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understood interactions in plants. Questions concerning the ‘missing’ carbon sink in terrestrial ecosystems under various global climate change scenarios have increased our interest in elucidating the role below-ground systems play in carbon sequestration and carbon/nutrient cycling. Fine root systems (roots ≤ 2 mm diameter + associated rhizosphere biota), in particular, play a critical role in forest ecosystem function, with more than 50% of annual net primary productivity allocated below ground in many forests. Similar to their aboveground ephemeral counterparts (leaves), fine roots are relatively short-lived, but are the principal tissues for below ground resource acquisition. Yet fine root system demography (i.e., annual production, lifespan, and timing of root initiation and mortality) and function remain one of the most difficult and least understood areas of study because of its complex biodiversity and dynamic nature. The opacity of the soil and complex nature of the root/rhizosphere biotic system pose unique challenges to tree biologists studying root system function and belowground biodiversity.

Because of these challenges, our understanding of root system structure and function in trees is based largely on highly controlled seedling and mesocosm studies. However, to scale from seedlings to mature trees, root system biologists must consider how root function (much of it driven by carbon and nutrient source–sink relationships) and root ontogeny change as seedlings mature (Table 1), and how the biodiversity of rhizosphere microorganisms in the field alters root system function. As trees age, whole-plant source–sink relationships change, and nutrient demands are buffered by stored reserves and internal recycling of N and P. Storage carbon plays a critical role in buffering day-to-day or seasonal fluctuations in the carbohydrate supply to roots. Balanced partitioning of recently fixed carbon between immediate use and storage is essential for plant growth and for survival during stress. If an environmental stress decreases the photosynthetic capacity of a tree, then the demand on carbon reserves increases. Because of their low buffering capacity, seedlings are more dependent upon recently acquired nutrients and recently fixed carbon than mature trees, exhibiting a more immediate response and greater susceptibility to environmental stresses than observed in older trees. Consequently, the biggest challenge facing root system biologists is finding new technologies that will allow us to examine *in situ* root system function and demography on trees of variable age or size, with an increased emphasis on mature trees.

As seedlings mature into saplings and trees, their perennial roots will modify the physical, chemical,

Root System Physiology

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Introduction

The biotic and abiotic interactions that occur between tree roots and the soil rhizosphere environment are easily the most complex and least

Table 1 Comparison of some structural and functional characteristics of seedlings and mature trees that will alter shoot/root relationships and root function

Structure/function	Seedling	Mature tree
Carbohydrate storage	Low	High
Carbon allocation	None to reproduction, higher to foliage than roots	Higher proportion to reproduction, roots, storage
Drought resistance	Low	High
Leaf conductance	High	Low
Dependence upon recently acquired nutrients	High	Low; buffered by stores
Nutrient retranslocation	Insignificant	High
Proportion of fine roots in secondary:primary growth	Low	High
Proportion of fine roots to total root biomass	High	Low
Proportion of photosynthetic tissues to total biomass	High	Low
Rate of net photosynthesis	High	Low
Root system growth and metabolism	Greater dependence on recently assimilated carbon	More buffered by storage carbon

Modified from Vogt KA, Publicover DA, Bloomfield J, *et al.* (1993) Belowground responses as indicators of environmental change. *Environmental and Experimental Botany* 1: 189–205.

and microbiological characteristics of their soil environment. Rhizosphere microorganisms such as mycorrhizae, *Rhizobium*, rhizobacteria, and mycorrhizal helper bacteria can stimulate tree growth through enhanced mineralization and nutrient acquisition, biological control of pathogens, and production of plant growth regulators. Tree roots in the field are generally colonized by a high diversity of mycorrhizal species, with the degree and rate of colonization by individual fungal species changing temporally, spatially, with tree or stand age, and with soil and climatic environments. Functioning of the mycorrhizal root and its overall effect on tree growth are mediated by a hierarchy of biotic and abiotic factors at the rhizosphere (soil chemistry, texture, moisture, temperature, and biota), community (plant competitors, animal associates, and tree pathogens) and ecosystem (precipitation patterns, temperature dynamics, and atmospheric chemistry) levels. Since over 90% of the world's land plants belong to families that are commonly mycorrhizal, root function of most trees cannot be examined without considering how mycorrhizas modify the soil environment and host growth. Mycorrhizal associations are discussed in greater detail elsewhere (*see Tree Physiology: Mycorrhizae*), but a limited discussion on how they alter tree root function is presented here. Although an entire book could be written on the subject of tree root physiology, I focus on the following aspects of tree root structure and function: root architecture and development, fine root system turnover, and fine root system function. For a more in-depth discussion of these and additional topics, I

refer the reader to the list of further reading at the end of this article.

