Table 8 Denitrifying bacteria in soil, and their metabolism and energy source – an example of the diverse range of organisms potentially involved in converting nitrate to gaseous N in forest soils

Denitrifying organism	*Metabolism*	*Energy source*
Pseudomonas	Chemoheterotroph	Soil organic matter
Paracoccus denitrificans	Chemoautotroph	H_2
Thiobacillus denitrificans	Chemoautotroph	Reduced S
Rhodopseudomonas	Photoautotroph	Light

a terminal electron acceptor when O_2 diffusion is limited by high soil moisture. There is also some evidence of N_2O production in woodland soils by heterotrophic fungi, where NO_3^- is used as an alternative for O_2 in respiration, and denitrification occurs simultaneously. Because of the broad range of processes with potential to produce N_2O in forest soils (summarized in **Table 8**), further studies are required to determine the impacts of forest management and climate change on N_2O emissions. There has been considerable interest in the impacts of forest management on methane (CH_4)-oxidizing bacteria because temperate forests are major sinks for atmospheric CH_4. For example, forest clear-cutting can reduce the activity of methane-oxidizing bacteria and therefore the net CH_4 consumption in forest soils; changes that apparently result from the inhibition of CH_4 oxidation by elevated soil inorganic N. Less invasive forms of management such as thinning have been associated with increased CH_4 consumption.

Impact on Species Composition and Abundance

Determining the impact of climate change and forest management on soil biota and the critical processes they mediate in forest soils remains a significant challenge for the future. For example, the current literature indicates that there is not enough information to predict the impact of increased atmospheric CO_2 on the soil microbial community. Progress towards this task will rely on linking, through empirical testing, functional groups and key species among the soil biota with key processes maintaining ecosystem stability, such as decomposition and nitrogen fixation. In this way the contributions of the huge diversity of soil biota may be simplified to allow a better understanding of changes in the soil environment on ecosystem processes and stability.

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Soil and its Relationship to Forest Productivity and Health

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Forest Soil and its Functions

Soil is a mixture of mineral materials, organic matter, water, air, and plant and animal life. It varies in depth from a few centimeters to several meters across most of the earth's terrestrial surface. Its rock, sand, silt, clay, and organic matter physical composition varies in texture and structure, which controls the infiltration, percolation, and storage of water and the balance between water and air in its pore space. The amount and nature of clay and organic matter and the influence of parent material and vegetation largely control its chemistry and level of fertility. Soil also contains and is made up of myriad macro-, meso-, and microorganisms, both plant and animal, essential for organic matter decomposition, nutrient cycling, energy conversion, and soil formation processes. Soils vary greatly across the landscape due to soil forming factors, including the nature of parent rocks and minerals from which they are derived, the amount of relief in the local topography, the types of plants and animals in and on the soil, the nature of the local climate, and the amount of time a soil has been in place. Soils can vary in age from a few years to millions of years.

Soils serve a variety of functions in forest ecosystems. They serve as a medium for tree growth; they anchor the tree physically and supply water and nutrients for uptake by tree roots; and they serve as water-transmitting layers on the earth's surface. During rain events or snowmelt, water moves into soil, percolates to a saturated zone or water table, and remerges downslope in streams and rivers. Absorption of water into soil regulates the flow and controls the quality of water in watersheds. Finally, soil serves as an ecosystem component. It controls the flow of energy, the cycling of chemical elements, the rate of organic matter decomposition, carbon sequestration, and biodiversity. The interaction of soil properties and processes determines forest health and productivity.

Forest Health and Productivity

Forest Health

Forest health is a qualitative term that refers to the general condition of a forest. A healthy forest is one that is relatively free of insect infestations, diseases, exotic weeds, and air pollution. All species making up the forest are able to grow at rates commensurate with the local climate, geographic position, and soil resource to complete their life cycles. A healthy forest can resist damage from catastrophic events like acute insect and disease attacks, fire, wind, and flooding, and fully recover from these perturbations to continue its life history functions over decades, centuries, or millennia. Soil influences forest health by securely anchoring trees' roots, by regulating energy flow among ecosystem components, and by controlling water and nutrient availability for the benefit of the entire forest system. The habitat of soil organisms that play a role in decomposition and nutrient cycling processes is also controlled by the presence and nature of the soil. During dry periods, droughty soils may predispose forests to insect and disease attack, but if the forest can recover normally, natural, periodic stress caused by soil-induced limits on water or nutrients is not considered unhealthy over the long term.

