Tree Root System Development

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Abstract

Tree root-system development is influenced by nursery cultural practices. These practices can result in modifications that will persist throughout the life of the tree. The primary root of a seedling is the site of first-order lateral root production. The number of these first-order roots developing, through secondary growth, into permanent laterals will determine the success of seedling establishment. As they move through the soil, roots respond to wounding by producing adventitious roots from the wounded area. Nursery cultural practices such as undercutting can mimic wounding. A mature tree's root system consists of 4-10 large lateral roots extending as far as 1-2 tree heights from the base, growing in the top 2 feet of soil, and maintaining several hundred million root tips, many of which are mycorrhizal. Depending on soil conditions, a few of the roots may grow to a depth of 5-6 feet . The below-ground portion of a tree is as important to the success of the tree as the above-ground portion. Mature root-system form can reasonably be estimated by the nursery manager. Seedlings with fewer than 5-6 permanent lateral roots at the time of transplanting should not be transplanted to the field because a low percentage of these seedlings will become successful competitors.

Introduction

It is reasonably easy to describe the above-ground parts of a favorite tree. The tree grows to a given height, has a specific diameter at breast-height, and has needles or deciduous leaves. Beyond that, the description becomes more difficult. The tree may be open-grown, which means it has many branches, but how frequently do the branches divide (branch-orders)? What is the surface-area of leaves needed to support the tree (leaf-area index)? It is very difficult to describe, or envision, the tree below ground because few intact, mature, root-systems have been exposed. Opinions are formed by examination of exposed roots of trees growing in rocky substrates. Even partly excavated root systems do not give a true picture because of the disturbance necessary in excavation.

Following is a discussion of the tree root-system, including the environment, the development of seedlings and mature root-systems, and the importance of mycorrhizae.

Root and shoot environments

Tree root and shoot systems exist in two very different environments. Normally a tree is fixed in one location for its entire life. Its shoot is exposed to the gaseous environment of the atmosphere. It is battered by strong winds

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mixed with rain, snow, or hail, scorched by the sun, or frozen by arctic air masses. The sun provides energy for photosynthesis but also delivers a large heat load that must be dissipated. The tree has evolved a rapidly growing stem that allows the plant to compete effectively for direct sunlight. This large stem requires large quantities of carbon to grow, and this carbon comes from the massive crown of branches and leaves that the stem supports. Such a large weight must be strongly anchored in the soil if the tree is to remain upright and competitive.

The root system grows in a very different environment. That environment is a porous medium containing approximately 45% solids, 5% organic matter, and 50% pore space by volume, half of which is ideally filled with air. The temperature extremes in the soil environment are not as great as in the atmosphere, nor do they change as rapidly. The soil is a harsh environment, however, for a succulent root tip required to work its way through pores that may be very small, filled completely with water instead of partially with air, and infested by a myriad of soil organisms constantly feeding on the carbon-rich primary root and its exudates.

The root system provides water and nutrients to the shoot,which in part allows the return of the carbon rich sugars needed for root growth. Roots, which are constantly stretched and contracted when the top sways in the wind, anchor the large, heavy top in the soil and keep it upright. Finally, the root system is the source of plant growth regulators, which move through the plant in very small quantities and act as signals of root activity. Thus, the root and shoot system of a huge tree are found in two very different environments and in conjunction with different stimuli, yet these two systems must coordinate functions to keep the organism alive and competitive. To promote a better understanding of root system development, we will follow the process of root growth from the seedling to the mature tree.

Seedling root system development

The first division in the embryo of a developing seed establishes its polarity (vertical axis). The embryo rapidly develops the radicle (basal end of the embryonic axis), cotyledons (leaf-like appendages or food storage appendages), plumule (meristematic growing tip of the embryo) and hypocotyl (the region between the cotyledons and radicle) (Figure 1). When the seed begins to germinate, it is usually the radicle that emerges first and develops into the primary root, thereby producing early anchorage and a source of nutrients and water. Two forms of germination occur, depending on the function and fate of the cotyledons. Conifers and many light-seeded deciduous species show epigeal germination, by which the cotyledons extend above the ground and function as photosynthetic tissue producing needed sugars for continued growth. Large seeded deciduous species, such as oak and walnut, display hypogeal germination, by which the cotyledons serve as food reserves and remain below ground. Emerging primary roots on hypogeal seedlings often grow longer and more rapidly than do those on epigeal seedlings, which must expend more energy developing a shoot to supply needed carbohydrates.

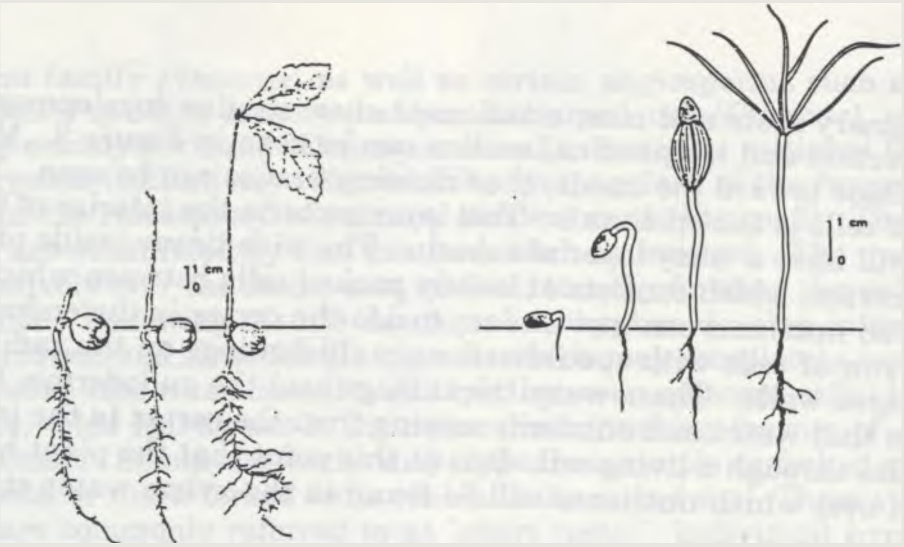

Figure 1. Hypogeal germination pattern of oak and epigeal pattern of pine. Note that the cotyledons of oak remain below ground in the seed and that those of pine are above ground and become the first photosynthetic tissue. (From USDA, 1974).