Root Architecture and Development

Root systems of higher plants show considerable architectural variation between species, within a species, and within an individual root system. This variability suggests that any genetic predisposition in root architecture is modified by the external soil environment. In long-lived perennial species, the degree of root plasticity is probably an adaptive response to spatially and temporally heterogeneous soil environments, enhancing a tree's ability to compete for limiting soil resources. Root systems of trees are often described as one of two types: those with taproots that grow rapidly downward, with taproot and lateral roots penetrating lower soil horizons, and those with more shallow, slower-growing primary roots and extensive, rapidly growing lateral roots. However, intraspecific variation in root growth is so great because of soil environmental modifications that interspecific comparisons can be difficult, and generalizations about species rooting depth and spatial deployment are misleading for many species. Certain species are more plastic than others with regard to environmental control of root architecture and spatial deployment in soils. For example, red maple (*Acer rubrum*) develops shallow, lateral roots in swamps and deep taproots in drier, upland soils, whereas some *Eucalyptus* species in dry areas develop a long taproot, but form a shallow root system on better sites.

In general, tree roots will grow in that portion of the soil where moisture, aeration, mechanical properties, and fertility are most favorable. A deep taproot system with a substantial number of lateral roots penetrating the lower soil horizons is typical of easily penetrable, often droughty soils. In contrast, shallow, platelike rooting is a response to edaphic limitations that restrict root growth to upper soil horizons, such as mechanical impedance of lower soil horizons or high water tables found in flooded soil environments. In more easily penetrable soils, the highest density of fine roots is often found in upper 0–10 cm soil horizons because these horizons are generally more aerated, have a higher organic matter content (with higher pools of organic N and P), are more fertile than deeper soils, and are well watered by summer precipitation. This is especially true in tropical and many temperate zone forests. In coniferous forests, rooting density in upper soil horizons tends to increase with stand age, presumably because canopy closure reduces understory competition and the litter layer becomes deeper and well established.

One of the common complaints among tree root biologists is the lack of standardization of root classification systems, making interstudy comparisons difficult and confusing. The problem is not a recent one, reflecting the complex and highly plastic nature of tree root systems growing in a dynamic environment. Studies dating from the early twentieth century used various classification systems that were intertwined with very elaborate, descriptive elements of form, often personalized by the various researchers. Lateral roots were described as: growth roots; long, main, and pioneer roots; surface roots, pioneers, seekers, and searchers; leaders; runners and

pioneers; extension roots; primary laterals; or simply laterals or long laterals. More recent ecological, physiological, and silvicultural studies often select a classification system (Table 2) based on the ease of use with their particular system (e.g., seedling versus mature tree, greenhouse versus field-grown plants) or experimental design (soil cores, ingrowth cores, minirhizotron observations, etc.). Unfortunately, most of these classification systems do not emphasize differences in morphology or root function, often lumping together roots that may have very different lifespans and function. This is particularly true for smaller-diameter roots ≤ 1.0 mm. Consequently, many researchers use a combination of classification systems to describe their roots. In those species such as *Pinus* that are strongly mycorrhizal, more emphasis needs to be placed on discriminating between mycorrhizal and nonmycorrhizal roots because of differences in lifespan, morphology, and function.

The heterorhizic root system is perhaps one of the most function-oriented classification systems that has withstood the test of time, in part because of its distinction between mycorrhizal and nonmycorrhizal roots. A heterorhizic root system is composed of long lateral and short roots, and is best typified in *Betula*, *Fagus*, and *Pinus*. Long laterals are first- and second-order roots (using developmental terminology) that generally originate in the root collar region, are considered permanent, and increase in diameter by undergoing secondary growth via a cambial layer. Individual long roots exhibit cyclic growth activity independent of each other, with pauses in growth often marked by metacutization. Metacutization is a process of lignification and suberization, resulting in

Table 2 Tree root classification systems

Developmental	Based on the order in which roots arise from primary root or taproot. First-order root arises from primary root or taproot; second-order root arises from first-order root; third-order root arises from second-order root. Often used in seedling studies when entire root is harvested since order of development is easily discernible
Architectural	Based on relationship to smallest root. The ordering system is the complete opposite of the developmental system, with smallest roots labeled first-order. Used in seedling or field studies
Heterorhizy	Long- and short-root habit exemplified by Betulaceae, Fagaceae, and Pinaceae. Long lateral roots are long-lived (many as old as the tree), are subdivided into various types depending upon diameter and point of origin, exhibit cyclic growth with pauses marked by metacutization, and are the framework of the root system. Classes of long roots, based on decreasing diameter, include: pioneer > mother > subordinate mother. Short roots are short-lived, typically ≤ 5 mm in length, do not undergo secondary growth, and are commonly mycorrhizal. Applicable to field studies
Woody/nonwoody roots	Used for some angiosperms not readily classified by long and short roots (e.g., red maple). Framework of permanent woody roots bearing many fans of relatively short-lived nonwoody roots. Nonwoody root fans consist of second- and higher-order nonwoody roots emerging from a first-order nonwoody root (developmental classification terminology)
Coarse/fine roots	Nonstandardized classification system based on root diameter only. The various root diameter classes vary with different studies, but fine roots are often defined as ≤ 2 mm. However, upper-diameter size limits for fine roots vary from 0.5 to 10 mm. Most often used in field ecosystem studies

a resting root that is protected against significant fluctuations in soil environmental conditions such as drought. Short roots are more ephemeral and arise from root primordia similar to those giving rise to long lateral roots, but are characterized by rounded tips with no true root cap, slow rates of cell division, short length, and no secondary growth. Short roots are considered important sites of water and nutrient uptake, and are commonly mycorrhizal, particularly in *Pinus*.

