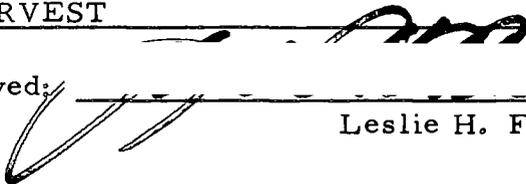


AN ABSTRACT OF THE THESIS OF

Mary Louise Hotze for the degree of Doctor of Philosophy

in Horticulture presented on May 5, 1976

Title: INDICATORS OF DECIDUOUS SHADE TREE DEVELOPMENT
USEFUL FOR TIMING CHEMICAL DEFOLIATION
AND HARVEST

Abstract approved:  Leslie H. Fuchigami

In the mild climate of the Pacific Northwest, the harvesting of deciduous shade trees in wholesale nurseries is prolonged from October to January because of autumn growth and prolonged leaf retention. Economically, it is advantageous to defoliate nursery trees at the earliest possible date. Premature defoliation, however, can cause die back or predispose trees to over-wintering damage or poor performance the subsequent year.

The purpose of this study was to identify and characterize the physiological stage of development at which leaves can be removed from deciduous trees without adversely affecting survival and regrowth. This physiological stage was termed "interfronoe."  Interfronoe could not be reliably predicted from visual growth phenomena such as leaf coloration, leaf fall, and terminal bud formation.

Preliminary data showed that stems and roots of plants unharmed by defoliation were less hydrated and contained higher concentrations of soluble carbohydrates than less mature plants which were damaged. It was hypothesized that osmotic potential of cells and the ionic status of cytoplasm were considerably different in interfronoe vs. pre-interfronoe plants, and that these differences could be used to predict interfronoe.

The hypothesis was tested by studying the influence of defoliation on uniform Cornus stolonifera Michx. plants grown under controlled SD or LD conditions for 10 wks, and 2 years of study on field-grown nursery stock. In the controlled study, xylem water potential and turgor pressure of SD-10 hr plants in interfronoe were generally lower than in pre-interfronoe plants grown at LD-16 hr days. Sequential hand defoliation showed that 60 days of SD treatment induced interfronoe in C. stolonifera. The xylem water potential also reached its lowest point after 60 days of SD exposure. Defoliation prior to interfronoe caused bud and stem die back and stimulated refoliation.

In 1974, phenological observations were made on 59 cultivars of 25 species. Observations were made of leaf expansion, autumn leaf coloration, and terminal bud formation. On 12 cultivars of 5 species, measurements were made of xylem water potential and osmotic potential on terminal shoots. Turgor pressure was calculated. The

timing of these phenological and physiological changes was correlated with weather data. Data on each species were grouped for a multiple discriminant function analysis to determine the most reliable interfronoe indicators. Response to hand defoliation was used as the standard for establishing when plants entered interfronoe. A combined index of interfronoe based on xylem water potential, osmotic potential, and turgor pressure predicted the onset of interfronoe with a high degree of accuracy in Acer, Malus, Quercus, and Sorbus. In terms of subsequent performance (growth), the time of interfronoe ranged from Sept 16 to Nov 11 in the species studied.

Seasonal changes in water status of 38 cultivars of 22 shade tree species were determined under field conditions in 1975 since certain changes in water status appeared to coincide with onset of interfronoe in 1974. Predawn xylem water potential, osmotic potential, and turgor pressure values (water status) were determined at 2 wk intervals from July 26 to Nov 21. A multiple discriminant function analysis indicated that stem water status was reliable for measuring interfronoe in cultivars of Acer, Betula, Carpinus, Crataegus, Fraxinus, Gleditsia, Malus, Platanus, Quercus, Sorbus, and Tilia studied.

Chemical defoliantes were safely used to hasten leaf abscission by 4-8 wk when water status was used to predict interfronoe. Comparatively low xylem water potential measurements effectively timed the application of chemical defoliantes.

Relationships between interfronoe, dormancy, and the rest period and quiescence phases of dormancy are discussed and illustrated diagrammatically.

