water and nutrient availability and a tree's ability to root and anchor itself. Forest productivity can be increased by silvicultural site treatments that mitigate naturally compacted soils and those compacted by trafficking of heavy equipment. Improving drainage of wet soils, and reducing evaporative demand of dry soils by conserving organic matter and harvest debris, increase forest productivity by optimizing the balance of air and water in soils. Conservation of soil organic matter and harvest slash during forest operations conserves essential nutrients and helps regulate their availability, especially nitrogen, phosphorus, and calcium that are found limiting in some forest soils. Careful management of all site and soil resources will ensure sustainable forest productivity and health for the production of products and ecosystem services such as water control, carbon sequestration, wildlife habitat, and biodiversity.

See also: **Health and Protection**: Biochemical and Physiological Aspects. **Soil Biology and Tree Growth**: Soil Biology; Soil Organic Matter Forms and Functions; Tree Roots and their Interaction with Soil. **Soil Development and Properties**: Forests and Soil Development; Landscape and Soil Classification for Forest Management; Nutrient Cycling; Nutrient Limitations and Fertilization; Soil Contamination and Amelioration; The Forest Floor; Waste Treatment and Recycling; Water Storage and Movement. **Tree Physiology**: A Whole Tree Perspective. **Wood Formation and Properties**: Wood Quality.

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Tree Roots and their Interaction with Soil

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Introduction

Root systems provide three key elements for the establishment and productivity of a tree: stability, uptake, and storage. Site characteristics such as slope, aspect, drainage, and land use history will directly and indirectly impact the success of these elements. Many species use the plasticity of their root system to adapt to site conditions, but others simply do not occur on sites incompatible with their normal root system. Edaphic factors such as temperature, soil water potential, oxygen concentration, mechanical resistance, and the content of nutrient ions will influence the growth and function of the roots themselves. At the same time, root systems have a profound effect on the physical and chemical characteristics of the multiple soil horizons. As roots grow, they stabilize, penetrate, enlarge cracks and crevices, and lower water and nutrient contents. Finally, root decay allows infiltration of water and surface materials downward through old root channels and organic material is concentrated within the soil profile.

Root System Characteristics

Root Mass and Configuration

Root systems provide stability or anchoring to trees and are most often characterized as one of three principle forms: taproot, heart root, or sinker root (**Figure 1**). Although site conditions will influence root growth and the array of diameter size classes, root form tends to be under a degree of genetic control. The taproot form is characterized by one

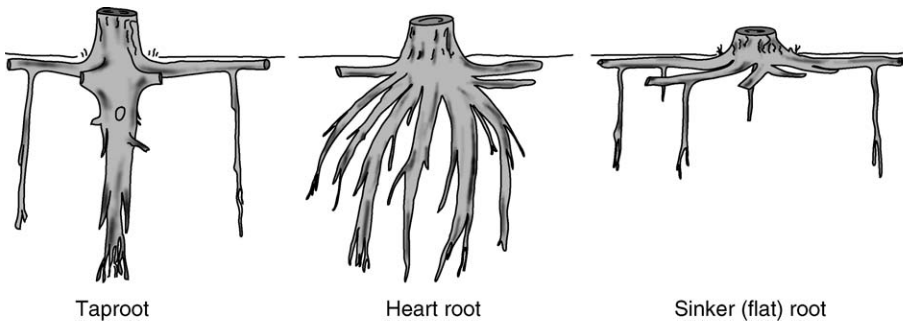

Figure 1 Principal tree root forms. Reproduced with permission from Fisher RF and Binkly D (2000) *Ecology and Management of Forest Soils*, Third Edition, Wiley.

primary, deeply penetrating taproot. Such root systems occur in species of *Carya*, *Juglans*, *Quercus*, *Pinus*, and *Abies*. Many taprooted species have extensive laterals and sinkers that allow them to survive on shallow soils or soils with seasonally high water tables. Species of *Larix*, *Betula*, *Carpinus*, and *Tilia* develop the heart root form which is characterized by numerous lateral and oblique roots radiating from the tree base. This form grows best on deep permeable soils and is more capable of exploiting fractures in bedrock than other root forms. The sinker or flat root form has an advantage on shallow soils and is characterized by shallow laterals from which vertical sinkers grow downward. This form is seen in species of *Populus*, *Fraxinus*, and *Picea* and can be found on a wide range of soil conditions.

