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TREE GROWTH IN RESPONSE TO ENVIRONMENTAL STRESSES [1]

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Abstract. Shade trees are subjected to a wide variety of environmental stresses which decrease growth and cause injury and mortality. Although trees often are classed as either stressed or unstressed, *all* trees are periodically stressed by unfavorable environmental conditions above or below ground, and often both. Exposure of trees to some stresses also predispose them to the effects of other stresses. Healthy trees require adequate supplies and balances of carbohydrates, growth regulating hormones, water, and minerals. Environmental stresses, alone or in combination, reduce tree growth by setting in motion a series of complex physiological events leading to deficiencies of these essential substances. Explaining growth reduction of stressed trees by correlating growth with a single physiological process such as photosynthesis oversimplifies the causal events involved. Examples are given of some of the mechanisms by which drought, high and low temperature, mineral deficiency or excess, and *environmental pollutants reduce growth and injure shade* trees. Arborists can make important contributions in selecting appropriate species, adequately preparing planting sites, and imposing cultural practices that will minimize exposure of trees to stress factors.

When I was invited to speak to you I was asked to emphasize how and why various environmental stresses affect growth of shade trees. Perhaps we should begin by examining what we mean by stress. Although Webster defines stress as pressure or strain it is clear that many different views are held about the meaning of stress. Tattar (1983) defines stress as a detrimental force or influence, while Selye (1952) considers stress to be "a state of non-specific tension in living matter." Barrett (1981) views stress as "a perturbation (stressor) applied to a system which is foreign to that system, or natural to that system

but applied at an excessive level (e.g., nitrogen, phosphorus, or water)." This is consistent with the view of Perkins (1974) that stress usually involves a specific extreme agent.

The predominant concept of stress is based on performance, with the tree in a state of stress when some measure of its performance falls below par. This encompasses the idea that stress can be induced by environmental factors which are either above or below the optimum range (24). However, stress may also result from competition between closely grown trees or between trees and grass. Messenger (1976) emphasized that shallow lateral roots of trees compete with grass roots for available water and mineral nutrients. Bould and Jarrett (1962) reported the growth and yield of apple trees were reduced largely as a result of competition between trees and grass cover crops for nitrogen. Van der Boon et al. (1963) noted that nitrogen contents of leaves and yields of apple trees were higher in plots where the grass sward was broken and maintained in a cultivated condition as compared to trees growing on plots with an intact grass sward. Harris (1966) attributed a decrease in diameter and height growth of *Magnolia grandiflora* and *Zelkova serrata* trees to established turf. Addition of nitrogen fertilizers stimulated growth of trees which had turf growing up to their trunks. It is important for arborists to distinguish between stressing agents that are part of the daily normal environment and those imposed by humans or acute events of infrequent oc-

currence. Often several environmental stresses affect trees simultaneously.

Plant ecologists naturally focus on stress as it affects communities of plants. Meier (1972) defined stress as any force that pushes the functioning of a critical subsystem beyond its ability to restore a relatively stable state of equilibrium. Regardless of how stress is defined, and irrespective of the specific stress or stresses involved, the concept as usually employed by ecologists involved interference with normal ecosystem functioning. Stress effects are dramatically obvious after thresholds of tolerance occur and, beyond those thresholds, recovery of the ecosystem is difficult (3). Barrett (1981) views stress ecology as the subdiscipline of ecology that attempts to characterize and quantify the impact of foreign perturbation on the structure and function of ecosystems.

Much too often trees have been simply considered to be either stressed or unstressed. Some entomologists and plant pathologists do not consider trees to be under stress until after they have responded to attacks by insects or fungi. Others consider trees to be stressed only after unfavorable environmental conditions have induced visible symptoms such as leaf chlorosis, necrosis, leaf shedding, twig dieback, etc. However, such trees already were stressed long before such visible symptoms became apparent. Hence, I think it very important for arborists to appreciate at the outset that *all* trees are periodically stressed to various degrees by many abiotic and biotic factors. Furthermore, a tree that might be unstressed or only mildly stressed at a given time can very shortly thereafter be undergoing severe stress as, for example, after a few days of high temperature and low air humidity, or after a day or two of soil flooding.

To appreciate the persistent nature of environmental stress on trees one need only recognize that because of mutual shading of leaves the interiors of tree crowns are continuously undergiong shading stress. For example, light intensity inside the crown of a citrus tree may be less than 2% or that outside the crown (66). In apple trees the rate of photosynthesis was three to four times higher in the outer crown than in the inner crown as a result of differences in mutual shading of leaves (65). In addition to such persistent stresses additional stresses are periodically imposed on trees for varying periods. For example, water deficits in tree crowns are recurrent and inevitable, as will be discussed later.

Some stresses predispose trees to the effects of other stresses. For example, a variety of dieback and decline diseases of trees are favored by abiotic stresses such as drought, flooding, extreme heat, mineral deficiency, and air pollution (76, 78). These diseases usually become evident after environmental stresses render trees susceptible to organisms of secondary action (32). Most of the disease damage in nursery and landscape trees is associated with endemic pathogens that have been present for considerable time. If the climatic conditions are favorable and the pathogens are aggressive they will attack vigorous trees and cause familiar diseases such as leaf spots and blights, rusts, and vascular wilts. However, many other endemic pathogens are not aggressive and only attack trees of low vigor. Such pathogens include those causing stem cankers, diebacks, declines, and some root rots. Outbreak of these diseases usually means that the trees were predisposed some time ago by stress. Exposure of trees to severe or prolonged stress may increase their susceptibility to disease at any time. However, stress is especially likely to induce disease injury in trees shortly after they have been transplanted or after they reach maturity and begin to decline in vigor (79).

Several dieback-decline diseases are triggered by water deficits in trees. Those include *Cytospora* canker of poplars (78), *Botryospheria dothidea* disease of several species (15), ash dieback (29, 32), and *Endothia gyrosa* canker dieback of pin oak (1, 75). Such diseases are also favored by biotic agents and, for many species, insect defoliation is of paramount importance in initiating the sequential events leading to expression of decline disease (32).

Dieback of *Fraxinus americana* is initiated by drought. Reduced growth of stems and twigs is followed by death of terminal buds and branches and by production of small and chlorotic leaves. Soon after initial symptoms are evident cankers develop on the branches and main stem. Beech bark disease is initiated when the beech scale

(Cryptococcus fagisuga) feeds on the bark. The mortality that follows a buildup of beech scale results from invasion of the scale-altered bark by the canker fungus, Nectria coccinea var. faginata. Decline of sugar maple trees often is associated with effects of deicing salts applied to roads (31) or low soil fertility (61). Symptoms include terminal dieback, crown deterioration, and production of clumps of leaves on sprouts. The root systems of defoliated trees often are killed by the shoestring fungus, Armillaria mellea (31). Oak decline occurs when healthy trees, predisposed by defoliation, drought, or frost are attacked by Armillaria mellea and the two-lined chestnut borer, Agrilus bilineatus. The effects of defoliation are especially serious when it occurs just after the trees have leafed out in early summer (when reserve carbohydrates are at a minimum). If defoliation stops, even after it occurred for more than one season, the trees may recover providing environmental conditions are favorable and trees have not been heavily invaded in their weakened condition by "opportunistic" organisms (31). Defoliation is followed not only by lowered amounts of photosynthetic products but also by conversion of reserve starches to glucose and fructose, which are present in relatively low amounts in undefoliated trees. These sugars provide an energy source for growth of organisms of secondary action such as Armillaria mellea and Agrilus bilineatus. Defoliation also induces other biochemical changes which lower resistance of trees to attack (32).