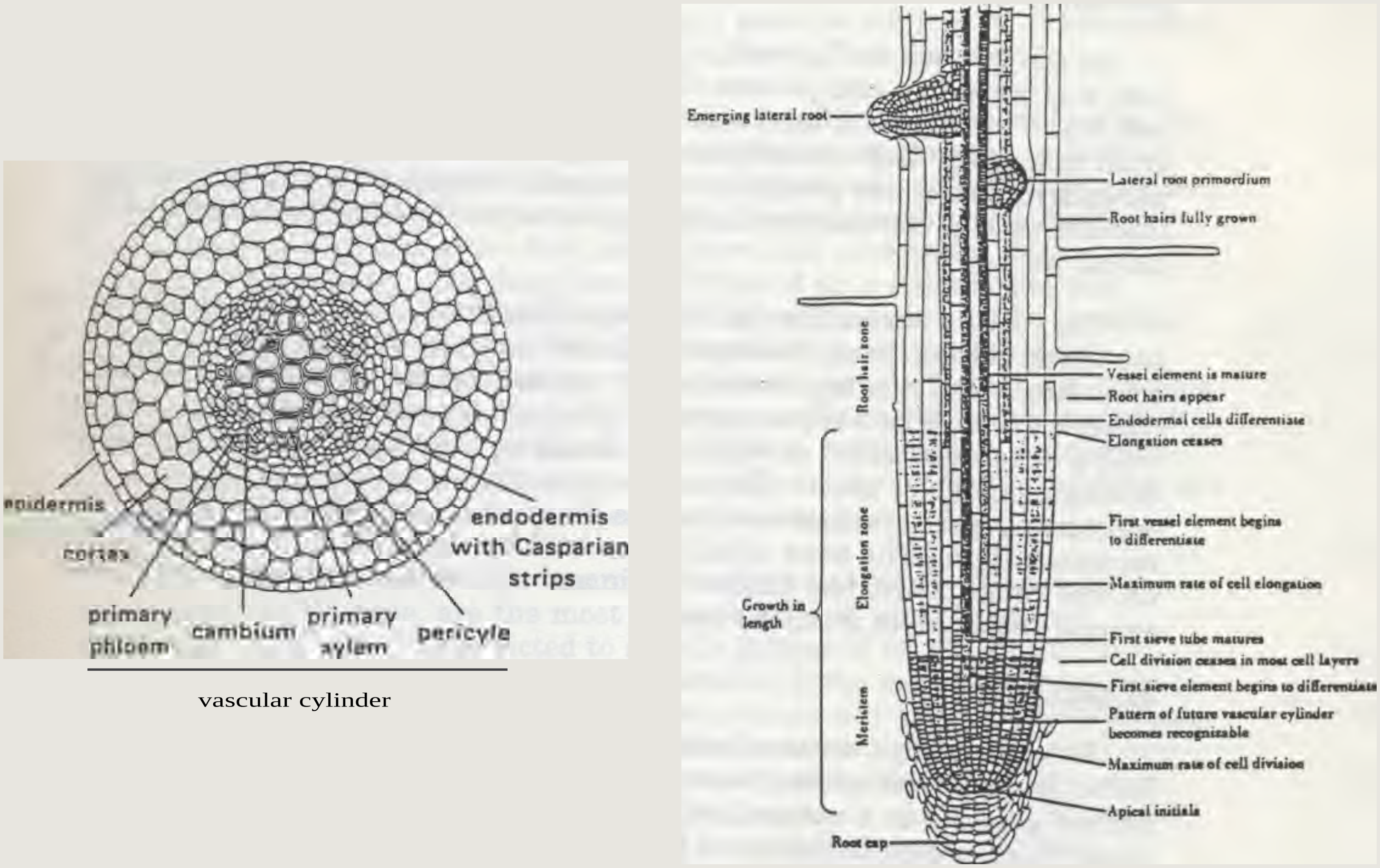

Figure 2. Cross-section and longitudinal-section of a primary root of a woody plant. Note the lateral root growth and that there is no secondary growth. (From Wilson and Loomis, 1967 and Ray,

Primary roots and most small roots show similar development. Their cross-section and longitudinal section can be seen in Figure 2. Moving from the outside toward the inside, the following tissues can be seen. The outer layer of cells is the epidermis. This layer protects the interior of the root and often will have a waxy layer of suberin. The wide tissue inside of the epidermis is the cortex, which consists of loosely packed cells between which water and dissolved nutrients can move. Just inside the cortex is the endodermis, a single row of cells with specialized waxy thickenings on the radial and transverse walls. These waxy thickenings seal the endodermis layer and require that water and nutrients moving from the cortex to the inside of the root pass through a living cell. It **is** at this point that the plant has some control over which nutrients will be found in the xylem water stream.

The endodermis protects the vascular cylinder, which is composed of the pericycle, the xylem and phloem, and eventually the cambium. The pericycle is the source of lateral roots and the cork cambium that may develop if the root produces secondary growth. The primary xyelm is found at the very center of the primary root and is usually in a pattern with two to five or more radiating branches. The primary phloem lies between the radiating xylem tissue branches. The primary cambium, which may give rise to later secondary growth, is located between the xylem and phloem.