When considering the functional implications of root architecture in trees, it is important to recognize that tree root systems contain various classes of roots that differ functionally and morphologically. Large woody roots are long-lived and are functionally important for carbohydrate and nutrient storage, for structural stability and anchorage, and as transport conduits between fine roots and stems. Since nonmycorrhizal and mycorrhizal fine roots function primarily in water and nutrient acquisition and are often short-lived, enhanced plasticity of the fine root system response versus larger woody roots may be more critical for capturing a heterogeneous supply of soil resources. Accumulating evidence from minirhizotron and other studies suggests that plasticity in fine root initiation, proliferation, and lifespan responses to changes in soil moisture, temperature, and fertilization are important for water and nutrient acquisition in heterogeneous soil environments. Fine root initiation from long-lived deep or other favorably located lateral roots is a competitive advantage for trees when competing with herbaceous understory species for limiting soil resources.

From a carbon standpoint, it may be more cost-effective to shed roots in an unfavorable soil location or during unfavorable times during the year and to construct new roots in potentially more favorable microsites, rather than maintaining existing roots that are less capable of acquiring water and nutrients. However, if the nutrient supply in the new location is short-lived, or a competitor occupies the site more effectively, then root proliferation would not be cost-effective; consequently, there is a certain amount of risk involved in this strategy. In forested ecosystems experiencing a seasonal drought typical of Mediterranean climates, upper soil horizons dry out during the long drought periods. Fine root systems often proliferate in these upper horizons during the wet periods (most likely because of the higher organic matter and nutrient content of soil in this layer), but experience high mortality during the drought. Trees become more dependent upon deep, more stable sources of water during these dry periods, and it is not unusual for fine roots to proliferate from preexisting woody roots in deeper

soil horizons. It has been suggested that functional specialization may occur in trees that have two distinct layers of fine root growth in the soil, with the upper layer of roots primarily responsible for nutrient uptake and the lower layer meeting the bulk of the tree's water demands.

Because of the technical difficulty in monitoring root growth *in situ*, most available experimental data on the functional implications of tree root growth and architecture are from destructive harvests or a continuous monitoring via minirhizotron technology of only a portion of the root system. Magnetic resonance imaging (MRI) is an innovative, nondestructive technique in which functional roots can be visualized as a three-dimensional image set within a potting container or intact soil core, and changes in root growth and architecture can be monitored *in situ* over time. The application of this technique to study roots in soil was initially explored over a decade ago. The technique is especially powerful because it provides not only spatial information describing the geometry of root extension through the soil, but it has the ability to distinguish functional from nonfunctional roots *in situ*, as well as the development of water depletion zones in the rhizosphere. The ability of MRI to distinguish functional roots within an undisturbed soil volume provides a unique and powerful tool for examining *in situ* functional implications of root growth and architecture in seedlings over time. New technologies used in combination, such as ground-penetrating radar and stable isotope technology, may provide a better understanding of functional implications of lateral root architecture and distribution of trees in the field.

Fine Root System Turnover: Carbon Costs

The larger woody supportive roots extending from the base of a tree are long-lived (often as old as the tree) and comprise most of the lateral root biomass. However, woody supportive roots account for little of the tree's total root length and metabolic carbon demand. In contrast, fine roots comprise only 5–10% of total root biomass, yet can account for up to 90% of the tree's total root length. In many forests, the annual carbon cost for fine root system production and maintenance may account for 30–75% of net primary productivity, indicating that fine root system carbon demands may represent one of the largest carbon sinks in forested ecosystems. However, estimates for both annual production and lifespan are biased by the methodology and calculations used, making cross-study comparisons difficult. Consequently, we have a poor understanding not only of what controls root lifespan, but how much annual

carbon is used to support fine root system (roots + mycorrhizal tips + extramatrical hyphae) growth, respiration, maintenance, nutrient uptake, carbon exudation, and storage reserves. Of these, root system respiration is probably the biggest carbon sink, accounting for up to half of the carbon that is allocated below ground. The high percentage of net primary productivity (NPP) allocated to tree root systems suggests that, although roots may be the most distant carbon sinks from source leaves, they are not the 'poor relations,' having more control over the amount of fixed carbon that is allocated to them than previously thought.

