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THE ROLE OF WATER STRESS IN TREE GROWTH¹

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Abstract. Urban trees often are subjected to soil and atmospheric stresses that reduce growth and vigor, increase susceptibility to insects and diseases, and cause premature death. Environmental stresses occasionally injure trees directly, as by freezing, but most injury is caused indirectly by inhibiting essential physiological processes. Water stress is particularly important because it is so frequent and affects so many processes. The injury caused by water stress can be reduced through prevention of stress by irrigation, postponement by development of extensive root systems and control of transpiration, and by selection of trees with a high tolerance of dehydration. More attention should be given to selection of species and individuals with high tolerance of the more destructive stresses such as water deficit, air pollution, and unfavorable soil conditions. This will require the cooperative efforts of arborists, physiologists, and tree breeders.

Trees in urban environments often are subjected to stresses that are more severe than those encountered by trees growing in the field or forest. This is because in nature trees tend to grow in habitats to which they are well adapted, but in urban environments they are planted for their aesthetic contribution, often with little or no consideration of the suitability of the environment. As a result of the arbitrary selection of planting sites, trees are subjected to drought, flooding, and other unfavorable soil conditions, air pollution, above normal temperatures and photoperiods, and mechanical injury more often than in their natural habitats. As a result urban trees often are unthrifty and have a shorter life expectancy than the same kinds of trees growing in a forest. Obviously, we need trees that are more tolerant of stresses, but to find them we need to identify the stresses and to understand how they affect trees.

How Environmental Stresses Affect Tree Growth

In order to understand why environmental stresses such as drought, flooded soil, and air pollution inhibit tree growth it is necessary to have a general understanding of how trees grow and react to their environment. As I have often told arborists and foresters, in order to grow trees efficiently one must understand how trees grow (Kramer, 1950; Kramer and Kozlowski, 1979, Chap. 1). Thus, although water stress is the major theme of this paper I will first attempt to develop a general philosophy concerning the effects of stress on plants.

It may be helpful to regard trees and other green plants as analogous to complex biochemical factories. However, unlike man-made factories, trees literally build themselves. After a seedling develops its first leaves it builds itself from nitrogen, minerals, and the sugar produced by photosynthesis from carbon dioxide and water. The source of energy is sunlight, the machinery for photosynthesis is the chloroplasts in the green leaves, and the raw materials are carbon dioxide, water, and minerals. The successful operation of the biochemical machinery depends on a favorable environment and on integration of the synthetic processes by growth regulators.

As shown in Figure 1, the quantity and quality of growth made by a tree depends on the interaction of two groups of factors, its hereditary potentialities or genotype and the environment in which it grows. Hereditary potentialities determine the differences among species and varieties, and even differences among individual trees of the same species or variety growing in a uniform environment. The differences between a red oak

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and a white oak or between a pine and a magnolia obviously are caused by differences in their heredity. Less obvious but equally important are the differences in rate of growth, winter hardiness, stress tolerance, and disease resistance seen among individuals of the same species growing side by side. Such individual differences among trees provide possibilities for selecting and breeding trees with increased tolerance of various environmental stresses, and modern biotechnology is providing the means of accomplishing this more rapidly than in the past.

The environment determines the extent to which the hereditary potentialities are attained, as shown by the differences in size of trees of the

same species growing in moist, fertile soil and in dry, infertile soil. The extreme effect of environmental and cultural conditions is seen in bonsai which have been dwarfed by cultural treatments and have a height that is only a small fraction of that of the same kinds of trees growing in nature.

Heredity and environment operate cooperatively through the physiological and biochemical processes of the tree to determine the quantity and quality of growth made, as shown in Figure 1. Thus the physiological processes of a tree are the machinery through which cultural treatments such as fertilization and irrigation, and environmental stresses such as drought, soil flooding, air pollu-

INTERACTION OF HEREDITY AND ENVIRONMENT

Hereditary Potentialities
Differences among species
and individuals in root
systems, tree form, leaf
morphology, etc.