As can be seen in Figure 2, roots mature from the tip, upward. Thus, the first mature xylem and phloem elements are found some distance behind the root tip. The apical initials, which lie just behind the root cap, are the source of all new cells. Cell division occurs frequently in this region, and basic parenchyma cells are produced. These parenchyma cells will differentiate into the various tissues previously mentioned as they get farther behind the apical meristem.

The root tip serves several important functions. First, it physically protects the apical initials from the harsh soil environment through which the root is extending. The root cap contains the mechanism for sensing gravity and thus controls the direction of root growth. The root cap also lubricates the root tip with a substance called mucigel, which allows the root tip to slip more freely through small soil pores. This material **is** rich in sugars and other substances and serves as a substrate for microorganisms important in soil mineralization. The zone of soil influenced by the root and associated mucigel, i.e. the rhizosphere, has unique biotic and abiotic characteristics not found several centimeters from the root.

Mycorrhizae

Because many root tips form a symbiotic relationship with various soil borne fungi, the simplified description above **is** not typically found in a root system growing in a natural soil medium The result of this symbiosis is a mycorrhiza, which benefits the plant by dramatically extending the root system into the tiny crevices of the soil, and which benefits the fungus by supplying a ready source of the sugars needed for growth. All members of the gymnosperm family *Pinaceae,* as well as certain angiosperms such as willow *(Salix),* aspen *(Populus),* hickory and pecan *(Carya),* oak *(Quercus),* and beech *(Fagus)* are ectomycorrhizal. Ectomycorrhizal infection is initiated from spores or hyphae (collectively referred to as 'propagules') of the fungal symbionts in the rhizosphere of primary (feeder) roots (Figure 3). These propagules are stimulated by root exudates such as mucigel. The propagules grow vegetatively over the feeder root surface, thereby forming the external fungal mantle. Following mantle development, hyphae develop intercellularly in the root cortex, and form the Hartig-net, which may completely replace the middle lamellae (the common cell wall layer between adjacent cells) between cortical cells. This Hartig-net is the major distinguishing feature of ectomycorrhizae. Ectomycorrhizae may appear as simple unforked roots, bifurcate roots, or multi-forked roots visible to the naked eye. These visible structures are commonly referred to as "short roots." Individual hyphae, numerous hyphae, or rhizomorphs may radiate from the fungus mantles on short roots into the soil and eventually unite with the base of fruiting bodies of the fungus.

Over 2100 species of ectomycorrhizal fungi are estimated to exist on trees in North America. Most fungi forming ectomycorrhizae with forest trees are Basidiomycetes, which produce mushrooms or puffballs as reproductive structures. However, certain of the Ascomycetes, such as truffles, are also symbiotic. The fruiting bodies of these fungi produce millions of above-ground spores, which are easily and widely disseminated by wind and water.

Under normal forest conditions, many species of fungi are involved in the ectomycorrhizal associations of a forest, a single tree species, an individual tree, or even a small segment of lateral root. In fact, as many as three species of fungi have been isolated from an individual ectomycorrhiza. A single fungus species may also enter into ectomycorrhizal association with numerous tree species. The fungi naturally found on a specific site are usually very competitive because they have evolved over time under a certain set of environmental conditions. When tree seedlings with introduced mycorrhizal fungi are planted in the field, native fungi (indigenous to the field site) quickly colonize the new growing root tips, replacing the fungal species introduced in the nursery. On harsh sites such as mine reclamation sites, where the native fungal population is low or non-existent, introduced fungi are an important component of the planted tree seedlings.

The endomycorrhizal fungi, commonly referred to as the "vesicular-arbuscular," or VA type, are the most widespread and important root symbionts. They are not restricted to specific groups of plants, but occur in practically all families of angiosperms, gymnosperms, and many pteridophytes and bryophytes. Most of the economically important agronomic grain and forage crops, as well as the major commercial fruit and nut trees and berries, normally form endomycorrhizae. Many of our most important forest trees, such as ash *(Fraxinus),* walnut *(Juglans),* sycamore *(Platanus),* cottonwood *(Populus),* and yellow poplar *(Liriodendron)* normally form endomycorrhizae. Although endomycorrhizal fungi can form a loose network of hyphae on primary root surfaces, they do not develop the dense fungal

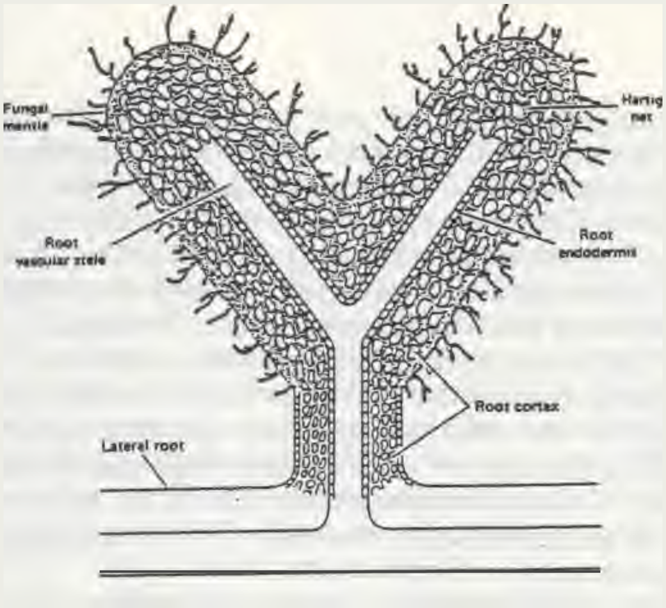

Figure 3. Diagram (not to scale) of an ectomycorrhiza of pine. Note the dichotomous branching of the short root. (From Marx, 1966).

