

recall a simlie which Charley Hess presented to us several years ago in which he likened the growth of a plant or the rooting of a cutting to a column which could be filled with liquid; the column having four series of holes on its sides. One series representing temperature, another water, a third light intensity, and the fourth mineral nutrition. In order to achieve the maximum amount of growth or degree of rooting of cuttings in a bed you must begin at the bottom of each series and plug the holes so that the liquid will rise in the cylinder. This has been a useful concept to me in evaluating the success or failure of our propagation efforts at Princeton.

The kinds of things that can be accomplished are wonderful if you have a perfect environment. I remember Jim Wells telling of a nursery on the West Coast of Scotland where conditions were so ideal that rhododendron cuttings were stuck and rooted directly in raised, open beds much as we would root hardwood cuttings of privet. I also remember going to Normandy in the spring of 1944 and a nurseryman there was top-grafting apple trees on high stems with nothing more than a little mud and a twist of straw around the scion and having complete success. As these examples indicate, when the environment is perfect from the plants point of view the results you can get are simply astounding. For this first symposium we are going to have a group of experts with us who are going to discuss four aspects of the environment and their interrelationships in plant propagation. The first speaker is Dr. Ted Kozlowski from the University of Wisconsin who is going to discuss some of the interrelations of water.

## **ROLE OF ENVIRONMENT IN PLANT PROPAGATION:**

### **WATER RELATIONS<sup>1</sup>**

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### **INTRODUCTION**

All plantsmen know that plants need water for growth. Water is essential for plants as the major constituent of physiologically active tissues. It is a reagent in photosynthesis and in hydrolytic processes as well as a solvent in which salts, sugars, and other solutes move from cell to cell. Water is also essential for maintenance of plant turgidity.

If we ask what the plant does with all the water it extracts from the

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soil we can only conclude that it allows most of it to evaporate from the shoots and uses only very small amounts in growth. It has been estimated, for example, that plants may use from 250 to 1,000 pounds of water to produce one pound of dry matter in growth of roots, stems, leaves, and reproductive tissues. Yet we know that if a plant cannot get water from the soil its growth is adversely affected and it may be killed. It should be obvious, therefore, that plants are extremely inefficient in their use of water and this is a matter of concern to all of us.

The plant propagator in particular must always be deeply concerned with plant-water relations. This is so not only because growth and survival of plants probably depend more on availability of water than on any other environmental factor, but also because the techniques of plant propagators unfortunately tend to create unusually severe internal water deficits in plants. For example, the preparation of cuttings and scions for rooting or grafting disrupts the path of normal water movement through the soil-plant-air continuum and thereby creates ideal conditions for desiccation of shoots.

This paper will allude briefly to some aspects of plant-water relations with which the plant propagator should be familiar. At the outset, I would like to emphasize the following major points:

(1) All plants growing in soil undergo internal water deficits. Such deficits develop periodically, even in plants growing in well-watered soils, when transpiration from shoots exceeds absorption of water through the roots.

(2) Growth and development of plants would proceed unimpaired and growth would be maximal only if a favorable internal water balance were maintained **continuously** during the life of a plant. Even temporary mild water deficits inhibit plant growth. The amounts of loss of plant growth as a result of unfavorable water balance are tremendous. In addition to restricting growth, water deficits modify various aspects of plant quality such as taste of fruits and density of wood (20, 24, 27).

(3) Growth limitations because of internal water deficits frequently are overlooked in situations where other deleterious agents operate, including plant competition, disease, or insect pests. Stunting and killing of desirable plants by "weed competition" commonly involves competition for water leading to a desiccation effect. Root diseases and insect injury to roots often interfere with absorption of water and thereby cause desiccation of shoots. In vascular wilt diseases, the desiccation of tops following vascular plugging often plays a major role in wilting of leaves and ultimate death of plants.

Leaf desiccation causes considerable winter injury to evergreens. During some warm winter or spring days transpiration is appreciable but water cannot be absorbed readily from cold or frozen soils and leaves consequently dry out.

Water deficits also play an important role in predisposing host plants to attacks by certain fungus pathogens and insects (26). Physiological changes which reflect decreasing vigor in trees often are a prerequisite to attack by certain insects. Copious exudation of oleoresins in gymnosperms and flow of sap or gum in angiosperms are correlated with resistance to bark beetle attacks. Vite' (45) showed that success of bark beetle attack was closely correlated with low oleoresin exudation pressures. Whereas initial attack occurred at random, only beetles in trees with low oleoresin exudation pressure made successful invasions which led to mass attacks later. Differences in susceptibility due to site and stand conditions were related to rates of flow of oleoresin and these, in turn, to stem hydration. Oleoresin exudation pressures decreased as internal water deficits in trees increased, indicating that drought often predisposed trees to attack by bark beetles.

(4) It is very difficult to appraise clearly the mechanisms by which water deficits adversely affect plant growth. One reason for this is that the internal water status of a plant is a dynamic parameter, influenced by conditions in the soil and atmosphere and regulated to various degrees in different situations and with different species by physiological factors. Another difficulty is that internal water deficits affect plant growth in many ways, both directly and indirectly. Hence, cause and effect relationships are difficult to assign (43).

(5) Internal water balance of plants is rapidly altered. Even well-rooted plants may have a very favorable internal water balance and within a matter of minutes they can develop severe internal water deficits, causing them to wilt. Thus, water deficiency develops much more rapidly than deficiency of other internal requirements for growth such as carbohydrates, hormones or minerals. For these several reasons it behooves plant propagators to be familiar with causes, effects, and control of water deficits in plants.

