

The emergence from dormancy is frequently regulated by a promoter–inhibitor system, where the principal promoter is gibberellic acid (GA₃) and the main inhibitor is abscisic acid (ABA). Low levels of inhibitor and high levels of promoter induce germination. According to some studies, it is not possible at present to determine the precise function of ABA in the induction of dormancy.

See also: **Genetics and Genetic Resources:** Cytogenetics of Forest Tree Species. **Tree Physiology:** Physiology of Sexual Reproduction in Trees.

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Shoot Growth and Canopy Development

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Introduction

As shoots grow and become numerous a canopy develops. The mass and surface area of the leaves in the canopy reach a maximum amount relatively early

in the life of a stand. Subsequent growth of the trunk and branches serves to lift the canopy higher and higher above the ground. The form and arrangement of the branches and leaves in the canopy are an important reflection of the architectural type. Tree architecture is difficult to study and describe because trees are very large, very long-lived, and have a complex hierarchy of components. Much of tree architecture is inherited. Trees look different because they have evolved in different climates – tropical palms (e.g., *Corypha elata*) versus alpine firs (e.g., *Abies alba*), coastal mangroves (e.g., *Rhizophora mangle*) versus savanna baobabs (e.g., *Adansonia digitata*) and niches (overstory Douglas-firs (*Pseudotsuga menziesii*) versus understory Pacific yews (*Taxus brevifolia*), overstory oaks (e.g., *Quercus alba*) versus understory dogwoods (e.g., *Cornus florida*). In addition to variation in the inherited types, there is tremendous genetic variation in response to the local environmental variables of solar radiation, competition, and availability of nutrients and water. The phytochrome-mediated response to plant shade is strongly inherited. Trees appear to grow toward the light, but are really growing away from shade. The intensity of competition determines the tree size and shape. Some species can grow larger than others under extreme competition. The xylem is well suited to support the tree and conduct water, but the hydraulic limits of the xylem to transport large volumes of water from the soil to the distant transpiring leaves also sets limits to tree size and form.

Tree Growth

Plant growth is defined as the increase in size by cell production and enlargement. Apical meristems at the tips of stems are responsible for primary growth to increase stem length and for the production of initials for the lateral appendages to the stem. The lateral meristem or cambium at the periphery of the stem between the xylem and phloem provides secondary growth to maintain vascular connections and increase mechanical support through increased diameter. Stems carry the leaves responsible for photosynthesis and the flowers responsible for reproduction. Although plant growth may appear simple from this description, when the entire scope of species is considered, growth provides an enormous variety of patterns in time and space that produce a bewildering array of architectures. Extensive studies of tree architecture have shown the existence of predictable types that reflect adaptation to environmental factors and competition.

The tree phenotype is the manifestation of the genetic information in the genotype acting through

developmental processes under the constraints of the environment to produce an adapted type. There is a huge genetic diversity of trees because they have become adapted to such a wide range of terrestrial environments from rain forests to arid deserts and from warm tropics to cold boreal regions. Because trees are long-lived sessile organisms and cannot move in space to escape environmental stresses that change through time, they have very high phenotypic plasticity that allows them to acclimatize to long- and short-term environmental changes. A site that provided plenty of light may become strongly shaded by competition. A site that was once adequately supplied with moisture may become too wet or too dry.

Almost all trees begin life near or at the soil surface. Because it is the primary site of energy exchange, plants at the bare soil surface experience the greatest extremes and the most rapid environmental changes. Small young trees experience a single soil and shoot environment. There are qualitative and quantitative changes in tree-environment interactions as the tree becomes larger.

Rapid early growth allows the tree to become established and escape the harsh conditions at the soil surface. The roots and shoots grow farther and farther away from the soil surface and the single plant begins to experience many different environments at the same time. The environmental extremes and rapid changes are not experienced by the large tree in the same way as the small tree, because most of the tree is far above or below the soil surface and the large tree shades the environment near its base. Consequently, there are quantitative and qualitative changes in shoot growth as a tree ages and becomes larger.