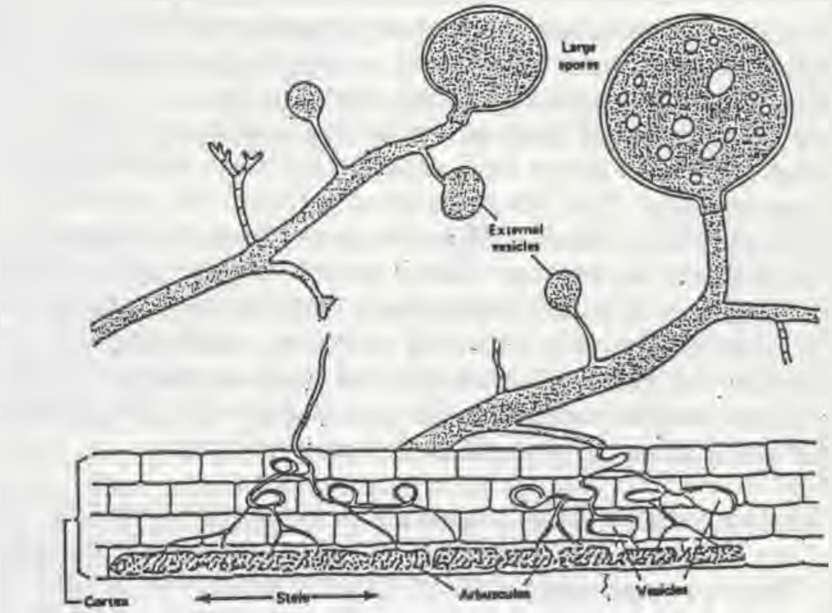

Figure 4. Diagram (not to scale) of an endomycorrhiza. Note there is no visible external modification of the root . (From Nicolson, 1967).

mantle typical of ectomycorrhizae (Figure 4). Endomycorrhizal fungi form large, conspicuous, thick-walled spores on the root surfaces, in the rhizosphere, and sometimes in the primary root tissues. Endomycorrhizal fungal hyphae penetrate the cell walls of the epidermis and then grow into the cortical cells of the root. These infective hyphae may develop specialized absorbing or nutrient-exchanging structures called "arbuscules" in the cortical cells. Arbuscules consist of dense clusters of very fine, dichotomously branched filaments, which may occupy the entire lumen of the cell. Vesicles are developed later, generally in the middle and outer cortex, and appear as terminal swellings either within or between cells. No external morphological changes occur in roots infected with endomycorrhizal fungi although, with some trees, a yellow or brown pigmentation of roots has been reported.

The fungi forming endomycorrhizae are mainly Phycomycetes. They do not produce large, above-ground fruiting bodies or wind-disseminated spores, as do most ectomycorrhizal fungi. Spread of these fungi, in soil, is by root contact, moving water, insects, or mammals. In the absence of a host, the spores of these fungi are able to survive for many years in the soil. As with the ectomycorrhizal fungus spores, these spores are apparently stimulated to germinate by the presence of root exudates. Once again, most soils have indigenous populations of endomycorrhizal fungal spores present in the soil, which germinate and replace the mycorrhizal fungal species introduced in the nursery.

The phenomenal part of the mycorrhizal story is that, from one mycorrhiza, 200-2,000 hyphae can extend up to six feet into the soil. Each hyphae can have as many as 120 lateral hyphae. The end result is that the root area on a mature tree can be increased 100X by the presence of mycorrhizae. Mycorrhizae are a natural component of any tree root system, and without them the tree would probably not survive.

Lateral root development

Lateral roots develop according to one of two scenarios. The first is development from the pericycle at some distance behind the extending root tip (Figure 2), which produces the "normal first-order" laterals seen on seedlings and providing the structural support for the development of second-order and higher roots (fine feeder roots). These laterals often form in rows associated with the design of the primary vascular system. Roots arising from the first-order laterals are called second-order roots. Continued branching of roots can produce up to fifth-order laterals.

In the second scenario, lateral roots arise because the root tip is constantly pushing through soil pores and is easily damaged or completely destroyed. The root system responds to injury by initiating adventitious lateral roots. These roots arise from parenchyma cells near the wound site. Adventitious lateral roots also arise when a sharp bend occurs in roots, as when they are bent by stones in their path. This response to wounding can be rather rapid so that in as little as 2-3 weeks, new roots emerge from a wound site. It is this response that forms the basis for the nursery cultural practice of undercutting, which stimulates more lateral root development.

An ideal seedling root system is one that contains a large number of first-order lateral roots from which higher-order lateral roots ultimately develop. This root system consists of several major first-order laterals, which provide the sites for all additional finer roots. The larger roots are primarily support and transport roots, whereas the higher-order roots are the absorbing roots. For a seedling to be successful in the field, it must have a large number of permanent first-order lateral roots (roots with diameters < 1mm , the diameter of a regular paper clip).

The dominance of first-order lateral roots is established early in life. By the time a seedling has completed its first growing season, most of the first-order lateral root pattern has already been established. Figure 5 demonstrates the development of permanent first-order laterals in a root system. One evidence of successful seedling establishment is the minimum number of permanent laterals developed. This number can be identified as seedlings are lifted from the nursery bed. For red and white oak a minimum of five to six permanent first-order lateral roots is needed for successful field establishment. For black walnut, the number of such permanent first-order lateral roots **is** eight to nine.