Physiological Growth Requirements

Knowledge of how healthy trees grow is essential to understanding how trees are affected by various stress factors (43). To that end I recall the prophetic statement of Kramer (1956) that "we will learn how to grow trees by learning how trees grow." By this he meant that environmental factors and cultural practices do not affect tree growth directly but rather do so by the intermediation of physiological processes. Thus it cannot be emphasized too strongly that normal growth of trees requires favorable balances and rates of physiological processes. Conversely, growth inhibition and death of trees in response to stress, are preceded by abnormal physiological events.

Throughout its life a tree is supplied by leaves and roots over increasingly longer distances with compounds essential for growth, including carbohydrates, growth hormones, water, and mineral nutrients. Hence normal growth requires close correlation among the physiological processes involved in synthesis or absorption and delivery of these substances to growing tissues. The physiological processes important in growth include absorption of water and mineral nutrients, photosynthesis, hormone synthesis, respiration, nitrogen and fat metabolism, synthesis and activity of a variety of enzymes, transport of various compounds from sites where produced to sites where they are used in growth, and conversion of foods to new protoplasm. Growing trees also require a continuous supply of respiratory energy for synthesizing new protoplasm, maintaining the structure of membranes, and transporting ions and molecules across membranes (55).

Carbohydrates. Photosynthesis, a process by which the energy of light is used by green leaves to synthesize carbohydrates from carbon dioxide and water, is essential for tree growth. About three-fourths of the dry weight of trees consists of transformed sugars that were produced by photosynthesis. Hence, growth depends on a rate of photosynthesis sufficiently high to provide carbohydrates to growing tissues. Carbohydrates are the chief constituents of cell walls, the starting point for synthesis of fats and proteins, and the important substrate for respiration. In trees sugars are converted to starch whenever a high level of sugar accumulates, and starch is transformed to sugar when sugar reserves are low and at low temperature (52).

Trees use both currently produced carbohydrates as well as stored reserves in growth. Large amounts of starch are stored in longitudinal and ray parenchyma cells of the sapwood. Seasonal depletion and accumulation of carbohydrate reserves are correlated with rates of tree growth. In most deciduous trees carbohydrate reserves decrease sharply during spring growth to a minimum in early summer and then increase to an autumn peak followed by a slight decline during the winter. In conifers carbohydrates show less seasonal fluctuation than do broadleaved trees, and conifers tend to ac-

cumulate some carbohydrates during the winter (55).

Hormonal growth regulators. Trees synthesize several growth hormones which control division, expansion, and differentiation of cells. Hormonal growth regulators include such growth promoters as auxins, gibberellins, cytokinins, and ethylene as well as growth inhibitors, such as abscisic acid. Each class of hormones can affect several aspects of growth. The plant hormones generally have an influence on growth a long distance from where they are produced and they affect growth in very small quantities. They act on enzyme systems which function in production and control of proteins, cellulose, and lignins. They also play a key role in bud and seed dormancy, shoot growth, cambial growth, and reproductive growth, with growth processes usually regulated by the combined effects of two or more hormones (55).

In dormant seeds the presence of a preponderance of a growth inhibitor prevents many seeds from germinating. Breaking of seed dormancy occurs following a shift in the balance of growth promoters over inhibitors. Embryo dormancy of seeds can be broken by exposing them to low temperatures ("stratification") or even long days which change the balance of growth hormones in favor of growth promoters over inhibitors. Germination of seeds with embryo dormancy can also be stimulated with applied growth-promoting hormonal compounds. However, not all seed dormancy can be broken by such treatments because some seeds fail to germinate if the embryo is immature, the seedcoats are impermeable to water and/or oxygen, or the seedcoats mechanically resist expansion of the embryo.

There is considerable similarity between embryo dormancy of seeds and dormancy of buds. In nature bud dormancy is broken by sustained exposure to the low temperatures of winter, which changes the balance of growth hormones in favor of growth promoters over inhibitors. Once such physiological dormancy is broken the buds need exposure to a critically high temperature before shoots begin to expand. Growth-regulating hormones, especially gibberellins and auxins, play an important role in elongation of shoots.

Growth hormones also have a central role in several aspects of cambial growth including division of cambial cells to produce wood and bark tissues, increase in size of cambial derivatives (wood and bark cells) and thickening of cell walls. Normal cambial growth is influenced by interactions involving auxins and gibberellins produced in the leaves and transported downward, cytokinins produced in the roots, and growth inhibitors and other substances. Evidence for the crucial regulatory role of hormones produced in shoots comes from correlations between bud growth in the spring and the downward movement of a cambial growth wave, as well as reduction of cambial growth in defoliated trees, disbudded trees, or girdled trees. If the inner bark (phloem) is blocked by a knife cut or injury, cambial growth below the phloem blockage stops rapidly, largely as a result of a deficiency of growth hormones (22). Reproductive growth is also regulated by hormonal interactions that control initiation, expansion, and maturation of flowers, fruits and seeds (55).

Water. Water is essential for growth of trees for several reasons: 1) It is a primary constitutent of protoplasm. Water content is high in growing tissues and may comprise as much as 90% of their fresh weight; and it is low in non-growing tissues, 2) water serves as a solvent in which substances involved in growth (e.g. minerals) are transported through trees to growing tissues, 3) water serves as a reagent in photosynthesis and hydrolytic processes, and 4) water maintains hydration of tissues and keeps them sufficiently turgid so cell and tissue enlargement can occur (55).

Mineral nutrients. Almost every mineral element that is present in the soil can be absorbed by trees, but not all elements are necessary for growth. A mineral element is considered essential if plants cannot complete their life cycle without it and if it is part of a molecule of a necessary plant constituent. The essentiality of certain mineral nutrients for growth is shown by their roles as constitutents of plant tissues (e.g. calcium in cell walls, magnesium in chlorophyll), catalysts in chemical reactions, constituents of buffer systems, and regulators of membrane permeability. Nitrogen, phosphorus, potassium, sulfur, calcium, and magnesium are required in rather large amounts, at least 1000 ppm. Other

elements, including iron, manganese, zinc, copper, boron, and chlorine are required in very small quantities and are toxic if present in large amounts (55).

Mechanisms of Growth Inhibition by Stress

To understand how growth of trees is affected by environmental stresses we must account for growth in length at stem and root tips, diameter growth by activity of cambial cells, and growth of reproductive structures. Furthermore, we need to explain control of such sequential phases of growth as cell division, cell expansion, and differentiation and maturation of cells. For example, cambial growth involves division of cambial cells and enlargement of the cambial derivatives. After the new cells enlarge such processes as secondary wall formation and lignification either continue or are initiated. During differentiation most cambial derivatives are altered into specialized elements found in the wood and bark.

Because change in the rate of tree growth is an integrated response to physiological changes that are regulated by many fluctuating and interacting environmental factors, it is difficult to quantify the contribution of an individual stress factor to reduction in growth. Some of the change in the environment of a tree is continuous and some is cyclic and the relative importance of individual stress factors varies over time. Another problem is that it sometimes is difficult to distinguish between correlation and cause and effect relations of environmental changes and tree growth. Still another problem is that the impact of an environmental stress or its alleviation on growth may not be apparent for a very long time. For example release of a tree from competition with other trees leads to increased diameter growth. However, the increased diameter growth only follows an increase in crown size and in leaf area which in turn leads to increased production and downward movement in stems of carbohydrates and hormonal growth regulators. Completion of the sequence of necessary physiological events that lead to appreciable increase in cambial growth in the lower stem may require more than one year (44).

