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EFFECTS AND CONSEQUENCES OF STRESS ON ROOT PHYSIOLOGY[1]

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Abstract. *Because roots are out of sight, they are too often out of mind when the effects of stress on overall tree condition are considered. A description and discussion of tree root structure and function is followed by some basic information on root physiology. The effects of various stresses, that affect the roots directly and indirectly, are considered in relation to root structure and physiology, and the consequences of altered root physiology on tree health is discussed.*

Because roots are "out of sight" they too often are "out of mind" when the effects of stress on tree health are evaluated. Stress from disturbances such as soil compaction, soil filling, and physical severance from trenching or scarification during construction can directly affect the roots. But there are also stresses induced by many factors that indirectly disturb the roots, seriously affecting root growth and other physiological processes. A tree represents the dynamic interaction and balance between the root and the shoot, so a change in one system must result in some change in the other. A knowledge of the structure and function of roots, their growth patterns, and other physiological processes is necessary to understand this interaction. In this paper I discuss how these direct and indirect stress factors affect roots, and how, in turn, the entire tree is affected.

Root Structure and Function

Roots absorb water and mineral nutrients and anchor the tree into the soil. Historically, these were considered the primary functions and, by many, the only functions. But other functions that are as important as these have since been recognized. Roots are the sites where most food reserves are stored, where synthesis of some of the growth regulators needed by the shoot takes place, and where inorganic nitrogen is converted into organic amides and amino acid compounds—the building blocks of proteins used in all parts of the tree.

Woody roots. The large lateral roots that form at the root-stem base and the tap root provide the major anchorage and support for the tree, and they are also important for lateral and upward transport of water, minerals, and organic compounds to the stem. Roots can be quite large at the root-stem base but they rapidly taper to a smaller diameter a short distance from the base, becoming long and thin. From these basal roots second-order woody roots which are long and thin can develop. Long woody roots provide anchorage but also function as a lateral transport system for water and nutrients and as explorers of vast quantities of soil. Large amounts of food reserve materials (mostly starch) are also stored here.

Nonwoody roots. The fine root system, which is nonwoody develops from and among the woody root system. These roots develop as lateral branches near the growing root tip of the long woody roots. The nonwoody roots branch and rebranch as many as five times and fill the soil space among the woody roots. These roots form in or grow up into the upper layers of the soil just

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beneath the litter. They provide minimal anchorage but because of their numbers they store significant amounts of carbohydrate. Their major function is to absorb water and minerals, produce amino acids and growth regulators, and form mycorrhizae. Mycorrhizae are root fungal structures that increase root surface area for absorption and aid especially in mineral absorption in soils that have marginal mineral content. Nonwoody roots are short-lived relative to the woody roots. Since they form near the growing tips of the woody roots, the major mass of fine roots is continuously being formed farther from the root-stem base. As the age of the tree increases, the distance for transport from the major portion of the nonwoody roots increases, as does the vulnerability to disruption.

Adventitious woody roots. These woody roots form at the root-stem base, sometimes from the stem but mostly from the large basal roots. Adventitious roots do produce nonwoody branches that explore previously colonized soil volumes. They sometimes develop when the stem is injured or as the tree becomes older. They also form in response to root injury, and several may form at a root tip that has been killed or severed. We know little about adventitious roots, especially about the mechanism which triggers or limits their formation. The ability to form adventitious roots in response to injury or stress may determine whether a tree survives or dies.

Root Growth

Root elongation. Root tips may grow year round depending on the soil temperature and moisture conditions. In temperate latitudes, however, there usually is a period of rest in the winter followed by renewed activity in the spring and another burst of activity in the fall. The exact growth pattern depends on growing conditions and species. In general, root elongation usually begins before or coincident with shoot growth, and initially depends heavily on stored reserves. Continued growth, however, seems to depend on new shoot growth. The roots apparently need growth substances that are produced in the shoots and transported to the roots. Thus, root elongation is not only vulnerable to the effects of stress that occurred in the previous growing season and influenced the storage of food reserves but also to the effects of stress during the current season.

Existing root tips of long woody roots grow and penetrate new soil volumes. Nonwoody branches form behind the growing tip and these roots quickly branch and rebranch to occupy the new soil volume and absorb minerals and water. Root tips on the existing nonwoody roots also grow, exploring new soil and providing new root tips for colonization by mycorrhizal fungi. New root tips form to replace those dead or injured ones; these may branch and be colonized by mycorrhizal fungi.

Radial growth. Yearly increases in root diameter occur only in the woody roots. This radial growth is greatest near the base of the tree and decreases rapidly away from the tree. This rapid decrease in radial growth results in a zone-of-rapid-taper where the roots are quite large where they attach to the tree but are narrow a short distance away.

Radial growth begins much later in the roots than in the shoots. It occurs after food reserves have been stored in the existing woody root tissue. Growth may be related to carbohydrate storage and may not occur until a threshold level of food reserves has been stored in the root. In the stem, formation of new wood for water and nutrient transport is critical to the tree's survival; in the roots, elongation, branching, and maintenance—which ensures water and mineral absorption—are equally critical to tree survival. Since both maintenance of the roots during the dormant season and initial root growth depend on stored food, storage has priority over growth.

In the roots, the entire woody cylinder functions in the transport of water and nutrients, so a lack of or reduction in radial growth for one or several seasons may not be critical for survival. However, when part of the cylinder is lost through wounding and compartmentalization, subsequent radial growth becomes important.