### MEASUREMENT OF WATER DEFICITS

As internal water deficits in plants control plant growth they need to be characterized and measured. This has been done in various ways, for example, by determining water content, relative water content (relative turgidity), saturation deficit, stomatal aperture, water potential, or shrinkage of plant tissues. The usefulness and limitations of these methods of determining water deficits in plants are discussed by Barrs (2).

Water that is subjected to molecular restraints is less free to enter into physiological reactions within plants than is pure free water. Restraints may result from differences in pressure, salt concentration, absorption at colloidal interfaces, confinement in capillaries, or inadequate water supply at a particular place. Many plant physiologists characterize water status of plants or soil in terms

of water potential — the difference in chemical potential of the water in the system and pure free water at the same temperature. This thermodynamic term represents the sum of all contributing factors to the water potential under any given set of external conditions. Its major components include 1) a pressure potential resulting from net pressure difference such as occurs as a result of turgor pressure in plants or hydraulic pressure in saturated soils, 2) a matric potential attributable to the colloidal matrix of the soil or plant system, and 3) a solute potential. The use of water potential to characterize water status in plants and soil has many advantages over other measurements (44).

### WATER RELATIONS DURING SEED GERMINATION

The effects of water deficits on seed germination have important implications in plant propagation and agriculture. Many plant propagators soak seeds to speed up germination. In regions of irrigation agriculture seed beds often are pre-irrigated and planted shortly thereafter. In areas of dry-land agriculture seeding usually follows a period of rain. When soil moisture supplies are low, catch crops such as milo (*Sorghum vulgare*) or safflower (*Carthamus tinctorius*) are often used (9).

Most seeds need to absorb water to trigger the metabolic processes associated with germination. Only small amounts of water are needed to initiate these biochemical activities. However, once such processes are underway, the seed and the germinant thereafter require increasingly larger amounts of water and in continuous supply. Desiccation after germination begins often is very harmful.

The degree of protoplasmic hydration necessary to stimulate seed germination varies greatly among species, and only a few examples will be given. Most seeds can absorb enough water for germination if soil is at field capacity. Some vegetable seeds, however, can germinate in soil which has dried to wilting percentage. Seeds of Hinoki cypress (*Chamaecyparis obtusa*), Japanese red pine (*Pinus densiflora*) and Japanese black pine (*Pinus thunbergiana*) germinated when soil moisture tension was 8 atm. or less. Above this value seed germination of each of these species declined as soil dried further. The greatest decrease in germination with increasing of soil moisture deficit occurred in *Chamaecyparis obtusa* (42). Kaufmann (15) studied the effects of water deficits on the rate of seed germination of sweet orange (*Citrus sinensis* 'Argentina'), sunflower (*Helianthus annuus* 'Mammoth Russian'), and lettuce (*Lactuca sativa* 'Phoenix'). Germination of lettuce or orange seeds occurred only when water deficits were low (at water potentials above  $-4.1$  or  $-4.7$  bars). Water availability was less critical for germination of sunflower seeds as they germinated well at  $-4.1$  and slowly at  $-8.0$  bars.

Some seeds can germinate in very dry soils. Owen (41) for example, showed that about 20 per cent of wheat seeds germinated when soil moisture content was below the permanent wilting percentage. The critical level of moisture stress at which germination was completely inhibited was not reached. It should be remembered that permeability of seed coats to water varies greatly among species. For example, the coats of many legume seeds inhibit water uptake. Some portions of seeds may also be more permeable than others. According to Koller and Roth (17), germination of *Panicum turgidum* seeds depended on whether the flat or convex side was in contact with the moist substrate.

Most seeds have an optimum period of moistening before germination. Species also vary in the capacity of their seeds to germinate following prolonged immersion in water. Soaking seeds of many species for a few hours often accelerates germination whereas prolonged immersion may injure seeds or decrease their viability. Soaking seeds of white pine (*Pinus strobus*) for 70 hours has harmful effects on germination. By comparison, seeds of tupelo gum (*Nyssa aquatica*) survive submersion of 7 months and of bald cypress (*Taxodium distichum*) for 30 months. However, these seeds do not germinate under water (38). It is well known that seeds of many weeds, especially those of aquatic habitats, can survive immersion for months.

Water also plays an important role in stimulating germination of seeds which are dormant because they contain water-soluble inhibitors. For example, seed germination in hot and dry regions often is geared to the short wet period of the year. When enough rain falls to wet the soil thoroughly the inhibitors are leached out of the seeds and the seeds are rehydrated, thereby creating internal conditions conducive to germination.

#### **DEVELOPMENT OF WATER DEFICITS IN LEAFY PLANTS**

Under ideal conditions with free access to unlimited water supplies leafy plants transpire vast amounts of water. However, the amount actually lost varies greatly with soil water availability and other factors. Most of the water lost escapes as vapor through the stomates which are the path of least resistance to diffusion of water vapor. Stomates generally are open in bright light and closed in the dark. They can also be closed by water deficits in the plant.

Internal water deficits in plants are controlled by relative rates of transpirational water loss from shoots and absorption of water through the roots. During the daytime more water is lost in transpiration than is replaced by absorption. Therefore, plants tend to be depleted of water during the day, especially on hot sunny days. During the night, however, both transpiration and absorption are low but the rate of

absorption exceeds transpiration and plants 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 translocation pathway from the soil through the plant and into the air. For example, some resistance to translocation of water occurs in the soil and in roots, stems, and leaves.