Recent studies using minirhizotron (Figure 1) and soil core methodologies suggest that fine root system lifespan is a function of stand characteristics, climate or latitude, tree or stand age, species and ecotype, soil environmental variables such as fertility, water availability, temperature, and soil depth at both

stand and microsite levels, carbon status of the tree, timing of root birth, root diameter, root class or type, root order, mycorrhizal colonization, root pathogens, and herbivory. The high variability in fine root system demography (timing of birth and death, and overall lifespan) at the soil microsite level suggests that soil environmental characteristics, in particular, modify stand, seasonal, and genetic controls, and that plasticity is an opportunistic response to a variable resource environment. The lifespan of fine roots in conifers is generally longer than in deciduous trees, ranging from less than 1 to over 20 years, depending upon root order and diameter, with lifespan generally increasing with root diameter.

In contrast to their aboveground ephemeral counterparts (leaves), fine roots of most trees do not appear to have any active separation from the parent in the form of abscission layer. Although lateral branch 'scars' have been observed on parent

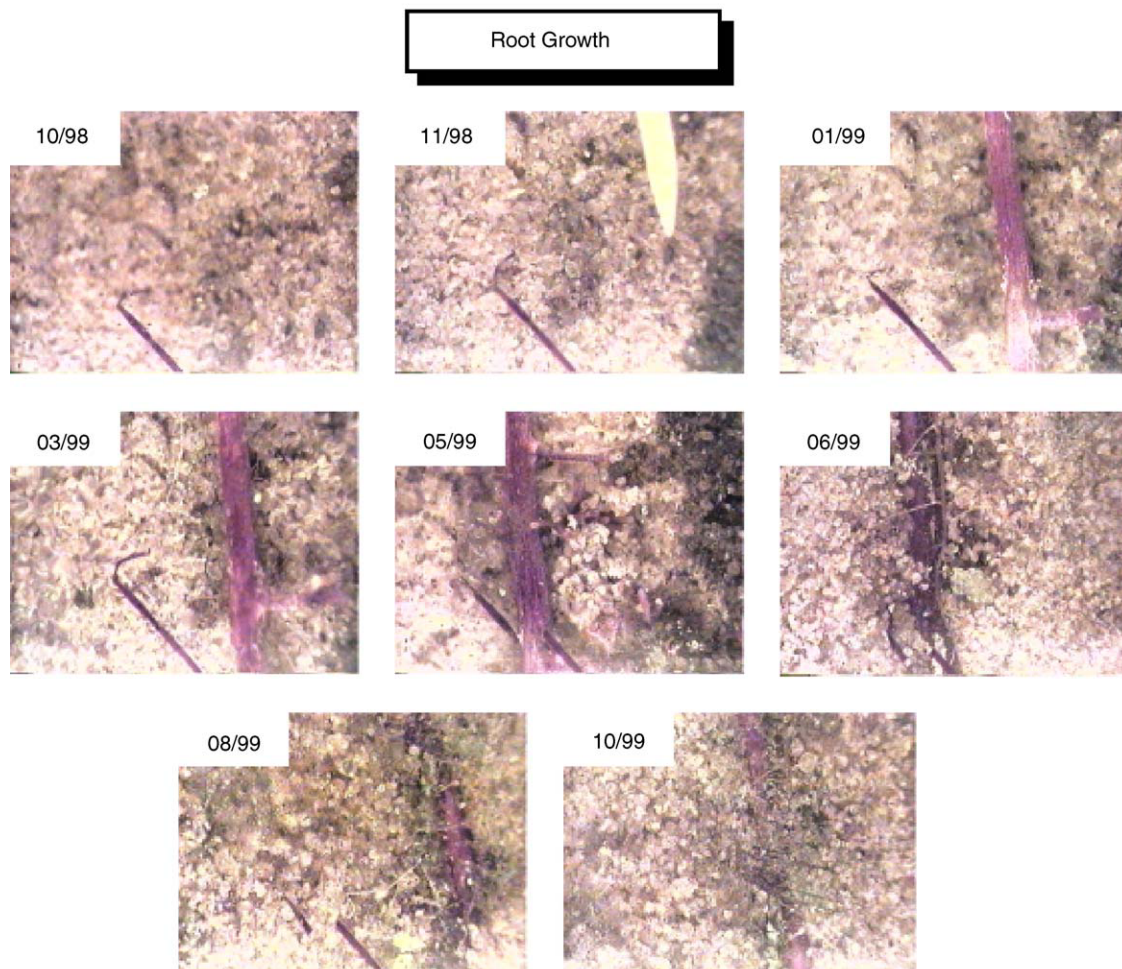


Figure 1 Example of how *in situ* root growth is followed over time using minirhizotron technology. A clear plastic tube is inserted in the ground at a 45° angle, and a camera is inserted into the tube at weekly or monthly intervals, recording images of the same root cohorts growing next to the tube. In the example, a new white root tip appears in 11/98, undergoes browning and secondary growth with bark development, and starts to degrade and disappear by 10/99.

roots in the field, the mechanism causing the mortality of branches is unknown. The development and morphology of the 'scars' have not been examined – the phellogen (bark cambium) of the parent root may simply seal the tissue off once the lateral root branch has started to senesce, as in a wounding response. In trees, suspension of root growth does not necessarily imply that the root is dying. The factors leading to growth suspension (a process called metacutization) may or may not be the same as those that result in root shedding. The mechanism by which roots are shed is poorly understood. It was once thought that roots have a predetermined lifespan and died when their finite supply of carbon was exhausted. However, experimental evidence indicates that root carbohydrate stores are dynamic, varying with season, on a diurnal basis, with age, environmental stress, and tree physiology, and can be replenished throughout the lifespan of the root. Experimental manipulation of the carbon supply has shown that root longevity is strongly influenced by the carbon status of the plant. The internal mechanism is probably one that ultimately restricts carbohydrate transport to the roots and, once root storage reserves have become exhausted, the affected roots will die.