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Indicators of Deciduous Shade Tree Development
Useful for Timing Chemical Defoliation
and Harvest

by

Mary Louise Hotze

A THESIS

submitted to

Oregon State University

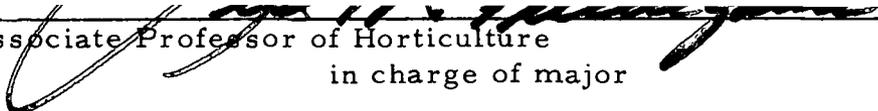
in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed May 1976

Commencement June 1976

APPROVED:


Associate Professor of Horticulture
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Date thesis is presented May 5, 1976

Typed by Mary Jo Stratton for Mary Louise Hotze

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INDICATORS OF DECIDUOUS SHADE TREE DEVELOPMENT
USEFUL FOR TIMING CHEMICAL DEFOLIATION
AND HARVEST

INTRODUCTION

The development of trees is seasonal. Adapted native plants survive because their cycles of growth and development are well synchronized with seasonal fluctuations. They respond to relatively subtle seasonal signals in the changing environment. These environmental signals set complex patterns of development into motion (48).

The growth and development of cultivated shade tree cultivars are often not well synchronized with the photoperiod, temperature, and rainfall in major production areas such as the Willamette Valley of Oregon where trees may grow 6 ft in one season. Such rapid and prolonged growth is desirable from the standpoint of production, but creates problems because harvests are delayed, ranging from Oct to Feb.

This study was designed to identify and physiologically characterize the stage of development at which the leaves could be removed from deciduous trees without affecting survival or regrowth. This distinct phase of development does not coincide with quiescence, dormancy, or the rest period. Hence, the term "interfronocce" was developed by the author to identify this stage. Interfronocce is of

Latin derivation: "intermissio" - interruption, cessation; "nocere" - to have a prejudicial influence; "frons" - foliage. Thus, the physiological stage of development at which leaves can be removed from deciduous trees without adversely affecting survival and regrowth after storage over winter.

The ultimate aim of the research was to develop a valid and simple index for predicting the onset of interfronoe of nursery trees. The timing of interfronoe can be identified experimentally by hand defoliating plants at various stages of development and assessing subsequent tree mortality, susceptibility to stresses (disease, mechanical, and temperature), refoliation, and growth and vigor. Several indirect physiological characteristics are useful in pinpointing interfronoe. The combination of physiological measurements used to predict interfronoe in these studies is called the interfronoe index.

To be useful to nurserymen, an interfronoe index should accurately identify the earliest possible time for safely applying chemical defoliants. More specifically, it should provide a simple means to:

1. Speed the harvest of deciduous trees and shorten the prolonged Oct-Feb digging season;
2. Identify the stage at which trees become less vulnerable to disease and physical damage.

3. Identify the stage at which trees are capable of developing resistance.

In short, the interfronoe index should help speed the harvest, assure overwintering survival of nursery stock in storage, and assure that replanted trees will grow well after shipment.

The deciduous shade tree industry needs chemical means of modifying plant development; specifically, chemical defoliant. There are many defoliant on the market (82) but optimum times of application and possible undesirable side effects are not well established. Until plant-hormone interactions are elucidated, effective defoliation practices are unpredictable. Resolving why and how the timing of defoliation is crucial to tree survival and performance is a first step in elucidating such interactions.

Digging foliated trees is impractical because leaf transpiration results in water stress, and bulk storage of leafy plants restricts air circulation and promotes decay. Leaves also add considerable weight during digging and grading and create cleaning problems in grading facilities (82). Early autumn digging of completely defoliated trees can be 15-fold more efficient than late digging in Oregon nurseries when fields are water-logged, but trees dug later are often less subject to injury and death in storage. A better resolution of defoliation timing and techniques will help resolve these compromises in nursery management.

The effects of manual leaf removal on desiccation, susceptibility to disease, speed of bud break, growth rate, and ultimate survival can be used to quantify plant response to defoliation. In itself, it does not provide information on possible side effects of chemical defoliant, but comparative studies can resolve such questions.

Defoliation of Trees

Defoliation of a tree can impair its physiological function for a variety of reasons. The degree of impairment depends upon the timing and extent of defoliation, and the occurrence of other stresses. Defoliation during the early part of the growing season is especially injurious. The influence of defoliation on growth has been investigated on several coniferous and hardwood species. Mechanical defoliation of tamarack during the growing season caused growth loss and mortality (39). Complete manual defoliation of longleaf pine seedlings (13) and jack pine (109) caused tree mortality; partial defoliation elicited adventitious bud growth and reductions in internodal increments.