It should be obvious that internal water deficits in plants will result from excessive transpiration or slow absorption of water from dry, cold, or poorly aerated soils or, more commonly, from a combination of both. Absorption of water and transpiration are partly controlled by different sets of factors. Transpiration is largely controlled by atmospheric factors (primarily light, humidity, temperature, wind) as well as by structure of leaves and opening and closing of stomates. Absorption is controlled by transpiration rate and also by the size and distribution of the root system and soil factors (primarily soil water availability, temperature, concentration of the soil solution, aeration, etc.). Temporary wilting of leaves in the afternoon often occurs because of excessive transpiration. This is not serious if the soil is well-watered because the leaves usually recover turgidity at night (when transpiration is low and absorption is somewhat higher). When soils begin to dry out, however, temporary wilting of leaves tends to become more permanent because leaves are less likely to recover turgidity at night (35, 36).

The recurrent daily development of internal water deficits in plants is shown by afternoon decreases in moisture content of plant tissues and by shrinkage of various plant parts including leaves, stems, roots, as well as fruits and cones (6, 7, 8, 20, 21, 25).

### EXPANSION AND CONTRACTION OF STEMS

As a result of recurrent dehydration and rehydration tree stems usually shrink slightly during the day and expand at night (Fig. 1) (18, 19, 22). Kozłowski and Winget (32) found that amounts of daily shrinking of tree stems in Wisconsin varied greatly during the summer, with small amounts occurring early in the growing season, followed by increased shrinkage in midseason, and greatly decreased shrinkage in late summer after transpiration had depleted the soil and tree reserves of water.

In addition to reversible diurnal stem shrinkage, seasonal shrinkage of stems occurs commonly during droughts. The radial decrease of stems during droughts often exceeds the amount of radial increase as a result of cambial growth during the same period. For example, many large white pine (*Pinus strobus*) stems in New England showed net weekly radial decreases during the summer (4). Dimock (11) reported that Douglas fir (*Pseudotsuga menziesii*) stems

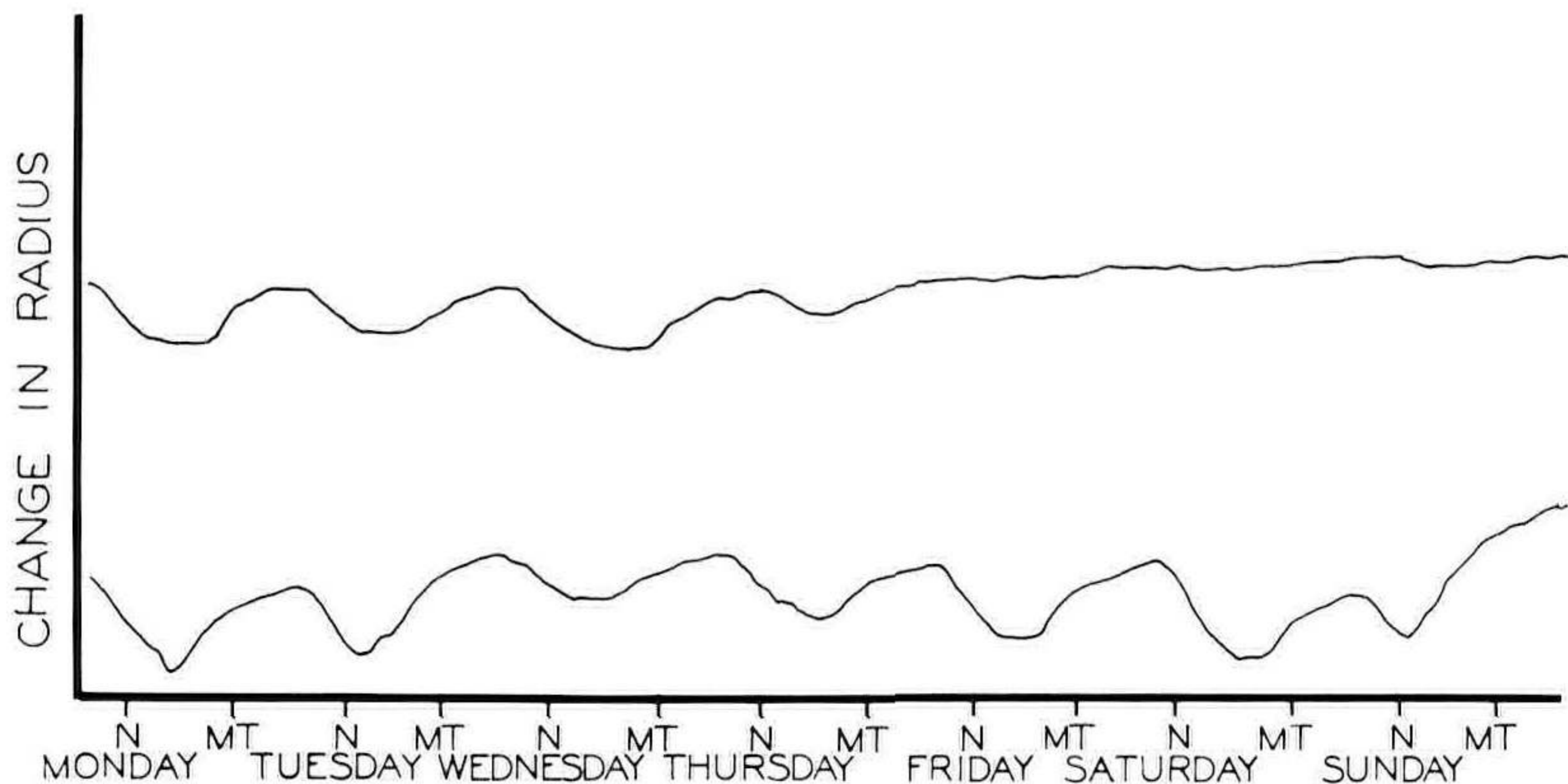


Fig. 1.

