 in) deep to cut the taproot. The seedlings were mechanically harvested bare root and held in temperature and humidity controlled storage facilities over the winter for spring planting. During the storage period, plants were graded by size, and roots are

Table 2. The linear relationship between the total number of lateral roots and the number ≥ 2 mm (0.08 in) diameter, existing on the upper 10 cm of the taproot after seedling harvest and taproot pruning compared to the number of lateral roots one growing season after replanting.

Species	Seedling lateral roots	R^2	P	Seedling lateral roots ≥2mm (0.08 in)	R^2	P	Lateral roots one year after replanting[z]
Alder, European black	15.0	0.001	0.946	7.4	0.048	0.601	11.5
Ash, Green	12.4	0.747	0.001	5.1	0.194	0.203	8.3
Aspen, quaking	5.8	0.013	0.855	5.2	0.186	0.393	5.0
Birch, European white	10.8	0.121	0.325	6.3	0.044	0.558	8.4
Birch, river	10.5	0.014	0.746	2.1	0.039	0.581	5.8
Black locust	11.1	0.048	0.543	3.3	0.001	0.964	6.7
Catalpa, northern	14.1	0.566	0.012	2.0	0.094	0.388	7.1
Cherry, Mazzard	11.7	0.094	0.383	4.0	0.138	0.291	7.4
Chokecherry	17.0	0.099	0.375	5.5	0.053	0.520	14.7
Elm, American	9.9	0.236	0.155	2.3	0.001	0.987	9.8
Elm, Siberian	20.2	0.202	0.224	4.8	0.019	0.723	14.2
Goldenchain tree	20.4	0.001	0.922	8.0	0.062	0.487	10.4
Hackberry, northern	9.6	0.026	0.656	3.2	0.156	0.259	8.6
Hawthorn, cockspur	11.3	0.352	0.215	1.8	0.156	0.259	3.7
Hawthorn, single seed	23.6	0.023	0.671	6.5	0.255	0.137	9.0
Honeylocust	5.6	0.097	0.380	1.4	0.501	0.022	5.5
Japanese pagodatree	6.7	0.024	0.669	3.3	0.009	0.790	4.6
Katsura tree	17.3	0.133	0.374	7.5	0.602	0.024	16.0
Kentucky coffee tree	7.0	0.015	0.730	3.1	0.001	0.920	10.6
Linden, littleleaf	9.1	0.194	0.275	1.8	0.045	0.614	4.4
Maple, Box elder	7.9	0.064	0.510	0.7	0.370	0.082	3.1
Maple, hedge	12.4	0.023	0.697	4.0	0.025	0.681	5.2
Maple, Norway	8.9	0.264	0.128	0.8	0.405	0.048	9.4
Maple, red	10.7	0.134	0.298	4.9	0.030	0.630	8.5
Maple, silver	17.9	0.391	0.072	4.2	0.266	0.155	7.6
Maple, sugar	18.1	0.006	0.820	2.4	0.454	0.033	12.1
Maple, sycamore	14.9	0.550	0.494	4.9	0.297	0.103	8.2
Oak, English	20.3	0.540	0.015	5.5	0.128	0.311	16.8
Oak, Northern red	14.4	0.663	0.008	1.4	0.393	0.071	3.6
Peashrub, Siberian	15.2	0.040	0.575	3.5	0.003	0.866	11.8
Plum, American	14.4	0.105	0.477	4.8	0.001	0.984	12.6
Plum, Myrobalan	17.8	0.118	0.331	3.0	0.001	0.967	8.8
Redbud	7.4	0.360	0.154	1.3	0.280	0.222	6.6
Russian olive	14.4	0.279	0.116	9.1	0.285	0.122	12.8
Tuliptree	17.7	0.147	0.273	7.4	0.001	0.943	9.4
Walnut, black	28.6	0.006	0.826	6.2	0.001	0.931	6.0
Zelkova, Japanese	17.7	0.024	0.670	5.7	0.032	0.616	13.1

[z]Linear regression ($P < 0.05$) was used to determine the relationship between lateral root persistence on the number and size of lateral roots present at the seedling transplant stage.

pruned to facilitate handling and mechanical planting as is customary in nursery field production. The taproot of each seedling was pruned at approximately 10 cm (4 in). Woody lateral roots were pruned at approximately 2.5 cm (1 in). Stems were cut to approximately 30 cm (12 in) tall.

