

Water is the most limiting ecological resource for most tree and forest sites. As soil-water content declines, trees become more stressed and begin to react to resource availability changes. A point is reached when water is so inadequately available that tree tissues and processes are damaged. Lack of water eventually leads to catastrophic biological failures and death.

Growing periods with little water can lead to decreased rates of diameter and height growth, poor resistance to other stresses, disruption of food production and distribution, and changes to the timing and rate of physiological processes, like fruit production and dormancy. More than eighty percent of the variation in tree growth is because of water supply. Effects of drought can be recognized throughout a tree.

Drought

The term "drought" denotes a period without precipitation, during which the water content of the soil is reduced to such an extent that trees can no longer extract sufficient water for normal life processes. Water contents in a tree under drought conditions disrupt life processes. Trees have developed a series of prioritized strategies for reacting to drought conditions (listed in order from least damaging to most damaging response):

- 1) recognizing ("sensing") soil / root water availability problems.
- 2) chemically altering (osmotic) cell contents.
- 3) closing stomates for longer periods.
- 4) increasing absorbing root production.
- 5) using food storage reserves.
- 6) close-off or close-down root activities (suberize roots).
- 7) initiate foliage, branch and/or root senescence.
- 8) set-up abscission and compartment lines.
- 9) seal-off (allow to die) and shed tissues / organs unable to maintain health.

As drought continues and trees respond to decreasing water availability, various symptoms and damage occurs. The next section of this publication reviews damage control problems in a tree.

Drought Damage Components

Wilting

Wilting is a visible effect of drought. As leaves dry, turgor pressure in leaf cells decrease causing leaf petiole drooping and leaf blade wilting. The amount of water lost before visible leaf wilting

The University of Georgia

THE UNIVERSITY OF GEORGIA, THE UNITED STATES DEPARTMENT OF AGRICULTURE, AND COUNTIES OF THE STATE COOPERATING. THE COOPERATIVE EXTENSION SERVICE OFFERS EDUCATIONAL PROGRAMS, ASSISTANCE AND MATERIALS TO ALL PEOPLE WITHOUT REGARD TO RACE, COLOR, NATIONAL ORIGIN, AGE, SEX OR HANDICAP STATUS. A UNIT OF THE UNIVERSITY SYSTEM OF GEORGIA. AN EQUAL OPPORTUNITY/AFFIRMATIVE ACTION ORGANIZATION

ע ושוואם אופוטשט ויט איז arnell School of Forest Resources Extension publication FOR99-010 WEB site = www.forestry.uga.edu/efr varies by species. Temporary wilting is the visible drooping of leaves during the day followed by rehydration and recovery during the night. Internal water deficits are reduced by morning in time for an additional water deficit to be induced the following day.

During long periods of dry soil, temporary wilting grades into permanent wilting. Permanently wilted trees do not recover at night. Permanently wilted trees recover only when additional water is added to the soil. Prolonged permanent wilting kills trees.

The relation between water loss from leaves and visible wilting is complicated by large differences among species in the amount of supporting tissues leaves contain. Leaves of black cherry (<u>Prunus</u>), dogwood (<u>Cornus</u>), birch (<u>Betula</u>), and basswood (<u>Tilia</u>) wilt readily. Leaf thickness and size do not prevent wilting as rhododendrons are extremely sensitive to drought with leaves that curl, then yellow and turn brown. By comparison, the leaves of holly and pine are supported with abundant sclerenchyma tissue (i.e. tough, strong tissue) and do not droop readily even after they lose considerable water.

Stomatal Control

One of the earliest responses in leaves to mild water stress is stomate closure. Stomates are the small valve-like openings usually active on the underside of the leaf that allows gas exchange and water loss. Stomates often close during early stages of drought, long before leaves permanently wilt. Different species vary greatly in their stomate closing response. Gymnosperms usually undergo more leaf dehydration than angiosperms before they close their stomates.

Many trees normally close stomates temporarily in the middle of the day in response to rapid water loss. Midday stomatal closure is generally followed by reopening and increased transpiration in the late afternoon. Final daily closure occurs as light intensity decreases just before sundown. The extent of midday stomatal closure depends upon air humidity and soil moisture availability. As soil dries, the daily duration of stomatal opening is reduced. When the soil is very dry, the stomates may not open at all.