Tree Architecture

The growth and proliferation of individual shoots lead to development of the tree and canopy architecture. Trees can be viewed as an assemblage of components or modules that are repeated and follow a hierarchy of types. Each component type more or less serves the same purpose, responds the same way to the environment, and is autonomous at its own level. The above-ground components of a tree in order of increasing size are: (1) apical meristem; (2) leaf; (3) shoot unit or metamere (node with its lateral appendage, usually a leaf, and structure in the axil of the lateral appendage and the proximal internode); (4) extension unit for a growth period; and (5) crown. The greatest diversity of tree architecture is found in the tropics where there are stable equable climates, a great diversity of climates, large areas of forest, and relatively little environmental change over thousands of years.

There are over 20 distinct architectural models among the tropical trees. Major functional characteristics determining models are the life span of the apical meristem and how the vegetative apical meristems differentiate. The apical meristem is of central importance, as it produces elongation growth and is the origin of the secondary or lateral meristem. In addition, many types of trees such as palms, palm-like trees, and tree ferns do not have a secondary meristem.

Apical meristems produce either a sexual or vegetative axis in an irreversible developmental process. The production of a sexual axis ends the life span of the apical meristem while the life span of the vegetative axis may continue indefinitely. Apical meristems show continuous or rhythmic growth. Continuous growth produces an axis with essentially equivalent internodes, leaves, and lateral branches. In contrast, rhythmic growth with alternating periods of growth and rest produces an axis with alternating long and short internodes and leaves and lateral branches that differ with internode length. Whether a species shows continuous or rhythmic growth has a substantial influence on its response to the environment and its form. Continuous growth is associated with unchanging environment and even when there are changes the tree responds by increasing or decreasing growth, but it does not produce resting buds. Examples include members of the family *Palmae*, the mangrove *Rhizophora mangle*, and species in the genera *Juniperus*, *Thuja*, and *Chamaecyparis*. Rhythmic growth is associated with a climate with substantially different seasons of growth and rest and the production of a resting bud. The genus *Pinus* is widespread and shows a lot of variation in growth pattern. Northern species such as *P. resinosa* often have a very rigid pattern of rhythmic growth that produces one shoot flush each year in the spring and is under strong genetic control. It shows little capacity to take advantage of prolonged favorable weather by producing more than one shoot in a year. In contrast, southern species such as *P. taeda* may show rhythmic production of one to several flushes depending on the weather.

Apical meristems produce either orthotropic or plagiotropic shoots. Orthotropic axes are erect, show radial symmetry, may have a spiral leaf arrangement, and are produced most often by the leading shoot. They are associated with vigorous young growth and tend to decrease in very old and severely stressed plants. Plagiotropic axes are horizontal, show dorsiventral symmetry, have a distichous leaf arrangement, and are produced most often by lateral shoots. They are associated with slow weak growth and tend to increase in very old trees and severely stressed

plants. These architectural characteristics are genetically controlled and constrain the ultimate tree form.

The majority of trees develop the form of a large central trunk with side branches while a relatively small number of trees, mainly those mentioned above with no secondary meristem, develop a single nonbranched axis. The excurrent or conical tree form is associated with conifers and cold climates with abundant snow and ice. The form obviously facilitates the shedding of ice and snow which could damage the crown if allowed to accumulate. The deliquescent tree form is associated with angiosperms and warm climates lacking snow and ice. This form may be an advantage where competition for light is extreme.

Shade Avoidance

The radiation environment is the most important factor determining shoot growth and canopy development. The leaves of trees are displayed to capture light energy, because plants need light energy for photosynthesis. Leaves and their stems have two options when subjected to shade: (1) adapt to functioning in the shade and (2) grow toward the unaltered light to increase photosynthesis. Shade leaves have greater photosynthetic efficiency in the low light because they develop greater surface area for light interception and they are thinner with less pubescence and less dense mesophyll cells for better light penetration and reduced reflection. In addition, shade leaves are oriented horizontally to intercept more light than the vertically oriented sun leaves. Shade plants increase the ratio of photosynthesizing machinery to respiring structural support material. Although plants can adapt to shade, those growing in the shade are usually not as vigorous as plants in full sun. Current research findings indicate that plants actually grow away from shade cast by competing plants. Competing plants change the quality of the light and this change is a signal that induces a growth increase response in internodes. The capacity to avoid plant shade was not important and probably did not evolve until plants became large enough to cast shade on their neighbors.