Forest Productivity Definition and Concepts

Forests that grow quickly and produce large amounts of biomass in a short period of time are said to be highly productive. For example, a mixed tropical forest in the Amazon basin of Brazil is more productive than a black spruce forest in Canada. Forest productivity is the rate of accumulation of forest dry matter per unit area per unit time. It is commonly expressed as net primary productivity (NPP). NPP includes the biomass accumulation of all plants' stems, leaves, roots, and reproductive structures, and it includes litterfall, root sloughing, and the plant biomass consumed by herbivores and plant and animal decomposers. NPP is expressed in units of dry mass accumulation per square meter per year ($\mathrm{g\,m^{-2}\,year^{-1}}$), or dry mass per hectare per year ($\mathrm{Mg\,ha^{-1}\,year^{-1}}$). The belowground component of NPP is difficult to measure. Most measures of NPP are for the more easily determined aboveground component only (ANPP).

Forest productivity can be depicted and defined as a logistic curve of production as a function of time (solid line in **Figure 1**). Just after forest establishment, when light, water, and nutrient resources are in ample supply, biomass increases exponentially until a point in time (inflection point) when resources are fully exploited by the forest. This usually coincides with stand closure and maximum leaf area development. After this point of inflection on the curve, production decreases exponentially due to light, water or nutrient limitations. Biomass accumulation reaches a maximum when light, water, or nutrient

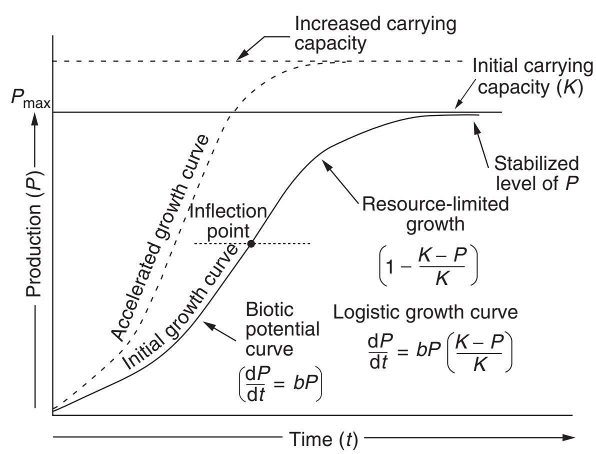

Figure 1 The forest biomass production curve is a logistic function based on the relative availability of light, water, and nutrient resources through time. Dashed lines show the potential for increasing productivity with site treatment over that of a nontreated condition (solid lines). Increasing soil quality (carrying capacity) increases productive potential (P_{max}), and alleviating water and nutrient limitations shortens the time required to reach carrying capacity. Reproduced with permission from Burger JA (2002) Soil and long-term site productivity values. In: Richardson J, Bjorheden R, Hakkila P, Lowe AT, and Smith CT (eds) *Bioenergy from Sustainable Forestry: Guiding Principles and Practice*, pp. 165–189. Dordrecht, The Netherlands: Kluwer.

resources limit the rate of photosynthetic carbon fixation to the level of carbon depletion via respiration; this is called the compensation point. This level of maximum production is the site's carrying capacity or potential.

Measuring Forest and Site Productivity

Historical production records from multiple harvests of fully stocked stands growing on the same site would provide the best and most direct measure of forest and site productivity; however, records for multiple growth cycles are not available for most forest sites. Foresters estimate forest productivity by measuring the rate of growth, or the volume accumulation of live, standing, aboveground woody biomass ($m^3\,ha^{-1}\,year^{-1}$) contained in the stems of desired crop trees. The mean, or average annual growth, is determined by dividing the total stand volume of live, standing tree stems by the total age of the tree stand; this is also called mean annual increment (MAI).