Root structure Root diameter is commonly used to differentiate function and often correlates with degree of suberization and longevity. Taproots primarily function as physical support, but also provide valuable storage. They comprise 10–30% of mature tree biomass and as much as 90% of total root biomass. Even though taproots have been documented to extend >20 m, the bulk of most root systems is 1.5 m from the surface and within the canopy drip line. Larger primary lateral roots emanate from the taproot in patterns influenced by genetics and site. Secondary laterals extend from primary laterals and combine to represent the bulk of the coarse root fraction. Coarse roots are >15 mm, generally have a well-developed bark, which is marked by lenticels and cracks which facilitate their contribution to water and nutrient uptake. These roots are perennial and contribute 5–20% of mature tree biomass and as much as 40% of the total root biomass. Fine roots are commonly referred to as the absorbing roots and in many species include any roots <15 mm. Roots 5–15 mm provide continuity of nutrient and water flow. Roots 2–5 mm are generally suberized roots that provide extension, uptake, and transport, but are not observably infected with mycorrhizae. Roots <2 mm are often termed feeder roots, as they principally function to absorb water and nutrients. Feeder roots are not suberized, can exhibit root hairs and may be noticeably infected by mycorrhizae. In some species, roots <1 mm diameter provide much greater surface area to dry weight correlation than do roots 1–2 mm, and are more accurately termed very fine feeder roots.

Root hairs and mycorrhizae are the smallest root features but are responsible for measurable increases in water and nutrient uptake. Root hairs are microscopic extensions of root epidermal cells which greatly increase the surface area of the root. They are delicate and easily ruptured when the soil is disturbed, suggesting why newly transplanted seedlings and plants need to be protected from water loss for the first few days after transplantation. Mycorrhizal fungi infect roots and can develop extensive hyphal networks which increase the uptake capacity of the system. The amount of ectomycorrhizal fungal mycelium can be so extensive that its total mass is comparable to the mass of fine roots themselves; however, the endomycorrhizae make up only a small mass of fungal material and are unlikely to exceed 10% of the fine root weight.

Root function Plant roots grow continuously, but their proliferation depends on the availability of water and minerals in their microenvironment. At the same time, the ability of plants to absorb both water and mineral nutrients from the soil is related to their capacity to develop an extensive root system.

Solute absorption occurs in a zone behind the root tip, where the processes of cell elongation and root hair formation occur (**Figure 2**). Within this zone of elongation, the pathway of least resistance occurs in the apoplast of the cortex up to the endodermis. Older root surfaces can absorb soil solution through cracks and breaks in cortical tissues, creating discontinuous zones of absorption along the root length. In roots of woody angiosperms and gymnosperms, a periderm arises and the epidermal and

