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## CONTROL OF WATER LOSS IN SHADE TREES<sup>1</sup>

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Trees are so constructed that they lose large amounts of water vapor to the air by transpiration. Their leaves are perforated with many stomata, microscopic-sized openings, each surrounded by two specialized guard cells. In broadleaved trees, stomata usually occur only on the undersurface of leaves, but in a few species they may be found on both the upper and lower surfaces.

Adding to conditions for high rates of water loss from individual leaves is the very extensive leaf area developed by trees. Trees vary greatly in the number of leaves, with conifers having many more than broadleaved trees of comparable age. Whereas a single mature broadleaved tree often bears leaves numbering in the tens of thousands, individual conifers often have millions. For example, a 36-year-old white spruce (*Picea glauca*) tree had over 5 million needles. In general, leaf size and leaf number in trees are negatively correlated. For example, a 21-year-old catalpa tree had 26,000 large leaves, whereas a citrus tree that was only 12 years old had almost 100,000 small leaves. But whether trees have very many small leaves or fewer large ones, they expose an extensive leaf surface that constantly evaporates water which must somehow be replaced.

Transpiration, the loss of water from trees in the form of vapor, is basically an evaporation process. It is modified somewhat by plant structure and stomatal control. Transpiration occurs in two stages involving: 1) evaporation from the

wet cell walls into intercellular spaces; and 2) diffusion of water vapor from the intercellular spaces into the outside air. Small amounts of water are lost directly through the epidermal layers of leaves but this amount varies with the thickness of the waxy layer on leaf surfaces, and very small amounts are lost through lenticels of twigs, even from deciduous trees in winter (Kramer and Kozlowski, 1960; Kozlowski, 1958, 1968b, 1971b).

The amounts of water taken up by trees and lost to the atmosphere by transpiration are very high indeed. For example, in the southern United States, forests are estimated to lose as much as 8,000 gallons of water per acre per day. A single silver maple (*Acer saccharinum*) tree that was 47 feet high had 177,000 leaves and was estimated to lose water at the rate of 58 gallons per hour during the late afternoon in July. Of course, no tree is likely to maintain such a high rate of transpiration very long. The rate of water loss is exceedingly variable, however, and differs greatly with season and site, species, soil moisture content, humidity of the air, age of tree, depth and extent of rooting, and it even varies in different parts of the same tree (Kozlowski, 1958, 1967, 1971a).

Internal water deficits in trees are controlled by relative rates of absorption and transpiration and by internal redistribution of water. During the day more water is lost from leaves by transpiration than is taken in by absorption through the roots because of resistance to water move-

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ment through the tree. The resulting internal water deficits usually are eliminated by a high rate of absorption overnight. At night the stomata are closed and transpiration is low or negligible (Kramer and Kozłowski, 1960).

For the reasons just cited, water contents of leaves vary daily, with the highest water contents occurring in the early morning. Leaf moisture contents decrease throughout the morning, reach a minimum sometime in the early afternoon, and then begin to increase sometime in the late afternoon. Moisture contents of tree trunks also vary daily and seasonally. On a seasonal basis, trunks of trees generally have the highest water contents in the spring, sometime around the beginning of bud opening. When the buds open and leaves emerge, transpiration accelerates and tends to deplete the stem of water throughout the summer. Water loss is replaced by absorption through the roots, but the overall seasonal trend nevertheless is toward a steady depletion of stem water during the summer until a minimum moisture content is reached, often just before leaf fall. This declining seasonal trend of water content of tree stems is altered by temporary replenishing of stem water through high rates of absorption during rainy periods (Kramer and Kozłowski, 1960).

It should be clear from the foregoing discussion that internal water deficits in trees occur very commonly and can be the result of either: 1) high transpiration; 2) slow absorption of water from dry, cold, or poorly aerated soil; or 3) a combination of both.

## EFFECTS OF WATER DEFICITS ON TREES

A high water content in trees is essential because water is a constituent of protoplasm, a reagent in important biological reactions, a solvent in which essential materials (e.g., minerals) are translocated, and a maintainer of turgidity. Even mild dehydration of trees is harmful (Kozłowski, 1966, 1968a, 1971b).