The shade signal is read by phytochrome in plants. Phytochrome has two interconvertible forms. One form (Pr) absorbs mainly red photons (maximum absorption 665 nm) and the other (Pfr) absorbs mainly far-red photons (maximum absorption 730 nm). The absorption by either form causes it to convert to the other form. Light in this range of the spectrum is little affected by clouds or rain but can be changed significantly by vegetation. Plants strongly

absorb red (R) and reflect far-red (FR) light; consequently, the R:FR ratio (ratio of photon flux at 660 nm and 730 nm) tends to be reduced by canopy shade. The R:FR ratio varies significantly with degree of shade (0.05–1.15 in canopy shade to 1.05–1.25 in full sun) and elicits large changes in the proportion of phytochrome in the Pfr form (Pfr/P ranges from 0.65 in full sun to 0.20 in deep shade). A wide variety of plant processes are known to respond to the R:FR ratio, including meristem activity, tissue differentiation (e.g., flowering versus vegetative), senescence, abscission, assimilate distribution, and chloroplast development (Table 1). Logarithmic stem elongation has been shown to have a strong inverse linear relation to the Pfr/P value. It has been shown that the strength of the elongation response to Pfr/P is genetically controlled and is very low in shade-tolerant plants and very high in shade-intolerant plants (Figure 1). It would be very interesting to learn whether the other plant responses to the R:FR ratio are similarly related to genetic variation in shade tolerance.

It appears that much of the plant response to shade is mediated by phytochrome. The very plastic response of trees to the radiation environment provides the capability to fine-tune tree architecture to achieve the greatest fitness. Even the germination of seeds is regulated by the light environment in some species. This capacity is under genetic control and plants adapt to a wide range of shade environments. The trees producing a canopy that creates the greatest change in the radiation environment (greatest change in R:FR ratio) generally show the smallest

Table 1 Shade avoidance responses

<i>Plant physiological process</i>	<i>Shade avoidance response</i>
Extension growth	Accelerated
Internode extension	Rapidly increased
Petiole extension	Rapidly increased
Leaf development	Retarded
Leaf area growth	Slightly reduced
Leaf thickness	Reduced
Apical dominance	Strengthened
Branching	Inhibited
Flowering	Accelerated
Rate of flowering	Greatly increased
Seed set	Severely reduced
Fruit development	Truncated
Senescence	Accelerated
Leaf senescence	Advanced
Leaf abscission	Advanced
Assimilate distribution	Marked change
Deposition in storage organ	Severe reduction

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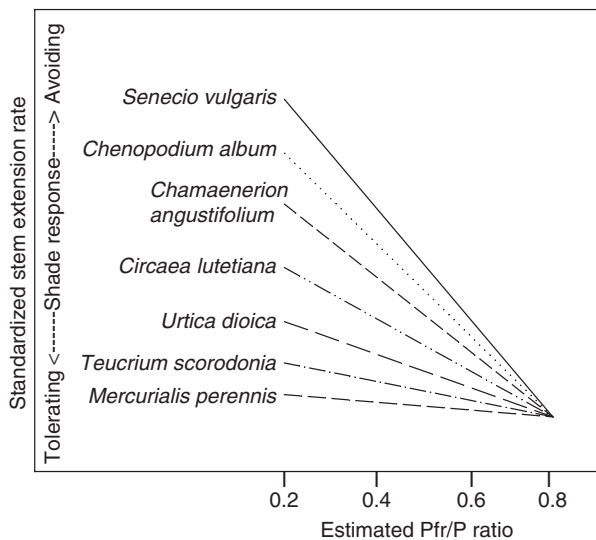


Figure 1 The elongation response to change in the Pfr/P ratio is much greater in plants that avoid shade than in those that tolerate shade. Reproduced with permission from Smith H (2000) Plant architecture and light signals. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth*, pp. 118–144. Oxford, UK: Blackwell.

response to changes in shade. In contrast, trees producing a canopy that creates the smallest change in the radiation environment generally show the greatest response to shade.