Forest sites that have the potential to produce biomass at a rapid rate are said to have high site quality. Site quality is the sum of the effect of all site factors on the capacity of a forest to produce biomass. MAI can be used for a relative measure of site quality. To estimate site quality, MAI is determined at the culmination of the increase in mean annual increment, the age at which mean annual increment peaks.

A faster, easier, but indirect measure of site quality is a tree's height relative to its age. Trees grow faster on good sites and slower on poor sites, while height remains well correlated to tree volume. As the quantity and quality of soil improves, trees grow at faster rates and will be taller at a given age (**Figure 2**). Their height growth is sensitive to site factors, but relatively independent of stand density. This height/age relationship is called the site index and is usually defined as the height of dominant and codominant trees in well-stocked, even-aged stands at a preselected or index age. Index ages of 25, 50, and 100 years are commonly used for fast-growing pines and eucalypts, hardwoods, and slow-growing northern conifers, respectively.

For the purpose of spatially mapping forest land and prescribing silvicultural treatments to areas based on site potential, site quality is commonly ranked by class, depicted by Roman numerals I through V, with site quality class I being the most productive and class V the least. **Table 1** shows the relationship between site quality, volume, product class, and value. As trees grow, diameter increases exponentially; therefore, volume and value increase exponentially. Wood in large tree stems is disproportionately more valuable than wood in small tree stems due to the products associated with each. For example, sawtimber is more valuable than firewood and results in a much greater return on investment from forest stands managed as a business enterprise.

Site and Soil and their Relationship to Forest Productivity

Overall, tropical rainforests have the greatest ANPP, followed by temperate and boreal forests. This gradient in productivity with latitude is mostly due to length of growing season, temperature, and amount of available water. ANPP increases as

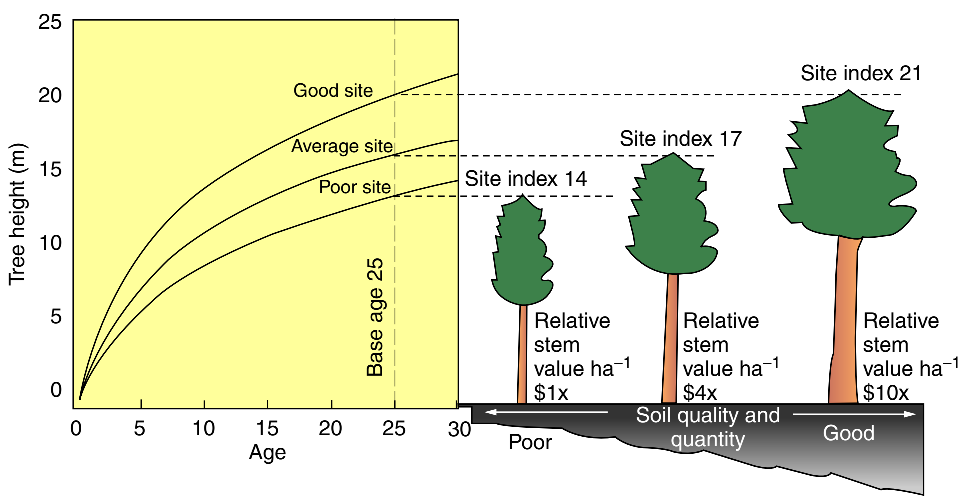

Figure 2 The depth and quality of soil influences the rate at which trees grow and accumulate biomass. Site index, the height of dominant and codominant trees in stands at an index age (e.g., age 50), is the most common method used by foresters to estimate site quality.

Table 1 The influence of site quality on wood production, product class, and return on investment; Appalachian oak is used for this example

Site quality class	*I*	*II*	*III*	*IV*	*V*
Oak site index (m)	26	23	20	17	14
Stem volume MAI ($m^3 ha^{-1} year^{-1}$)	8.0	6.2	4.6	3.0	1.8
Commercial use and value	Furniture, veneer	Sawtimber	Railroad ties	Firewood	None
Return on investment (%)[a]	10	7	3	0	−5

[a] Return on investment estimates were based on average stumpage values and management costs for the Appalachian region during 2001. Emphasis is on the relative difference in values among site quality classes; absolute values vary with regional economic conditions.