### Stomatal Closure

Closure of stomata is one of the earliest

responses to drought. The stomata close when the water content decreases in the guard cells that surround the stomatal pore. As the guard cells lose water and turgidity declines, the stomatal pore closes; when the guard cells again absorb water the pore opens and the cells become turgid. The plant is turgid when in a normal healthy state. Turgidity results from water uptake and a higher turgor pressure within cells. Tissues lacking turgidity are sometimes described as flaccid and in a state of wilting.

Dehydration of trees is checked considerably by earlier closure of stomata during each day of a developing drought and by temporary closing of stomata during midday. However, the closing of stomata during a drought may not prevent killing of a tree which loses much water directly through the leaf epidermis by evaporation after stomatal closure has occurred. Evergreen trees usually undergo more leaf dehydration than deciduous trees before they close their stomata.

Leaves may recover slowly after a severe drought, but this may cause severe damage to stomata, which may open slowly or not at all when the tree is finally watered. On a given tree the stomata of shade leaves are more sensitive than sun leaves to water losses. Also the stomata of young leaves tend to close faster than do those of old leaves.

### Wilting

As leaves dehydrate and lose water they eventually wilt. Wilting varies in degree and may be classified as: 1) incipient; 2) temporary; or 3) permanent. Incipient wilting does not cause drooping of leaves. Temporary wilting involves drooping of leaves during the day and recovery from wilting during the night. During a sustained drought, plants temporarily wilted may become permanently wilted. Recovery from permanent wilting requires rewetting of the soil. Trees which stay in a state of permanent wilting for an extended period may die.

### **Decrease in Vegetative and Reproductive Growth**

Growth in diameter of trees is particularly sensitive to water supply. During dry years trees produce narrow annual rings of wood. During a summer drought, cambial growth either slows or stops altogether, depending on drought severity, and accelerates or begins again following rain or irrigation. Cambial growth in response to dry and wet periods may result in formation of "false" or "multiple rings" of wood in stems. These often have been mistaken for annual rings of wood, leading to incorrect estimates of tree age (Kozlowski, 1971b).

Drought decreases the rate of diameter growth in trees not only in one year but also in later years. A summer drought affects the number of leaf initials which form in new buds for the shoots of the following year, and the consequent reduction in foliage reduces the amount of growth requirements, such as carbohydrates and hormones, that are translocated downward.

Flowering and fruiting of trees are influenced by availability of water at any stage during flower bud formation, flowering, pollination, fertilization, embryo growth, or fruit and seed development. However, it is difficult to make broad generalizations on the effects of drought on reproductive growth, partly because timing of the cycle of reproductive growth varies widely.

Flower bud formation often is suppressed by drought but the effect may not be obvious until the following year at flowering time. Sometimes, however, a mild water deficit at a critical time will increase initiation of flower buds by decreasing growth of vegetative tissues. Both the size and quality of fruits are improved by an adequate water supply before and during the period of fruit enlargement.

### **Injury**

Various tissues and organs of trees often are injured or killed by drought, without necessarily killing the tree. Leaf responses to drought include curling, "scorching", marginal browning,

early autumn coloration, and premature dropping.

Considerable winter and early spring leaf scorching and defoliation occur in evergreen shrubs and trees. When the injury is severe, all the leaves and buds (often the plants) are killed. More commonly, however, the leaves are killed but the buds are not and the plants survive. Eventually the dead leaves are shed, with the most obvious symptoms occurring on the sides exposed to the wind or sun. Such winter desiccation injury often has been erroneously attributed to direct thermal effects.

Winter desiccation injury occurs when absorption of water cannot keep up with transpirational losses. Appreciable transpiration often occurs as the air warms up sufficiently during winter or spring days to steepen the vapor pressure gradient between the leaves and surrounding air. Since the soil is cold or frozen, water cannot be absorbed through the roots rapidly enough to replace transpirational losses and the leaves become desiccated. Among the important causes for decreased absorption of water at low temperatures are physical effects on root resistance, increased water viscosity, and decreased permeability of root cell membranes. Other factors such as decrease in rate of root growth, hydraulic conductivity, and root metabolism may also contribute to decreased absorption, but these appear to be less important (Kramer and Kozlowski, 1960).

Following prolonged and severe droughts, stems may become so desiccated that they crack. In some species, death of bark in vertical strips and longitudinal cracking may result from water deficits. Drought cracks may or may not heal and, if they do not, they provide openings for invasion by decay fungi and insects.