According to Levitt (1980) a stress may adversely affect plants in at least three ways: 1) stress may induce a direct *plastic* strain. Such direct stress injury is recognized by the speed of its appearance. An example is the killing of young tree leaves by freezing. 2) Stress may induce a reversible *elastic* strain which does not injure plants. Once the stress is removed the plant is restored to its original physiological state. For example, stomata close and the rate of photosynthesis decreases during a drought but they usually reopen and photosynthesis is restored when the soil is irrigated. If an elastic strain is maintained for a long enough time an irreversible plastic strain may result and injure the plant. 3) Stress may injure a plant by giving rise to a second stress. For example, low relative humidity of the air may produce a leaf water deficit which, in turn, may injure the plant. Levitt's classification is a useful introductory guide to mechanisms by which unfavorable environmental conditions and cultural practices might affect growth of trees.

Control of growth of both vegetative and reproductive tissues of a tree involves close interdependency between the crown and root system. Leaves supply carbohydrates and hormonal growth regulators necessary for growth of all tissues. Roots in turn supply water, mineral nutrients and certain hormonal growth regulators essential for growth of both root and crown tissues.

In addressing the question of how growth is reduced in trees that are not visibly injured by stress (e.g. how elastic strains operate) it is important to recognize that, over time, several complex physiological changes occur concurrently or sequentially and in the aggregate contribute to growth changes in stressed trees.

Imposition of an environmental stress on one part of a tree is transmitted to distant tissues and organs and eventually decreases growth of the entire tree (41, 55). For example, cold soil will decrease absorption of water and mineral nutrients. Decreased absorption of water will result in leaf dehydration (since absorption of water cannot keep up with transpirational loss) followed by closure of stomatal pores. As stomata close the diffusion of CO_2 into leaves is arrested, leading to lowered synthesis of carbohydrates and hormones, and a reduction in downward translocation of these essential substances to growing stem and root tissues. This sequence of

events further decreases root growth which decreases absorption of water even more, etc.

Much too often the reduction in growth following exposure of a tree to stress has been "explained" by reduced photosynthesis leading to a deficiency of carbohydrates. Actually, the mechanism of such growth reduction is considerably more complicated. For example, defoliation of trees by insects reduces the total amount of carbohydrates produced by photosynthesis and leads to a decrease in carbohydrate reserves (69). However, the decrease in cambial growth following defoliation is not traceable entirely to starvation. Accompanying the reduction of available carbohydrates by defoliation there is a decrese in synthesis and downward transport of hormonal growth regulators from the tree crown. Our experiments showed that girdling of tree stems rapidly and drastically decreased cambial growth below the girdles. The reduced growth did not appear to be caused directly by deficiency of carbohydrates by defoliation there is a decrease in in the form of starch was present below the stem girdles. Rather it appeared that cambial growth was arrested by regulatory influences on utilization of carbohydrates in growth (22, 23). Such observations emphasize the importance of a continuous supply of downwardly translocated hormonal growth regulators for cambial growth. It should also be remembered that in many trees the rate of cambial growth is rapidly reduced by late-summer droughts when tree stems have large carbohydrate reserves (39). Only about a third of the extractable carbohydrates of apple trees was depleted during growth (73). Furthermore cambial growth can be stimulated by long days even when the added light is of such low intensity that it does not appreciably influence the amount of available carbohydrates (52). Hence there is considerable evidence of the importance of growth hormones produced in tree crowns on control of cambial growth when carbohydrate supplies are adequate.

Responses of Trees to Various Environmental Stresses

The remainder of this discussion will characterize certain aspects of the mechanisms by which drought, temperature, mineral supply,

and environmental pollution decrease growth and injure trees.

Water deficits. Tree crowns expose a tremendous leaf area to the air and lose a great deal of water by transpiration. Hence, internal water deficits occur very commonly in trees and adversely affect their growth (47). Water deficits are controlled by relative rates of loss of water vapor from leaves (transpiration) and absorption of water through the roots. During the daytime more water is lost in transpiration than is replaced by absorption. Therefore, leaves tend to become dehydrated during the day, especially on hot sunny days. During the night, however, both transpiration and absorption are low but the rate of absorption is higher than the rate of transpiration so trees tend to refill with water. The rate of absorption of water by roots during the day lags behind transpiration even if the soil is well watered. Such an absorption lag is the result of resistance to water movement in various parts of its pathway from the soil through the tree and into the air. For example, some resistance to movement of water occurs in the soil and in roots, stems, and leaves.

Internal water deficits in trees may result from excessive transpiration or slow absorption of water from dry, cold, or poorly aerated soil or, more commonly, from a combination of both. Transpiration is largely controlled by atmospheric factors (primarily light, humidity, temperature, and wind) as well as by the structure of leaves and opening and closing of stomatal pores. Absorption of water is controlled by the rate of water loss by leaves, size and distribution of the root system, and various soil factors (primarily soil water availabilty, temperature, concentration of the soil solution, aeration, etc.). Temporary wilting of leaves in the afternoon sometimes occurs because of excessive transpiration. This is not serious if the soil is well-watered because the leaves usually rehydrate at night (when transpiration is low and absorption of water is somewhat higher). When soils being to dry out however, temporary wilting of leaves tends to become more permanent because leaves are less likely to recover turgidity at night (55).

As a drought develops, leaf cells progressively dehydrate and the reduced turgor of leaf cells in-

hibits cell expansion. At the same time the stomata close, thereby reducing the rate of photosynthesis by impeding absorption of CO_2 through stomatal pores. Changes in hormonal growth regulators occur also. If drought is prolonged the reduced transport of carbohydrates and hormonal growth regulators from leaves to roots will reduce root growth which will decrease absorption of water and mineral nutrients.

The most important initial cause of death of transplanted trees is drying out of leaves. Exposure of bare-rooted trees to drying for even short periods may rapidly cause severe water stresses in trees, resulting in reduced growth and mortality (50, 51). Even after transplanted trees are reset in the ground, excessive transpirational water loss occurs because roots often grow too slowly to absorb enough water to keep up with transpirational losses. Trees that survive transplanting may show growth reduction for several years.

Winter Dehydration Injury. Much winter injury of evergreens occurs because of drying out of leaves rather than by direct thermal effects. Because the soil is cold or frozen the rate of absorption of water by roots is much too slow to replace water losses by leaves in transpiration. Hence the leaves become dehydrated and often scorched (47). Usually the leaves are killed and eventually shed while the buds survive. Winter dehydration of leaves is one of the most important factors that limit the range of conifers (47, 48, 77, 85).

Effects of Water Deficits on Physiological Processes and Growth

Stomatal aperture. Stomata are very sensitive to water stress and tend to close during relatively early stages of leaf dehydration, often long before visible wilting of leaves is evident. When water-stressed trees are irrigated the closed stomata sometimes open slowly and some may not open at all even after leaf turgor is restored (18).