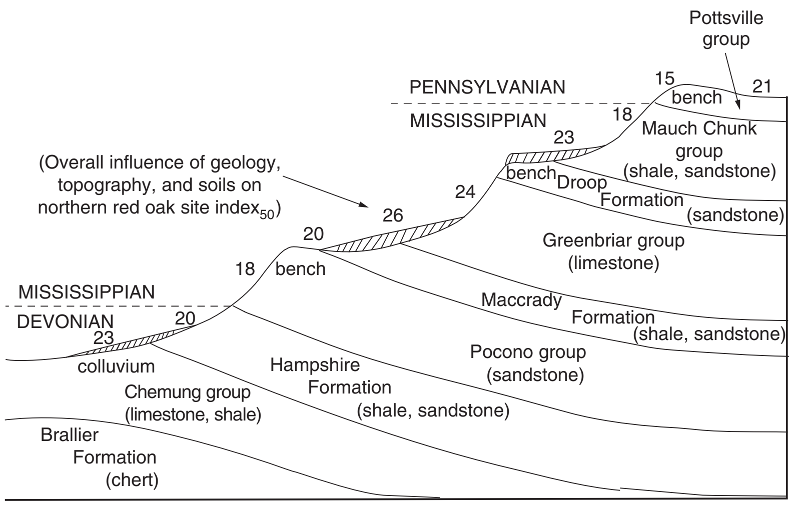

Figure 3 Hillslope in the Appalachian Mountains region of West Virginia. Site quality varies greatly on this hillslope gradient due to geologic, topographic, and soil features.

growing season, temperature, and available water increase. Across this gradient, ANPP varies by more than an order of magnitude, from more than $20\,Mg\,ha^{-1}\,year^{-1}$ for tropical rainforests to less than $2\,Mg\,ha^{-1}\,year^{-1}$ for boreal forests. Within a region of relatively uniform temperature and rainfall, ANPP can vary tenfold due to topographic position, geology, and soil quality. These site and soil factors influence tree growth primarily through water and nutrient availability.

Geologic and Topographic Site Factors

Soils are formed from residual material or from material transported and deposited by water, wind, ice, or gravity. The productivity of residual soils is influenced by rock and mineral type and the rate at which they weather. Limestones and shales weather faster than most sandstones creating deeper, more fertile soils. Common igneous and metamorphic soil-forming rocks are generally more resistant to weathering, although most are rich in minerals required by plants. Soils derived from transported materials are generally very productive, as they are found in low landscape positions and consist of existing soil materials transported from higher elevations. The position, orientation, and layering of geologic materials also influences soil weathering rates, soil water movement and storage, and depth of rooting. In the northern hemisphere, steep, mid-slope positions with southwest aspects have the shallowest soils and highest evaporative demand. The deepest, most productive soils are found on northeast-facing slopes at slope bottoms. Topographic features influence productivity predominantly by controlling plant available water and controlling the harmful effects of fire, wind, snow, and ice. On flatter terrain, slight changes of only a few centimeters in elevation can influence the depth to a water table and the effective soil depth that trees can exploit. In the case of soils with high water table, productivity is more often nutrient limited due to insufficient aerated soil volume.

Figure 3, a not-to-scale drawing of an actual hillslope in the Appalachian Mountains of the USA, illustrates the interaction of geologic, topographic, and soil factors influencing site productivity. The site index of northern red oak (*Quercus rubra*), a native species that occurs naturally across the entire hillslope gradient, ranges from 15 to 26 meters as a function of these interacting factors. It is most productive at mid-slope, growing in colluvium and residuum of a limestone-derived soil. It is least productive growing on bench positions above weathering-resistant, quartzitic meta-sandstone layers (Pocono and Pottsville formations). Its productivity is intermediate on soils derived from shale formations. Productivity is intermediate (higher than expected due to site factors alone) at the top of the mountain due to higher rainfall caused by orographic precipitation.