A loss of photosynthetic capacity during the growing season may render trees more susceptible to damage from other stresses. Defoliation, for example, has been recognized as one of the primary factors predisposing tree hosts of Armillaria mellea to infection (148).

Insect defoliation of Acer saccharum was a predisposing factor to maple blight (36).

Many deciduous tree species are especially sensitive to defoliation at certain stages of development. Generally, this period ranges from mid-June through August in temperate zone species of the northern hemisphere. In some species, it extends to mid-November. Giese (36) found that defoliation of sugar maple in mid-August in northern Wisconsin caused bud and branch die back. Defoliated branches leafed out but did not form mature buds before autumn frosts and die back resulted.

Typically, mature temperate zone plants grow during the first half of summer and then extension growth ceases and terminal buds form. Juvenile trees grow much later into the summer. Dormant-quiet buds may be forced into growth by defoliation until interfronoe.

Interfronoe is a developmental stage distinct from rest. Rest is defined as the stage of bud dormancy caused by internal physiological blocks which prevent growth even under ideal external conditions for growth. It applies to normally foliated or defoliated plants. Rest status is tested by observing bud growth, or lack thereof, after placing non-defoliated plants under long days and favorable temperatures. Interfronoe occurs 4-6 wk prior to rest in Cornus stolonifera (Fuchigami, personal communication). It is not

known why defoliation prior to interfronoe causes refoliation and bud and branch die back. The answer may well be complex. Leaf removal eliminates photoperiodic perception sites, a source of phytohormones, and the major transpirational surface of plants. Defoliation likely alters a sequential and inter-related series of metabolic adjustments. Physiological and biophysical changes involved in the numerous adaptive responses which occur in the autumn are almost certainly involved (151) particularly those influenced by food reserves, hormones synthesized in the leaves, and the water status in different parts of the plant.

Wargo et al. (149) found that severely defoliated trees which refoliated the same season had greatly reduced levels of starch in the roots. Their root starch levels were one-tenth as high as in non-defoliated trees and one-third as high as normal trees. Trees that were lightly to moderately defoliated did not refoliate the same season, and their root starch levels were equal to those in non-defoliated trees. The amount of food reserves is supposed to be closely correlated to growth in the early part of the growing season (74). Branch and bud die back caused by premature defoliation appears to involve more than a simple depletion of root food reserves (Fuchigami and Mackaness, unpublished data, 144, 151, 162).

Many hormonal changes and resulting physiological alterations occur in plants during late summer and autumn. Examples include:

Environment:

Shortening days induce leaf senescence and cold acclimation, etc. (1, 32, 33, 41, 52, 54, 84, 85, 97, 106, 107, 116, 137, 138, 143, 144, 145, 151)

Spectral changes in sunlight can alter cold acclimation, etc. (151).

Warm days and cool nights enhance cold acclimation (32, 33).

Plant:

ABA production increases as leaves mature (37, 38, 79, 84, 161, 162).

Auxin-stimulated ethylene production occurs in different concentrations in different tissues (84).

The upward flow of cytokinins in xylar sap declines to low level (92).

Results of hormone level alteration:

Ethylene induces auxin-inhibited growth (6, 50, 119, 120)

Ethylene promotes nucleic acid and enzyme synthesis which promotes leaf abscission, breaks rest in buds, inhibits lateral bud development in concert with auxin (4, 22, 23, 46, 59, 86, 119, 141).

ABA causes cessation of shoot growth, blocks RNA synthesis, thus inhibiting GA-induced enzyme production (46, 79).

ABA induces changing levels of GA and other promoters (61, 92, 122, 146, 162).

A plant from which mature leaves are removed before interfronocce may regrow because of insufficient levels of inhibitors and low auxin levels. In these thesis studies young leaves around the terminal bud were also removed when plants were manually defoliated. Refoliation was not vigorous, perhaps because of low auxin levels. The natural

autumnal decline of cytokinins is likely accentuated by leaf removal which probably reduces the upward movement of cytokinins in the xylar sap. Hormonal balances altered by defoliation may influence respiratory regulation. There may be a fast burning of food reserves.