Fine roots appear to have an indeterminate lifespan and die when environmental conditions become unfavorable (e.g., during a long drought), and/or the carbon cost of maintaining roots becomes too great relative to other carbon sinks in the tree. The high root mortality associated with heavy fruiting in *Prunus* and *Citrus*, or with stresses (e.g., defoliation) that can result in carbon shortages in trees may be necessary to maintain whole-tree carbon balance. Atmospheric pollutants such as ozone can affect root growth in trees by reducing the supply of photosynthate available for transport to roots due to inhibitory effects on photosynthesis and leaf growth, and increased leaf carbohydrate demands resulting from accelerated leaf turnover, membrane repair processes, and synthesis of antioxidants. Since most tree–fungal interactions are mediated through a carbon/nutrient exchange within the association, the extent of mycorrhizal formation is particularly sensitive to the availability of carbohydrate from the shoot, and thus, any environmental stress that alters this availability.

Because most forest soils are N- and/or P-deficient, many tree species have coevolved a high dependence on mycorrhizal associations. Mycorrhizae account for 5–80% of total fine root system biomass in conifers, and up to an additional 5–20% of net primary productivity. Hyphae of mycorrhizal fungi have a smaller diameter than roots and cost roughly

10% more to construct, but vastly increase the exploitation potential of tree roots because of their high surface area. In ectomycorrhizae, short roots are covered with a mantle of hyphae from which extramatrical hyphae extend into the soil (Figure 2). Over 200 individual hyphae have been observed emerging from a single mycorrhizal tip. An individual hypha may extend more than 2 m and form more than 100 lateral branches. Mycorrhizal associations come at a considerable carbon cost to the tree, but they offer protective benefits against root pathogens, increase the exploitation potential of a root system for immobile nutrients such as phosphate, ammonium, copper, and zinc, protect trees from heavy metals, and help maintain the tree's water status during dry periods.

Although construction costs of mycorrhizal root tips are higher than nonmycorrhizal roots, there is some evidence suggesting that mycorrhizal roots live longer than uncolonized roots on the same tree. This may be due in part to their protective effect against root pathogens, or to the mycorrhizal root's efficient ability to exploit limiting resources from the soil, ultimately increasing carbon flow into mycorrhizal roots. Endomycorrhizal and ectomycorrhizal fungi protect roots from pathogenic organisms possibly by: (1) producing antibiotics and antifungal chemicals (such as phenolic compounds); (2) encouraging the growth of beneficial microorganisms in the rhizosphere; and/or (3) physically protecting the root tips. Unlike woody and fine lateral roots, mycorrhizal roots do not undergo secondary growth, and are more susceptible to pathogenic invasion. Consequently, protecting the root from pathogens is in the mycorrhizal fungi's best interest. Roots of trees brown as they age and undergo secondary growth. In the region immediately proximal to an uncolonized white tip, browning occurs as epidermal and cortical



Figure 2 Ectomycorrhizal root of *Pinus* spp. Note extramatrical hyphae emanating from bifurcated root tip. Courtesy of Dr. Larry Peterson.

tissues break down and fill with condensed tannins. The tannin and suberin deposits are believed to serve a protective function against both pathogenic and mutualist fungi in this tannin zone and in tissue that has undergone secondary growth with a well-developed periderm.

Fine Root System Function: Nutrient Uptake

Supplying trees with nutrients is one of the major functions of their root systems. Perennial root systems of trees can modify rhizosphere soil over time, often enhancing the soil chemical environment by increasing its organic matter content and nutrient and water retention capacities, and making it a more hospitable place for beneficial rhizosphere microbes. Although the soil solution is the immediate source of nutrients for plants, it is in equilibrium with nutrients in the solid soil phase. When depleted by roots, the soil solution can be replenished by desorption and ion-exchange reactions. Whether energy is expended in uptake (traditionally referred to as active uptake) and if uptake is under metabolic control are in part determined by whether uptake is with or against the electrochemical gradient and if the ion is transported across the plasma membrane from the root apoplast into the symplasm.