Soil Factors

Soils have basic physical, chemical, and biologic properties that influence soil climate and fertility, the two general conditions that influence forest productivity and health. The complex structural and functional components of soil climate and fertility are conceptualized in the drawing in **Figure 4**. Soil depth, horizonation, texture, structure, and porosity determine the rate of flow and storage of heat, water, and air that in turn influence rates of metabolic activity in roots and their growth. Soil fertility and nutrient availability is determined, in part, by organic matter decomposition and mineralization, and the weathering of soil parent materials. The extent to which soil climate and fertility processes are optimized determines the availability of water, oxygen, and nutrients for uptake by forest plants.

Measurable soil factors influencing tree growth include total depth or depth of certain layers, organic matter content, nutrient content, air/water balance, and depth to a water table or restricting layer. There are dozens of studies in the literature that correlate ANPP with soil properties. Different soil properties are more influential than others in different regions. For example, numerous correlation studies have shown that, in the Atlantic coastal plain region of the USA, southern pine growth is most influenced, in order of listing, by thickness of the subsoil, depth of the surface soil, drainage, depth to mottling, nutrient content, and organic matter content. In the northwest region of the USA, mixed conifers are most influenced by soil depth, surface soil texture, water-holding capacity, nutrient content, subsoil texture, and coarse fragment content.

Increasing Forest Productivity by Increasing Soil Quality

Forest productivity is determined by tree genetic potential, soil and site factors, and silvicultural inputs. Therefore, forest productivity can be increased (dashed line in **Figure 1**) by improving the genetic make-up of the trees, and by temporarily alleviating deficiencies in water and nitrogen by irrigating or fertilizing. These silvicultural inputs usually shorten the length of time required for biomass to reach the site's carrying capacity, which is one way to increase forest productivity (shorter rotations). A second way of increasing productivity is to increase site carrying capacity for additional

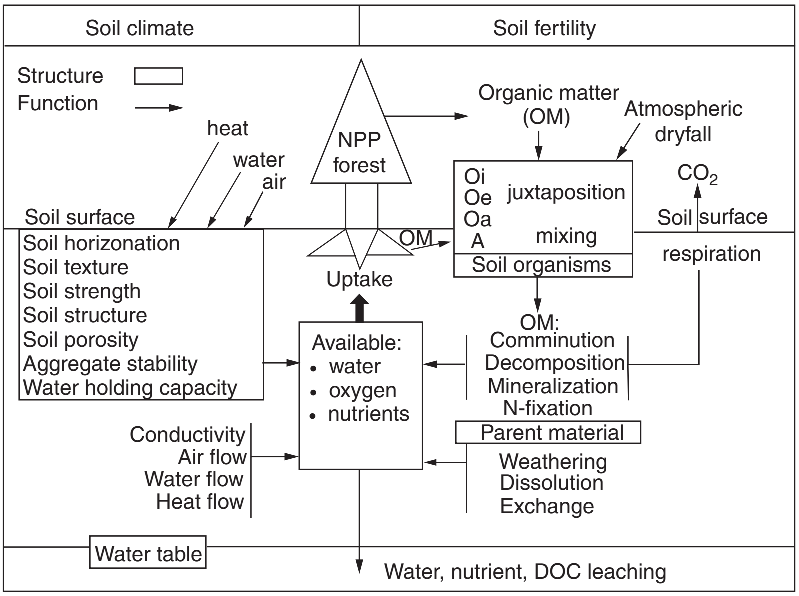

Figure 4 Conceptual model of soil properties and processes influencing forest productivity. DOC, dissolved organic carbon; NPP, net primary productivity. Reproduced with permission from Burger JA (2002) Soil and long-term site productivity values. In: Richardson J, Bjorheden R, Hakkila P, Lowe AT, and Smith CT (eds) *Bioenergy from Sustainable Forestry: Guiding Principles and Practice*, pp. 165–189. Dordrecht, The Netherlands: Kluwer.

production potential. Carrying capacity can be increased with site treatments that cause a more or less permanent change in site carrying capacity, such as increasing effective rooting depth by eliminating barriers to root growth, by draining wet soils, by adjusting soil acidity or alkalinity, or by adding phosphorus to deficient soils. These modifications of the soil resource raise the P_{max} on the y axis in **Figure 1**. The dashed production curve depicts an increase in forest productivity due to an increase in site quality or carrying capacity, and a further increase due to a shorter growth cycle.