After root pruning, and before planting, the seedlings were individually tagged and photographed from two directions against a measurement grid, rotated 90 degrees between photographs. Seedlings were planted in the production fields at J. Frank Schmidt Nursery in Boring, Oregon, at the original soil line depth, with 30 cm (12 in) spacing within rows, and 1.5 m (5 ft) between rows. They were grown with standard nursery maintenance, and then dug bare root after one season because root architecture is largely established by one year after replanting (Watson and Hewitt 2020).

The number and diameter of lateral roots on each seedling before planting were determined from the photographs taken after root pruning. This was necessary due to time constraints and to avoid desiccation of the root systems during handling. After harvest, number and diameter of both lateral roots above the cut end, and new roots initiated from the cut end, were recorded directly from the plants. The sum of root diameters was used for comparison of the relative overall development of lateral roots, and new roots initiated from the cut taproot.

Statistical analysis was performed using SigmaPlot for Windows Verson 14.0 (Systat Software, Inc.). The relative development of lateral root vs. regenerated roots of each species was compared using t-tests ($P < 0.05$). Linear regression ($P < 0.05$) was used to determine the relationship between lateral root persistence (dependent variable) on the number and size of lateral roots present at the seedling transplant stage (independent variables).

Results and Discussion

The taproot pruning that is performed on seedlings in the nursery results in the loss of lateral roots and formation of an adventitious root flare at the cut end (Hewitt and Watson 2009). Variation in response of individual species to taproot pruning may affect the architecture of the structural root system of each species differently. The number and size of lateral roots present as a seedling could influence

Table 3. Development (sum of diameters) of lateral and regenerated roots of 37 species one year after transplanting[z].

Species	Lateral roots[y]		Regenerated roots[x]	
Alder, European black	57.5		59.4	
Ash, Green	40.3	*	31.1	
Aspen, quaking	27.6		53.6	**
Birch, European white	52.2		31.9	
Birch, river	28.4		51.9	**
Black locust	37.9		72.5	***
Catalpa, northern	29.8		64.2	***
Cherry, Mazzard	67.9		71.0	
Chokecherry	57.4	***	29.4	
Elm, American	28.8		46.4	**
Elm, Siberian	48.4		51.3	
Godenchain tree	41.1		61.8	*
Hackberry, northern	34.5		42.9	
Hawthorn, cockspur	12.0		46.5	**
Hawthorn, single seed	30.5		46.7	**
Honeylocust	14.1		47.2	***
Japanese pagodatree	17.2		59.8	***
Katsura tree	63.4	***	28.0	
Kentucky coffee tree	23.6		40.7	*
Linden, littleleaf	19.5		43.9	**
Maple, Box elder	14.6		73.3	***
Maple, hedge	23.6		43.1	*
Maple, Norway	28.7		52.0	
Maple, red	48.1	*	25.0	
Maple, silver	34.2		55.4	**
Maple, sugar	25.0		40.6	
Maple, sycamore	39.5		85.0	***
Oak, English	27.3		42.6	*
Oak, Northern red	9.6		31.8	***
Peashrub, Siberian	42.2		37.0	
Plum, American	37.0		49.9	
Plum, Myrobalan	46.2		87.9	***
Redbud	30.7		29.3	
Russian olive	66.0	***	22.9	
Tuliptree	35.3	*	26.4	
Walnut, black	25.7		34.7	
Zelkova, Japanese	49.4		38.4	

[z]The number of lateral root vs. regenerated roots of each species was compared using t-tests. Significance is indicated as: * $P<0.05$, **$P<0.01$, ***$P<0.001$.

[y]Sum of diameters of lateral roots above cut end of the taproot.

[x]Sum of diameters of new roots initiated from the cut end of the taproot.

the future architecture of the tree root system. These characteristics have potential to be easily used to visually grade seedling root systems in the interest of producing better tree root systems.

There was no consistent relationship between the number of lateral roots above the remaining portion of the taproot after pruning (10 cm, 4 in) as a seeding, and the number of lateral roots present one year after replanting, in most species. Of the 37 species used in the study, the number of lateral roots present one year after replanting could only be predicted by the number of seedling lateral roots in four species (green ash, northern catalpa, English oak, northern red oak). The number of seedling lateral roots of those four species was not similar to each other, or unique as a group, and varied (12.4 to 20.3) across the middle third of the overall range (5.6 to 28.6) (Table 2).