Photosynthesis. Much interest has been shown in effects of water supply on photosynthesis of trees. The rate of photosynthesis begins to decrease when leaves are only slightly dehydrated and continues to decline during a prolonged drought until the rate becomes negligible. Photosynthesis is reduced early during a drought because stomatal closure reduces CO_2 diffusion into leaves. As the leaves become more severely dehydrated the photosynthetic process is inhibited through adverse effects on chloroplast activity. In the long term, total photosynthesis is also reduced because of inhibition of leaf formation and expansion and also because of shedding of leaves. Drought induces leaf abscission in some trees following changes in balances of growth hormones and synthesis of enzymes that hydrolyze the middle lamella between cells of the abscission layer. In other trees the leaves simply dehydrate and wither as a drought intensifies (44).

Growth. Shoot growth is reduced by the effects of water deficits on bud formation, internode elongation, and on initiation and expansion of leaves (12, 87). Most of the reduced leaf area as a result of drought has been linked to slowing of cell expansion. Enlargement of leaf cells depends on cell turgor and is very sensitive to dehydration. Water deficits that are too mild to close stomata and reduce the rate of photosynthesis often inhibit cell expansion (33). In many species cell expansion is so sensitive to water deficits that leaves expand only during the night when water loss from leaves by transpiration is negligible (10).

Division of cambial cells to produce wood and bark cells, as well as enlargement and differentiation of cambial derivatives, are regulated by water supply. The number of wood cells produced, seasonal duration of production of wood cells, the time of initiation of latewood (summerwood), and duration of latewood production are regulated by the internal water balance of trees. Trees often respond to drought by slowing production of wood cells, but cambial activity readily resumes after a rain (88). Water deficits not only decrease the number of wood cells formed but also inhibit cell expansion.

Water deficits affect cambial growth both directly and indirectly. Water deficits may directly inhibit cambial activity when cell turgor is low enough to prevent hormonal growth regulators from acting. During a drought, growth may be reduced indirectly through decreased synthesis and downward transport in the stem of hormonal growth regulators (47, 88).

The slowing of root growth during a dry period and growth acceleration after a rain are well

known. Soil water deficits reduce the rate of root elongation, root branching, and root thickening. In addition roots growing in dry soil often become suberized to their tips, resulting in reduced capacity for absorption of water. On dry sites the growth of roots often is limited to the depth to which the soil is wetted.

Production of fruits and seeds can be arrested by drought at any stage of reproductive growth, including flower bud initiation, opening of flowers, pollination, fertilization, embryo growth, or fruit and seed enlargement. The importance of water to reproductive growth has been shown by correlation of rainfall with flowering and fruiting and by irrigation studies. The effects of irrigation vary with the amount and distribution of rainfall, extent of internal water deficit, stage of reproductive growth, soil type, tree species, weather conditions, and amount and timing of irrigation (47, 55).

Drought Tolerance

Some trees survive drought better than others do. Drought tolerance of trees varies primarily because of differences in adaptations for drought avoidance and, less importantly, because of variations in capacity to withstand protoplasmic dehydration. Adaptations for drought avoidance may be present in leaves, roots, or stems. The most important leaf adaptations include small or few leaves; small, few, or sunken stomata; rapid stomatal closure during drought; and heavy wax deposition on leaf surfaces. All of these prevent excessive water loss. Deep rooting and extensive root branching to produce a high root-shoot ratio contribute to drought tolerance by allowing for high rates of absorption of water to replace the water that is lost by transpiration (42).

Temperature Stress

Growth of most trees is optimal in the range of 20-35°C, depending on species. At higher or lower temperatures the rate of growth declines, with the effect mediated by altered carbohydrate, hormone, water, and mineral relations. Trees often are injured at very high or very low temperatures (48).

Freezing injury. Spring and autumn frosts may injure trees, with the extent of injury varying with the degree of cold hardiness in affected tissues at the time of the freeze and with the duration of the freezing temperature. Susceptibility to stem canker fungi increases greatly at levels of freezing that do not damage tissues in the absence of pathogens (79). Much injury is caused by low temperatures in the spring following a period of mild weather during which trees begin to grow. A common response to freezing is killing of shoots, especially those of late-season growth flushes that did not have time to harden. Freezing during the growing season may also injure the cambium to produce "frost rings" which sometimes resemble annual rings. However, frost rings can be identified microscopically by abnormally developed wood cells and displaced wood rays. Frost rings are more common in small twigs than in large branches or the main stem. They also occur more frequently in trees with thin bark than in those with thick bark. Alternate freezing and thawing sometimes induce frost cracks or sunscald on tree stems. Sunscald lesions not only become sites for entry of fungi and insects but also injure the inner bark and block transport of carbohydrates and growth hormones. Freezing temperatures also kill roots, especially the small, physiologically important ones. Another response is frost heaving when roots became frozen in a block of ice and more ice forms below. Frost-heaved seedlings often die as their exposed roots become dehydrated (55.)

Cold hardiness. Many trees can survive low winter temperatures without injury but the same trees are killed if they are exposed to temperatures only a few degrees below 0°C in the middle of the summer. Trees such as trembling aspen and white birch may resist freezing in midwinter to −80°C, but southern pines and magnolias develop winter hardiness down to only −15°C. There is also considerable difference in cold hardiness of different organs and tissues on the same tree. Roots normally are very sensitive to cold in the winter. Vegetative buds that begin to open in the spring are especially susceptible to freezing. Severe winters may wipe out a fruit or seed crop because flower buds and conelets are very susceptible to frost injury.

Cold hardiness of temperate-zone trees develops each year in three sequential stages. The first stage, which begins before the first frost,

involves metabolic changes that condition the tree to respond to low temperatures during the second stage of acclimation. Whereas the first stage is induced by shortening days, the second is triggered by the first frost. The third stage is induced by very low temperatures (85).

Several internal changes are involved in development of frost hardiness. In most species sugars accumulate in the autumn as trees become frost hardy and they decrease in the spring as cold hardiness is lost. The sugars may increase cold hardiness by (1) depressing the freezing point, (2) accumulating in cell vacuoles and decreasing the amount of ice formed and, hence, decreasing cell dehydration and (3) inducing various "protective changes" which are not too-well understood (59). Another important change during development of cold hardiness is an increase in water soluble proteins. Changes in these proteins may involve an increase in water-binding proteins that may decrease free water in cells, rendering formation of ice in cells less likely (55).

Most cold-hardy trees survive very low temperatures in a frozen condition but a few avoid freezing by undergoing deep undercooling. Freezing injury may result from direct freezing of cell contents, or indirectly when cells are dehydrated as a result of extracellular freezing. Leaves usually are killed when ice crystals form within cells, but they may survive if the ice crystals form in intercellular spaces. When plants that have been frost-hardened are cooled slowly, ice forms first in intercellular spaces and water moves out of cells to the ice nuclei. Hence the concentration of the cell sap is increased and its freezing point is lowered. When cold-hardened leaves are cooled very rapidly they may be injured, partly because water is not extracted from cells fast enough to prevent formation of ice crystals within cells. According to Levitt (1980), most freezing injury in plants results from dehydration of cells.

Growth. Many investigators have noted variations in vegetative and reproductive growth as the temperature was altered. For example, height growth of trees decreases with increase in altitude, reflecting an inhibitory effect on the rate of growth and on the seasonal duration of growth (48).

Temperature influences wood production through its effects on seasonal initiation of cambial growth and on its rate and duration (39). The seasonal duration of cambial growth varies greatly with latitude. Near Hudson Bay, Canada, cambial growth of Norway spruce lasted for two months; (62); at Chalk River, Ontario for three months (25). In the southern United States cambial growth of conifers may continue for six to eight months, and in the tropics may occur throughout the year.

