

Root Growth and Root Regeneration Testing on Hardwoods

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Introduction

Root regeneration tests, their rationale and the methods for root regeneration testing on bareroot seedlings have been described by Burdette (1987) and Ritchie (1985). Simply put, bareroot seedlings must regenerate new roots so they establish intimate contact with the soil. The sooner this occurs, the more readily will the seedling be able to uptake the water and nutrients it needs to support vigorous first year growth. Greenhouse root regeneration tests are an inexpensive, robust and relatively fast way to measure seedling vigor (Feret 1987). As these test results often correlate well to field performance, they are one of several tools available to the nurseryman for evaluating seedling vigor and quality.

While few will argue that robust root regeneration is a good thing for bareroot seedling stock, there are no easy answers on how to grow seedlings in the nursery with high root regeneration potential. An understanding of root development and its control will contribute to the formation of new and creative solutions to the problem. In this article I present some of the information on what is known of root development and suggest ways to use this information for the growing of better bareroot hardwood nursery stock.

Development of Roots

An examination of the literature suggests the following tenets apply to tree roots:

1. Successful soil exploitation is dependent on a finely divided root system.
2. Physical laws demand support for the tree. Therefore, since stiffness is proportional to the 4th power of the diameter, few large support roots are most efficient for tree support.
3. Development of roots can be envisioned as two phases: PRIMARY development and SECONDARY growth promoting the radial growth of individual woody roots.
4. There is both temporal, and physiological overlap in growth phases.
5. For both phases there is evidence in the literature for strong competition between the different parts of the root system and the shoot.

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The overall development of roots in nursery seedlings is a complex process. Even though there are excellent studies of root growth and development in the literature (ie. Nambiar 1980, Wilcox 1968), many questions remain. Extending roots develop lateral root primordia in the direction of base to tip (acropetally). Number and size of primordia is controlled by shoot auxins. The root apex produces cytokinins, and other substances which inhibit lateral root primordia development. Thus, lateral root development is a balance between shoot produced auxin production and root tip produced hormone inhibitors of lateral root primordia. In some species adventitious roots (roots that do not originate from the pericycle but rather arise from areas exterior to the stele) may form between lateral root primordia.

The eventual size of a root is determined by two factors. Roots are retained by the plant as permanent roots when the primary root diameter is large relative to the parent root diameter and the primary xylem diameter (PXD) is some minimum percentage (i.e. 25%) of that of the parent root (Horsley and Wilson 1971). Generally large roots arise from large primordia. Feeder roots of fine structure and small diameters do not generally become a part of the permanent structural root system (Wilcox 1964).

The control of the spacing of secondary laterals along first order laterals is apparently a function of root growth rate. Longer roots produce fewer permanent secondary laterals than shorter laterals. This is not the trend near the base of the shoot where a high frequency of root branching is found in many species (Coutts 1987).

The distribution of large main first order lateral roots on the taproot is very different from the spacing of second order laterals (Coutts 1987). First order lateral roots tend to develop more frequently and are more vigorous near the shoot base. In this basal area first order laterals are often disproportional in size (ie. large for their age).

Roots of high growth potential tend to be found near the root bases and along second order laterals. Primordia forming these roots are apparently formed late in the year when the root system is otherwise dormant or in the period of slow root extension in the early spring.

Adventitious roots may often form at the shoot base. These adventitious roots, when large in diameter and having a large steel (or PXD) can form permanent members of the structural root system in both gymnosperms and angiosperms. While adventitious roots are not connected to the vascular system of the structural roots in the same manner as roots originating in the pericycle, it is arguable as to whether they are as "good" as normal roots in water uptake. Many examples can be found to illustrate the usefulness of adventitious roots to the plant (ie. Coutts 1983). In fact, rooted cuttings survive exclusively on adventitious root systems.

Roots with large root tips tend to live longer and have a higher probability for secondary radial growth. Environmental conditions including nutrient availability, mechanical impedance, temperature and

moisture availability all have a potential impact on root tip size. Thus, the root environment can have a major impact on the overall morphology of a tree (and seedling) root system (Nambiar 1980).