Recent advances in phytochrome research have provided significant knowledge of plant response to shade. It has been common knowledge for a long time that tree stem and leaf growth are affected by light and for the most part there was a sense that intensity of light was the main signal. It has become clear that light quality as it is altered by vegetation is a major signal in photomorphogenesis. Shoot growth and canopy development are guided by the radiation environment. Genes encoding for several phytochromes responsible for very different processes, including seed germination, flowering, elongation, and tuberization, have been found in *Arabidopsis*.

Current research activity seeks to determine how to manipulate the shade avoidance response mediated by phytochrome through genetic means. There are many mutants that have provided new information. A transgenic crop has been produced that appears to have reduced shade avoidance. It has reduced stem elongation which presumably allows greater energy investment in the part of the plant to be harvested, the fruit. In the case of trees, it may be more productive to search for ways to increase the shade avoidance response to produce more stemwood. The large number of phytochromes and their interactions will make the genetic engineering of shade avoidance a long and meticulous process. But

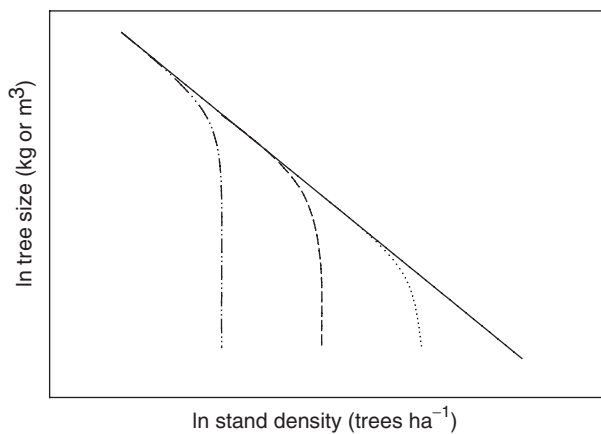


Figure 2 The maximum size–density relation for even-aged single species stands has a slope close to $-3/2$ when $\ln$ (tree size) is plotted against $\ln$ (density). Trees in low-density stands increase in size until they reach the maximum attainable for the given density. Further increase in size will only occur when density decreases through mortality.

it will certainly proceed faster than traditional breeding for the same trait.

The Maximum Size–Density Relation

The maximum size–density relation depends on the assumptions that trees of a certain species all have the same allometric growth and that trees on a fully occupied site will experience self-thinning. Trees growing in even-aged single-species stands will grow to a certain size that depends on density and they can not grow larger unless density is reduced by mortality (Figure 2). This appears to be consistent with the concept of a maximum biological productivity. Furthermore, the size–density relation is independent of site quality and stand age. The relationship between average plant size and stand density is bounded asymptotically by the $-3/2$ power rule:

$$s = ap^{-3/2}$$

where s = plant weight or volume, a = a constant, and ρ = stand density. This can also be written as:

$$\ln s = \ln a - 3/2 \ln \rho$$

The relation is common to all species studied to date and, although the slope varies somewhat, it is usually close to $-3/2$. The height of the line does vary considerably by species. At a stand density of 2470 trees ha^{-1} *Abies magnifica* and *Sequoia sempervirens* will attain a maximum average stand diameter of 25.4 cm; density must be reduced to 2050 for *A. concolor* and *Pinus ponderosa*, 1470 for *Pseudotsuga menziesii*, 1110 for *Pinus taeda* and 990 for *P. palustris* to achieve the same diameter. Apparently,

the efficiency with which each species occupies space varies considerably among species. The maximum size–density relation is a powerful tool for determining tree size and shape.