Secondary growth

For primary roots to become large permanent roots, they must begin to develop secondary growth. This occurs when the primary cambium, which is between the primary xylem and phloem elements of the vascular cylinder, begins to grow (Figure 6). Parenchyma cells between the unconnected primary cambial zones become meristematic and ultimately produce a continuous cambial ring. Once the cambium is completely connected, secondary xylem is produced towards the inside and secondary phloem towards the outside. Because the pericycle, endodermis, cortex and epidermis are not meristematic they are unable to keep up with the circumferencial growth of the vascular cambium and begin to break apart and are sloughed off. A cork cambium, similar to the one in the stem, is initiated in the pericycle but ultimately arises in the secondary phloem. Once the cork cambium produces bark-like tissue, water uptake is hampered through that portion of the root.

Episodic growth

The last major topic that needs to be covered with respect to seedling root system development is that of episodic growth. Different plant parts can be considered carbon "sources" and/or "sinks." The sources are plant parts that supply carbon, and the sinks are plant parts in need of carbon for growth. The source-sink roles of various tissues change over time, depending on whether or not active growth is occurring. When one part of the plant acts as a sink, the rest of the plant may act as a source. This means that, while growth is taking place in one part of the plant, it is not taking place in the rest of the plant. This relation **is** frequently seen between shoot and root growth. When

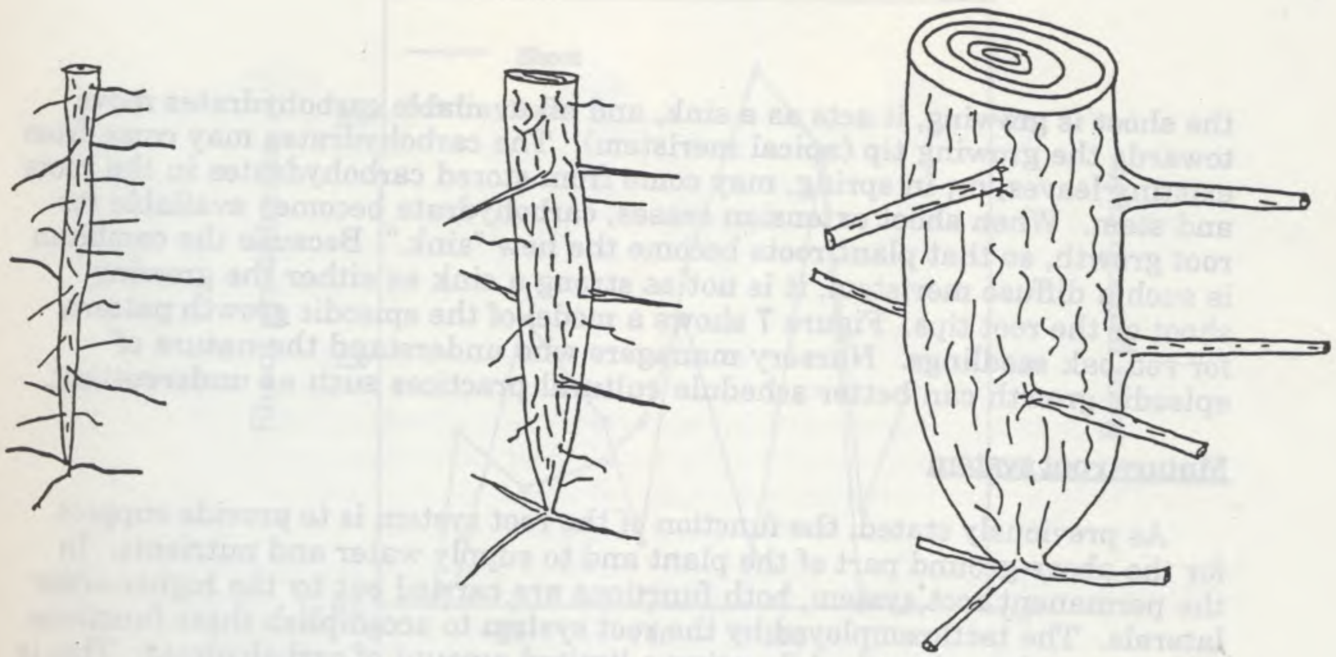

Figure 5. Model of root development from seedling to sapling as developed from work done by the Hardwood Nursery Cooperative. Note that the number of permanent first-order roots is determined early and persists throughout the life of the tree.

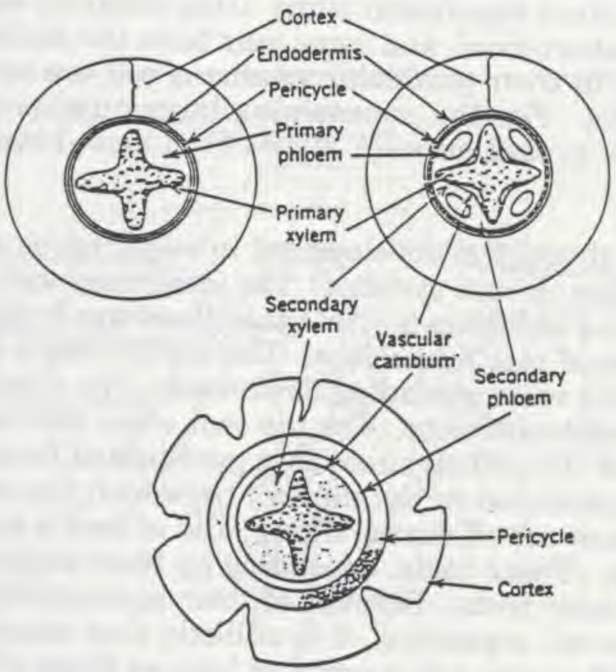

Figure 6. Secondary growth in a woody root. Note that tissue from the pericycle outward ultimately disappears. (From Kramer, 1969).

the shoot is growing, it acts as a sink, and all available carbohydrates move towards the growing tip (apical meristem). The carbohydrates may come from existing leaves, or, in spring, may come from stored carbohydrates in the roots and stem. When shoot extension ceases, carbohydrate becomes available for root growth, so that plant roots become the new "sink." Because the cambium is such a diffuse meristem, it is not as strong a sink as either the growing shoot or the root tips. Figure 7 shows a model of the episodic growth pattern for red oak seedlings. Nursery managers who understand the nature of episodic growth can better schedule cultural practices such as undercutting.