Large structural roots, either first or higher order laterals, support the tree and serve as the vascular framework for the feeder root system. The number of structural roots is relatively small, compared to the number of long roots and the very large number of high order lateral feeder roots. Generally trees seem to have fewer than 12 major support roots (Coutts 1987). It is generally believed that structural root dominance is established early in seedling development. Dominance remains until root systems are damaged (as in transplanting) by mechanical strain or pathogens. For tree roots to become structural, it appears they must have a large PXD, but this does not ensure their dominance.

Secondary thickening of the taproot occurs early in the growth of trees with the taproot type of root system. As trees age the taproot becomes progressively less competitive with the structural lateral root system. Roots which are quiescent in their lateral growth for years may resume rapid radial growth as a tree ages and the tap root loses dominance (Preisig et al. 1979).

Differential radial growth of structural roots may be modified by nutrient availability or other environmental modifiers of metabolism (such as flooding). There is considerable debate as to whether this secondary growth is caused by actual nutrient availability or is caused by hormonal regulation by root tips (see Coutts 1987 for a discussion). Vascular connections between environmentally affected portions of the root system and unaffected parts of the root system can greatly modify the severity of environmental perturbations. The literature is replete with conflicting data as to whether radial growth of roots is more controlled by substances produced at the root tip or from the shoot. It is likely that both the shoot-produced hormones and root-produced hormones impact radial secondary development.

Under natural conditions the environmental factors influencing root secondary growth appear to be both mechanical and physiological. Mechanical stress at the base of trees would appear to stimulate root (and stem) secondary growth in the so-called zone of rapid taper, the stem area surrounding the root collar. Similarly, disproportionate secondary root thickening appears to occur in bent or concave surfaces of the roots. Exposure of roots to light usually precipitates secondary thickening, and this thickening may extend distally from the exposed part. Flooding may also cause differential secondary growth in the root system, shifting growth to parts of the root system where aeration is above minimum levels for active metabolism. Generally speaking, it would appear that the environment of primary roots is more important for secondary growth than is the environment of the root immediately surrounding the cambium where secondary radial growth occurs (Coutts 1987).

Shoot - root balance

In considering seedling quality, forest tree nurserymen often discuss shoot/root ratios as an important criterion of quality. Usually dry weight of the shoot is considered relative to the dry weight of the root. While there are several alternative ways to think about the shoot/root ratio, one is to consider the "plumbing" of the seedling and its balance between roots and the shoot. Shinozaki et al. (1964) proposed a pipe theory to enhance the understanding of tree architecture. They suggested that the cross-sectional area of the sapwood in the stem is related to the cross-sectional area of the vascular system in the above portions of the tree. Coutts (1987) has extended the idea to the root-shoot relationship. He suggested that the cross-sectional area of the shoot is also related to the cross-sectional area of the root vascular system. The root vascular system must be in "balance" with the shoot vascular system; but what the "balance" is, or should be, remains undefined. Plants attain a balance using several adaptive strategies. Palms, for instance, produce large numbers of small fine roots while oaks tend to produce a large-root structural system branched to a well distributed feeder root system. Little is known of the adaptive significance of these differences.

There is evidence that the interaction between the shoot and the root leads to homeostatic development of the plant. Lockard and Schneider (1981) cite examples from the horticulture literature showing that rootstock vigor has no influence on the shoot/root ratio; although the ratio may be greatly affected by site conditions and environment.

Transplant root quality

Root regeneration of bareroot transplants is likely impacted by at least some, if not most, of the factors influencing root growth in general. Roots of transplanted seedlings must regenerate if seedlings are to become well established. Root regeneration in conifers tends to follow a seasonal pattern. Roots are generally dormant in early winter; when given optimal conditions for growth, new roots fail to grow (regenerate). As dormancy is released by the accumulation of chilling hours, roots will grow in an optimum environment. Root regeneration and growth is generally correlated with the dormancy release index (DRI) (Ritchie and Dunlop 1980), increasing as DRI increases. At some time just prior to bud break (in loblolly and white pine ca. 2 weeks) root regeneration ability exhibits a precipitous drop (Ferret et al. in press). Once buds flush and shoot growth occurs roots may again grow in an episodic relationship to the shoot growth patterns (Ledig and Perry 1969).