### **EFFECTS OF TRANSPLANTING ON TREES**

It cannot be emphasized too strongly that water deficits of recently transplanted trees are infinitely more serious than those which develop periodically in well-rooted trees. Trees which are uprooted and moved with bare roots, or even with a root ball of soil, undergo a mas-

sive physiological shock because their capacity for water absorption is greatly diminished while transpiration demands continue. Transplants often lose water faster than they absorb it. Many small absorbing roots are lost and the previously well-established contact of the whole root system to a large volume of water-supplying soil is greatly disrupted.

With the above considerations in mind, experiments were conducted on transplanting shock, leaf anatomy in relation to transpiration, stomatal responses to environmental factors, and control of water balance in transplanted trees by decreasing transpiration and increasing absorption of water.

### Transplanting Shock

Many arborists have considered midsummer transplanting to be successful if the trees survive. However, such reports generally do not compare growth of transplanted trees with undisturbed control trees. Therefore, experiments were conducted in the greenhouse, nursery, and in the field on water balance, growth, and survival of trees that were transplanted during the summer.

In a forest nursery six species of hardwood seedlings in full leaf were lifted in midsummer on a cloudy day and either replanted immediately on the same site or after 30 minutes of root exposure. *Fraxinus americana*, *F. pennsylvanica*, and *Betula alleghaniensis* survived midsummer planting better than *Quercus alba*, *Q. macrocarpa*, or *Q. rubra*. Nevertheless, transplanting was not considered successful for any species because most of the seedlings which survived were severely injured.

In the University of Wisconsin Arboretum, *Picea glauca* trees about 3 feet high were dug in late June with a root ball of soil and were transplanted immediately. Additional trees were dug at the same time and left on the ground in a balled condition for 1 or 4 weeks. The root ball was wrapped in polyethylene. Three years later some of the trees that had been transplanted immediately after lifting were dead and the survivors in this group were only about half as high as the control trees that had not been

transplanted. Mortality was still higher in trees that were balled for 1 week before transplanting. Practically all the trees, which had been kept in a balled condition for 4 weeks before transplanting, were dead. Furthermore, growth in the few survivors was very restricted.

In another experiment 27 3-year-old *Populus deltoides* trees were selected from plantings at the Arlington Farm of the University of Wisconsin. The trees were randomly divided into three groups of nine trees each. The trees in one group were lifted and the soil shaken from the roots before the trees were immediately transplanted at another site within the plantation. Trees of the second group were lifted with a ball of soil approximately 2 feet in diameter. The ball was tightly wrapped with polyethylene. The balled trees were immediately moved to another site within the plantation and replanted after the polyethylene was removed. Trees of the third group were not disturbed and served as controls. The trees were transplanted between July 21 and July 25. During transplanting bare-rooted and balled trees were alternated so that different environmental conditions on the different days would influence survival of trees in both transplanting treatments. The sites for transplanting were selected so that transplanted trees would be exposed to similar light and wind conditions.

The succulent and developing leaves wilted rapidly after transplanting of both bare-rooted and balled trees. Within 24 hours, most leaves on trees which had been transplanted were desiccated and many had abscised. Although most of the leaves died on trees which were balled and transplanted, several such trees retained a few isolated green leaves. Moisture for these leaves probably was supplied by roots in the ball. Transplanting in midsummer had very detrimental effects on the trees but did not kill them. All of the trees sprouted about 2 or 3 weeks after transplanting. However, the terminal shoots were damaged and any subsequent growth from the sprouts would result in poor form of the trees.

Before the trees were transplanted, measurements of terminal shoot length and counts of

leaves on terminal shoots were taken for control trees and trees to be transplanted. Determination of the changes in these measurements as they were influenced by transplanting treatments were planned, but were not made because of the severe shock and damage resulting from transplanting.

In a related experiment, 25% Foligard anti-transpirant was applied to some *Populus deltoides* trees before they were transplanted in August. Application of the antitranspirant was followed by less severe wilting than in unsprayed, transplanted trees. Nevertheless, transplanting was unsuccessful in treated trees because they developed severe water deficits and were injured or died.