Mature root system

As previously stated, the function of the root system is to provide support for the above-ground part of the plant and to supply water and nutrients. In the permanent root system, both functions are carried out by the higher-order laterals. The tactic employed by the root system to accomplish these functions is to forage through soil while using a limited amount of carbohydrate. This is accomplished in several ways. First, the root systems of trees are extensive, rather than intensive, as is the case among many grasses. A grass plant has a large volume of roots in a relatively small volume of soil the shoot doesn't require much support against gravity or wind. The tree, however, needs more support to maintain an upright position. This is accomplished by extending relatively few roots to great distances from the base of the tree. The tree root system is therefore extensive, not exploiting every possible bit of soil volume. Secondly, large numbers of small non-woody feeder roots satisfy the needs for water and nutrient absorption while using minimal carbohydrate. These roots are relatively short-lived, and some may have the ability to be dormant when soil conditions in their particular volume of soil are not conducive to water and nutrient uptake. Finally, maintaining large numbers of mycorrhizae with their extensive hyphal network allows even more branching out within the soil environment.

With this strategy of development in mind, let us review the general structure of mature root systems. The ideal tree, with all possible roots, would look like the one in Figure 8. Note that there are a number of major kinds of structural lateral root formations. The surface roots are mainly horizontal or flat, with sinker roots extending downward. The roots extending at an oblique angle are called heart roots. The tap root often still contains the original apical meristem from the primary root that germinated from the seedling. If the seedling was produced in the nursery, however, the original tap root meristem would have been cut off during lifting; and at best a series of side tap roots might develop. These roots, depending on their angle of growth, might also be classified as heart roots. Because of their succeptibilities to damage during growth and to soil organisms, it **is** unlikely that many of the original meristems of the roots will survive as long as those of the shoots do.

Some have been quick to characterize a particular species as being a tap-rooted, heart-rooted or sinker-rooted species (Figure 9). It is more realistic, however, to characterize a species root system according to the sites where it grows. A tree growing on a deep, well-drained, sandy soil might have a single

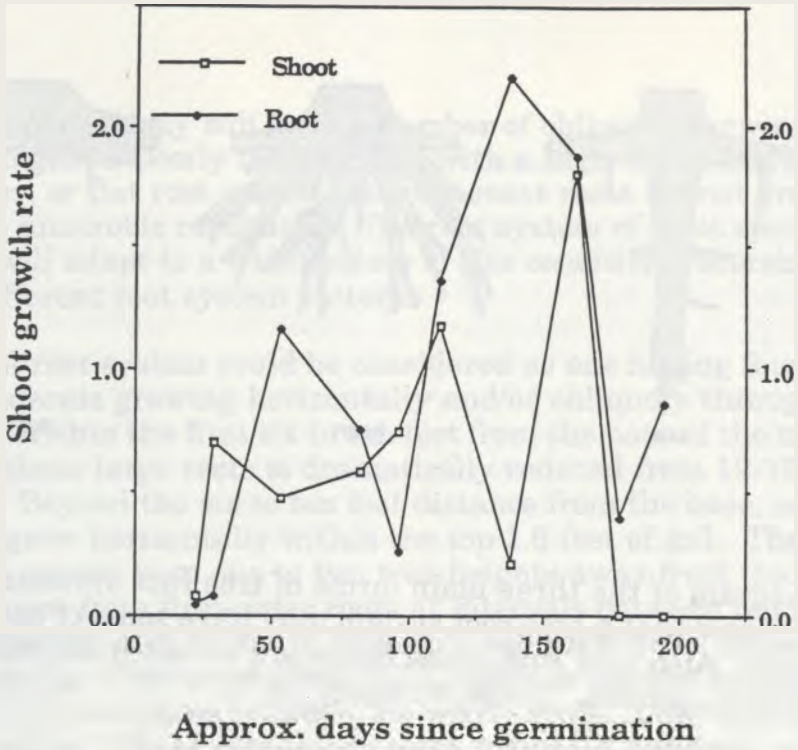

Figure 7. The episodic growth pattern of red oak during its first year of growth. Note that when the roots are actively growing, shoot growth slows dramatically and vice versa. Data from work done by the Hardwood Nursery Cooperative.