The conifer model is important in nursery practice since it is imperative the nurseryman lift seedlings prior to the spring season root growth potential drop. By doing this, planted seedlings are assured an opportunity for soil-root contact because new roots will grow as soon after transplanting as soil temperatures warm (ca. above 10C). The literature is replete with reports of root regeneration and its importance, modification and relationship to conifer seedling survival and early growth (Burdette 1987).

It must be recognized that generalizations about root growth are tenuous, especially when discussing root growth and root regeneration periodicity. In spite of this, most likely models must be constructed as points of reference. The conifer seedling root growth model seems to agree with hardwood seedling models for root growth with an important exception. As with conifers, hardwood seedlings depend on "signals" from the shoot (or buds) for the initiation of new root growth and root regeneration. Observations by Farmer (1975), Larson (1970) and Richardson (1958) have shown that roots in hardwood seedlings are dependant on the shoot for growth initiation. However the timing of most spring root growth in hardwoods is coincident with shoot growth, not prior to shoot growth as in conifers. Root growth in hardwoods generally does not occur until shoot dormancy is broken by chilling (Farmer 1975). While some roots may grow prior to bud burst, or during the winter when soil temperature and moisture are favorable, most roots in hardwood seedlings grow when the shoot is active.

Root regeneration and growth differences between conifers and hardwoods have important implications for the nurseryman. Timing of lifting prior to bud break may not be as important in hardwoods as in conifers. However, for both groups of plants, lifting prior to bud break is likely important. Obtaining hardwood root systems capable of regenerating new roots when seedlings break bud in the spring is just as important to the hardwood nurseryman as it is to the conifer grower. The central questions are: What plant mechanisms are responsible for large numbers of root primordia in bare root seedlings and how does the nurseryman manage growth conditions and seedling stock in the nursery to activate these mechanisms?

Answering these central questions will be essential for the development of high quality hardwood nursery stock. Two basic approaches seem warranted: 1. Genetic selection for seedling stock with inherently large number of lateral root primordia in the root zone within 6 inches of the root collar, and 2. determining the cultural treatments needed to stimulate the expression of these primordia.

Enhancement of root regeneration potential

Genetic selection may be one way to improve the root growth potential of hardwood seedlings. It has long been known that species and provenances of conifers have varying root growth potential (RGP) when grown under the same nursery cultural conditions. Burdette (1987) and data presented by Johnson et al. (1988), Carlson (1985), DeWald et al. (1985), and Jenkinson (1975) suggest genetic control of conifer seedling RGP is moderate to high. Barnes (1989) recently demonstrated a 100% advantage in RGP of pitch X loblolly pine hybrids compared to loblolly pine when grown in a Virginia nursery. This increase was related to the increased lateral root biomass in hybrid seedlings. In conifers then, there is ample evidence that number and/or expression of root primordia is genetic and therefore can be genetically managed in the nursery by carefully selecting seed source.

In hardwoods there is scant information on genetic control of seedling root system characters. It has long been known that root genotypes interact with shoot genotypes in dramatic patterns (**see** Lockard and Schneider 1981). These interactions are at least in part explained by the interaction of shoot produced auxins and root produced cytokinins. Farmer's (1975) data supports the hypothesis that red oak seedling root regeneration is under genetic control. Fruit breeders have reported genetic control of root regeneration in cherry rootstocks (Gruppe 1985) and observations on the need for orchard staking suggest root system structure is also under genetic control (Zagaja et al. 1988). Khajjidoni and Land (1989) found sycamore roots varied by family and this variation led to variation in root regeneration. Several nurseries are experimenting with genetic selection and in the future more will be known of its potential. Nursery management of select genotypes which respond well to cultural manipulations also may significantly enhance bareroot seedling quality.