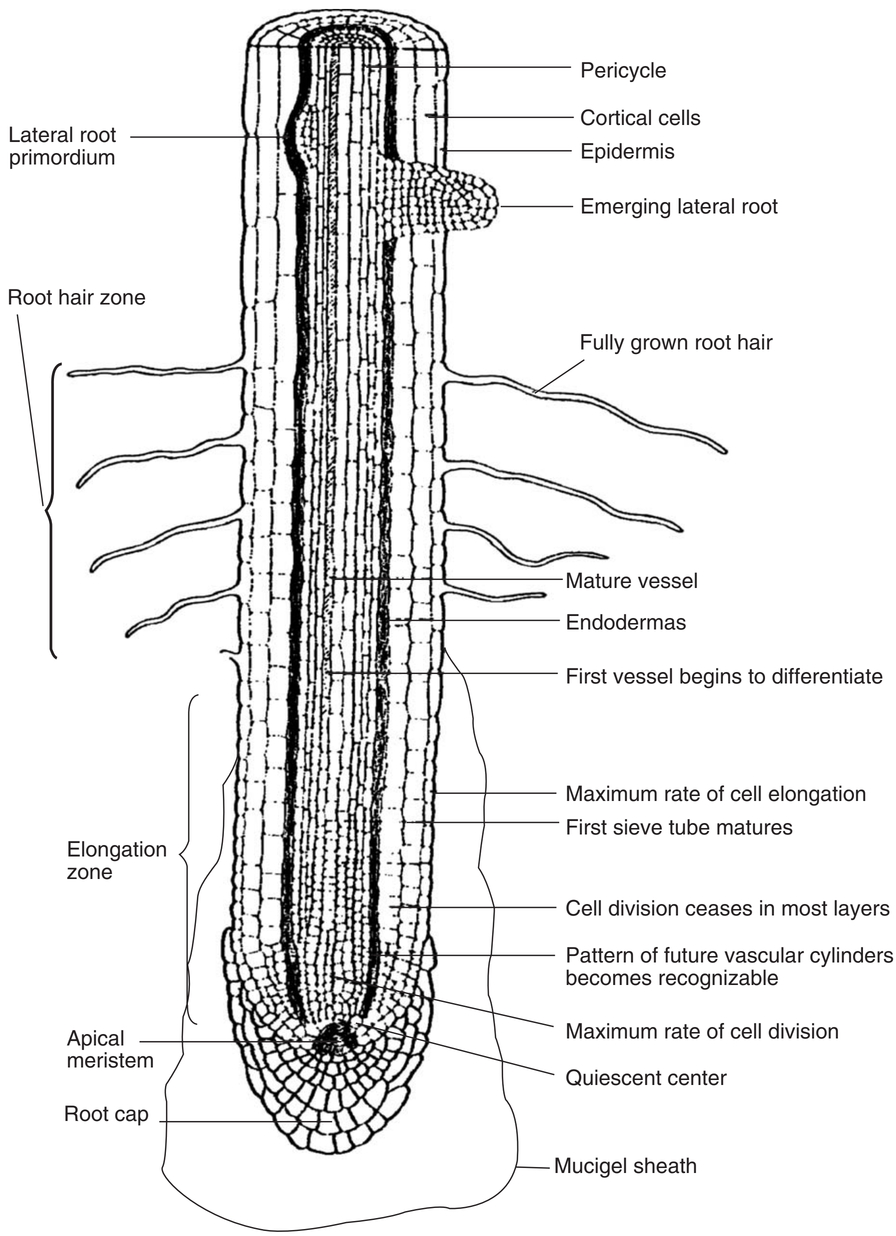

Figure 2 Schematic of root thin section. Reproduced with permission from Lake JV, Gregory PJ and Rose DA (1987) *SEBS 30 Root Development Function*. Cambridge University Press.

cortical tissues exterior to it are shed leaving a highly variable, but appreciably permeable layer of cork cells. Because these roots dominate the root system in mature plants, this contribution to the water supply of the plant must outweigh that of the younger unsuberized tissues.

Water contacts roots in two ways: (1) mass flow of water (Darcy's law) to the root, or (2) interception of water as roots grow through moist soil. The rate of water flow through soils depends on the size of the pressure gradient and on the hydraulic conductivity of the soil which will vary with soil texture. As water is absorbed from the soil near the rhizosphere, the water potential of the soil decreases and a gradient toward the root is created. As more of the soil spaces become filled with air, there are fewer contiguous channels through which water can easily flow. Root hairs may traverse air gaps between the root and moist soil particles. When a soil dries out enough, the water potential can fall below what is called the permanent wilting point. This is the point at which the water potential of the soil is so low that plants could not regain turgor even if all transpiration were stopped. The permanent wilting point is not a unique property of the soil, but depends on the plant species.