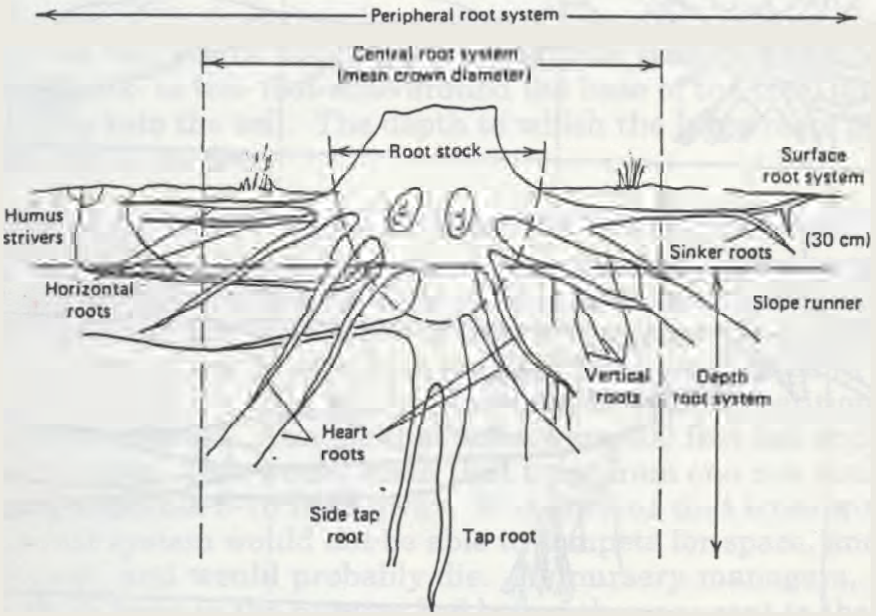

Figure 8. Diagramatic model of a tree root system, with the various kinds of roots that may develop. (From Hocker, 1979).

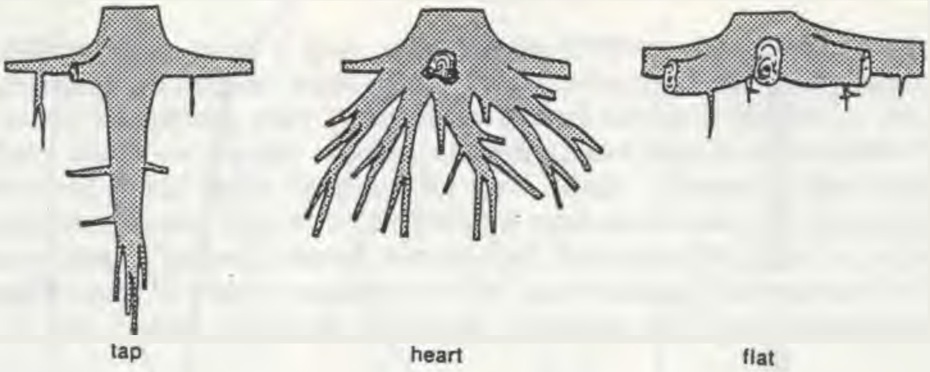

Figure 9. Diagram of the three main forms of tree root systems. Note from Figure 8 that a tree root system may have some of each of these roots. Also note that these forms are as much site specific as species specific. (From Armson, 1977).

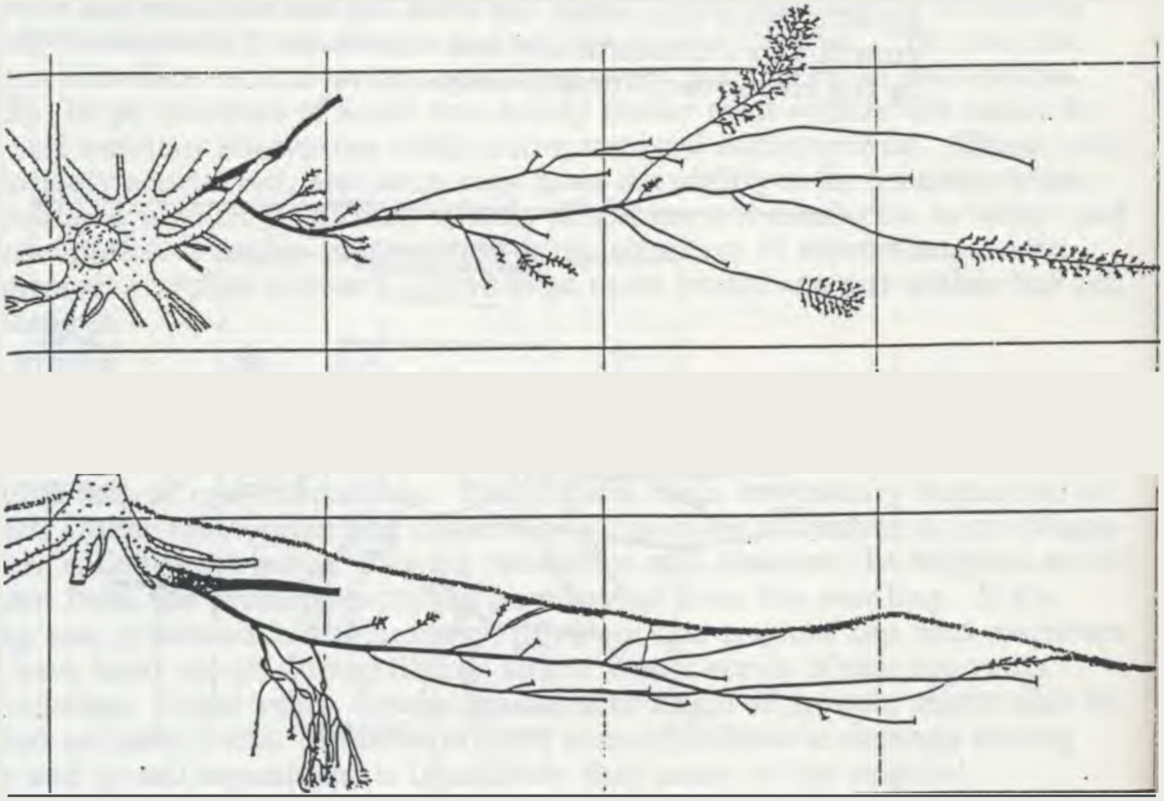

Figure 10. Root system form, including higher-order roots. Note that the lines are 1 m apart. Also note that, in the lower diagram, the soil surface slopes down to the right. (From Lyford, 1980).

tap root, but more likely will have a number of obliquely growing heart roots. A tree growing on a poorly drained soil, with a high water-table, will probably have a sinker, or flat root system, because most roots cannot grow in saturated soil, with its anaerobic conditions. The root system of most species is very plastic and will adapt to a wide variety of site conditions, thereby producing a variety of different root system patterns.