An experiment was also conducted on the effect of root exposure on water balance of *Pinus resinosa* seedlings. Changes in stem shrinkage and water balance of leaves were determined for potted seedlings and for repotted seedlings (June 15) which had bare roots exposed for 15 minutes, 1 hour, 24 hours, or 48 hours. A continuous record of changes in stem diameter was obtained with dendrographs and daily changes in stem diameters of the seedlings were also measured with a micrometer caliper. Diameters of stems of control (undisturbed) seedlings did not fluctuate diurnally. Changes in diameters of seedlings which had their roots exposed for 15 minutes or 1 hour were very similar to those of the controls except after June 26 in the case of the seedlings with roots exposed for 15 minutes. The diameter of the stem of the seedlings with roots exposed for 15 minutes did not fluctuate diurnally and declined in diameter only slightly until June 26. Beginning with June 26 and through June 28 stem diameter showed a stair-step pattern of shrinkage, with shrinkage occurring during the day and little or no change in diameter at night. Seedlings with roots exposed for 24 hours or 48 hours also showed a stair-step pattern of stem shrinkage. There was a very rapid and large decrease in stem diameter during the afternoon of the first day the roots of the seedlings were exposed. Thereafter a smaller amount of irreversible stem shrinkage occurred each day until

June 21, even after the seedlings were repotted and watered. Stem shrinkage occurred during the day and there was little or no change in stem diameter at night. After June 20, there was little further shrinkage of stems.

Diameters of stems, measured daily with a micrometer caliper, of four controls and of a seedling with roots exposed for 15 minutes or 1 hour did not significantly change from June 16 to June 22. In contrast, stem diameters of seedlings with roots exposed for 24 hours or 48 hours declined from the beginning of root exposure until the seedlings were repotted. After repotting, little significant change in stem diameters occurred.

Irreversible shrinkage of stems of seedlings with roots exposed was indicative of the subsequent death of the seedlings with the exception of a seedling with roots exposed for 1 hour which did not show stem shrinkage at least during the period measurements were made and which subsequently died. All seedlings with roots exposed died except one seedling with roots exposed for 15 minutes and one with roots exposed for 1 hour. All control seedlings remained healthy.

Differences in moisture content of current, 1-year-old, and 2-year-old needles on control trees were evident, with moisture content of current needles markedly greater than that of either 1-year-old or 2-year-old needles. Exposure of roots caused a decline in the moisture content of needles of all three age classes. The decline in moisture content of current needles was most marked and, after 48 hours of root exposure, moisture content of current needles was only slightly greater than that of 1-year-old and 2-year-old needles. The decline in moisture content of all age classes of needles as a result of root exposure was not statistically significant after 15 minutes or 1 hour exposure, except for a greater moisture content in current needles of seedlings exposed for 15 minutes than in current needles of control seedlings. This difference probably resulted because the roots of the seedlings which were bare-rooted were placed in a water-bath overnight to loosen the soil from the roots. This treatment apparently caused a

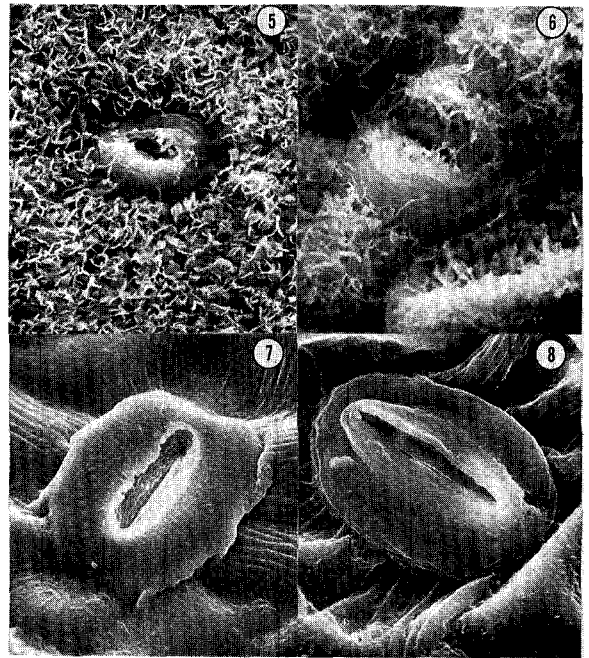
higher initial moisture content in current needles of root-exposed than in control seedlings, and the effect of the higher initial moisture content was still evident even after roots were exposed for 15 minutes.