Low soil temperature inhibits both root initiation and growth of existing roots. Roots begin to grow shortly after the soil becomes frost-free in the spring. Root growth of trees may occur during each month of the year in the southern states.

Temperature regulates yield of seeds and fruits by influencing floral initiation, bud dormancy, opening of flowers, fruit set, and growth of fruits. The southward extension of northern trees often is limited because in some years winter temperatures are not low enough to induce breaking of bud dormancy (55).

Low soil temperatures decrease absorption of water by increasing the resistance to water movement across living root cells. A decreased rate of root growth and metabolism also result in lowered absorption of water. Low soil temperature reduces both passive and active uptake of minerals (55).

High temperature. High temperatures often reduce growth and injure trees. Direct injury, which usually is caused by temperatures of 45°C or higher, involves a very rapid tree response. Indirect injury, caused by temperatures in the range of 15 to 40°C may not be evident for days after exposure to the high temperature.

Examples of direct heat injury include stem lesions such as "sunscald" or "bark scorch" caused by drying of the inner bark and cambium, stem lesions of seedlings at the soil line, and lesions on some fleshy fruits. Sunscalded tissues often are colonized by stem canker organisms. Direct injury may be caused by protein denaturation, injury to cell menbranes, and lipid liquefaction (59).

Several mechanisms may be involved in indirect heat injury. the rate of photosynthesis increases with rising temperature but, at a critically high temperature, the rate levels off while the rate of

respiration continues to increase. This leads to depletion of carbohydrate reserves. Sometimes indirect heat injury is associated with formation of toxic compounds and breakdown of proteins (59). Leaf scorching and shedding associated with hot, dry winds often are traceable to high rates of transpiration and dehydration of leaves (42, 47).

Mineral Stress

Either a deficiency or excess of mineral nutrients may adversely affect tree growth. The most obvious early effect of mineral deficiency is yellowing of leaves (chlorosis), reflecting reduced chlorophyll synthesis. Leaves are very sensitive indicators of mineral deficiency, tending to be small and pale in color. They may develop dead areas of tissue at their tips, or between major veins. Deficiency symptoms of elements that are relatively immobile in plants (iron, manganese, boron, and calcium) appear first in the younger leaves. In contrast, deficiency symptoms of mobile elements (nitrogen, phosphorus, potassium, magnesium) appear first in the older leaves.

Mineral deficiencies lead to chlorosis, reduced photosynthesis and hormone synthesis, as well as death of leaves, shoots, and other tissues. However, because of various interactions and feedback responses, it often is difficult to ascertain how a deficiency of a particular mineral element produces an observed effect. For example, nitrogen deficiency may reduce growth because of a lack of nitrogen for synthesis of protoplasm, but there is also an associated reduction in synthesis of enzymes and chlorophyll as well as a reduction in the leaf area. Hence the rate of photosynthesis is reduced, lowering the supply of carbohydrates available for growth. A single mineral element often has several roles in plants, and it often is difficult to determine which role or combination of roles accounts for the observed symptoms (55).

Addition of too much fertilizer sometimes causes injury or decreases growth of trees. A high concentration of salts in the soil may increase the osmotic pressure of the soil solution sufficiently to reduce absorption of water, increase leaf water deficits, and injure tissues by dehydration when the rate of transpiration is high. As mentioned, severe dehydration of leaves closes stomata and reduces photosynthesis. Furthermore, high salt concentrations in the soil may injure young feeder roots by extracting water from them. This is especially likely for roots of trees growing on sandy soils. The amount of root injury caused by too much fertilizer depends on species, type and amount of fertilizer, and time of application (55).

Environmental Pollution

In the immediate and foreseeable future arborists will need to be very concerned about the effects of environmental pollution on shade trees. Not only is accumulation of pollutants greatest where there is the highest concentration of people and industry but emission of some air pollutants is increasing at an alarming rate. Postel (1984) compiled data from various sources which indicate that we may continue to expect large increases in sulfur dioxide and nitrogen oxides which are among the most phytotoxic pollutants known.

Trees are adversely affected by a wide variety of environmental pollutants. Among the most important of these are sulfur dioxide (SO_2), ozone (O_3), fluorides (F), oxides of nitrogen (NO_x), particulates (including cement kiln dusts and foundry dusts), heavy metals, salt spray, deicing salts, and such applied biocides as herbicides, fungicides, insecticides, and antitranspirants. Trees themselves produce some toxic compounds (allelochems) which inhibit seed germination and growth of neighboring plants. For example, black walnut roots produce juglone, a phytotoxic compound (74).

Acute injury usually becomes evident after rapid absorption of high concentrations of gaseous air pollutants. Chronic injury, which follows absorption of low concentrations of air pollutants for a long time, usually causes chlorosis and leaf senescence. In conifer needles, tipburn is caused by high concentrations of pollutants, and chlorosis by low concentrations. Air pollutants may also injure fruits (8). Pollutants not only injure trees but also influence their metabolism and reduce their growth without causing visible injury.

Air pollutants inhibit various aspects of tree growth, including height growth (13) and cambial

growth (7). Cambial growth may be reduced without visible leaf injury (37). Pollutants also lower the rate of dry weight increase of leaves, stems, and roots (81), and may decrease both the yield and quality of flowers, fruits, and seeds (82).

The responses of trees to pollutants vary greatly with tree species and cultivars, pollutant dosage, type and combinations of pollutants, age of trees, environmental factors, and interactions of pollutants with plant diseases and insects (45, 46, 49).

Conifers usually are more susceptible than broadleaved trees to air pollutants. Differences among species, clones and cultivars in pollution tolerance reflect variations in capacity for avoidance of uptake of pollutants or in biochemical tolerance of pollutants, with the former much more important. Inasmuch as gaseous air pollutants cause injury after they enter leaves through stomatal pores, such characteristics as small and few stomata decrease the amount of pollutant absorbed. More SO_2 was absorbed by *Fraxinus americana* seedlings, with large stomata, than by *Acer saccharum* seedlings with small stomata (34). *Betula nigra* seedlings absorbed more SO_2 and were injured more than *Betula papyrifera* seedlings, further emphasizing the importance of stomatal characteristics in pollution tolerance. Stomatal sizes of California species and shrubs provided a good index of SO_2 uptake and tolerance (86).

Only rarely are trees affected by a single polluting substance. Rather they are influenced by two or more pollutants at the same time. Usually the harmful effects of combined pollutants are greater than the effects of a single pollutant.

Young seedlings are more susceptible than old seedlings or mature trees to a given dosage of an air pollutant. Seedlings in the cotyledon stage are particularly susceptible (14). In mature trees sensitivity to pollutants varies with leaf age. For example, the younger fully expanded leaves and those near full expansion are more sensitive to SO_2 than old leaves, and small, expanding leaves are least sensitive.

The effect of a pollutant is greatly influenced by environmental regimes during as well as before and after a pollution episode. The effects of light intensity, temperature, soil moisture, and relative humidity, all of which influence stomatal opening and closing, affect the amount of gaseous air pollutants absorbed and, therefore, influence injury and growth responses (45, 59). By inducing stomatal closure, flooding of soil may decrease absorption of pollutants (68).