The ideal root system could be considered as one having four to ten large first-order laterals growing horizontally and/or obliquely through the soil (Figure 10). Within the first six to ten feet from the base of the tree, the diameter of these large roots is dramatically reduced from 12-15 inches to one inch or less. Beyond the six to ten foot distance from the base, most of the larger roots grow horizontally within the top 1.5 feet of soil. The first-order laterals may extend from one to two tree-heights away from the base. Second-order roots grow from first-order roots at intervals between ten and 40 inches. Non-woody roots 1 mm or less in diameter will grow from the second- and third-order roots. They can be from 0.25 inches to six feet in length and often branch to fill in the spaces between the woody roots. They may also grow in an upward direction. These non-woody roots maintain hundreds of thousands of root tips. It has been conservatively estimated that a mature red oak could have up to 500 million root tips, a large number of which would be mycorrhizal. Thirty to eighty percent of these fine roots die annually. As much as 60-70% of the carbon produced by the tree may go into root system construction and maintenance. The biomass of the root system accounts for 15-25% of the total tree biomass. Mycorrhizae may add an additional 8% to that figure.

In a forest, even with the extensive nature of tree root systems, there is no area in the surface soil where woody roots are farther than five to ten inches apart. Within the six- to ten- foot-zone around the base of the tree, large roots will grow obliquely into the soil. The depth to which the large roots grow seldom exceeds five to six feet.

Imagine drawing a tree to scale on a sheet of 8.5 X 11 inch paper. If the tree were 100 feet tall and that height scaled to five inches, then the roots would extend only 0.25 inches below the soil line. The lateral roots would extend five or more inches in either direction. Most of the roots beyond the six- to ten- foot-zone from the base could not be seen because they would be located in the line indicating the surface of the soil. Also try to visualize the competition between tree root systems in a forest. Assume that trees were 100 feet tall and planted at 10 X 10 feet spacing. This would mean that trees from one row could be competing with trees from 9-10 rows away. It is obvious that trees without a well-developed root system would not be able to compete for space, and would remain suppressed, and would probably die. As nursery managers, we must try to identify these trees in the nursery bed before they are sent to the field.

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environmental factors influencing growth

Water is a key to growth. After cell division occurs, new cells will not expand unless there is water to hydrate them. A young, unlignified cell may be 80-90% water. As important as water is, tree root systems do not "seek" water. Roots grow in soil that has good aeration and sufficient water. If there is not sufficient water, root tips will go dormant or may die and be sloughed off. Even if there is water in soil just beyond a several inch dry zone, the roots will not grow through that zone just because there is water on the other side. In addition, water is absorbed passively by the root system. It is the evaporation of water from stomates in the leaves, which produces tension in the water column extending down into the roots, that pulls water up through the tree.

Nutrients, for the most part, are also absorbed passively by the root system, for roots do not "seek" nutrients, either. Mycorrhizae are very important in enabling tree root systems to absorb sufficient quantities of immobile soil nutrients such as phosphorus. This function is a passive one in that a root system with mycorrhizal hyphae exploits more soil volume than does a root system without mycorrhizae. In addition, transport of elements through fungal hyphae is generally faster than movement through the soil solution. The presence of mycorrhizae on nursery seedlings may be a function of soil fertility. When there are high levels of readily available phosphorus in the soil, mycorrhizal production is much less. Nursery managers should be aware of this fact and use less fertilizer if they want to stimulate good mycorrhizal development. However, the fungal species available to colonize seedling roots in the nursery are often not the ones that will be present in the field. These non-native fungi will be quickly replaced after planting unless the field site has been drastically modified.

Soil temperatures also influence root development. Because soils respond slowly to ambient temperature changes, roots often find themselves in a temperature environment very different from that of the shoot. In spring, when good conditions for shoot growth exist, soil conditions may still be too cold for growth. Likewise, in the fall, soil temperature can remain warm enough for root growth long after shoot growth has ceased. The critical temperature for root growth lies in the range of 40-85 F. Temperatures that are too warm may also stop growth. The slow process of heat movement through soil reduces the likelihood of temperatures being too high for root growth at depths of more than a few inches.

Finally, soil conditions such as texture and structure can have a major impact on root-system form and growth. As suggested earlier, coarse textured, well-drained soils tend to produce deeper root systems than do fine textured, poorly-drained soils. Soil structure can be even more important for root development. Structure is related to the organization of macro- and micropores in the soil. Over time, macropores are developed in a soil as a result of freezing and thawing, and wetting and drying, as well as of root and soil organism activity. These macropores can be easily destroyed by compaction and tillage.

Nursery implications

The nursery manager can have a dramatic influence on the root system characteristics of seedlings shipped from the nursery. By controlling bed density and supplies of water and nutrients, root/shoot ratios can be manipulated in favor of the former. Root systems should be favored because they are the part of the plant most heavily disturbed during lifting and handling. Because root systems respond to injury, undercutting can be used to stimulate more lateral root development. Because roots and shoots grow at different times, the nursery manager must be aware that a particular cultural practice might have an unexpected effect. Seedlings should be lifted only when the shoots and roots are dormant, but dormant shoots don't always indicate dormant roots, especially in the fall. Finally, only seedlings with large numbers of permanent first-order lateral roots should be shipped to the field for planting. It is cheaper, in the long run, to cull the inferior seedlings at the nursery rather than to wait for them to demonstrate their inferiority in the field.

The control of root system development is a key to producing quality seedlings and, ultimately, a quality plantation or forest.

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