These several experiments emphasized the great advantage of transplanting trees when they are not in a full-leaf condition. Transplanting broadleaved trees with fully expanded foliage, when atmospheric conditions are conducive to high transpirational loss (high temperature, low relative humidity), is likely to result in severe water deficits, greatly reduced growth of surviving trees, and death of many trees.

### STOMATAL CHARACTERISTICS AND TRANSPIRATION

Trees vary greatly in leaf anatomy and transpiration rates. Variations in stomatal size and frequency as well as in the stomatal apparatus are important in comparing transpiration capacity of different species. With these considerations in mind, stomatal characteristics of over 30 species of trees were examined.

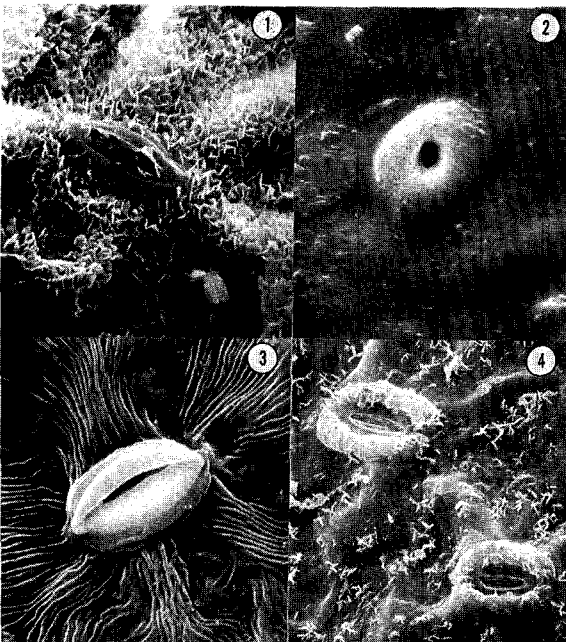
Some trees developed anatomical characteristics to reduce water loss (e.g., sunken stomata, thick waxy cuticular layers, leaf hairs, etc.) (Figs. 1-14). The guard cells of *Acer*

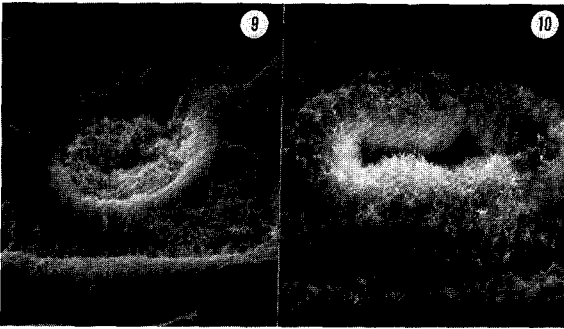


**Figs. 1-8.** Scanning electron micrographs of the lower leaf surfaces of eight species of broadleaved trees. Fig. 1. *Cercis canadensis*. Fig. 2. *Citrus mitis*. Fig. 3. *Fraxinus americana*. Fig. 4. *Quercus macrocarpa*. Fig. 5. *Acer saccharum*. Fig. 6. *Acer saccharinum*. Fig. 7. *Ulmus americana*. Fig. 8. *Betula papyrifera*.

*saccharum* and *Fraxinus americana* stomata were level with the leaf surface (Figs. 11, 12). Those of *Quercus macrocarpa* projected above the leaf surface (Fig. 13). *Pinus* had sunken stomata, with the guard cells a part of the second layer of cells (the hypodermis) rather than the epidermal layer (Fig. 14).