Over the past two years a cooperative study has been conducted on seedling quality in high-quality hardwoods: white oak, red oak and black walnut. The purpose of the study has been to gather data on root attributes and their relationship to survival and growth. Cooperators have been the states of Missouri, Iowa, Indiana, Illinois and Ohio. Dr. Richard Schultz, Iowa State University at Ames and the U.S. Forest Service are additional cooperators. The root regeneration data generated by this study is of particular relevance to this paper.

Root regeneration was measured in red oak seedlings from 3 nurseries. Three treatments were applied as a factorial design including three planting densities (3, 6 and 9 seedlings per ft. ²) crossed with root pruning (with and without). These treatments led to a wide range in plant sizes and root regeneration values. The data is then useful for analysis of root regeneration and the relative impacts of nurseries and treatments. Confounded in nursery effects are seed source and lifting date relative to climatic conditions and chilling hours at each nursery.

The results of the root growth potential (RGP) analysis led to the following. Root regeneration was significantly ($p < .05$) affected by nursery, treatment, and nursery*treatment interactions. The ANOVA model accounted for 26% of the variation in RGP. Of this 26% of the variation in RGP, nursery effects comprised 78% of the variation. Treatment effects comprised 8% of the variation and nursery*treatment interactions comprised 13% of the variation observed. RGP values ranged from a nursery high of 49 new roots to a nursery low of 15 new roots.

In contrast to the RGP analysis, and using root collar diameter (RCD) as a gross measure of size variation in the same red oak seedlings, it was found that about 50% of the variation in RCD was due to nursery and 50% due to treatment. RCD ranged from a nursery high of 7.9 mm to a nursery low of 6.6 mm. Therefore it may be that while treatments in the nursery significantly affect seedling size, they do not have nearly as great an effect on the root regeneration potential of red oak seedlings. This may be because nursery cultural treatments do not impact the number of first order laterals as much as they impact other plant parts (Nambiar 1980).

From the analysis of variance it can be concluded that for RGP enhancement, it is not nearly as important how red oaks are grown, but rather what nursery grows them. The analysis does not help us understand why nurseries vary so much in red oak RGP. It may be soil type, cultural conditions such as irrigation schedules, nutrient status etc., genotypes grown, time seedlings were lifted, or any combination of these and other factors.

One important finding of this study is the fact that nursery and treatment effects only account for 26% of the variation in RGP and only 18% of the variation in RCD. This means that nearly 75% of the variation in seedlings remains unaccounted for.

The unaccounted for sources of variation need to be elucidated before we as nurserymen can manipulate root parameters. We know how to manipulate seedling sizes and from our experience with the above study, and others, we can rest assured that almost all hardwood seedlings will break bud normally when transplanted. The vexing problem remains of determining why some hardwood seedlings will grow well after transplanting, while others will not.

The relationships between seedling parameters and RGP are interesting to examine because they shed some light on the problem. The relationship between RGP and new shoot dry weight was the strongest ($p < 0.001$) relationship observed. Correlations were $r = 0.47$ ($n = 414$), 0.50 ($n = 180$) and 0.70 ($n = 220$) for red oak, white oak and black walnut respectively. In other words, bareroot seedlings with good top growth following transplanting also grow new roots on a proportional basis. So RGP really tells us not much more than shoot growth observations. The real question is what comes first; do the new roots support more top growth or does good top growth produce auxin signals to the root system making it grow well? Since both root and shoot growth appear to occur simultaneously, the question can not be answered by observation alone.

From the data of our hardwood seedling studies we have also found that, for red oak and white oak, the root measure most closely and significantly ($p < 0.001$) related to RGP is lateral root dry weight. In red oak the correlation between RGP and lateral root dry weight was $r = 0.27$ ($n = 414$) and for white oak $r = 0.36$ ($n = 180$). Since lateral root dry weight is significantly ($p < 0.001$) correlated to all other measures of seedling **size (ie. root collar diameter, tap root weight, stem weight)**, it seems that large seedlings simply have more lateral root biomass, more RGP and more new first year shoot growth.