There is normally a major reduction in stem water content in the autumn at the time of maturation of the pith cells (93). Removing leaves prior to interfronoe interferes with transpiration and undoubtedly affects plant water status. Perhaps the normal reduction in plant water content is delayed. The autumnal decrease in water content is attributed in part to root suberization (78, 93). If the roots are not fully suberized at the time of defoliation, this could further complicate interfronoe development.

Correlations between Environmental Factors
Affecting Interfronoe and Patterns of
Primary Shoot Growth

Periodicity of tree shoot growth is observed in all types of environments. In tropical trees, individual shoots pass through alternate periods of growth and dormancy (1, 41). One school of thought is that cyclic growth periodicity in tropical trees is attributable to "internal factors" that are independent of the environment. This view is based on asynchronous growth patterns and lack of correlation between environmental factors and growth periodicity (41). Other researchers believe that subtle environmental factors control the growth periodicity in tropical trees (1).

Increasing night length brings about the onset of bud dormancy in many woody plants. Cessation of shoot growth in species native to high latitudes and high elevations is often correlated with daylength (162). This photoperiodic effect is modified or overridden by temperature in some species. Other plants are insensitive to photoperiod (162). In the temperate zone tree growth is intermittent. Shortening days induce cessation of tree growth in many species, while others stop growing during the longest days of summer while temperature and soil moisture are conducive to growth. Other subtle environmental changes in the microclimate (e.g., water stress, light intensity, or temperature) may shift promoter/inhibitor balances causing either renewed activity or cessation of growth.

Although all trees of the temperate zones show intermittent growth, the manner in which primary growth occurs is highly variable among species. Kramer and Kozlowski (78) studied the rates and duration of growth in many young coniferous and deciduous trees. Nutritional relationships, patterns of bud release, and growth form of trees are affected by the pattern of primary growth. Patterns of shoot extension of intermittently growing trees may be grouped into four categories (162):

1. A single flush of terminal growth followed by formation of a resting bud (Quercus, Carya, Fraxinus, Sorbus, and many conifers).

2. Recurrent flushes of terminal growth with terminal bud formation at the end of each flush (Pinus of southern and southeastern U.S. and most evergreens and deciduous trees of the subtropics and tropics).
3. A flush of growth followed by shoot-tip abortion (Ulmus, Betula, Salix, Corylus, Ostrya, Syringa, Tilia, Robinia, Cercidiphyllum, Rhamnus, Carpinus, Platanus, Gleditsia, Diospyros, Catalpa, and Fagus).
4. A sustained flush of growth for extension of late-formed leaves prior to terminal bud formation (Liriodendron tulipifera and Liquidambar styraciflua L.).

Variations in growth cessation or initiation between the four categories of trees listed above are compounded by variations within each of the four categories. Growth cessation and initiation are thought to be under hormonal control (61, 106, 107, 139, 140, 141, 142, 145). Oversimplifications of this complex process are evident when growth cessation or initiation are attributed to a single hormone. A major growth inhibiting role has been attributed to ABA (64, 146). More recently, the role of promoter-inhibitor balances has been discussed, including ABA, auxins, cytokinins, gibberellins, and ethylene. Hormonal interactions in endogenous growth control are poorly understood (112, 122, 131).

A comprehensive theory is needed to explain the distinct cyclic periods of growth and dormancy in plants. Leopold (84) proposes that growth cessation involves balances between inhibitory and promotive plant hormones, particularly ABA and gibberellic acid. He suggests that the growth cessation stage is probably a state of

suppressed nucleic acid competence. Environmental cues for growth cessation lead to changes in the plant hormone components, which in turn serve to switch the nucleic acid system off (2, 146). On the contrary, cold acclimation and hardiness research indicate that growth cessation is an active time of physiological changes with increases in quantity and control by nucleic acids (46, 151).

Plant-Water Relations and Interfroncoce

A mature tree is generally less sensitive to moisture stress than a young tree (128) because the roots have colonized the available soil volume more intensively and extensively. Under normal conditions, the root and foliar systems establish an approximate balance that is adapted to the moisture supply (14). In root-pruned and transplanted nursery stock this balance is often upset.

Plant response to water stress has been the subject of several reviews in the past 10 years (28, 53, 70, 71, 73, 77, 118, 123). Recent reviews have emphasized: water interactions with biological macromolecules and membranes (60, 62, 129); water stress effects on metabolism and physiology (21, 77, 89, 123, 124, 132, 136); and water stress effects on growth, morphology, and ontogeny (35, 79, 121, 124, 160).