Environmental Factors
Soil conditions
Atmospheric conditions
Biotic factors - cultural
treatments, competition,
and pests



PHYSIOLOGICAL PROCESSES

Photosynthesis
Transpiration
Water status
etc.



QUANTITY AND QUALITY
OF GROWTH

Fig. 1. Diagram showing how heredity and environment interact through the physiological processes of a tree to determine the quantity and quality of growth.

tion, insect pests, and diseases affect growth. If a tree breeding program or a cultural treatment increases growth it is by improving the functioning of the physiological machinery. If environmental stresses and pests reduce growth it is because they inhibit essential physiological processes.

This concept of the role of physiological processes in the response of trees to environmental stresses can be illustrated by a few examples:

Irrigation prevents water deficits and injury to physiological processes.

Fertilization supplies the nutrient elements required as building materials, as catalytic agents associated with enzymes, as buffers, in maintenance of osmotic pressure, and for other physiological functions.

Soil flooding inhibits root respiration, reducing growth and killing roots, reducing the absorption of water and minerals, and disturbing other physiological processes. It also often is accompanied by accumulation of substances toxic to roots.

Low temperatures cause freezing injury to shoots and cold soil reduces root growth and inhibits water and mineral absorption.

Abnormally high temperatures, characteristic of many urban environments, especially at night, cause excessive use of carbohydrates in respiration.

Abnormally long photoperiods, caused by street lights, hinder development of dormancy.

Air pollution damages cell membranes and inhibits enzyme activity which affects many physiological processes, including photosynthesis.

Defoliating insects reduce the leaf area available for photosynthesis.

Pathogens often reduce the leaf area and sometimes block the conducting tissue, and some produce toxins that affect other physiological processes.

Specific environmental stresses often have multiple effects with complex interactions. For example, increasing the CO₂ concentration of the at-

mosphere usually causes partial closure of stomata. This decreases the rate of transpiration per unit of leaf area, which is injurious, but partial closure of stomata also decreases injury from SO₂, which is beneficial. Water stress has even more complex effects, as we will see later.

Water Stress

Water stress is the most common limitation on tree growth in forests. Zahner (1969) reported that 80% of the year to year variation in diameter growth of forest trees in humid areas can be related to differences in rainfall and the related variations in water stress. In fact, the relationship between precipitation and tree growth is so close that the width of rings of old trees is used to predict past rainfall conditions (Fritts, 1976). Water stress also is common in urban trees; although Berrang et al. (1985) reported that it was less common than soil saturation in New York City. However, the tops of trees growing in soil that is periodically saturated often are injured by water deficits because injury to their roots reduces water absorption.

The relationship between rainfall and growth exists because directly or indirectly water deficit affects almost every process in plants. This is explained by the following list of some general functions of water:

1. It is a *constituent* forming over 50% of the fresh weight of trees.
2. It is *the solvent* in which gases and minerals enter and leave cells.
3. It is a *reactant* in photosynthesis and other important processes.
4. It is essential for *maintenance of the turgor* necessary for cell enlargement, opening of stomata, and other plant processes.

The effects of water stress on tree growth may be classified as directly resulting from loss of turgor and indirectly resulting from disturbance of physiological processes that may or may not be related to loss of turgor. The most important direct effect is decrease in cell enlargement, which results in decreased leaf area, decreased width of annual rings, and decreased size of trees. The first visible effect of water stress is wilting, followed by leaf scorching and defoliation. Among the important indirect effects are those resulting from

closure of stomata, inhibition of the photosynthetic machinery, disturbance of enzyme-mediated steps in metabolic processes such as carbohydrate and nitrogen metabolism, and the functioning of growth regulators. Some interactions are shown in Fig. 2.

In summary, water deficits injure trees by inhibiting a variety of processes involved in growth, resulting in small unthrifty trees that are more susceptible to injury or death from other stresses than vigorously growing trees. More detailed discussions of the effects of water stress can be found in the series of books on water deficits and plant growth edited by Kozlowski (1968-1983) and in Kramer (1983).