Dendrograph record showing shrinkage of red pine (*Pinus resinosa*) stems in the afternoon followed by expansion during the night. The upper curve is for July 10-17 and the lower curve for August 21-28. Note lack of stem shrinkage and expansion during the latter part of the week (upper curve) when cloudy and rainy weather occurred. From Kozlowski (25).

shrank consistently during a 6-week period in the summer. Buell, Small, and Monk (5) demonstrated that during a severe drought in New Jersey in August of 1957 tree stems shrank so much that their diameters were smaller than they were before the growing season started. When internal water balance was finally restored by rains in December the tree stems expanded rapidly. Kozlowski, Winget, and Torrie (33) recorded marked swelling of tree stems on each day following a rain during the summer.

#### EXPANSION AND CONTRACTION OF REPRODUCTIVE TISSUES

There is considerable evidence of shrinkage of reproductive tissues during the day and expansion at night because of hydration changes (20, 21). Excessive transpirational losses of water in the afternoon create high water deficits in the leaves and water is extracted from the fruits. At night when stomates close the fruits tend to refill with water. Diurnal expansion and shrinkage of fruits have been reported for a variety of fruits including cherries, oranges, apples, plums, walnuts, pears, avocados, and acorns, as well as cones or strobili of gymnosperms (21). Our experiments showed that Montmorency cherry (*Prunus cerasus*) fruits that were in a mid-stage of development often shrank during the morning and afternoon and they expanded beginning in late afternoon and continuing into the night (Fig. 2). The time of beginning as well as the amount and duration of diurnal shrinkage of cherry fruits varied with the stage of fruit development, soil moisture availability, weather, and degree of internal water stress in the tree (23).

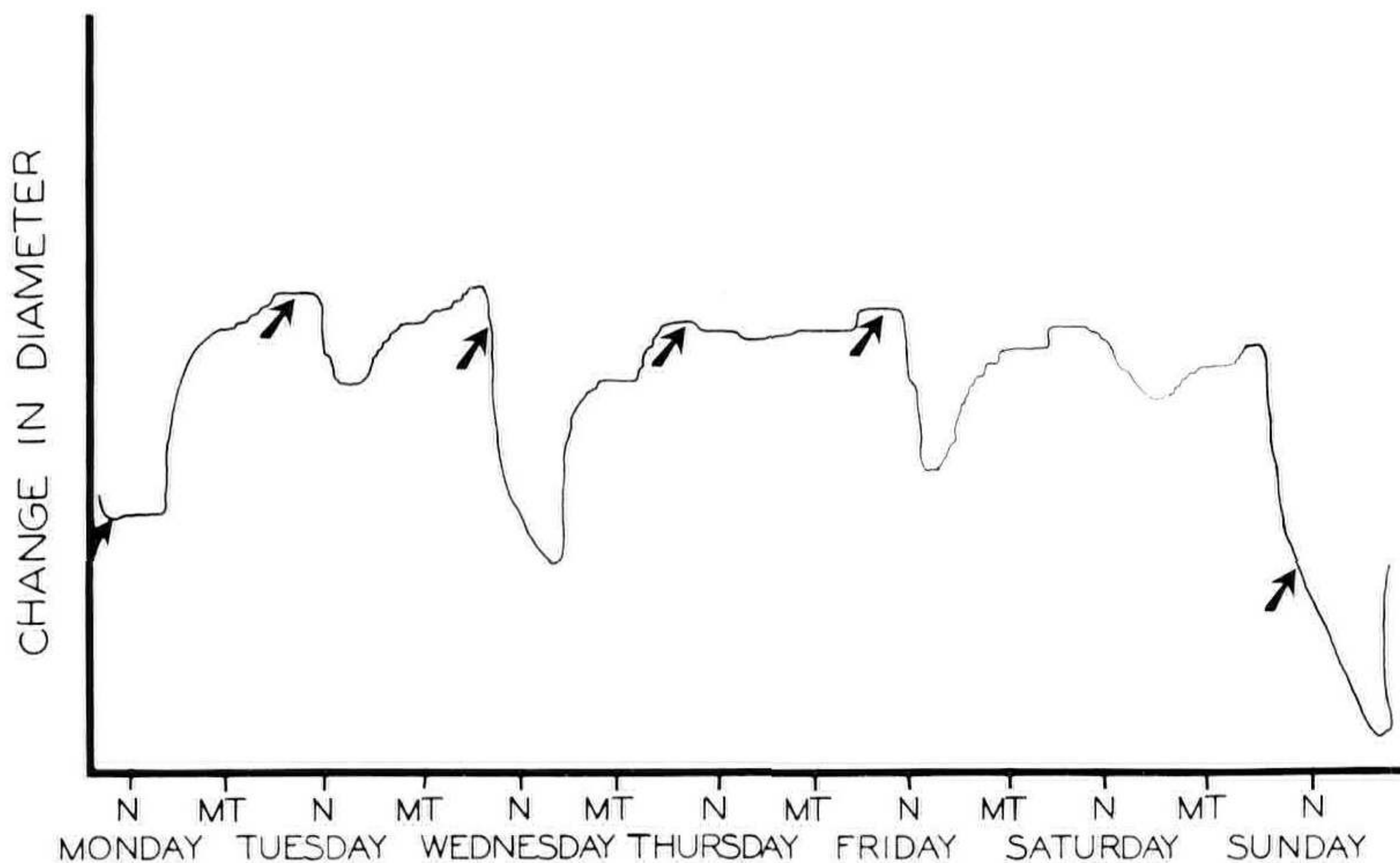


Fig. 2.