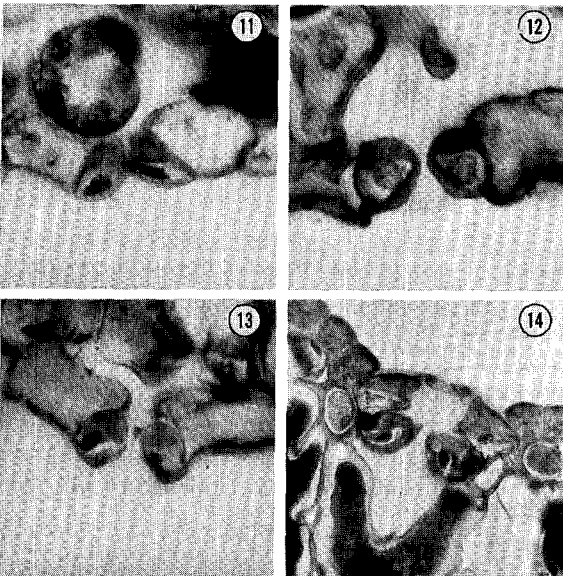
Stomatal length and frequency also varied markedly among species. Length of guard cells varied from 17 to 56  $\mu$  and stomatal frequency from about 100 to 600 stomata per  $\text{mm}^2$ . Generally a species with small stomata tended to have many of them. For example, *Acer saccharum*, *A. saccharinum* and *Rhus typhina* had numerous small stomata whereas *Betula papyrifera*, *Fraxinus pennsylvanica*, *Ginkgo biloba*, *Gleditsia triacanthos*, *Salix fragilis*, and *Vitis vinifera* had few large stomata. Oaks (*Quercus rubra*, *Q. macrocarpa*, and *Q. palustris*) had both numerous and large stomata. Stomatal size and frequency often varied greatly in the same genus as in different species of *Crataegus* or *Fraxinus* (Davies et al., 1972).





**Figs. 9 and 10.** Scanning electron micrographs of needle surfaces of pines. Fig. 9. *Pinus resinosa*. Fig. 10. *Pinus strobus*.

Marked variations also were shown among species in their waxy leaf coatings. *Fraxinus americana* had a protruding cuticular lip over the guard cells (Fig. 3). The stomatal pores of *Acer saccharum* and *Cercis canadensis* were partially or totally occluded with cuticular wax (Figs. 1, 5) whereas those of *Ulmus americana*, and *Betula papyrifera* were not (Figs. 7, 8). The stomatal pores of *Pinus resinosa* were occluded with an amorphous cuticular wax. By comparison, the stomatal pores of *Pinus strobus* were surrounded by plate-like wax but were unoccluded (Figs. 9, 10).



**Figs. 11-14.** Light microscope cross-sections of leaves, showing stomatal structure. Fig. 11. *Acer saccharum*. Fig. 12. *Fraxinus americana*. Fig. 13. *Quercus macrocarpa*. Fig. 14. *Pinus resinosa*.

### Stomatal Response to Environmental Changes

Whether a tree can grow vigorously depends to a large extent on whether it can photosynthesize rapidly and keep transpirational water loss low. With these considerations in mind, variations between and within species in transpiration, photosynthesis, and water use efficiency in relation to leaf structure, stomatal size, stomatal frequency, and control of stomatal opening were studied in shade tree species. Plant responses under environmental stress were determined for plants which varied markedly in stomatal size and frequency.

**Temperature.** Experiments were conducted on seedlings of five species of trees which occur along an ecological gradient from xeric to mesic: *Quercus macrocarpa*, *Q. velutina*, *Q. alba*, *Q. rubra*, and *Acer saccharum*. Leaf resistance and rates of transpiration and photosynthesis as well as water use efficiency were calculated for each species over a temperature range of 20 to 40°C and a light intensity range of 200 to 3200 ft. c. (Wuenscher and Kozłowski, 1971a, 1971b).

All species showed a linear increase in transpiration with increased leaf temperature, up to 35°C. At high light intensities transpiration of *Q. velutina* and *Q. rubra* decreased above 35°C. All species also showed a significant increase in transpiration resistance with increased leaf temperature. The increase was linear throughout most of the temperature range. Linear correlation and regression analyses were made between leaf temperature and transpiration resistance for pooled data from all light intensities. The rate of increase of transpiration resistance with rise in leaf temperature was greatest for *Q. velutina* and least for *Q. alba* and *A. saccharum*. Rates of increase were intermediate and about equal for *Q. macrocarpa* and *Q. rubra*.

Water use efficiency, the ratio of water loss resistance to CO<sub>2</sub> uptake resistance, increased with increasing leaf temperature up to 35°C and decreased at higher temperatures. Water use efficiency also increased with increasing light intensity up to some value at which it leveled off or decreased slightly. Efficiency of water used varied in the following order: *Q. velutina*

>*Q. macrocarpa* >*Q. rubra* = *Q. alba* >*Acer saccharum*. At 40°C the water use efficiency of four species declined greatly, whereas that of *Q. velutina* declined only slightly. Under most conditions, water use efficiency of *Q. velutina* was more than 4 times greater than in *Acer saccharum*.