Hydraulic Architecture

The leaves displayed by branches in the canopy to capture light energy and fix carbon also transpire large amounts of water. Transpiration is a consequence of opening stomata to exchange CO₂. In addition, it serves at least three other purposes: (1) it moderates leaf temperature variation by evaporative cooling; (2) it transports mineral ions from the soil to leaves and ends of branches; and (3) it transports information about the environment from the roots to the leaves and branches. The necessity to transport large amounts of water from the soil to the leaves requires a special architecture of stems and leaves dictated by the properties of water, the physical environment, and the plant.

As soon as the stomata open, water evaporates from the inside of the leaf, causing a drop in water potential. Water moves into the roots from the soil and up the xylem from the roots to replace the transpired water. It moves along xylem conduits down a water potential gradient. The water is under tension and resists cavitation due to cohesive forces. The xylem provides a rigid conducting system of tubes where the secondary cell walls are the tubes and the lumens are the conducting voids filled with water. Gymnosperm xylem is composed mainly of very small closed tracheids, and in angiosperms the conducting elements are mainly vessels, thousands of times larger than tracheids, composed of stacked vessel elements with perforated end-walls. Water moves between conducting elements through pits along the sides and ends.

Flow through the xylem is proportional to its conductance and the driving force. Conductance depends on diameter of the lumens, conduit number, roughness of the interior walls, and restrictions of the pits. The driving force is a pressure difference in water potential set up by transpiration from the leaves. To maintain water flow the xylem must be constructed to have a conductance sufficient to transport water under a driving force that can be created and sustained in the conduits. The average driving force across the entire plant is essentially the water potential difference between the root tip and the leaf tip per unit of length (MPa m^{−1}). The driving force may not be of the same magnitude throughout the plant. If the water potential gradient is too small anywhere along the xylem the water will not move.

Water flow occurs when the water potential difference is adequate to create a flow. The greatest potential differences and greatest water flows occur when soil water is plentiful and the water potential is high. As soil water declines the water potential in the plant also declines to maintain water flow. Eventually, water potential in the plant will decline to a level that increases the risk for cavitation, a break in the water column filled with air or water vapor. Water flow in a conduit ends when a cavitation occurs and does not resume until it is refilled. If cavitations become numerous and transpiration continues, water potential must drop further to maintain flow in the remaining flow channels. The decreasing water potential may provoke runaway cavitation, a vicious cycle of increasing cavitation and decreasing water potential that can continue and eventually result in total failure of the xylem to conduct water. There is a lot of evidence that trees often approach low water potentials close to the threshold for catastrophic cavitation at midday on sunny days. Stomata close just in time to prevent disaster. In fact, some persons wonder if that is not the main purpose for stomata.

There is a potential for xylem characteristics that promote high conductivity and those that protect against cavitations to have conflicting effects. Conductivity can be increased by producing larger-diameter conducting elements with few flow constrictions between them; however, there is some evidence these qualities may increase the vulnerability to cavitation. Although it seems that high conductivity and low vulnerability to cavitation would be beneficial traits, the research results concerning a possible trade-off between these two traits are not conclusive. On the other hand, high vulnerability of certain plant parts could turn them into expendable parts that cavitate to protect the rest of the plant from excessively low water potentials.

Canopy architecture must meet the requirement that the xylem conduct sufficient water to meet transpiration demands. The capacity to absorb and transport water to the transpiring leaves depends on conductivity and vulnerability to cavitation of the xylem and rhizosphere. For a given root area/leaf area ratio this capacity is determined by hydraulic properties of the xylem and soil (Figure 3).

Stem length and leaf area will be determined by the hydraulic properties of the xylem in addition to root absorbing capacity and the capacity of the soil to provide water.