Roots absorb mineral nutrients at low concentrations from the soil solution and translocate them to various parts of the plant for utilization. Uptake can be active (as is the case of phosphorus) or passive (as is the cases for calcium, magnesium, and other cations). Experimental evidence supports nutrient absorption at the apical region of the root axes, and along the entire root surface, depending on the nutrient being investigated. Soil chemistry and parent material will greatly influence the bonding and binding of anions and cations to clay lattices and soil colloids, thereby determining the degree of availability. Rainfall and soil texture will also impact uptake capacity, as tortuosity and pore size distribution impact mass flow and desorbtion characteristics.

Tree root systems are vital in their capacity to store water, nutrients, and carbohydrates. It is well documented that tree boles shrink and swell within a day in response to water use patterns, and studies have observed a similar pattern in large lateral roots. However, the degree of elasticity and propensity for deep water recharge remain important study points. The tremendous reservoir of nutrients in root systems is not retranslocated from roots before they die, thus they are returned to the soil where they can be utilized by other plants. At the same time, tree roots are an immediate source of labile and stored carbohydrates. Starch storage in mid-rotation loblolly pine (*Pinus taeda*) has been documented to contribute $>14\%$ of the total carbon needed for annual tree growth.

Root systems also produce hormones that function to regulate whole tree growth. Roots are known to produce and export cytokinins and abscicic acid (ABA) to the xylem sap. When dehydration of the root medium occurs, the cytokinin content in the xylem decreases and a large increase in ABA concentrations can be measured in the roots. The ABA content of the leaf epidermis is closely related to the degree of stomatal closure even without a change in leaf water potential, and stomatal closure can occur even if only part of the root system is dehydrated. In addition, while the absolute magnitude of osmotic adjustment is less in roots than in leaves, as a percentage of the original tissue potential it can be greater in roots than in leaves. These adjustments may only slightly increase water extraction from previously explored soil, but they also enhance turgor and maintain root growth.

Root longevity There is little disagreement that taproots and coarse roots can be as old as the bole itself, and generally root diameters increase with age. The common misconception is that fine roots live only a very short time. In fact, research has shown that fine roots of pine can live 8 years or more. Evidence suggests that fine roots of other species also have a substantially longer lifespan than previously believed.

The anatomy and morphology in parts of the root system vary greatly according to the age of the tissue and the soil environment. In the apical zone of the root, cells are thin-walled, rich in cytoplasm, and have a high rate of respiration. However, relatively old tissues with thick-walled suberized endodermis and few passage cells can be effective in transport of phosphorus and potassium. The movement of calcium and magnesium into the xylem is, by contrast, greatly restricted by the development of suberized lamellae in the endodermis, suggesting normal transport across the plasma membrane of young endodermal cells.

Mycorrhizal Infection

Mycorrhizae are widespread in natural conditions and extensively infect tree species, creating mutualistic relationships through which the fungi receive sugars from the host plant, in exchange for increasing mineral uptake efficiency. Mycorrhizae occur in two major classes: ectotrophic and endotrophic. The ectotrophic mycorrhizal fungi typically form a thick sheath or mantle of fungal mycelium around the roots, with some of the mycelium penetrating between cortical cells. This network of internal hyphae is called the Hartig net. Endotrophic or vesicular–arbuscular (VA) mycorrhizal fungi do not produce a fungal mantle around the root, but form ovoid structures called vesicles and branched structures call arbuscules within plant root cells.