Another study showed that, over a range of temperatures, transpiration resistance was lower and water loss was higher in *Fraxinus americana* than in *Acer saccharum* seedlings. *Fraxinus* had very little capacity to avoid drought by control of stomatal aperture.

*Light Intensity.* Experiments were conducted on stomatal aperture (diffusion resistance) of *Fraxinus americana*, *Acer saccharum*, *Quercus macrocarpa*, *Citrus mitis*, and *Cercis canadensis* seedlings over a range of light intensities of 800 lux to 32,000 lux (Davies and Kozlowski, 1974b).

Equilibrium leaf resistances varied with light intensity and species. *Acer* stomata began to close when light intensity decreased below 16,000 lux. By comparison *Fraxinus* and *Quercus* stomata did not begin to close until light intensity fell below 6,500 lux. *Cercis* stomata remained open until light intensity dropped below 5,000 lux and *Citrus* stomata began to close at 3,200 lux.

When light intensity was rapidly changed from 0 to 32,000 lux and the reverse, stomata opened faster than they closed in *Fraxinus* and *Quercus* while in *Citrus* they closed faster than they opened. Opening and closing times were not different from each other in *Acer* and *Cercis*. In each species both opening and closing of stomata of green plants were much more responsive to changes in light intensity than were stomata of chlorotic plants.

*Humidity.* A comparison was made of stomatal opening and closing in response to changes in humidity. Seedlings of *Fraxinus americana* and *Acer saccharum* were subjected to relative humidity changes from 20 to 80% (Temperature 25°C) at two light intensities (6,500 and 32,000 lux) (Davies and Kozlowski, 1974a).

Increases in humidity caused stomatal opening; decrease in humidity caused stomatal closure. A change in humidity at high light intensity affected stomatal responses less than humidity changes at low light intensity. Both opening and closing of stomata in response to humidity change occurred much faster in *Acer* than in *Fraxinus*. In both species, after a change in humidity, stomatal opening occurred faster than stomatal closing. This was much more obvious in *Acer* than *Fraxinus*. The significance of this work is that if a plant can respond to humidity it will close its stomata before it is subjected to water stress.

*Wind.* Experiments were conducted in the wind tunnel of the University of Wisconsin Biotron on effects of wind on transpiration and stomatal resistance of *Fraxinus americana*, *Acer saccharum*, and *Pinus resinosa* seedlings. Wind was alternately on and off for 24-hour periods. Light intensity was 3000 ft. c. on a 16-hour day, temperature was 28°C and relative humidity approximately 50% (Davies et al., 1974).

Transpiration rates per unit of leaf dry weight in both wind and still air varied as follows: *Fraxinus* *Acer* *Pinus*. Transpiration over a 24-hour period was increased by wind in *Fraxinus*, decreased in *Acer*, and was unaffected in *Pinus*. These species differences reflected variations in stomatal size, structure, and control of stomatal aperture. Whereas *Acer* stomata closed rapidly when exposed to wind, those of *Fraxinus* did not. Rapid stomatal closure resulted in high turgor and reduction in water loss despite an increase in the plant-air vapor pressure gradient. In *Fraxinus*, with relatively insensitive stomata, wind had less effect on stomatal closure and plant turgor was not maintained. In *Fraxinus*, despite eventual stomatal closure, seedlings in wind lost more water than those in still air. In pine, with sunken stomata which were occluded with cuticular waxes, wind apparently had little effect on transpirational water loss.

#### Within-Species Variations in Stomatal Control

Experiments were conducted on the relation of internal leaf anatomy, stomatal size, stoma-