How to Decrease Injury From Water Stress

Successful growth of trees depends on maintaining a favorable water balance. This is analogous to maintenance of a favorable bank balance, which depends on the ratio of deposits

to withdrawals.

Deposits = *Water absorption*

Withdrawals = *Water loss by transpiration*

Balance = *Tree water status*

The tree water status ranges from fully turgid through temporary wilting to permanent wilting and death from dehydration, and the arborist's problem is to prevent the development of injurious water deficits. This is difficult because urban trees are planted in situations unfavorable for absorption, but favorable for water loss. For example, a shade tree 35 feet high might bear 25,000 leaves with a surface area on one side of 2000 square feet. In midsummer such a tree might lose 35 gallons of water per day or 1000 gallons in a month. This is equivalent to the readily available water in a cylinder of sandy loam soil 25 feet in diameter and 2.5 to 3.0 feet deep. The tops of trees with root systems restricted to small volumes of soil or injured by waterlogged soil therefore often suffer from water stress. Measurement of water stress is discussed in another paper of this group.

The soil is a reservoir for water and minerals, but its role as a medium for root growth also is very important. For example, Coile (1948) found that the growth of pines in the southeastern United States was more closely related to those physical properties of the soil that determine its suitability for root growth than to the chemical properties associated with soil fertility. Soil factors affecting root growth will be discussed in more detail in later papers. However, arborists should be warned that over irrigation may be more injurious than under irrigation, and use of water high in salt often aggravates the injury.

There are three approaches to minimizing injury from plant water stress, *prevention*, *postponement*, and *increased tolerance*. Most tree water stress results from drought, that is from lack of sufficient rainfall to replace the water removed from soil by evaporation and transpiration. The only way to prevent water stress caused by drought is irrigation. The frequency of irrigation necessary to prevent severe water deficits depends on such variables as the depth and extent of the root system, the water holding capacity of the soil, the exposure of the top, the rate of evapotranspiration, and the desiccation tolerance of the species.

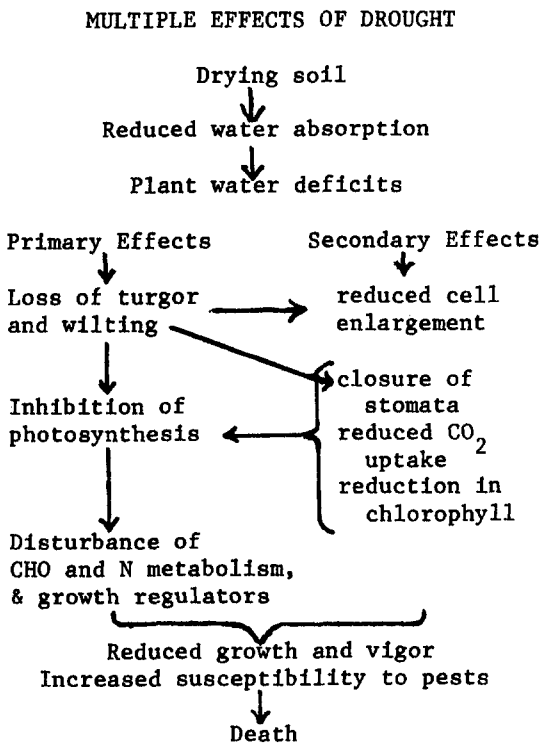


Fig. 2. Diagram showing some of the ways in which water stress affects tree growth.

This emphasizes the need for use of good judgement in timing the irrigation of trees. Increasing water shortages and various legal restrictions on the use of water are creating increasing difficulties for unlimited use of water on ornamental plants. This is likely to focus more attention on the use of trees and shrubs that use less water or are more tolerant of dehydration.