Mechanisms of Pollution Effects

The adverse effects of environmental pollutants are very complex and may involve changes in food, water, mineral, and hormone relations (67). Pollutants variously affect chlorophyll synthesis and breakdown, photosynthesis, hormone relations, membrane permeability, carbohydrate and protein reserves, and activity of enzymes. The necrosis, flecking, and bronzing of leaves that follow absorption of gaseous air pollutants are associated with loss of water from cells and effects of altered water relations on cell metabolism (28). Pollutants may first affect leaf tissues and later influence trees through changes in the soil such as leaching of mineral nutrients, accumulation of heavy metals, and mobilization of aluminum which is phytotoxic. It is not possible to explain in terms of a single central mechanism the way in which phytotoxic pollutants reduce growth and injure trees because of the different effects of the many chemically diverse compounds involved, the influence of many interacting environmental factors on the impact of pollutants, and variations in pollution tolerance of different tree species, clones, and cultivars (45, 46, 49).

Much attention has been given to the effects of pollution on photosynthesis. Many different pollutants variously reduce the rate of photosynthesis, including SO_2 (38), O_3 (5), fluorides (36), cement and coal dusts (2), and heavy metals (11, 56, 57). Agricultural biocides that reduce the rate of photosynthesis include some insecticides (4), and fungicides (55), herbicides (55), and antitranspirants (16). Occlusion of stomatal pores by some film-type antitranspirants often is followed by leaf chlorosis, necrosis, and reduction in tree growth (19, 58). Pollutants may alter the rate of photosynthesis by changing stomatal aperture and clogging of stomata (thus reducing CO_2 absorption by leaves), changing optical properties of leaves, changing the heat balance of leaves, causing destruction of chlorophyll, and changing the

activity of enzymes involved in photosynthesis. Total photosynthesis often is lowered by reduced leaf growth as well as necrosis and shedding of leaves (55).

More than one mechanism is also involved in effects of pollutants on reproductive growth. Often the yield of fruits and seeds is decreased after a reduction in physiological efficiency of the leaves. Reproductive growth may also be reduced by effects of pollutants on flowering and fruiting and by direct injury to reproductive structures. For example, air pollutants inhibit pollen germination and growth of the pollen tube (35). Some air pollutants are also toxic to pollinating insects (8).

Conclusions

Not only are urban trees grown in areas with restricted root and crown space, but they are also subjected to changes in water tables and injury through construction activities. Furthermore they often are exposed to the harmful effects of herbicides, deicing salts, and increasing amounts of air pollutants. In order to grow trees successfully in such artificial and hostile environments, the arborist will require knowledge about the processes involved in tree growth and the environmental stresses that control those processes. Such information will increase his ability to skillfully alter and manipulate the environment in order to assure that physiological processes of trees will be favorably coordinated throughout their development. In meeting these challenges the arborist should give primary attention to selection of trees most likely to survive local stresses, as well as to site improvement and use of cultural practices that will alleviate environmental stresses long before they become severe.

Natural selection has tended to produce populations of trees adapted to the environmental conditions in which they have evolved. Arborists can avoid harmful effects of environmental stresses by giving careful attention to the origin of planting stock for specific sites, especially periodically dry or cold ones. For species with extensive north-south ranges, trees from southern seed sources tend to grow faster, leaf out later in the spring, and continue shoot growth later into the autumn. They also are less frost tolerant. These trends largely reflect adaptations to cold and warm regions;

hence it is always wise to use trees of native stock growing as near as possible to the planting site. The U.S. Forest Service recommends that, if possible, planting stock should be produced from seed collected within 100 miles horizontally and 1000 feet vertically of a planting site.

The arborist must be constantly alert to the extreme sensitivity of urban trees to a variety of abiotic and biotic stresses. Whereas control measures for tree diseases caused by primary, highly pathogenic fungi should be directed at the pathogen, those for dieback-decline diseases should emphasize prevention of predisposing stress factors. When insects are primary predisposing factors the use of insecticides can decrease infestations. The effects of predisposing environmental stresses can be prevented or alleviated by judicious irrigation, application of fertilizer, reducing competition from sod by mulching over the root zone, avoiding soil compaction by covering walkways with wood chips or other mulches, pruning of tree crowns during droughts, and removing weak or dead branches to promote wound healing and reduction of decay (27, 30, 31, 71).

The arborist should be aware that trees can quickly change from a non-stressed to a stressed condition. In particular, transplanted trees often undergo a sudden, massive physiological shock. This is because the roots of transplants do not grow fast enough to absorb water in sufficient amounts to keep up with transpirational water losses. The water relations of transplants can be improved by careful selection of trees and root pruning in the nursery long before the transplanting process. Root pruning stimulates root branching and production of many small absorbing roots. Hence, root pruning eventually leads to efficient absorption of water by transplanted trees. Other useful techniques include transplanting broadleaved trees in a leafless condition if possible, transplanting under appropriate environmental conditions, maintaining favorable crown-root ratios, judiciously using antitranspirants, lifting trees from the nursery when they are still dormant, selecting healthy trees with a high potential for root growth, proper handling of planting stock, and very careful supervision of transplanting and post-transplanting practices (27, 30, 41, 50,

51).

The impacts of air pollutants are likely to become increasingly important. Despite many efforts to control pollution, the amount of SO_2 in the air is expected to increase because of greater use of highly polluting fuels. The Environmental Protection Agency (1978) predicted that overall emissions of sulfur oxides would be 10% higher in 1990 than in 1975. In some regions the amounts released will be even higher. For example, based on emission regulations in force in 1978, Lincoln and Rubin (1980) estimated that release of SO_2 in 1990 in the northeastern states may increase by as much as 60% over 1975 levels. And even if emission regulations for new industrial facilities become more stringent, the increase in SO_2 was projected as near 24%. This means that in selecting trees for a given site, arborists will need to give much more attention to pollution tolerance of trees and proportionally less to some other desirable characteristics. Several published lists of tolerance of trees to individual air pollutants are available (see, for example, 20). These can be used to much greater advantage than they have in the past.