tal frequency, and control of stomatal aperture on transpiration rates of six *Populus* clones (two clones of *P. maximowiczii*; one clone from each of the species *P. deltoides*, *P. nigra*, and *P. trichocarpa*; and one hybrid, *P. maximowiczii* x *P. nigra* (Siwecki and Kozlowski, 1973). Water loss of excised leaves, as determined with transpiration decline curves, varied widely among clones as did internal leaf anatomy, stomatal size, stomatal frequency, and control of stomatal aperture. Transpiration rates were more closely related to stomatal size, frequency, and control than to internal leaf anatomy. No consistent pattern was shown over all clones in correlation of transpiration rate with any individual feature of internal leaf anatomy examined (leaf thickness, epidermal thickness, amount of palisade parenchyma, amount of spongy parenchyma, percent of combined thickness of spongy mesophyll plus epidermal layers, or percent of palisade parenchyma). Very high transpiration capacity of *P. trichocarpa* was correlated with low stomatal resistance associated with large stomata (but low stomatal frequency). The high rate of water loss in *P. maximowiczii* x *P. nigra* was correlated with high stomatal frequency. In both of these clones the capacity to keep stomata open for a long time also contributed to their high transpiration rate. Although *P. deltoides* and *P. nigra* leaves had relatively large stomata, their generally low rates of transpiration were attributed to early stomatal closure.

### Biological Implications of Stomatal Control

Stomatal diffusion resistance may be a function of stomatal size, stomatal frequency, and capacity for stomatal closure under conditions of environmental stress. However, stomatal control often is more important than stomatal size or frequency in controlling water loss and photosynthesis. Inter- and intraspecific variations in stomatal control occur commonly and have very important biological implications in relation to drought resistance and injury by atmospheric pollutants.

Wide variations occurred among species in control of stomatal aperture. *Acer saccharum*,

with a stomatal apparatus that is relatively sensitive to environmental stress (low light, high temperature, low humidity, wind) was more drought resistant than *Fraxinus americana* with relatively insensitive stomata.

Our experiments showed that species differences in stomatal control and water use efficiency influenced their occurrence along an ecological gradient. Stomatal resistance with increasing temperature generally decreased from xerophytic to mesophytic species. Of the five species studied, *Quercus velutina* had the highest water use efficiency and was the most drought resistant species. It fixed CO<sub>2</sub> rapidly while losing little water. Hence, it can grow successfully on hot dry sites. By comparison, *Acer saccharum* exhibited relatively low water use efficiency. It lost much more water than *Quercus velutina*. Thus, for normal growth it requires a site with more available water or low evaporative demand.

*Pollution Injury.* Several investigators have shown an important relationship between stomatal diffusion resistance and injury to plants by atmospheric pollutants. In our laboratory we compared SO<sub>2</sub> injury and sulfur deposition rate in *Acer saccharum* (high stomatal diffusion resistance) and *Fraxinus americana* (low stomatal diffusion resistance). SO<sub>2</sub> injury occurred much faster in *Fraxinus* than in *Acer*. The sulfur deposition rate was much greater in *Fraxinus*, emphasizing the importance of high stomatal resistance in impeding SO<sub>2</sub> uptake in *Acer*. We may expect also that under windy conditions *Acer* would close its stomata rapidly and be injured less than *Fraxinus* by pollutants.

### Relation of Stomatal Characteristics to Top-Root Ratio

Despite the foregoing stress on differences in stomatal characteristics, it should be strongly emphasized that in considering transplanting any species, primary attention should be given to the ratio of the transpiring surface of a tree to its absorbing surface (top-root ratio). This ratio is important because it determines to a large degree whether absorption of water can keep up

with transpiration and whether the transplant is likely to dry out to critical levels. *Acer saccharum* leaves, for example, had a relatively low transpiration rate per unit of leaf area because their stomata were small and partially occluded with wax and because they closed rapidly in response to environmental stress. These drought-avoiding characteristics of individual leaves of *Acer* should not obscure the important fact that development of an extensive leaf area in this species will result in high total transpirational loss and desiccation injury, even if the rate of water loss per unit of leaf area is low.

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## ABSTRACT

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Insecticide sprays are commonly timed to coincide with the period or periods in a particular insects' developmental cycle when it is most vulnerable. Year-to-year temperature variations may make calendar spray timing data collected one year inaccurate for some other years in the same geographic area. If insects' developmental cycles and blooming dates of ornamental plants are similarly affected by temperature variations, a valid correlation can be drawn, and the blossoming times of the plants can be used as accurate indicators of the times when the particular insects are most vulnerable to insecticide applications. To test these correlations, the life cycle of the eastern spruce gall aphid, *Adelges abietis*, was chosen. A valid correlation between blooming stages of the ornamental shrub *Magnolia soulangiana* and spring initiation of egg laying by eastern spruce gall aphid seems to be apparent. Similar correlations are probably valid for other ornamental pests.