Postponement of plant water stress can be accomplished by improving the absorbing system and by decreasing the rate of transpiration. One of the best insurances against tree water stress is deep, much branched root systems, and a high root-shoot ratio that can supply water as rapidly as it is lost from the top. Much of the injury to recently planted trees occurs because of slow regeneration of root systems, especially on large trees (Watson, 1985). However, urban trees often are planted where soil conditions limit root development. This suggests that research is needed to develop trees with root systems that are more tolerant of unfavorable conditions such as very compact and poorly aerated soils. There are large differences in depth of rooting among species and the shallow rooted dogwood wilts long before the deeper rooted oaks and pines with which it grows. There probably also are large differences among individual trees within a species, providing opportunities for selection. There also are important differences among species in root tolerance of the poor soil aeration (Kozlowski, 1984, 1986; Yelenosky, 1964) that is a common problem with urban trees (Berrang et al., 1985).

The other possibility for postponement of plant dehydration is better control of water loss from both plants and soil. Control of plant water loss depends chiefly on stomatal behavior and thickness of cuticle. Stomata that close promptly when leaf water stress develops, combined with a relatively impermeable layer of cuticle covering the epidermis, significantly reduce water loss from trees and delay the development of water stress. There should be good opportunities to select both species and cultivars among species with better than average control of transpiration. The use of antitranspirants may be beneficial under some conditions, but problems accompany their use (Davies and Kozlowski, 1974). Shedding of leaves often occurs in water stressed trees and

this also decreases water loss. Use of mulch on the soil decreases the loss of water by evaporation from the soil surface and often improves infiltration of water supplied by rain or irrigation.

If drought is prolonged the benefits from adaptations that postpone dehydration eventually are exhausted and severe dehydration begins to develop. At this point survival depends on protoplasmic tolerance of dehydration, or the degree to which plant tissue can be dried before it is killed. There are significant differences in this respect between the trees and shrubs native to semiarid regions subject to annual droughts and those from humid regions where droughts are less frequent and less severe. For example, acacia, eucalypts, and olives are generally more tolerant of dehydration than beeches, birches, or elms. Also trees that grow on dry sites such as blackjack and post oak are more tolerant of dehydration than the red oaks that typically grow on moist soils in the same region (Bourdeau, 1954). Larcher (1975) provides some information on the drought tolerance of a wide variety of plants, including many trees. These differences provide opportunities for selecting species most likely to survive on dry sites. Also, it is likely that significant differences with respect to drought tolerance could be found among individual trees of a species if they were systematically screened.

Summary and Conclusions

Urban trees often are subjected to stresses more severe than those suffered by trees in the forest, resulting in lower vigor and shorter life.

Environmental stresses such as drought, flooding, and air pollution reduce growth and kill trees by inhibiting physiological processes that are essential for growth and survival.

Water stress is one of the most frequent and most injurious environmental stresses because it affects so many physiological processes. Reduction in the degree of injury caused by water stress can be brought about by prevention or postponement of stress, or by increased tolerance of desiccation.

Because of the large amount of genetic variability among trees it seems worthwhile to search for some of the following characteristics:

Roots more tolerant of deficient aera-

tion and high salt; and better able to penetrate compact soils, resulting in a larger root-shoot ratio.

Leaves with thicker cuticle and more responsive stomata, resulting in decreased water loss.

Trees with more protoplasmic tolerance of dehydration and air pollutants such as SO₂ and ozone.

Trees with more protoplasmic tolerance of cold and heat.

Investigations of this sort require the cooperative efforts of arborists who are familiar with problems at the environmental level, physiologists who can identify the physiological effects of environmental stresses, and tree breeders with experience in tree improvement programs.

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Abstract

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The demise of a once-stately tree will be blamed on a particularly cold winter or on a severe drought. Seldom will the owner suspect the true culprit: construction damage. Preventing damage to trees during construction isn't difficult. It just takes commitment. However, that commitment must come from the owner, the landscape architect, the contractor and everyone else on the design team. Pre-planning can take various forms. Many contractors, following suggestions by the designer, put up barriers around natural areas to be preserved. These define the "construction envelope" for all to see. In attempting to preserve at least some of the natural environment, remember that it can be damaged in many ways. The six most frequent are: grade changes, soil compaction, changes in drainage, changes in soil pH, root breakage or removal, and mechanical wounding.