Results from analysis of the black walnut data are similar to the results of the oak analysis except for a stronger correlation between RGP and new spring shoot growth ($r = 0.70$; $n = 220$; $p < 0.001$). For black walnut there was also a significant relationship between both lateral root and taproot dry weight and RGP ($r = 0.24$ and $r = 0.27$ respectively; $n = 220$; $p < 0.001$). For the oak species, there was no significant relationship between taproot dry weight and RGP. As with the oaks, there were significant relationships between root biomass and shoot biomass; seedlings with large root systems had correspondingly large tops.

Conclusions

Data from our studies and the literature suggest homeostatic development of the root and shoot relationship. It seems logical to assume it will be difficult to alter this homeostatic relationship with cultural treatments. It also seems logical to assume lateral root biomass is the single most important morphological attribute for RGP, ie. new root **formation after transplanting. Thus, if we are to improve the RGP of hardwood seedlings, we must alter the taproot:lateral root biomass ratio. This is especially true for oak species.**

There are likely several ways of improving lateral root biomass. First, it may be that cultural treatments will affect the ratio. Undercutting coupled with lateral root pruning at the proper stages of seedling development may accomplish our goal of decreasing the ratio of taproot:lateral root biomass by temporarily reducing the number of growing root tips to allow shoot auxin stimulation of new primordia. Johnson (1989) has shown that undercutting can lead to increased survival of bareroot oak seedlings.

Manipulating moisture availability at the proper stage of seedling development may also accomplish our goal by increasing the number of lateral root primordia close to the basal sector of the root system. **By** providing a better growth regime in and around the root collar rather than deep in the zone where the taproot is forming, root biomass accumulation in both spring and autumn treated seedlings will be preferential in this area. This might be best accomplished by frequent shallow irrigation practices.

The basic physiology of the seedling might be modified by exogenous applications of auxins, causing the seedling to produce proportionally more primary growth in the root system (Struve and Arnold 1986). It may also be that genetic selections could be made for plants having heritable variation in primary root growth attributes.

Genetic selection of desirable root ideotypes may allow amplification of nursery cultural treatments. Genetic selection for seedlings with inherently large numbers of lateral root primordia will likely respond best to manipulations like undercutting and irrigation.

Whichever techniques are attempted (and I believe all approaches should be attempted), it is the primary root development that has to be modified in the nursery. This means that it is early season first year growth that must be modified as that is when to basic root system framework is established.

The challenge to those of us in research and to nurserymen is to gather empirical and quantitative data on seedling growth manipulating treatments. Communicating results and further discussions will likely yield to greatly improved hardwood seedling quality.

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Ontario Root System Management Practices

Glenn McLeod*

Introduction

I would like to cover the Ontario approach to, and objectives of, root system management in our coniferous nursery stock. My talk is divided into the following sections:

- terminology
- Ontario objectives
- controlling factors
- species response

Terminology

Root Pruning - the preferred term is undercutting. This is the mechanical cutting of roots, in situ, in the seedbed or transplant bed.

Horizontal - is the drawing of a thin sharp blade under the seedbed/transplant bed, parallel to the soil surface. The blade severs roots extending below the set depth.

Vertical - is the severing of lateral roots by passing cutting blades or rolling coulters between the seedling rows. Lateral roots which grow from one row into another will be cut. Lateral roots which extend down the row will not be severed.

Box - is a combination of horizontal and vertical pruning with the added feature of cutting roots between trees in each seedling row. Lateral roots are cut in all four sides and horizontal undercutting severs the roots at the bottom of the box.

Root Wrenching - utilizing a horizontal angled blade to cause the physical disturbance of loosening and aerating the bed and the root system. Wrenching is carried out with a thicker, broader blade than root pruning. The loosening and aerating action breaks up the root:soil contract.