Fungal mycelia extend into the soil, forming hyphal rhizomorphs and hyphal strands supporting fruiting bodies. This extension of fungal hyphae beyond the nutrient-depleted soil zones near roots increases the capacity of the root system to absorb nutrients. Ectotrophic mycorrhizae may also proliferate in the organic layer of the soil and hydrolyze organic phosphorus for the root. Studies have shown that mycorrhizal fungi can transport phosphate at a rate more than four times higher than that of an uninfected root.

A key factor in the extent of mycelial development is the nutrient status of the host plant and site. Deficiency of a nutrient such as phosphorus tends to promote mycorrhizal infection, whereas, infection tends to be suppressed in well-fertilized soil. A correlation also exists between volume of root surface fungi and bacteria (closely related to biomass), and shoot nitrogen. Although such a correlation could be caused by the microorganisms increasing the plant's nitrogen uptake, it is more likely that increased nitrogen in the plant causes increased microbial growth through increased exudation. This interaction has significant application in forest systems where species competition, spacing, and site preparation continue to impact site productivity.

Tree Allometry

Allometry is an empirical expression of the distribution of biomass between aboveground and belowground tissues. In general this relationship will be species specific and it will shift as a stand develops. Trees generally shift from a predominance of belowground tissue to aboveground tissues with age and stand development; however, it may be difficult to separate this pattern from seasonal effects. Site conditions including temperature, planting density, and competition do not usually change the root to shoot ratio (R/S), but may impact the rate of growth and the absolute root density.

It is frequently reported that the relative allocation of carbon for root growth decreases drastically with fertilization, and that trees respond to improved site fertility by shifting the allocation of tree mass belowground on infertile sites and aboveground on fertile sites. Research also shows shifts in root size distribution toward fewer fine roots in response to increased site fertility. However, roots proliferate in microsites with high nutrient contents and it is most likely that total tree growth changes rather than the allometry of that growth changing. Similar arguments can be made for impacts of competition. In any event, even insignificant shifts in allometry may be biologically important to stand productivity and longer-term carbon storage.

Soil Conditions and Root Growth

Soil Texture

Root form is closely associated with tree species, but the mixture of sand, silt, and clay in a soil will impact water availability and resistance to root penetration, thereby influencing the expression of that form. Higher clay contents increase resistance to penetration, may restrict vertical and horizontal root growth, and can result in thinner roots and slower growth. Sandy soils provide lower resistance to penetration, allow extension through large pore spaces, and can contain roots that are on average of greater diameter.

Bulk density is the representation of mass of soil per unit volume. The lower a bulk density reading, the lower the resistance to root penetration, while the higher the bulk density, the greater the resistance to root penetration. Within a range of values, root growth is possible regardless of soil texture or water availability, but beyond a value of approximately $2.65\,g\,cm^3$, root penetration is restricted.

Impeded roots are known to develop a layer of suberized lamellae close to the root tip which greatly increase resistance to the radial flow of water, and delay re-establishment of continuous films of water when roots are moistened after a period of desiccation. Uptake of potassium would not be affected in impeded roots, but transfer of calcium and magnesium across the root would be hindered.

Historically it has been accepted that roots will grow unrestricted only in pores of diameter greater than their own, and only enter those of at least a similar size to the root tip. While this growth strategy may be predominantly true, advancement of root and mycorrhizal research has shown that a root tip needs only a single cell to pass through a pore space before it continues to extend through unrestricted media. Extension of root tips and hyphae through restricted pore sizes in many soil structures leads to the physical breakdown of organic and inorganic impediments.

Soil Moisture

Clearly there are tree species better adapted at living on wetter sites than drier sites, and vice versa. A large portion of this adaptation is in how plant roots adjust to and thrive in conditions of low oxygen. The supply of oxygen to the roots is essential for cellular respiration, the source of metabolic energy that drives mineral uptake processes. In general, roots require a minimum oxygen level and will cease to elongate when water levels are high. Unsuberized roots may become thicker in response to high water levels, but whether the cause for this is expansion of individual cells, or growth of additional cells is not known.