The chemical potential of water in plants is affected by hydrostatic pressure or tension, colligative effects of solutes, and

interaction with matrices of solids (cell wall) and macromolecules (53). Hence, ψ (water potential) is the algebraic sum of the component potentials arising from the effects of pressure (ψ_p), of solutes (ψ_s), and of matrix (ψ_m). Component potentials in plant-water relations are usually written as $\psi = \psi_p + \psi_s$. Matric potential is usually studied in systems with varying water contents (10) because it arises from forces exerted by adsorbed water, adsorbed solutes, and surface tension (7).

In fully turgid tissue the initial decreases in tissue water content cause large decreases in ψ making it more negative. Decreases in ψ_p are usually much more marked than decreases in ψ_s and account for the major part of the diminution in ψ (53). Hsiao (53) notes that decreases in ψ_s follow the simple osmotic relationship with solution volume. After more water is lost and ψ_p falls to a negligible level, decreases in ψ_s alone account for most of the further decrease in ψ . At this point the change in ψ per unit change in tissue water is small compared with that of the turgid state because ψ_p ceases to be a factor.

Water potential (ψ) is the fundamental measure of plant water status. Tissue ψ is a useful indicator of plant water status, and gradients of ψ govern water transport. Hsiao (53) indicated that ψ values per se may not be crucial in determining plant behavior. Effects of reductions in ψ on growth (110, 111) and on some metabolic

processes (45) were minimized or eliminated if turgor was maintained by providing the tissue with an easily absorbable solute. This was true even though tissue ψ remained at a reduced level. The maintenance of turgor appeared to be the critical factor in maintaining growth and regulating metabolic processes in the plant.

A hypothesis of this study, based on preliminary correlative data, was that changes in a plant's water status would coincide with the onset of interfrooze development. Physiological processes which are affected by water deficits and which change during interfrooze include:

Slowing down

The initiation and differentiation of vegetative and reproductive primordia in apical meristems.

Enlargement of cells thus differentiated.

Cell division and wall synthesis.

Protochlorophyll formation and nitrate reductase level.

Cytokinin level.

Transpiration and respiration.

Protein and carbohydrate synthesis and metabolism (53, 124).

Accumulations of ABA, proline, and CO_2 sufficient to partially account for stomatal closure (53, 124).

Suberization of the root system affecting its capacity to absorb water and nutrients (53, 124).

Hastening senescence of leaves (58, 59, 94, 95).

The significance of a plant's self-imposed reduction in tissue ψ during late summer is apparent. Reduction in stem and root moisture content is associated with acclimation to low temperature (93). Water stress can induce cold acclimation in red-osier dogwood (18), and artificial dehydration of excised stems will induce a limited (5 to 10°C) but rapid increase in cold tolerance (87). The hydration of plant tissues is under endogenous physiological control. Plants lose water and acclimate effectively in the summer and autumn even when soils are saturated.

Roots are a major source of resistance to water flow through plants (75, 76, 77). A 1.5-fold decrease in relative stomatal resistance of leaves and a 3.5-fold increase in resistance to water flow through roots at 0.15 bars tension occurred in red-osier dogwood prior to cold hardening to -12°C (93). It was suggested that a decrease in permeability of root cells to water occurred during this initial stage of acclimation (to -12°C). Suberization of root surfaces further reduced water uptake as plants became hardy to -45°C.

Initiation of vegetative and reproductive primordia in apical meristems ceases as soon as water stress is imposed and resumes soon after stress is removed. Cell wall synthesis appears to be quite sensitive to a drop of a few bars in ψ (19). There is some indication that this is due to increased ψ_p and not to lowered ψ_s . It is unclear whether curtailed wall synthesis is a cause or result of

reduced growth during stress. Cleland (19) showed that glucose incorporation decreased where there was a 3 to 4 bar reduction in coleoptile ψ_p , but that growth essentially stopped. This suggests that growth is more sensitive to water stress than wall synthesis. Reduced cell enlargement results from a lack of turgor (19).

The typical late summer cessation of growth in trees is due to a large number of environmental factors. Water stress is likely involved to some extent, but probably is not a predominant factor. Water stress in tissues of plants which are approaching maturity tends to hasten senescence (123).