Literature Cited

1. Appel, D.N., R.J. Stipes, and S.S. Brown. 1979. *Influence of water stress on Endothia gyrosa canker development in containerized pin oaks.* Phytopathology 69: 534.
2. Auclair, D. 1977. *I. Effets des poussieres sur la photosynthese. II. Influence des polluants particulaires sur la photosynthese du pin sylvestre et du peuplier.* Annal. des Sciences Forestieres 34: 45-57.
3. Auerbach, S.I. 1981. Ecosystem response to stress: a review of concepts and approaches. p. 29-41. In G.W. Barrett and R. Rosenberg, (eds.) *Stress Effects on Natural Ecosystems.* Wiley, Chichester.
4. Ayers, J.C., and J.A. Barden. 1975. *Net photosynthesis and dark respiration of apple leaves as affected by pesticides.* J. Am. Soc. Hort. Sci. 100: 24-28.
5. Barnes, R.L. 1972. *Effects of chronic exposure to ozone on photosynthesis and respiration of pines.* Environ. Pollut. 3: 133-138.
6. Barrett, G.W. 1981. Stress ecology: An integrative approach. p. 3-12. In G.W. Barrett and R. Rosenberg, (eds.) Stress Effects on Natural Ecosystems. Wiley, New York.
7. Benoit, L.F., J.M. Skelly, L.D. Moore, and L.S. Dochinger. 1982. *Radial growth reductions of Pinus strobus L. correlated with foliar ozone sensitivity as an indicator of ozone-induced losses in eastern forests.* Can. J. For. Res. 12: 673-678.
8. Bonte, J. 1982. Effects of air pollutants on flowering and fruiting. p. 207-223. In M.H. Unsworth and D.P. Ormrod, (eds.) Pollution in Agriculture and Horticulture. Butterworths, London.
9. Bould, C. and R.M. Jarrett. 1962. *The effects of cover crops and NPK fertilizers on growth, crop yield and leaf nutrient status of young dessert apple trees.* J. Hort. Sci. 37: 58-82.
10. Boyer, J.S. 1968. *Relationship of water potential to growth of leaves.* Plant Physiol. 43: 1056-1062.
11. Carlson, R.W. and F.A. Bazzaz. 1977. *Growth reduction in American sycamore (Platanus occidentalis L.) caused by Pb-Cd interaction.* Environ. Pollut. 12: 243-253.
12. Clements, J.R. 1970. *Shoot responses of young red pine to watering applied over two seasons.* Can. J. Bot. 48: 75-80.
13. Constantinidou, H.A. and T.T. Kozlowski. 1979. *Effects of sulfur dioxide and ozone on Ulmus americana seedlings. I. Visible injury and growth.* Can. J. Bot. 57: 170-175.
14. Constantinidou, H.A., T.T. Kozlowski, and K. Jensen. 1976. *Effects of sulfur dioxide on Pinus resinosa seedlings in the cotyledon stage.* J. Environ. Qual. 5: 141-144.
15. Crist, C.R. and D.F. Schoeneweiss. 1975. *The influence of controlled stress on susceptibility of European white birch stems to attack by Botryosphaeria dothidea.* Phytopathology 65: 369-373.
16. Davies, W.J. and T.T. Kozlowski. 1974. *Short- and long-term effects of antitranspirants on water relations and photosynthesis of woody plants.* J. Am. Soc. Hort. Sci. 99: 297-304.
17. Davies, W.J. and T.T. Kozlowski. 1975. *Effects of applied abscisic acid and plant water stress on transpiration of woody angiosperms.* For. Sci. 22: 191-195.
18. Davies, W.J. and T.T. Kozlowski. 1977. *Variations among woody plants in stomatal conductance and photosynthesis during and after drought.* Plant and Soil 46: 435-444.
19. Davies, W.J., T.T. Kozlowski, and K.J. Lee. 1974. *Stomatal characteristics of Pinus resinosa and Pinus strobus in relation to transpiration and antitranspirant efficiency.* Can. J. For. Res. 4: 571-574.
20. Davis, D.D. and H.D. Gerhold. 1976. Selection of trees for tolerance of air pollutants. p. 61-66 In Better Trees for Metropolitan Landscapes (F.S. Santamour, H.D. Gerhold, and S. Little, eds.) U.S. Forest Service, General Tech. Rept. NE-22.
21. Environmental Protection Agency. 1978. Research outlook. 1978. EPA-600/9 78-001.
22. Evert, R.F. and T.T. Kozlowski. 1967. *Effect of isolation of bark on cambial activity and development of xylem and phloem in trembling aspen.* Amer. J. Bot. 54: 1045-1055.
23. Evert, R.F., T.T. Kozlowski, and J.D. Davis. 1972. *Influence of phloem blockage on cambial growth of Acer saccharum.* Amer. J. Bot. 49: 632-641.
24. Franz, E.H. 1981. A general formulation of stress phenomena in ecological systems p. 49-54. In G.W. Barrett and R. Rosenberg, (eds.) Stress Effects on Natural Ecosystems. Wiley, Chichester.
25. Fraser, D.A. 1962. *Apical and radial growth of white spruce (Picea glauca (Moench) Voss) at Chalk River, Ontario, Canada.* Can. J. Bot. 40: 659-668.
26. Harris, R.W. 1966. *Influence of turf grass on young landscape trees.* Proc. Int. Hort. Congr. 17: 80.
27. Harris, R.W. 1983. Arboriculture. Prentice-Hall.

Englewood Cliffs, New Jersey.

28. Heath, R.L. 1980. *Initial events in injury to plants by air pollutants.* Ann. Rev. Plant Physiol. 31: 395-489.

29. Hibben, C.R. and S.B. Silverborg. 1978. *Severity and causes of oak dieback.* J. Arboric. 4: 274-279.

30. Himelick, E.B. 1981. Transplanting Manual for Trees and Shrubs. Int. Soc. Arboriculture, Urbana, Illinois.

31. Houston, D.R. 1981. Stress triggered tree diseases. The diebacks and declines. U.S. Dept. of Agriculture Forest Service NE-INF-41-81.

32. Houston, D.R. 1984. *Stress related to diseases.* Arboric. J. 8: 137-149.

33. Hsiao, T.C. 1973. *Plant responses to water stress.* Ann. Rev. Plant Physiol. 24: 519-570.

34. Jensen, K.F. and T.T. Kozlowski. 1975. *Absorption and translocation of sulfur dioxide by seedlings of four forest tree species.* J. Environ. Qual. 4: 379-382.

35. Karnosky, D.F. and G.R. Stairs. 1974. *The effects of SO_2 on in vitro forest tree pollen germination and tube elongation.* J. Environ. Qual. 3: 406-409.

36. Keller, T. 1977. *Der Einfluss von Fluorimmisionen auf die Nettoassimilation von Waldbaumarten.* Mitt. Schweiz. Anst. Forstl. Versuchswes. 53: 161-198.

37. Keller, T. 1980. *The effect of a continuous springtime fumigation with SO_2 on CO_2 uptake and structure of the annual ring in spruce.* Can. J. For. Res. 10: 1-6.

38. Keller, T. 1983. Air pollutants deposition and effects on plants p. 285-294. **In** B. Ulrich and J. Pankrath, (eds.) Effects of Accumulation of Air Pollutants in Forest Ecosystems. Reidel Publishing Co., Dordrecht, Netherlands.

39. Kozlowski, T.T. 1962. Photosynthesis, climate, and tree growth. p. 149-164. **In** T.T. Kozlowski, (ed.) Tree Growth. Ronald Press, New York.

40. Kozlowski, T.T. 1967. *Physiological implications in afforestation.* Proc. Sixth World Forestry Congr. Vol. II: 1304-1316.

41. Kozlowski, T.T. 1969. *Tree physiology and forest pests.* J. For. 69: 118-123.

42. Kozlowski, T.T. 1976. Water relations and tree improvement. p. 307-327 **In** M. Cannell and F.T. Last, (eds.) Tree Physiology and Yield Improvement. Academic Press, London.

43. Kozlowski, T.T. 1978. How healthy plants grow. p. 19-51. **In** J. Horsfall and E. Cowling, (eds.) Plant Disease, Vol. III. Academic Press, New York.

44. Kozlowski, T.T. 1979. Tree Growth and Environmental Stresses. University of Washington Press, Seattle, Wa.

45. Kozlowski, T.T. 1980a. *Impacts of air pollution on forest ecosystems.* BioScience 30: 88-93.

46. Kozlowski, T.T. 1980b. *Responses of shade trees to pollution.* J. Arboric. 6: 29-41.

47. Kozlowski, T.T. 1982a. *Water supply and tree growth. Part I. Water deficits.* Forestry Abstracts 43: 57-95.

48. Kozlowski, T.T. 1982b. Reduction in yield of forest and fruit trees by water and temperature stress. p. 67-88 **In** C.D. Raper and P.J. Kramer, (eds.) Crop Reactions to Water and Temperature Stresses in Humid Temperate Climates. Westview Press, Boulder, Colorado.