Recurrent daily shrinkage and expansion of fruits of Montmorency cherry (*Prunus cerasus*) as a result of changes in internal water balance. The arrows indicate time of irrigation. From Kozlowski (25).

Even when the soil was well-watered leaf thickness of Calamondin orange (*Citrus nitus*) began to decrease around sunrise when stomata opened and transpiration began. The fruit, however, did not begin to contract until about 1.5 hours after sunrise. Transpiration for about 1.5 hours apparently resulted in a water potential gradient from the fruit to leaves and water was translocated from the fruit along a free energy gradient (29). Klepper (16) found that such a gradient existed between fruits and leaves of pear trees. During droughts daily shrinkage of fruits and leaves continued until later in the day than when trees were well-irrigated.

Bartholomew (3) showed that during the afternoon of a hot, dry day lemons attached to trees shrank, but they expanded at night. Lemons attached to the tree lost a third more water than detached ones, emphasizing that attached lemons were a water-reservoir for other tissues. The drier the soil became the greater was the amount of water withdrawn from the fruits. Other evidence indicates that fruits act as water reservoirs in plants. For example, shoots pruned from plants bearing fruits do not wilt as rapidly as non-bearing shoots. Also fruits on pruned-off branches usually soften faster than fruits picked off the tree (23).

The cones of gymnosperms also undergo periodic water deficits, with the amount of diurnal shrinkage varying with the stage of cone development. Early in their development cones of white spruce (*Picea glauca*), red pine (*Pinus resinosa*), and jack pine (*Pinus banksiana*) exhibited a predominantly stepwise increase in diameter with little or no midday shrinkage. After the major surge of early-



season cone growth was completed, the cones showed recurrent shrinkage during the day and expansion at night. Maturing cones showed progressive overall shrinkage prior to opening. Percentage moisture of maturing cones decreased markedly in late summer (7, 10).

### WATER RELATIONS OF TRANSPLANTS

Undoubtedly the most important cause of reduced growth or death of transplants is desiccation resulting from excessive transpiration and reduced absorption of water. Transplants undergo a massive physiological shock, because their uprooting and subsequent handling in a barerooted condition may cause critical drying. Even after plants are reset in the ground, excessive water loss occurs since roots grow often too slowly to absorb enough water to keep up with transpirational losses (34, 36). Trees which survive transplanting often exhibit reduced growth long afterward (24). For example, leader growth of white spruce was reduced by half in the first year after replanting. Furthermore, growth of some trees was reduced for as much as ten years following transplanting (39).