Water stress has profound effect on hormonal distribution, particularly cytokinins and ABA (89). Wright (156) first observed an increase in an inhibitor, later identified as ABA (157), when excised wheat leaves wilted. When water stressed leaves decreased 9% in fresh weight, the ABA content increased several-fold in 2 hr (156) and as much as 40-fold in 4 hr (156). Similar ABA increases during water stress have since been observed in intact plants of several species (98, 100, 103, 161).

It has long been known that ethylene induces abscission (119). Leaf abscission occurs in response to water stress in many plants. In cotton (95) abscission of bolls or leaves was more or less proportional to the daily water deficit as indicated by predawn leaf ψ measurements. Circumstantial evidence suggests that abscission

induced by water stress may be controlled by endogenous ethylene production. Ethylene production by petioles on intact cotton plants tended to increase within hours after water deficits developed, and declined quickly on rewatering (95).

When exogenous ethylene and CO_2 were supplied to cotton plants (59), ethylene did not induce abscission at high ψ , but greatly enhanced abscission at low ψ . The threshold water deficit required for abscission was reduced by exogenous ethylene. Thus water stress seemed to predispose leaves to ethylene-induced abscission. CO_2 is often an inhibitor of ethylene action (119). In these studies it counteracted somewhat the promotive effect of exogenous ethylene on leaf abscission of stressed seedlings.

Nurserymen occasionally hasten the abscission of leaves of deciduous trees by subjecting the trees to various forms of water stress such as withholding irrigation water or undercutting and side pruning the root systems. Ethephon has also been used to enhance leaf abscission since it releases ethylene upon decomposing. The results of the studies reported herein indicate that these practices could be used more safely and effectively if precise measurements of ψ were used to program timing of Ethephon application.

Research Approach

As previously mentioned, the purpose of this study was to

identify and characterize the physiological stage of development at which leaves can be removed from deciduous trees without adversely affecting survival and regrowth. This physiological stage was termed interfronocce.

Preliminary data showed that stems and roots of plants unharmed by defoliation were less hydrated and contained higher concentrations of soluble carbohydrates than less mature plants which were damaged. It was hypothesized that osmotic potential of cells and the ionic status of cytoplasm were considerably different in interfronocce vs. pre-interfronocce plants, and that these differences could be used to predict interfronocce.

The hypothesis was tested by studying the influence of SD or LD treatment on uniform Cornus stolonifera Michx. plants grown under controlled conditions for 10 wks, and 2 years of study on field-grown nursery stock. In the controlled study, xylem water potential and turgor pressure of SD-10 hr plants in interfronocce were generally lower than in pre-interfronocce plants grown at LD-16 hr days. Sequential hand defoliation showed that 60 days of SD induction induced interfronocce in C. stolonifera. The xylem water potential also reached its lowest point after 60 short days. Defoliating prior to interfronocce caused bud and stem die back and stimulated refoliation.

In 1974, phenological observations were made on 59 cultivars of 25 species: number of trees with expanding leaves, times of autumn leaf coloration and terminal bud formation. On 12 cultivars of 5 species, xylem water potential, osmotic potential, and turgor pressure were made on terminal shoots. The timing of these phenological and physiological changes was correlated with weather data. Data on each species were grouped for a multiple discriminant function analysis to determine the most reliable interfronoe indicators. Response to hand defoliation was used as the standard for establishing when plants entered interfronoe. A combined index of interfronoe based on xylem water potential, osmotic potential, and turgor pressure predicted the onset of interfronoe with a high degree of accuracy in Acer, Malus, Quercus, and Sorbus. In terms of subsequent performance (growth), the critical time of defoliating ranged from Sept 16 to Nov 11 in the species studied, depending on specific cultivar receptivity to environmental stimuli.

Seasonal changes in water status of 38 cultivars of 22 shade tree species were determined under field conditions in 1975 since water status changes apparently coincided with onset of interfronoe. Predawn xylem water potential, osmotic potential, and turgor pressure values (water status) were determined at 2 wk intervals from July 26-Nov 21. A multiple discriminant function analysis indicated that stem water status was reliable for measuring interfronoe in

Acer, Betula, Carpinus, Crataegus, Fraxinus, Gleditsia, Malus,
Platanus, Quercus, Sorbus and Tilia.