How Stresses Affect Roots

Stress factors can affect roots directly by killing them, or by preventing or reducing elongation and branching, radial growth, and mycorrhizae formation. Stresses also indirectly affect roots through their adverse influence on photosynthesis and other physiological processes in the plant. Stresses can reduce the amount of carbohydrate available for use and storage in the roots, retard the production of regulators and other substances needed for growth and other functions in the roots, or interfere in the transport of these materials to the roots.

Drought can affect roots both directly and indirectly. Root tips can die from lack of water. Insufficient internal water pressure reduces root-tip elongation. Drying of soil prevents root penetration. Drought affects root growth indirectly by reducing the amount of food produced by the leaves and translocated to the roots for growth and storage. Thus, drought can reduce root growth during the current season and also at the beginning of the next season through its effect on food reserves.

Defoliation by insects, foliage diseases, or chemicals indirectly influences root growth by reducing the amount of food for use and storage, and by affecting growth regulators which are manufactured in the leaves and transported to the roots. Like drought, defoliation can affect root growth and physiology both during the current growing season and in the next.

Soil compaction can physically crush roots and kill them. It restricts root penetration through soil and therefore reduces elongation and branching. Compaction also suffocates roots by reducing or eliminating the available oxygen for normal respiration. Toxic compounds develop internally and roots die.

Waterlogging suffocates roots by eliminating oxygen needed for normal respiration. Toxic materials develop internally and externally in the soil and kill the roots, especially the tips.

Construction activities can sever roots from the tree. The extent of the separation of the nonwoody absorbing system from the transport system depends on the size of the tree and the distance from the base where the separation occurred. Even if adventitious roots form on the severed roots, the amount of transporting woody tissue is reduced significantly because all of the woody tissue present at the time the root is wounded becomes nonfunctional, and there must be new radial growth to replace the lost tissue. Roots can be suffocated when fill is placed about them. The effect is similar to that from soil compaction and waterlogging. Construction also can result in growth barriers which physically prevent roots from penetrating new soil or which force them to grow into soils that have inadequate mineral nutrients, moisture, or air.

Root disease organisms can affect nonwoody roots directly and kill them. They also can girdle larger transport roots and prevent transport of nutrients to the nonwoody roots, which die.

Stem wounds and diseases have compounding effects. They reduce or prevent the transport of nutrients from the stem to the root system which then is adversely affected, and they also can restrict transport of water and nutrients to the leaves. This reduces the productivity of the leaves, which, in turn, reduces carbohydrates and other growth substances available for root growth, which reduces the amount of water and nutrients absorbed, and so on.

Competition from sod probably is one of the least appreciated "stresses" on trees. While not a stress per se, it can exacerbate the effects of certain stresses such as drought and nutrient deficiencies. The roots of grass intermingle with the trees' roots in the upper soil and compete directly with them for water and minerals. Sod also increases the amount of runoff, which reduces the amount of water entering the soil. Damage also can occur to tree roots from application of lime, herbicides, and insecticides associated with lawn care.

Consequences of Altered Root Growth and Physiology

The major consequence of an impaired root system is the reduction in water and mineral absorption and transport to the leaves. Leaves can be smaller than normal because of insufficient water absorption during leaf expansion. Also, they may be less productive because when the transpiration rate exceeds water absorption rate, the stomates (air and water exchange openings) of leaves close down to lessen water loss, which reduces the rate of photosynthesis. Reduced mineral absorption can result in chlorotic foliage and the overall food-producing efficiency of the plant can be lowered. Specific processes can be affected if absorption of a particular mineral element is limited.

Nitrogen metabolism is affected. Amino acids formed in the roots are transported to the leaves where they are converted to all of the amino compounds necessary for protein formation, especially in the rapidly growing tips of shoots and roots. When protein formation is curtailed because of reduced levels of amino acids, growth of the rapidly growing tissue slows down. This means less terminal and radial growth in both the shoot and root.

Growth regulators that are formed in the roots and transported to the shoots are also affected and can reduce terminal growth, especially internode elongation. This may result in inefficient leaf distribution with respect to capturing sunlight and result in a less productive leaf system.

Since mycorrhizal fungi depend on tree roots for carbohydrates, stresses can affect mycorrhizae formation. Mycorrhizae may die from insufficient carbohydrates in the root tips: water and mineral absorption is reduced. Where trees are growing in rich deep soil, the loss of mycorrhizae may not be of major consequence. But where trees are growing in shallow soils that are marginal nutritionally and lack water-holding capacity, the loss of mycorrhizae could spell their doom. And nonmycorrhizae roots are less resistant to disease organisms.

An unhealthy crown of a tree may simply reflect an unhealthy root system. The stress that caused this condition may not be obvious and may even have happened in the previous growing season. Understanding how stresses affect the roots can help you diagnose the problem, the cause, and hopefully, the cure.

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ABSTRACT

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What is the best propagating medium to use? Cuttings are being rooted by someone in almost every conceivable combination of available materials. A medium must have certain qualities. It should be clean and relatively sterile. It should be relatively easy to handle preferably, lightweight. It should be available at a reasonable cost. It should be firm enough so it can provide a suitable structure into which cuttings can be set and held upright and in place. It should be able to absorb and retain a fair quantity of water to keep the cuttings in good condition, yet not become water-logged and soggy. Any surplus water that may be applied should drain through easily and rapidly, leaving the mass at a uniform and even level of moisture. Above all, this moist medium should contain small but well-defined pockets of air between the particles so that the bases of the cuttings can have an adequate supply of oxygen.