Soils at field capacity have 10–30% of the volume composed of air-filled spaces, and this percentage decreases as water content increases. Under most conditions, the oxygen supply in air-filled pore spaces is in the range of 15–20% but plant roots cannot obtain oxygen when soils are flooded, and anaerobic environments are created. In wetlands and along the shores of oceans, lakes, rivers, and ponds, pore spaces become saturated with water, the rates of water and nutrient absorption are suppressed, and death of roots can occur. While some woody species are tolerant to flooding during dormancy, formation of adventitious roots and aerenchyma after flooding (linked to increased ethylene production) has been shown to alleviate the effects of root injury to some species.

In contrast to flood-sensitive species, wetland vegetation is well adapted to growth for extended periods in saturated soil. Even when shoots are partially submerged, they grow vigorously and show no signs of stress. In these plants, the stem and roots develop longitudinally interconnected, gas-filled channels, known as aerenchyma, which provide a low-resistant pathway for diffusion of oxygen and other gases. Hypoxia stimulates greater production of ACC and ethylene, and the latter promotes the breakdown (lysis) of cells in the root cortex. As roots extend into oxygen deficient soil, continuous formation of aerenchymas just behind the tip allows oxygen movement within the root to supply the apical zone. This retained oxygen aerates the apical meristem and allows growth to continue 50 cm or more into anaerobic soil.

Under adverse soil conditions the extension of roots is retarded and differentiation is slowed less than extension. In this way, cell maturation occurs much closer to the apex than in rapidly extending roots. Suberization of roots in response to dry soil conditions corresponds to a cessation of root extension and formation of a continuous suberized layer just beneath the root cap. Thus the hypodermis and endodermis are found to develop closer to the apex when soil conditions are unfavorable. As long as desiccation does not cause cortex cells to collapse, the root apices are able to rupture the suberized layer and extension resumes within a few days of soil rehydration.

Temperature

Soil temperature influences both adsorption of water and nutrients by existing roots and affects future root growth. As soil temperature increases, root carbohydrate demands increase due to increased respiration and as the carbon sink strength of the roots increases. In the long term, shoot biomass production is decreased at the expense of root maintenance and growth. Conversely, changes in phospholipids in the roots, as a response to gradual shifts in temperature, may influence transport processes across cell membranes by maintaining them in a fluid condition at lower temperatures. This cell membrane level mechanism may serve as a root adaptation to seasonal changes in soil temperature.

The optimum root temperature for shoot growth is a function of the R/S ratio. Optimum root growth occurs at approximately 35°C for subtropical plants, 27.7°C for warm temperate plants, and 20°C for cool temperate plants. There are ranges of temperature within which plants and microorganism can grow and function, but it is important to remember that temperature impacts are not independent for roots and shoots. Increasing root temperature decreases the R/S ratio, just as increasing shoot temperature increases the R/S ratio.

Nutrient Availability

Tree roots usually favor a slightly acidic pH, one in which fungi predominate the rhizosphere. A low pH favors the weathering of rocks, the release of ions such as potassium, magnesium, calcium, and manganese, and the increased solubility of carbonate, sulfate and phosphate salts present in the soil solution. Increasing solubility facilitates absorption by the root.

The inorganic particles of the soil solid phase act as a reservoir of nutrients such as potassium, calcium, magnesium, and iron. Also associated with this solid phase are organic particles containing nitrogen, phosphorus, and sulfur. Nutrient movement to the root surface can occur by mass flow and by diffusion. Mass flow describes movement of nutrients along with the convective flow of water moving through the soil toward the root. The amount of nutrient provided to the root by mass flow will be dependent on the rate of water flow to the plant and the concentration of nutrients in solution. Where water flow is high and nutrient concentrations are high, mass flow can play an important role in nutrient supply.