Recent research findings have pointed to the possibility that plants can fine-tune water use through signaling soil water availability and controlling xylem conductivity. Roots may be sending a

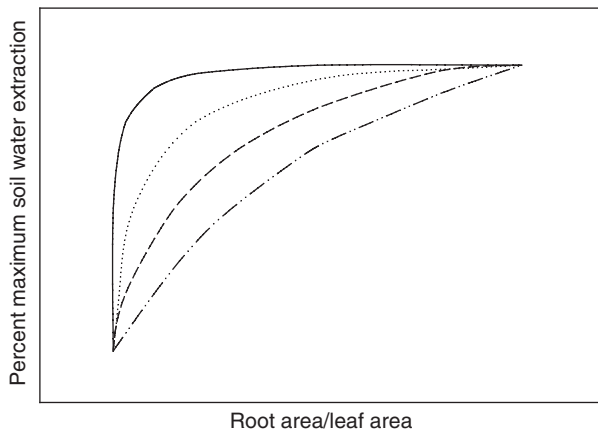


Figure 3 The maximum soil water extraction potential before cavitation causes failure to conduct somewhere in the soil–plant system occurs at the highest attainable root area/leaf area ratio. Decreasing soil water extraction potential occurs with declining root area/leaf area ratio due to loss of conductivity first in the xylem and later in the rhizosphere. Each curve represents the relation between extraction potential and root area/leaf area ratio for a different soil and xylem type. The upper curve could be a loam soil and drought-resistant species highly resistant to cavitation and the lower curves a sandy soil and drought-susceptible species not resistant to cavitation. Modified with permission from Hacke UG, Sperry JS, Ewers BE, *et al.* (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124: 494–505.

signal in the water flow to the leaves to regulate stomatal opening depending on soil water status. Research has indicated that the ion content in the xylem sap influences hydrogels and xylem conductivity. Hydrogels in the pit membranes between xylem elements may open and close pit pores to increase and decrease conductivity to different parts of the canopy. The question is whether the phloem or some other mechanism adjusts xylem conductivity depending on canopy demands. Both mechanisms of fine-tuning water use would mean the tree would be less subject to low water potentials and water stress. Tree architecture could be more closely tuned to environmental demands without heavy overbuilding to produce xylem with excess conductivity or excess protection against cavitation.

Conclusions

Tree growth is started by linear primary growth of the apical meristem which is followed by volume growth of the secondary lateral meristem. Although this constrains the plant form, trees have evolved a startling variety of architectural types. The shoot is elaborated and multiplied to produce a canopy which serves the purpose of capturing light energy and facilitating the reproduction of adapted types through flowering. Inherited architectural types have

been identified and described. They range from the steeply conical forms that shed snow and ice in cold climates to the deliquescent crowns that dominate the forest and capture a good share of the solar radiation in dense tropical forests. The greatest variety of inherited architectural types is found in tropical forests.

The main environmental factor shaping canopy development is the radiation environment. Phytochrome is the substance in plants that interprets the radiation environment and elicits a light response in almost all growth activities. Although plants appear to grow to the light, the elongation response to light is a mechanism to avoid shade. Increased understanding of the shade response improves the interpretation of canopy development and produces better management of stand density. Despite genetic engineering being tedious and complicated because of interactions among the different phytochromes and a potential for negative effects of genetic transformations, it appears to show a lot of promise for increasing harvest yield in trees. It is easy to imagine there may be economic value for an increased shade avoidance response that produces trees that grow faster in height, straighter, and with fewer branches. The size and shape of trees in dense stands follow a trajectory defined by the maximum size–density relation. An interesting question is whether phytochrome plays a role in the effects of competition described by this relation.

Trees must transport large amounts of water to transpiring leaves. Recent research suggests that the conducting system from the roots, through the xylem to the leaves is far more than just passive tubes responding to physical laws. Xylem morphology and anatomy balance conductivity with protection against cavitation. Cavitation in some plant parts may protect others against low water potential. Signaling within the plant and variable xylem conductivity may permit fine-tuning of water use by the tree. These mechanisms may allow tree architecture that is not excessively expensive and overbuilt to protect against water stress.

See also: **Ecology:** Forest Canopies. **Tree Physiology:** A Whole Tree Perspective; Canopy Processes; Xylem Physiology.

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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