If desiccation and mechanical injury during harvest, storage, and handling of the seedlings damages fine roots (less than 2 mm (0.08 in) diameter), woody roots may be more likely to persist after replanting the seedlings. Of the 37 species, the number of lateral roots 2 mm (0.08 in) diameter, or larger, as a seedling could only predict the number of lateral roots present one year after replanting in four species (honeylocust, katsura, Norway maple, and sugar maple). The number of seedling lateral roots greater than 2 mm (0.08 in) diameter in these four species varied widely (0.8 to 7.5) across the range of all species (0.7 to 9.1) (Table 2). In nearly every species, there were at least 25 percent more lateral roots one year after replanting, than there were roots 2 mm (0.08 in), or larger, as a seedling. Over half of all species had at least 50 percent more (Table 2). Even if the 2 mm (0.08 in) seedling roots did persist, the growth of other smaller roots, and/or the production of new, faster-growing adventitious roots, as has been reported for oaks (Pagès et al. 1992), would make the relationship between woody seedling roots and lateral roots one year later difficult to detect.

All species regenerated new roots from the cut end of the taproot. Root pruning stimulates root growth from the cut end of the seedling taproot as the plant attempts to restore the pre-pruning shoot-root ratio (Maggs 1964, Richards and Rowe 1977, Harris et al. 2001, Hewitt and Watson 2009). About half of the species (19 of 37) showed stronger regenerated root development than lateral root development one year after replanting the seedlings (Table 3). Both fibrous rooted species (eg. maples) and taprooted species (eg. oaks) exhibited this response. Relatively stronger lateral roots were only exhibited in six species (tulip tree, chokecherry, Norway maple, sugar maple, northern hackberry, and green ash). All six species would be considered to be fibrous rooted. However, other species that would also be considered fibrous rooted did not develop dominant lateral roots. Lateral or regenerated root dominance after replanting does not seem to be related to this type of general characterization of the root system.

The dominance of adventitious roots from the cut end of the taproot over lateral roots may be attributed to their anatomy. Replacement taproots are generally thicker and woodier than typical lateral roots (Wilson et al. 2007). They have large meristems from the primordium stage (Coutts 1987) which is likely to provide them with a higher growth potential (Hackett, 1969).

Growing conditions could also be a factor. The Oregon growing season is long (227 days, March 30-November 12), and winters are relatively mild, compared to many of the native habitats where these species originated. If the longer growing season resulted in a longer time between the cessation of shoot growth and leaf drop with leaves still photosynthesizing, there may have been an ample supply of carbohydrate translocated to the root system while warm soils could support additional root growth. Growth of taproots can be more responsive to carbohydrate availability than lateral roots (Thaler and Pages 1996, Willaume and Pages 2006). If the same relationship exists between lateral roots and the multiple adventitious roots (regenerated taproots) produced from the cut end of the taproot, the regenerated taproots may be better able to take advantage of the available carbohydrate supply.

None of the species included in this study, with the exception of chokecherry and quaking aspen, are native to

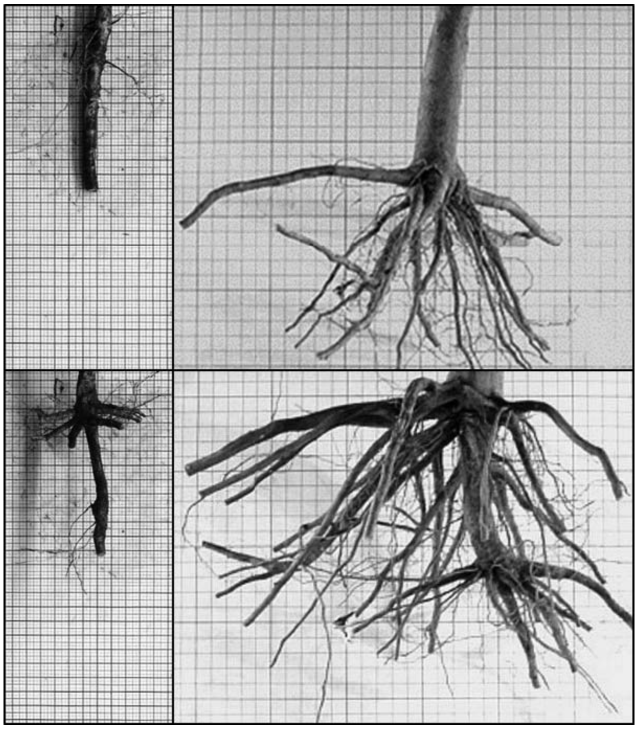

Fig. 1. **An example of a one-year-old Mazzard cherry seedling with only fine lateral roots (upper left) and one with primarily large woody laterals (lower left). Root architecture developed as could be expected. Roots regenerated from the cut end on both plants (upper and lower right). Fine roots did not survive transplanting, and no adventitious roots were produced on the remaining portion of the taproot above the cut on the upper seedling, leaving only the regenerated roots (upper right). The larger lateral roots persisted on the other seedling in addition to the regenerated roots (lower right).**