Diffusion occurs when mineral nutrients move from a region of higher concentration to a region of lower concentration. Because active nutrient uptake by the root will lower nutrient concentrations at the root surface, concentration gradients are created surrounding the root. Diffusion of nutrients can supply nutrients to the root surface from areas of high concentration to areas of lower concentration. When diffusion is too slow, a nutrient depletion zone is formed adjacent to the root surface.

Carbon Dynamics of Tree Roots

Growth

Production and growth of roots require more plant resources and energy than production or growth of aboveground tissues. This idea is largely driven by attempts to complete and balance models with only a black-box understanding of root production and turnover. Research has shown that the carbon compounds used by roots, in order of preference, are carbohydrates > amino acids > soluble proteins > insoluble proteins. Because carbon is fixed during photosynthesis, site properties that are linked to photosynthetic capabilities and sink strength will impact root growth.

Root growth varies seasonally in response to carbon fixation by leaves and demand by various parts of the tree. Deciduous species have wide range in photosynthetic capacity, while evergreen species maintain some photosynthetic capacity all year. Under these two scenarios we understand that an excess of carbohydrates would be available to deciduous species roots only after leaf-out in the spring, whereas evergreen root production would be bimodal, with excess carbohydrates produced in the early spring and autumn.

Root development is critical during seedling establishment. Establishment may be limited by site-specific properties (such as nitrogen or phosphorus availability, or aeration) or by process-limiting situations (such as establishment of a mycorrhizal hyphal network, production of absorbing root surface area, or allocation of resources between sources and sinks).

Exudates

Interest in the rhizosphere effect on microbial activity and plant health did not gain momentum until about 1955. Since that time, researchers have calculated that carbon released from roots growing in soil can amount to approximately 20% of the total plant dry matter. Exudates are produced from carbohydrates which are primarily synthesized in the shoot during photosynthesis and then translocated to the root system. A majority of total root exudates, approximately 60%, are cations and to a lesser extent anions. The carbon components of root exudates are typically composed of 66% organic acids, 29% carbohydrates, and 5% amino acids.

The presence of microorganisms in the rhizosphere increases root exudation, either through physical damage to the root tissues, or through release of metabolites from the microorganisms which affect root physiology. In this way, measuring microbial population in the rhizosphere in response to various factors indirectly assays exudation. Research has generally shown that change in any biological or physical factor that affects plant growth also affects the quantity of exudates released by roots. The principal factors affecting the type and quantity of substances released by roots into the rhizosphere include species and developmental stage of plant, soil physical stress factors, plant nutrition, mechanical or disease injury, microbial activities, and foliar-applied chemicals.

Decomposition

Decomposition of root systems provides a network of continuous root channels, and improves soil porosity. Roots are the principal source of organic matter in the deeper soil layers, and their decomposition directly and indirectly influences nutrient release. Studies of several tree species indicate that decomposition rate decreases as a function of increasing root diameter. Decomposition of large lateral roots and taproots can potentially impact nutrient release over several decades while decomposition of fine roots affects nutrient release on a seasonal basis.

Typically, a 'wet' forest has more living than dead roots, while a 'dry' forest has more dead than living roots. The major influence of increasing soil moisture is to improve decomposition and mineralization of dead roots and their nutrients. Because carbon dioxide, produced as a by-product of decomposition of organic material, equilibrates with the soil water, we can measure changes in respiration and link this to biological activity. Conversely, site disturbances including fire and clear-cuts will affect biological respiration presumably with little change in belowground biomass.

See also: **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Physiology**: Mycorrhizae; Nutritional Physiology of Trees; Root System Physiology.

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Soil Organic Matter Forms and Functions

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Introduction

Soil organic matter is important in determining both relatively stable soil properties as well as dynamics of soil systems. This article focuses on the contribution of organic matter to mineral soil horizons dominated by inorganic sand, silt, and clay-sized particles. The role of the organic forest floor is described elsewhere (*see* **Soil Development and Properties**: The Forest