In most cases it is not practical to irrigate forest stands. Instead, foresters shift limiting water resources to crop trees by eliminating competing vegetation and by thinning crop trees at appropriate times during the growth cycle. ANPP is not increased, but the amount of merchantable wood is increased by shifting resources to fewer, merchantable trees at the expense of nonmerchantable vegetation. Nitrogen is often growth limiting in both managed and nonmanaged forests throughout the world. In managed forests, deficiencies can be aggravated by removing harvest slash and soil organic matter in the process of preparing the site for planting, and by accelerating nitrogen mineralization through soil tillage. Deficiencies usually occur in managed, even-aged forests during or just after canopy closure. Adding nitrogen at mid-rotation temporarily fertilizes the trees, but usually has little long-term effect on soil fertility. Multiple additions of nitrogen through time are usually needed to completely alleviate deficiencies. Because nitrogen additions fertilize the trees with little permanent effect on the soil, forest productivity increases, but site quality remains unchanged.

Phosphorus limits forest productivity in some forested regions of the world where total soil phosphorus levels are inherently low, or where phosphorus is chemically or physically bound and unavailable to plants. Deficiencies are alleviated by applying phosphorus at time of planting or site preparation. Because of the unique chemistry of soil phosphorus, it remains for long periods of time, increasing fertility for the length of the growth cycle and beyond. This long-lasting effect improves soil quality and increases site carrying capacity.

High soil strength and soil air and water imbalances are physical problems that can be addressed with site treatments. In all cases, forest practices that improve soil physical properties increase the amount and quality of the rooting environment. The amount of soil available for rooting is usually a function of depth, but can be a function of physical impedance or the inability of roots to physically penetrate soil, especially when dry. The physical quality of soil is mostly a function of soil structure and consistence that allows water and air to flow and be stored at optimum amounts. Naturally compacted soils, or soils compacted by machine trafficking, can be subsoiled, bedded, or harrowed to create better rooting environments. Poorly drained soils can be ditched to lower the water table, and sites can be bedded to elevate planted seedlings above water-saturated soil.

Forest productivity can also decrease if soil quality is damaged by forestry practice. Soil damage is usually an unintended side effect of forest harvesting, with the exception of chronic air pollution causing soil acidification and base leaching in forest soils of some industrialized regions of the world. Forest harvesting on wet soils compacts and puddles soils, which can restrict root growth and impede normal soil drainage. Site clearing after harvest, either mechanically or with intense fire, can remove significant amounts of organic matter and nitrogen, causing nutrient deficiencies at some point in the growth cycle. Forest practices and site treatments invariably change a variety of soil properties and processes, with both positive and negative effects. Sustainable forestry practices will ensure that the net effect is positive for sustainable forest productivity and health.

Human communities throughout the world desire forests that sustain plant and animal productivity, maintain balanced hydrologic, carbon, and mineral nutrient cycles, and maintain protective and environmental forest functions. Forest soils play an important role in each of these functions. Research for a better understanding of soil and its relationship to forest productivity and health is ongoing. Given that soils have complex properties and processes and are highly variable across the landscape, carefully prescribed soil- and site-specific forest management practices and treatments should ensure the maintenance of soil quality in both extensive and intensively managed forests.

Summary

Forest health is the condition of a forest relative to being free of insect, disease, water, and nutrient stresses, and to its ability to survive and recover from catastrophic events like fire, tornadic winds, and floods. Forest productivity is the rate of forest biomass accumulation per unit area per unit time. Forest productivity is controlled by the genetics of the species and individuals that make up the forest, and site and soil factors that include local climate, geology, topography, and soil properties that control 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