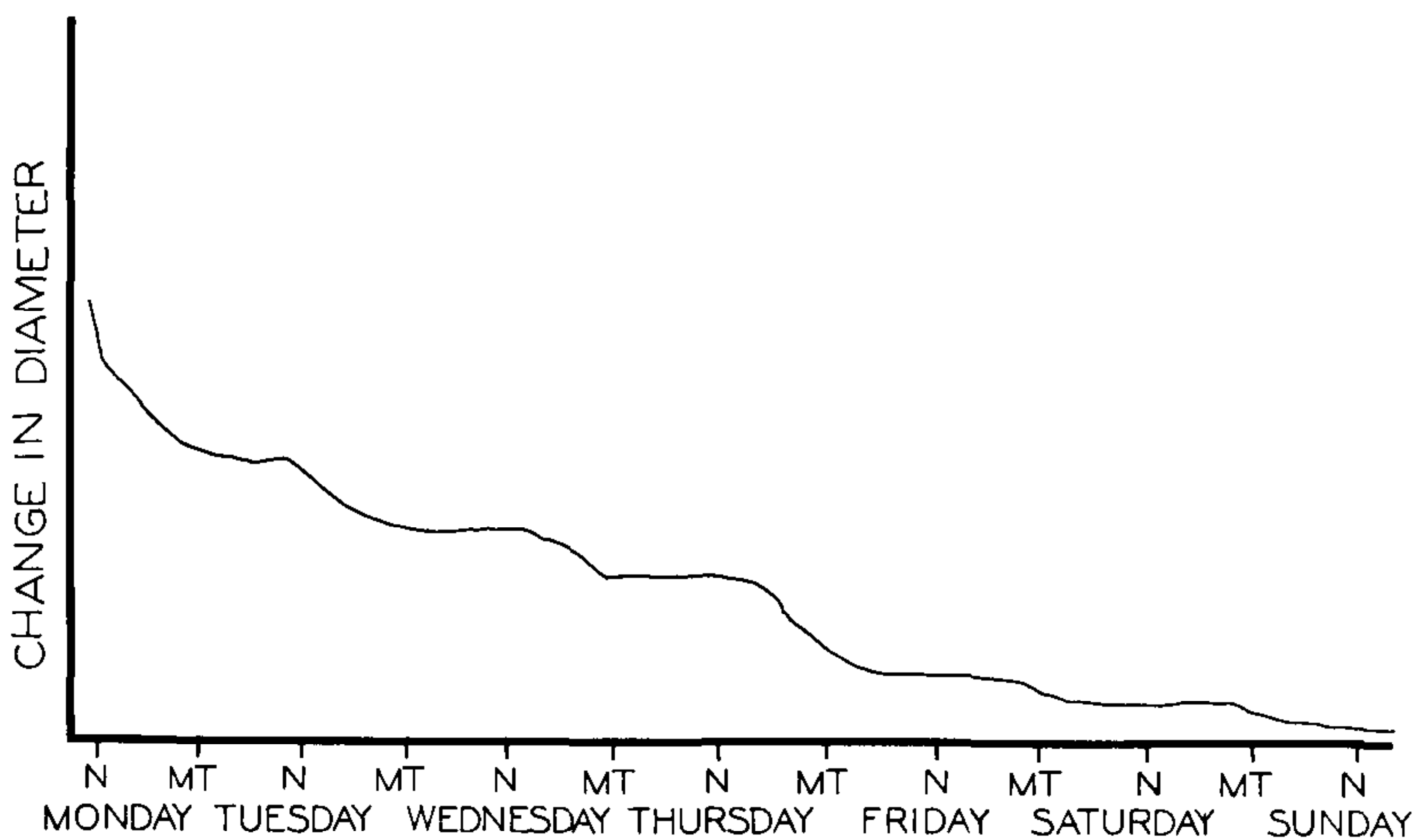


Fig. 3.

Progressive stem shrinkage resulting from excessive water loss from a young red pine (*Pinus resinosa*) tree during the first week after transplanting. From Kozlowski (25).

A very small percentage of trees removed from the nursery will rapidly restore a favorable internal water balance on out-planting. Actually, many transplants undergo very severe water deficits from the time they are lifted from the nursery until their roots become reestablished after planting. This takes a long time. Transpiration continues meanwhile and shoots may develop very severe water stresses. Research by Watanabe (47) in Japan showed that

moisture content of leaves of many transplanted one-year-old camphor (*Cinnamomum camphora*) seedlings often dropped to 30 per cent of that of control seedlings.

Our experiments confirmed development of severe water deficits in trees following transplanting. Even though soil moisture was maintained in the readily available range, many transplanted trees lost large amounts of water and stem diameters decreased each day (Fig. 3) (22). This indicated that transpirational losses repeatedly exceeded absorption rates, emphasizing the harmful effects of disrupting the soil-plant-air continuum during transplanting. Extreme variability of stem shrinkage among transplants pointed up the uncertainty of early reestablishment of individual trees. Such variations in reestablishment usually are related to differences in internal water deficits which often are due to differences in root-shoot balance of seedlings, variations in root regenerating potential, and amount of damage to fine roots in transplanting.

The capacity of transplants to resume root growth rapidly often is critical to survival. Capillary movement of water from wet to dry regions in soils at or below field capacity is slow. When there is little or no capillary water movement toward roots, continuous root extension becomes essential for absorption of enough water to sustain growth (37). As Kramer (34) stated, the water in the mass of soil into which roots do not grow is essentially unavailable to plants. This means that plants with an inherent capacity to develop rapidly growing root systems are most likely to maintain a favorable water balance after transplanting.

If the root surface is not adequate to supply transpirational losses, internal water deficits are likely to develop. Reduction of the size of the root system relative to size of the shoot by fertilizers, eradicants, mechanical injury, diseases, or insects often causes severe water deficits in the top.

### CONTROL OF WATER BALANCE

Plants have three basic means for controlling their internal water balance — absorption, transpiration, and internal redistribution. A favorable internal water balance is fostered by high absorption and low transpiration rates. Absorption of water can be promoted by keeping soil moisture supplies readily available. Although this seems to be widely understood it too often is neglected in practice, especially following transplanting. Much apparent drought resistance is traceable to deep and branched root systems of plants. Hence, some plant breeders are giving attention to development of seedlings with deeply penetrating and profusely branching root systems.

Allen (1) demonstrated that most outplanted longleaf pine (*Pinus palustris*) trees died simply because they lost water faster than their

recently disturbed and damaged roots could supply it. Reducing the amount of needle surface by clipping affected the top-root balance and decreased transpiration. Average increases in survival of transplants following clipping of needles varied from 10 to 30 percent, and sometimes exceeded 50 percent.

Plant propagators can do much to insure that transplants do not desiccate to critical levels. Use of polythene packaging has been helpful in conserving moisture of planting stock (12). It should be remembered that exposure of nursery stock to drying for even short periods of time may have serious effects on their growth and survival, but this varies with species and condition of the plants at the time they are exposed (29). In one experiment, exposure of Douglas-fir nursery stock for as little as 4 minutes affected survival (13). In another experiment Hermann (14) exposed two-year-old Douglas-fir plants at 90 degrees F and 30 percent relative humidity for periods up to 120 minutes. Survival by November of the year of field planting decreased with each added length of exposure. Critical limits of exposure varied with the physiological condition of the nursery stock. Whereas seedlings lifted in the autumn could not survive more than a few minutes of exposure, those lifted in the winter could survive exposure up to 30 minutes. These differences appeared to be related to capacity for root regeneration. Prolonged storage of nursery stock also increased susceptibility to exposure. Even if long exposures did not reduce survival, they caused slow growth of transplants. Thus the importance of keeping exposure of nursery stock to a minimum during transplanting was demonstrated.