Stomatal closure will not prevent water loss. Trees lose significant amounts of water directly through the leaf surface after the stomates close. Trees also lose water through lenticels on twigs, branches, roots, and stems. Trees in a dormant condition without leaves also lose water. Water loss from tree surfaces depend upon tissue temperature – the higher the temperature, the more water loss.

One effect of severe drought is permanent damage that slows or prevents stomatal opening when the tree is rewatered. Additional water supplies after a sever drought period will allow leaves to recover from wilting, but stomate opening (necessary for food production) to pre-drought conditions, may not occur for a long period after rehydration.

Trees resist excessive rates of water loss through stomatal regulation. Stomates can be controlled by growth regulators transported from the roots during droughts. Drought effects on roots, stomates and other leaf cells can limit photosynthesis by decreasing carbon1dioxide uptake, increasing food use for maintenance, and by damaging enzynme systems.

Leaf Shedding

Premature senescence and shedding of leaves can be induced by drought. The loss of leaves during drought can involve either true abscission, or leaves may wither and die. In normal abscission, an organized leaf senescence process which includes the loss of chlorophyll, precedes leaf shedding. With severe drought, leaves may be shed while still full of valuable materials.

Yellow poplar (Liriodendron) is notorious for shedding many leaves during summer droughts,

sycamore (<u>Platanus</u>) sheds some leaves, and buckeye (<u>Aesculus</u>) may shed all of its leaves as drought continues. On the other hand, leaves of dogwood (<u>Cornus</u>) usually wilt and die rather than abscise. If water becomes available later in the growing season, some trees defoliated by drought may produce a second crop of leaves from previously dormant buds. Many times these leaves are stunted.

Sometimes drought1caused leaf shedding may not occur until after rehydration. Abscission can be initiated by water stress but cannot be completed without adequate water to shear-off connections betwen cell walls. The oldest leaves are usually shed first. Injury to foliage and defoliation are most apparent in portions of the crown that are in full sun. These leaves show drought associated signs of leaf rolling, folding, curling, and shedding. The actual physical process of knocking1off leaves is associated with animals, wind, or rain.

Effects on Photosynthesis

A major drought effect is the reduction of photosynthesis. This is caused by a decline in leaf expansion, reduction of photosynthetic machinery, premature leaf senescence, and associated reduction in food production. When trees under drought are watered, photosynthesis may or may not return to normal. Recovery will depend upon species, relative humidity, drought severity and duration. It takes more time to recover photosynthetic rates after watering than for recovery of transpiration.

Considerable time is required for leaf cells to rebuild full photosynthetic machinery. Failure of water-stressed trees to recover photosynthetic capacity after rewatering may indicate permanent damage, including injury to chloroplasts, damage to stomates, and death of root tips. Often drought can damage stomates and inhibit their capacity to open despite recovery of leaf turgor. When stomatal and non-stomatal limitations to photosynthesis are compared, the stomatal limitations can be quite small. This means that other processes besides carbon-dioxide uptake through open stomates are being damaged by drought.

Root damage also effects drought recovery. For example, photosynthesis of loblolly pine seedlings are reduced for a period of several weeks when root tips are injured by drought, even after water has been restored.

Growth Inhibition

Growth of vegetative and reproductive tissues are constrained by cell initiation shortages, cell enlargement problems, and inefficient food supplies. Cell enlargement depends upon hydraulic pressure for expansion and is especially sensitive to water stress. Cell division in generating new cells is also decreased by drought.

Shoot Growth – Internal water deficits in trees constrain growth of shoots by influencing development of new shoot units (nodes and internodes). A period of drought has a carry-over effect in many species from the year of bud formation to the year of expansion of that bud into a shoot. Drought also has a short-term effect by inhibiting expansion of shoots within any one year. The timing of leaf expansion is obviously later than that of shoot expansion. If shoot expansion finishes early, a summer drought may affect leaf expansion but not shoot expansion.

Shoots of some trees elongate in only a few weeks in late spring. This growth form is called fixed or determinant growth. Other species elongate shoots over a period of several months which is called multiple flushing or continuous growth. A late July drought may not affect current-year shoot elongation in species with fixed growth, like oaks. Oak shoots expand only during the early part of the growing season. A late July drought can inhibit expansion of shoots from multiple flushing species, like

sycamore, which elongate its shoots during much of the summer. Spring and Summer droughts damages both types of trees.

In the southern pines, late summer droughts will influence expansion of shoots in the upper crown to a greater extent than those in the lower crown. This is because the number of seasonal growth flushes varies with shoot location in the crown. Shoots in the upper crown normally exhibit more seasonal growth flushes than those in the lower crown. Buds of some lower branches may not open at all.