The radial pathways for ion and water movement are extracellular (apoplastic) and intracellular (symplastic). The apoplastic pathway is a system of pores and wall surfaces outside the plasma membranes of epidermal, cortical, and stelar parenchyma cells, with the Casparian band in the endodermis blocking apoplastic passage of ions into the stele. In the symplastic pathway, plasmodesmata provide continuity or passage between the cytoplasm of living cells, offering a pathway of low resistance. In trees, nutrient uptake along the root axis varies with the nutrient. Uptake of some nutrients, such as calcium and iron, appear to be restricted to apical zones, while uptake of others (such as phosphate and nitrate) occur in older tissues of roots, even those undergoing secondary growth. How nutrients are transported across the periderm of fine roots is unknown, but field and greenhouse studies suggest that it does occur.

The ability of tree roots to acquire nutrients from a given volume of soil may vary with species, genotype, degree of mycorrhizal colonization, and rhizosphere microbial populations. Many plant nutritionists prefer to use the term 'acquisition' when referring to nutrient uptake by roots because it emphasizes that more is involved in getting inorganic nutrients into plants than ion transport across cell

walls. Nutrient acquisition is the dynamic interaction between plant, soil, and rhizosphere microbial properties, and is a function of root growth and development, overall plant growth, nutritional status of the plant, uptake (kinetic) properties of the root transporter, concentration of nutrient at the root surface, transport properties from the soil to root (including mass flow and diffusion), mobilization of ions by roots (including desorption, dissolution, and hydrolysis of organic compounds), and mobilization by associated rhizosphere microorganisms (including mycorrhizal and bacterial associates). In mobilization, root exudates (H^+ , HCO_3^- , reducing agents, chelating agents, and organic anions) are released into the rhizosphere to alter rhizosphere pH, to balance the electrochemical gradient resulting from anion and cation uptake, and to make some ions more available for plant uptake while excluding others (e.g., heavy metals). In addition, enzymes such as phosphatase are released by rhizosphere microorganisms and roots of some tree species, mobilizing organic sources of P that would otherwise be unavailable for uptake.

The nutritional characteristics of seedlings and mature trees, in particular, the nutrient transport systems, and what regulates these systems, are poorly understood. Although genotypic variation in nutrient uptake has been observed in many species, whether the differences are a result of genetically controlled differences in the transport system (e.g., maximum rate of uptake capacity (V_{max}) or affinity of the transporter for the ion (K_m)), or are simply a consequence of differences in growth, is less clear. Studies addressing how growth controls nutrient uptake at the root plasma membrane are scarce. Many studies with herbaceous and woody species (the latter, seedling studies only) have found a positive correlation between nutrient uptake rates and relative growth, suggesting that plant 'demand' is an important determinant of nutrient uptake rate. However, in trees, nutrient storage may be as strong a nutrient sink as growth. Thus, any relationship between growth and nutrient uptake will be confounded by a tree's inherent capacity for storage and nutrient retranslocation from other plant tissues.

The stimulation of physiological uptake capacity and root growth in nutrient-rich zones and their suppression in nutrient-poor zones are well-documented responses to a spatially heterogeneous supply of nutrients in herbaceous species, and more recently, in some woody species. These compensatory responses may enable trees to grow in naturally heterogeneous soil environments by allocating limiting resources in ways that maximize nutrient absorption. Although the stimulation of uptake capacity

in nutrient-rich patches is a well-documented response, the mechanism regulating uptake is not fully understood. Split-root experiments with herbaceous species have suggested that, when roots encounter a P-rich zone, uptake capacity not only increases but is maintained, despite high internal P concentrations in those roots. Accumulating evidence with herbaceous plants suggests that shoot 'demand' regulates N and P uptake and loading into the xylem, possibly via cycling of that nutrient in the phloem. Regulation of nutrient uptake in trees is complicated by their perennial long-lived habits, high storage capacities, and seasonal remobilization of certain nutrients, in particular, N and P. Recent studies suggest that organic forms of N and P in trees are more important storage forms of those nutrients than inorganic forms. In roots, immediate assimilation of N and P into an organic form would keep cytoplasmic concentrations of the inorganic form low, maintaining or stimulating continued uptake of that nutrient.

For nutrients that are highly mobile in the soil (e.g., NO_3^-), a high uptake capacity (a physiological response) is an important component of root competition where depletion zones of adjacent roots overlap. However, for immobile ions such as inorganic phosphate (P_i), stimulation of root growth in a nutrient-rich zone might be more critical than an increase in physiological uptake capacity. Phosphate concentrations of most soils are seldom higher than $10 \mu\text{mol}^{-1} \text{P}$. Diffusion of P to the root may limit P_i uptake more than any kinetic parameter controlling influx, i.e., V_{max} and even K_m . In soil-grown plants, higher uptake rates by roots growing in a P-rich zone will soon become limited by low P_i concentrations in the rhizosphere. Highly branched root systems are believed to be more efficient at exploiting soil for immobile ions such as NH_4^+ and phosphate. Consequently, for immobile nutrients, nutrient acquisition is probably most enhanced by increasing the surface area available for absorption via root proliferation, an alteration of root architecture, root hair initiation, or mycorrhizal colonization. In general, the finer the root, the greater the return per unit investment of carbon.