Much attention is being given to influencing internal water balance of plants by controlling transpirational water loss. The benefits of preventing or reducing transpirational losses of cuttings by water mists are well known to plant propagators and will not be discussed further. Attention has also been given by plant breeders to producing plants with thick cutin and very responsive stomata which will conserve water during droughts. Reducing energy absorption by modifying leaf color or leaf arrangement may also be helpful.

There is a great deal of interest in maintaining a favorable water balance in plants by use of antitranspirants. Over the years scores of compounds have been applied, including oils, plastic films, wax emulsions, and metabolic inhibitors. The results have been variable. Film type antitranspirants reduced transpiration effectively in some cases but not others. Many leaf coatings which physically blocked stomata, have been disappointing. Whereas they reduced transpiration, they also checked photosynthesis and eventually the treated plants died or their growth was greatly reduced.

The fairly recent discovery that antitranspirants which operate as metabolic inhibitors can prevent opening of stomata in the light and induce closure of already open stomates was a very important con-

tribution (48, 49). Zelitch (48) observed that hydroxysulfonates effectively inhibited the enzyme glycolic oxidase and caused rapid changes in products formed during photosynthesis. When somewhat wilted plants were supplied with such an inhibitor of glycolic oxidase, the rate of transpiration decreased and the leaves became turgid faster than did leaves of control plants. The metabolic antitranspirant appeared to influence the osmotic pressure of guard cells and thus controlled stomatal aperture. Zelitch and Waggoner (50, 51) reported that phenylmercuric acetate sprayed on leaves at concentrations of  $10^{-4}$  M caused stomates to close for about 2 weeks. In our laboratory



Fig. 4.

Stages (left to right) in stomatal closure of white birch (*Betula papyrifera*) leaves following treatment with phenylmercuric acetate. From Waisel, Borger, and Kozłowski (46).

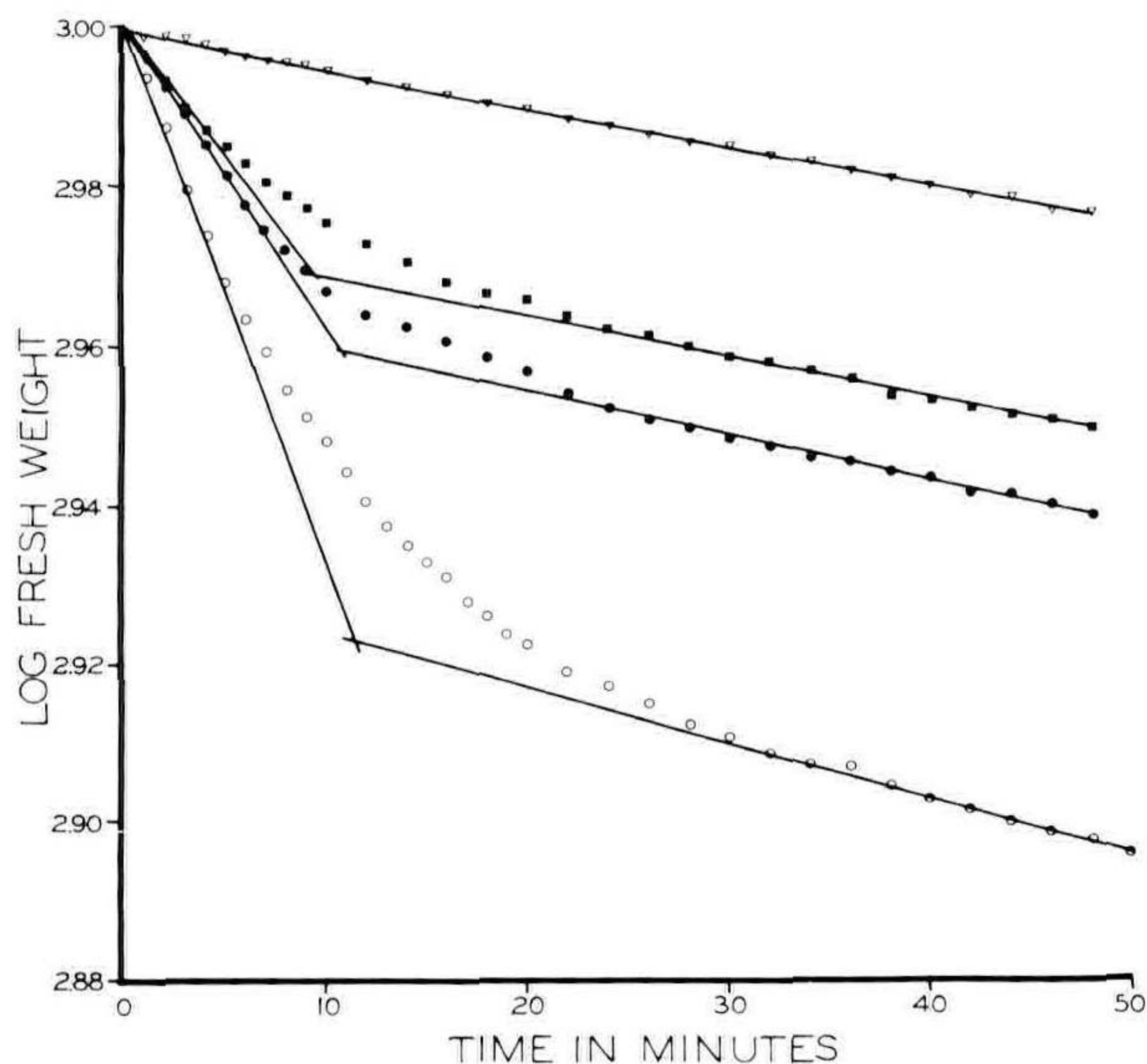


Fig. 5.