Cambial Growth – Drought will effect the width of the annual ring, the distribution of the annual ring along the trunk and branches, duration of cambial growth, proportion of xylem to phloem, and timing and duration of latewood production. Cambial growth slows or accelerates with rainfall.

Cambial growth is constrained by water supply of both the current and previous year. Last year's annual ring sets growth material supply limits on this year's growth. This year's drought will effect next year's cambial growth. Such a delayed effect is the result of drought impacts upon crown development, food production, and tree health. Drought will produce both rapid and delayed responses along the cambium.

Root Growth – Water in soil not penetrated by tree roots is largely unavailable. Trees with widely penetrating and branching root systems absorb water effectively. This type of root system acts to prevent or postpone drought injury. When first exposed to drought, the allocation of food to root growth may increase. This provides more root absorptive area per unit area of foliage and increases the volume of soil colonized. Extended drought leads to roots being suberized to prevent water loss to the soil.

A high root — shoot ratio reflects high water-absorbing capacity. Good water absorbing ability coupled with a low transpiration rate for the amount of food produced (high water-use efficiency), allow trees a better chance to survive drought conditions.

The annual root system (absorbing roots) take up a majority of the water in a tree. Annual roots are not the woody roots seen when a tree is dug. Large woody roots have bark. Any bark crack or damage is quickly sealed-off so little water flows through these areas. It is the young roots, the roots easily damaged by drought, that are the major absorbers of water and essential elements in a tree.

Biological Lag Effects

In fixed growth species, environmental conditions during the year of bud formation can control next year's shoot lengths to a greater degree than the environmental conditions during the year of shoot expansion. Shoot formation in fixed growth species is a two-year process involving bud development the first year and extension of parts within the bud during the second year.

Drought during the year of bud formation in fixed growth trees decreases the number of new leaves formed in the bud and the new stem segments (internodes) present. Drought then influence the number of leaves, leaf surface area, and twig extension the following year when those buds expand.

Summer droughts can greatly reduce shoot elongation in species that exhibit continuous growth or multiple flushing. Drought may not inhibit the first growth flush, but may decrease the number of stem units formed in the new bud that will expand during the second (or third, etc.) flush of growth. If drought continues, all growth flushes will be effected.

Drought Hardening

Trees that have previously been subjected to water stress suffer less injury from drought than trees not previously stressed. Trees watered daily have higher rates of stomatal and surface water loses than trees watered less frequently. Optimum, unstressed pre-conditioning can lead to more severe damage from drought conditions.

Pest Problems

Drought predisposes trees to pests because of lower food reserves, poorer response to pest attack, and poorer adjustment to pest damage. Unhealthy trees are more prone to pest problems. Drought creates unhealthy trees. Attacks on trees by boring insects that live in the inner bark and outer wood can be more severe in dry years than in years when little water stress develops. Little water and elevated temperatures can also damage pest populations.

Supplemental watering of trees can be timed to help trees recover water and minimize pest problems on surrounding plants. Watering from dusk to dawn does not increase the normal wet period on plant surfaces since dew usually forms around dusk. Watering during the normal wet period will not change pest/host dynamics. Watering that extends the wet period into the morning or begins the wet period earlier in the evening can initiate many pest problems.

Visible Symptoms

In deciduous trees, curling, bending, rolling, mottling, marginal browning (scorching,) chlorosis, shedding, and early autumn coloration of leaves are well-known responses to drought. In conifers, drought may cause yellowing and browning of needle tips.

As drought intensifies, its harmful effects may be expressed in dieback of twigs and branches in tree crowns. Leaves in the top-most branch ends generate the lowest water potentials, and decline and die. Drought effects on roots cause inhibition of elongation, branching, and cambial growth. Drought affects root / soil contact (root drys and contracts) and mechanically changes tree wind-firmness. Drought also minimizes stem growth.

Among the important adaptations for minimizing drought damage in tree crowns are: shedding of leaves; production of small or fewer leaves; rapid closure of stomates; thick leaf waxes; effective compartmentalization (sealing-off) of twigs and branches; and, greater development of food producing leaf cells.

The most important drought-minimizing adaptations of tree roots are: production of an extensive root system (high root-shoot ratio); high root regeneration potential; production of adventitious roots near the soil surface; and, effective suberization and compartmentalization of root areas.