Spatial and temporal nutrient heterogeneity occurs in soils from both natural and managed ecosystems at scales relevant to individual plants; consequently, a plastic response in root physiology and/or in growth would be an important competitive trait. Temporal pulses of nutrients become available to plants during spring snow melt, during autumnal leaf fall, with seasonal rains, etc. Spatial patchiness of supply is common in most soils and greatest for immobile nutrients such as P_i . Soil tillage may increase the size

of the patch, but not eliminate it. Fine root proliferation in a nutrient-rich patch is not necessarily cost-effective if the ion is highly mobile, the patch is short-lived, or a competitor occupies the patch more effectively. The degree of root proliferation is influenced by soil concentration and whole-plant demand for that nutrient, and may be species-specific. Root system response to patches may differ among species from different successional stages or nutrient status. For example, fast-growing species from nutrient-rich habitats may exhibit higher plasticity in physiological rates of uptake and root morphology, while slow-growing species from nutrient-poor habitats may conserve carbon by depending upon long-lived root systems, and respond to soil heterogeneity primarily by increasing uptake rates. However, this latter strategy would be less effective for acquiring immobile ions such as P_i and ammonium.

Because of their extensive hyphal network, mycorrhizal associations increase the exploitation potential of a root system for immobile nutrients such as phosphate, ammonium, copper, and zinc. Nutritional benefits of mycorrhizae are most significant in N- and P-deficient soils. Except in the most productive forests, N and/or often P concentrations in the soil generally limit growth of most trees, especially during periods when nutrient demands are high. Consequently, it is not surprising that many tree species, particularly coniferous species, have coevolved a mutualistic dependence on mycorrhizal associations, with development most pronounced in infertile than fertile soils, or where nutrients become available in seasonal flushes. It has been estimated that, when root growth is restricted, external hyphae of endomycorrhizae can deliver up to 80% and 25% of the plant's P and N requirements, respectively, with greater nutritional benefits possible in ectomycorrhizal associations.

Ectomycorrhizae improve host N and P nutrition in deficient soils by accessing organic pools that would otherwise be inaccessible to roots – this is particularly critical in forest ecosystems, where the largest pools of N (and P) are the organic pools. Proteins and other organic N compounds are bound in recalcitrant forms of organic matter or are chemically fixed in clays, which protect them from rapid microbial breakdown. Thus, even though soil N greatly exceeds plant N, many forested ecosystems are N-limited because only a small fraction of total N is available in an inorganic form to plants. However, mycorrhizae allow woody plants to compete with soil microorganisms for organic forms of both N and P. The ability of ericoid and ectomycorrhizae to use protein as a growth substrate is correlated with the production of extracellular acid

proteinases in external hyphae, whereas extracellular acid phosphatases and phytase catalyze the release of P_i from organic complexes in the soil. Some tree species, particularly those that are adapted to highly organic, nutrient-deficient soils, appear to have proteinase, phosphatase, and phytase activity in nonmycorrhizal roots. However, because nonmycorrhizal roots are at a spatial disadvantage in competition with microorganisms, activity levels in nonmycorrhizal roots in the field are probably low compared with mycorrhizal roots. It is important to note that, although mycorrhizae increase the supply of N and P available to the host root apoplast, further uptake and transport of these nutrients across the root plasmamembrane into the symplast and ultimately xylem are dependent upon characteristics of the tree's transport system.

In the process of cation and anion uptake, roots of plants excrete protons, bicarbonate ions, and organic acids to their rhizospheres to maintain an electrical charge balance. However, in doing so, rhizosphere pH can be altered. Since the solubility of many nutrients in the soil is pH-dependent, plant roots can enhance solubility of a limiting nutrient (such as P) or decrease the solubility of potentially toxic elements (e.g., Al) simply by altering their rhizosphere pH. Other forms of root exudates associated with nutrient uptake include sugars, amino acids, acid proteinases, phosphatases, and phytases. The efflux of organic substrates from roots such as exudates, mucilages, lysates, and water-insoluble components associated with growth (sloughing of root cap cells and cell wall debris) are a significant source of carbon for microbial and mycorrhizal associates because they are easily assimilated. Colonization by mycorrhizal fungi is generally higher in roots with high (sugar) exudation rates. Microbial use of rhizodeposited carbon substrates has a major influence of nutrient availability in the rhizosphere, with the overall benefits to the tree (and forest) most likely justifying the carbon cost. Unfortunately, our understanding of root exudation, both benefits and costs, is limited by the technological difficulty in measuring this process *in situ*, particularly since any disturbance to the root will alter exudation and respiratory losses.