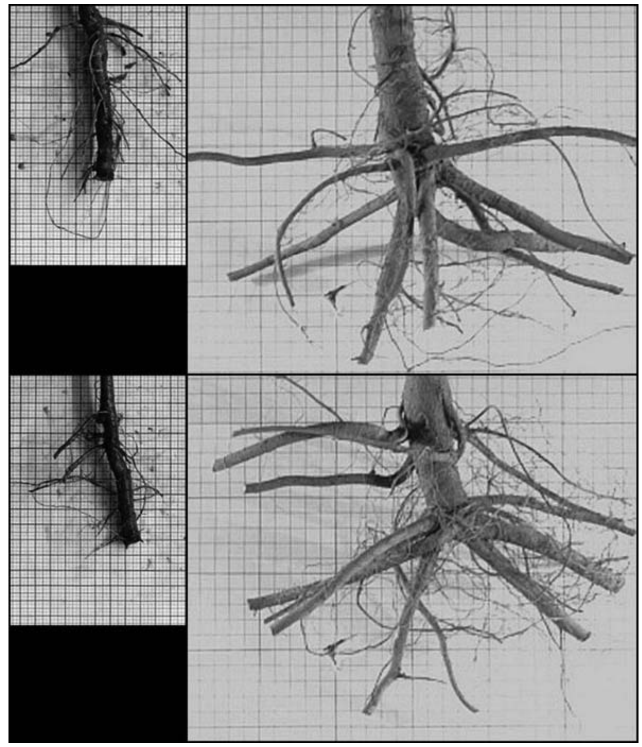

Fig. 2. **One-year-old Siberian elm seedlings with several woody lateral roots (upper and lower left). Both regenerated roots from the cut end, but the lateral roots did not increase appreciably in size on one (upper right), while they did on the other (lower right). This difference in root architecture development could not have been predicted from the seedlings at planting.**

Oregon. Even for those, seed sources better matched with the locations where plants will be shipped and planted may be used by the grower. Growing conditions (climate, soils) in Oregon are among the best in the temperate world, and likely more favorable than species native habitats in the eastern United States, Europe or Asia (Table 1). Ample summer irrigation and fertilization applied by growers to maximize growth would make the growing conditions even more different that the native habitats, presumably better. Little is known about how root systems respond to a longer growing season and better growing conditions than their native habitat. It may be possible that better growing conditions in Oregon than where they are native also contributed to greater development of regenerated roots.

The number, or size, of lateral roots as seedlings could not be used to predict future root architecture in most species. High variability in root data can limit statistical significance and mask relationships in research. Coefficients of variation in this work was often greater than 100% of the mean, and as high as 257 percent. In practice, high variability in root architecture development can make grading root systems difficult. This can be illustrated with examples of individual plants.

Figure 1 shows two Mazzard cherries from the study group of trees that had very different root architecture as seedlings. One (upper left) had just a few very small lateral roots. These small, non-woody roots did not persist through the transplanting process, and no adventitious roots were produced above the cut. The only roots present a year after replanting are roots regenerated from the cut end (upper right). The other seedling had several large woody lateral roots as a seedling of the same age (lower left) that persisted and increased in size over the next year. New roots were also regenerated from the cut end of the taproot (lower right). In these two plants, root architecture developed as could have been predicted.

In contrast, Figure 2 shows two Siberian elms which had very similar root architecture as seedlings. Each had several small woody lateral roots (upper and lower left). Both produced new roots from the cut end, but the lateral roots did not increase appreciably in size on one (upper right), while they did on the other (lower right). This difference in root architecture development would not have been predicted as seedlings. These examples illustrate how root architecture development cannot be easily predicted from seedling root systems.

Earlier work (Hewitt and Watson 2009) on a limited number of species showed that roots regenerated from the cut end of the taproot become a large component of the root system. This study confirmed this does occur on all 37 species included in this study. The majority of species (84 percent) had equal or greater regenerated root development than lateral root development one year after seedlings were replanted. The architecture of the root system is already established by this time (Watson and Hewitt 2020). Even when regenerated root development was significantly lower than lateral root development, the regenerated roots still comprised up to 44 percent of the root system.

The high variability and unpredictability of young root systems exhibited in this work shows the challenge of producing consistent, high quality root systems. Naturally regenerated root systems are not of consistent high quality either (Single 2009), but in nature, the natural selection process can select for the best from many plants over time. Quality selection in nursery production does not have the same luxury of time and high attrition. Seedlings with poor root systems need to be identified, and discarded or corrected, early in the production cycle. Additional work is needed on how this might be accomplished.

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