Effect of phenylmercuric acetate (PMA) on stomatal closure as shown by transpiration-decline curves of treated and untreated leaves of white birch (*Betula papyrifera*). ( $\Delta$  —  $10^{-3}$  M PMA;  $\blacksquare$  —  $10^{-4}$  M PMA;  $\bullet$  —  $10^{-5}$  M PMA;  $\circ$  — control. From Waisel, Borger, and Kozłowski (46).

we have also been able to induce stomatal closure of white birch (*Betula papyrifera*) leaves with phenylmercuric acetate sprays (4, 5). Although these results are exciting I cannot reemphasize too strongly that, because of toxic side effects, we need to do much more research with these metabolic antitranspirants. We observed for example that after leaves of white ash (*Fraxinus americana*) were dipped into alkenyl or decenylsuccinic acid (DSA) the efficiency of the cutinized layer of leaves in preventing water loss was decreased (30). We also found that sprays of DSA at concentrations of  $1 \times 10^{-1}$  M or greater applied to red pine trees in the summer, injured the leaves and adversely affected late summer development of buds. Shoot growth in the year after application of DSA was adversely affected (31). Thus the problems of dosages and kinds of chemicals to use are many. Extreme caution in the use of metabolic antitranspirants, in our present stage of knowledge, seems to be in order. Nevertheless, because the stakes are so high and some progress has been made in bringing about stomatal closure by metabolic inhibitors, we should continue research along these lines.

### DROUGHT RESISTANCE

Drought resistance of plants depends on their capacity to endure dehydration or to prevent it. Very great desiccation resistance is found in nearly all the main groups of lower plants. In contrast, very few species of higher plants can withstand water loss at least below 50 percent of the saturation water content without injury or death.

Plants have many different structural features which contribute to drought tolerance and it seems futile to seek a single cause in any one species (20). Contributing adaptations may be found in roots, stems, or leaves. Plant survival in xeric habitats often bears a close relation to depth and spread of root systems. Whereas shallow-rooted plants often show marked damage during dry periods those with unusually deep roots are drought-tolerant. Reduction of the transpiring surface by leaf abscission during the dry season is another effective adaptation to drought. This is more important in angiosperms than gymnosperms, and is considered the most important factor in water economy and survival of desert plants of the Near East. In that region larger winter leaves abscise in summer and are replaced by smaller ones. The total reduction in leaf dry weight may be as high as 85 percent. Even in trees in a leafless state, some transpiration occurs through twigs, branches, and buds. Therefore, slow water absorption is necessary in leafless plants (28).

Another factor in drought tolerance is capacity for rapid stomatal closure during droughts. After stomatal closure occurs, cuticular control of transpiration becomes very important. Some species lose almost no water through the epidermis whereas others lose large amounts and therefore have little resistance to drought (40). In some

species drought resistance often is vested in more than one structural feature in the same plant. In Brazil, for example, transpiration of certain trees and shrubs is greatly reduced by stomatal closure during early phases of drought, but as drought severity increases, leaf abscission follows (20).

Certain plants are able to conserve water by rolling of their leaves. In some grasses, with thickened epidermis walls reinforced by a ring of fibers and few stomata sunken in grooves, leaf rolling is very effective in preventing water loss. Such grasses, (*Stipa spp.*), in the Mediterranean region reduced transpiration by 60 percent through rolling of their leaves. It should be emphasized also that in many plants leaf rolling occurs at high water deficits only and the leaf may die before the mechanism can prove helpful.

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BILL FLEMER: Thank you very much, Ted. As you can see this is a rather complex subject and one which is not conducive to being handled by a 10-minute talk.

Our next speaker is well known to us all — Dr. Sidney Waxman. Sid is going to discuss another aspect of the environment which we must manipulate in propagating plants, and that is light, its duration, its quality and its intensity; Sid.

## LIGHT: DURATION, QUALITY, INTENSITY

SIDNEY WAXMAN

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Before discussing any of the various aspects of light or its influences on plant growth, it must first be understood that there are three basic factors: light intensity, light quality and light duration which all interact with each other. The overall influence on vegetative growth, flowering or some other response is the product of these three factors operating simultaneously. There are many other factors that may alter a plant's response to light; the most important one is temperature.

### I. LIGHT INTENSITY

Jan Ingen-Housz, in articles dating back to 1779, was among the first to recognize that light was an important factor in photosynthesis. He reported on experiments in which he found that "plants purified the air only in light, whereas in the dark the same tissues made the air impure". He also noted that this process became more active with a higher intensity of light and that under heavily shaded conditions "the plants acted upon the air just as animals." In 1800 it was first considered by Jean Senebier, that the oxygen given off during photosynthesis came from the carbon dioxide absorbed by the plant. Senebier also reported, when using stained glass of various colors, that it was the red rays of the spectrum that were chiefly effective in the photosynthetic process.