Fine Root System Function: Water Uptake

Plant water deficit has been implicated more than any other environmental stress as the most important soil parameter limiting carbon fixation, growth, and net primary production on a global scale. Up to 80–90% of the variation in diameter growth in trees can be attributed to variations in rainfall and plant water stress. Excellent reviews on the importance of

water on tree growth, the absorption of water and the ascent of sap are provided in the further reading section. This section will focus instead on how tree roots respond to water stress. In dry soils, trees with large canopies and/or poor stomatal control are particularly susceptible to water stress. If water loss via leaf transpiration exceeds water absorption by roots, a tree must regulate its water use, find additional water sources, or find other means of conserving water while meeting metabolic and growth requirements to avoid hydraulic failure. Some hydraulic models have suggested that in the soil → root → leaf → atmosphere hydraulic pathway, xylem of fine roots may be the weak link and act as hydraulic 'fuses' analogous to the protective function of electrical fuses. By localizing any break or cavitation in the hydraulic pathway to the more vulnerable but ephemeral fine roots, trees can minimize root replacement and xylem-refilling costs. The tree can get rid of fine roots that no longer have access to a reliable water supply and allocate more carbon to root growth in soil microsites or horizons with a more abundant and stable supply of water.

Trees are capable of growing in a wide range of soils that differ greatly in their hydraulic characteristics, presenting different challenges to roots trying to extract water from them. For example, coarse soils lose more moisture and conductivity at higher water potentials than fine soils because of weaker capillary forces retaining water in the larger pore spaces. Consequently, plants growing in sandy soils may become water-stressed at relatively high soil water potentials compared to plants in fine soils. Trees can differ considerably in their potential for water extraction, depending upon root-to-leaf ratio, rooting depth and density, degree of mycorrhizal colonization, and their resistance to cavitation. Since water is absorbed via roots and lost via transpiration in leaves, the ratio of fine root area to leaf area must be high enough to avoid hydraulic failure in the rhizosphere (i.e., loss of hydraulic contact between the root and soil), while approaching maximum extraction potential. Not unexpectedly, both nutrient and water deficits in the soil generally lead to similar shifts in whole-tree carbon allocation, i.e., more carbon is generally allocated to root growth to enhance the exploitation potential of fine root systems. However, in coarse soils with high soil porosity, a tree's response to fertilization amendments could compromise its drought tolerance because fertilization generally decreases the fine root-to-leaf area ratio.

In arid environments and in forests that are subjected to seasonal drought, deep taproots and lateral roots growing in lower soil horizons (with a more stable water supply) may support much of the

tree's water demands during times of water stress. Upper soil horizons are more subject to large fluctuations in water content than deeper soil horizons because of evaporation and plant water uptake, whereas deeper soil horizons are likely to be buffered by ground water recharge. In arid and semiarid environments, it is not uncommon for taproots to extend 10–20 m into the soil to tap into a more stable water source. Using stable hydrogen isotopic analysis of source water, several researchers have found that even riparian trees in arid and semiarid regions utilize ground water instead of less reliable surface water sources (i.e., stream water and precipitation). This utilization strategy may in part be due to the large fluctuations in stream discharge rates that generally occur during the lifetime of most trees in riparian habitats, helping the trees to survive periods of low discharge during extreme droughts.

Although deep roots provide access to a stable water source, trees are generally more dependent upon fine root growth in the more nutrient-rich upper soil horizons to meet the bulk of their nutrient requirements. Consequently, trees in forests experiencing seasonal drought often experience fine root proliferation in upper soil horizons during the wetter periods to maximize nutrient exploitation of these horizons, but high mortality during the seasonal drought. In less arid environments, this ability to switch among different water sources could increase a plant's ability to compete for limiting water resources when upper soil horizons dry out. Whether nutrient uptake by surface roots in the drier upper horizons continues to occur during this switch to deeper water sources is most likely a function of plant nutrient demands, soil moisture in these upper horizons, soil porosity, the degree of fine root system production, and whether hydraulic lift may be rewetting these drier horizons. In hydraulic lift, water absorbed by deep roots of trees or shrubs passes through roots in the drier, upper soil horizons, and rewets rhizosphere soil during periods when transpiration ceases (generally at night). The process is believed to be primarily passive, driven by root and soil water potential gradients. The 'lifted' rhizosphere water in these upper soil horizons is then reabsorbed the next day and transpired. Hydraulic lift has been demonstrated in tree species occurring in arid, semiarid, and even in some mesic forest environments. The persistence of hydraulic lift over long periods in otherwise dry upper horizon soils could prolong the lifespan and activities of fine root systems in upper soil horizons, improve ion mobility in rhizosphere soil, and maintain nutrient uptake in the more nutrient-rich upper horizon soils.

The root–soil interface, or rhizosphere, is a dynamic environment between the tree root, rhizo-

sphere biota (both microbes and mycorrhizas), and soil environment. With the exception of nitrogen-fixing organisms and mycorrhizae, we know very little about how rhizosphere microbes (including those microbes associated with mycorrhizae) may alter root function and tree growth. It is impossible to study tree root physiology and forest (belowground) ecosystem function without considering rhizosphere biota. With increasing demands for shorter rotations and faster-growing trees in plantations, existing fertility of forest soils must be improved. A greater consideration of how forest management practices alter soil biology and root function could ultimately lead to more efficient tree root systems.

See also: Tree Physiology: A Whole Tree Perspective; Mycorrhizae; Nutritional Physiology of Trees.

Further Reading

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