49. Kozlowski, T.T. 1985. Effects of SO_2 on plant community structure. **In** W.E. Winner, H.A. Mooney, and R. Goldstein, (eds.) Effects of SO_2 on Plant Productivity. Stanford University Press, Stanford, Ca.

50. Kozlowski, T.T. and W.J. Davies. 1975a. *Control of water balance in transplanted trees.* J. Arboric. 1: 1-10.

51. Kozlowski, T.T. and W.J. Davies. 1975b. *Control of water loss in shade trees.* J. Arboric. 1: 81-90.

52. Kozlowski, T.T. and T. Keller. 1966. *Food relations of woody plants.* Bot. Rev. 32: 293-382.

53. Kramer, P.J. 1956. *The role of physiology in forestry.* For. Chron. 32: 297-308.

54. Kramer, P.J. 1984. Water Relations of Plants. Academic Press, New York.

55. Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press, New York.

56. Lamoreaux, R.J. and W.R. Chaney. 1978a. *Photosynthesis and transpiration of excised silver maple leaves exposed to cadmium and sulphur dioxide.* Environ. Pollut. 17: 259-268.

57. Lamoreaux, R.J. and W.R. Chaney. 1978b. *The effect of cadmium on net photosynthesis, transpiration and dark respiration of excised silver maple leaves.* Physiol. Plant. 43: 231-236.

58. Lee, K.J. and T.T. Kozlowski. 1974. *Effect of silicone antitranspirants on woody plants.* Plant and Soil 40: 493-506.

59. Levitt, J. 1980. Responses of Plants to Environmental Stresses. Vol. I. Chilling, Freezing, and High Temperature Stresses. Academic Press, New York.

60. Lincoln. D.R. and E.S. Rubin. 1980. *Air pollution emissions from increased industrial coal use in the northeastern United States.* J. Air Pollution Contr. Assoc. 30: 1310-1315.

61. Mader, D.L., B.W. Thompson, and J.P. Wells. 1969. Influence of nitrogen on sugar maple decline. Mass. Agric. Expt. Sta. Bull. 582.

62. Marr, J.W. 1948. *Ecology of the forest-tundra ecotone on the east coast of Hudson Bay.* Ecol. Monogr. 18: 117-144.

63. Meier, R.L. 1972. *Communications stress.* Ann. Rev. Ecol. Syst. 3: 298-314.

64. Messenger, A.S. 1976. *Root competition; grass effects on trees.* J. Arboric. 2: 228-230.

65. Mika, A. and R. Antoszewski. 1972. *Effect of leaf position and tree shape on the rate of photosynthesis in the apple tree.* Photosynthetica 6: 381-386.

66. Monselise, S.P. 1951. *Light distribution in citrus trees.* Bull. Res. Council Israel 1: 36-53.

67. Mudd, J.B. and T.T. Kozlowski, (eds.) 1975. Responses of Plants to Air Pollution. Academic Press, New York.

68. Norby, R.J. and T.T. Kozlowski. 1983. *Flooding and SO_2 stress interaction in Betula papyrifera and B. nigra seedlings.* For. Sci. 29: 739-750.

69. Parker, J. and D.R. Houston. 1971. *Effects of repeated defoliation on root and root collar extractives of sugar maple trees.* For. Sci. 17: 71-95.

70. Perkins, R.J. 1974. *Stress and its relation to the ecosystem.* Int. J. Ecol. Environ. Sci. 1: 119-127.

71. Pirone, P.P. 1978. Tree Maintenance. Oxford Univ. Press, New York.

72. Postel. S. 1984. Air pollution, acid rain, and the future of forests. Worldwatch Paper 58. Washington, D.C.

73. Priestley, C.A. 1962. Carbohydrate resources within the perennial plant. Commonwealth Bur. Hort. and Plantation Crops. Tech. Commun. 27.

74. Rice, E. 1984. Allelopathy. Second Edition. Academic Press, New York.

75. Roanes, M.K., R.J. Stipes, P.M. Phipps, and O.K. Miller, Jr. 1974. *Endothia gyrosa, causal pathogen of pin oak blight.* Mycologia 66: 1042-1047.

76. Roberts, B.R. 1977. *The response of urban trees to abiotic stress.* J. Arboric. 3: 75-78.
77. Sakai, A. 1970. *Mechanism of desiccation damage of conifers wintering in soil-frozen areas.* Ecology 51: 657-664.
78. Schoeneweiss, D.F. 1978. *The influence of stress on diseases of nursery and landscape plants.* J. Arboric. 4: 217-225.
79. Schoeneweiss, D.F. 1981. *Infectious diseases of trees associated with water and freezing stress.* J. Arboric. 7: 13-18.
80. Selye, H. 1952. The Story of the Adaptation Syndrome. Acta Inc., Montreal, Canada.
81. Shanklin, J. and T.T. Kozlowski. 1984. *Effect of temperature preconditioning on response of Fraxinus pennsylvanica seedlings to SO$_2$.* Environ. Pollut. 36: 311-326.
82. Smith, W.H. 1981. Air Pollution and Forests. Springer-Verlag, New York.
83. Tattar, T.A. 1983. *Stress management for trees.* J. Arboric. 9: 25-27.
84. Van der Boon, I., A. Pouwer, and N.M. de Vos. 1963. *Nitrogen dressing in orchards with a grass sward.* Sixteenth Int. Hort. Congr. Proc. 3: 151-157.
85. Weiser, C.J. 1970. *Cold resistance and injury in woody plants.* Science 169: 1269-1278.
86. Winner, W.E., G.W. Koch, and H.A. Mooney. 1982. *Ecology of SO$_2$ resistance. IV. Predicting metabolic responses of fumigated trees and shrubs.* Oecologia 52:16-21.
87. Zahner, R. 1962. *Terminal growth and wood formation by juvenile loblolly pine under two soil moisture regimes.* For. Sci. 8: 345-352.
88. Zahner, R. 1968. Water deficits and growth of trees. p. 191-254 **In** T.T. Kozlowski, (ed.) Water Deficits and Plant Growth. Vol. II Academic Press, New York.

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ABSTRACTS

GREY, G.W. 1984. **Painless shrub pruning.** Am. Forests 90(5): 13-16.

There are nine things you need to know before you prune: 1) what it is, 2) the difference between pruning and shearing, 3) why you want to prune it, 4) what nature intends it to look like, 5) when it leafs, blooms, and fruits, 6) when to prune it, 7) how it will respond to pruning, 8) how to prune, and 9) when to remove it.

SHIGO, A.L. 1984. **Tree decay and pruning.** Arboricultural Journal 8: 1-12.

The major aims of pruning for amenity trees have been to control growth and maintain desired shapes. It is possible to prune in such a way that no more decay will develop than develops normally when branches are shed. Proper pruning techniques will come from a better understanding of trees. Trees repond to injuries and infections by setting boundaries to resist the spread of microorganisms. The boundaries also resist the spread of microorganisms from dying branches into the joining stem. Pruning cuts should not be made behind the branch bark ridge. Such cuts remove the protective boundaries, allowing microorganisms to spread rapidly into the system. When branches are pruned properly, there is no need for wound dressings. When branches are pruned improperly, no amount or type of wound dressing will help.