The multiple discriminant function analysis (3) results in a linear function of interfronoe. For two levels of interfronoe (interfronoe vs. pre-interfronoe), two linear functions are developed, which differentiate the best predictors of interfronoe. Many variables can be inserted into the linear function as coefficients. Since the coefficients for the linear function are chosen to maximize the minimum distance between levels of interfronoe, it is possible to discriminate which variables are the best indicators of interfronoe by the percent of correctly classified interfronoe cases based on using those variables.

At the initiation of this experiment, a large set of observed variables were used and appropriate data were entered into each of the functions. It resulted in classification of the data variables into one of the two phases. Using xylem water potential, osmotic potential and turgor pressure as variables and two phases of interfronoe, the analysis produced two functions:

$$\text{Phase}_1 = A_{10} + A_{11} (\text{XWP}) + A_{12} (\text{OP}) + A_{13} (\text{TP})$$

$$\text{Phase}_2 = A_{20} + A_{21} (\text{XWP}) + A_{22} (\text{OP}) + A_{23} (\text{TP})$$

such that A_{10} and A_{20} are constants for Phase 1 and 2 of interfronoe, A_{11} and A_{21} are classification function coefficients for XWP,

A_{12} and A_{22} are classification function coefficients for OP, and A_{13} and A_{23} are classification function coefficients for TP. To classify a new case, if Phase 1 is greater than Phase 2 the new case is classified as Phase 1 of interfronocce. If Phase 2 is greater than Phase 1, the new case is classified in Phase 2 of interfronocce.

The balance of this thesis is presented in the form of two manuscripts written for submission to HortScience and Jour Am Soc Hort Sci respectively. The Appendix contains tables of data which will not be submitted for publication, but which are referred to in the manuscripts in their present form.

WATER STATUS OF RED-OSIER DOGWOOD AT
DIFFERENT PHOTOPERIODS¹

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Additional index words. defoliation, dormancy, xylem water potential

Abstract. The influence of photoperiod on plant water status was studied. Red-osier dogwood plants (Cornus stolonifera Michx.) were subjected to short (SD-10 hr) or long (LD-16 hr) photoperiods for 10 wks. Biweekly observations were made of xylem water potential and osmotic potential. Responses of stems to sequential hand defoliation were evaluated biweekly to establish the earliest stage of development at which plants could be defoliated without reducing survival or subsequent regrowth. This stage of plant development is termed interfronoe. In the SD treatment, interfronoe occurred after 60 days, while LD plants never reached interfronoe. Stems of plants defoliated prior to interfronoe died outright or suffered tip dieback. A low xylem water potential (increasingly negative) coincided with the interfronoe in SD plants. Xylem water potential measurements appear to be a useful means of predicting interfronoe.

¹Received for publication Published with the approval of the director of the Oregon State University Experiment Station as Journal Series No. From a dissertation submitted by the senior author in partial fulfillment of the requirements for the PhD degree at Oregon State University.

Introduction

The status of plant hydration is dependent upon soil moisture availability, atmospheric conditions, and the plant's ability to control water losses or uptake (123). As deciduous trees adapt from intensive transpiration in the summer to minimum transpiration after leaf abscission in the fall, water availability and movement in the plant are substantially altered (84).

A reduction in stem and root moisture content is associated with acclimation to low temperatures (85). Controlled desiccation induces cold acclimation in red-osier dogwood (18). It appears that the decrease in hydration of overwintering stems during cold acclimation results from decreased stomatal resistance and increased root resistance to water movement (93). Despite saturated soil, plant water content decreases in late summer and early autumn when plants acclimate.

Preliminary data showed that stems and roots of plants unharmed by defoliation were less hydrated and contained higher concentrations of soluble carbohydrates than less mature plants which were damaged. It was hypothesized that osmotic potential of cells and the ionic status of cytoplasm were considerably different in interfronoe vs. pre-interfronoe plants, and that these differences could be used to predict interfronoe. This distinct phase of development does not coincide with quiescence, dormancy, or rest period.

Hence, the term interfronoce was developed by the author to identify this stage of development. Interfronoce is of Latin derivation: "intermissio" - interruption, cessation; "nocere" - to have a prejudicial influence; "frons" - foliage. The physiological stage of development at which leaves can be removed from deciduous trees without adversely affecting survival and regrowth after storage over winter.

The ultimate aim of the research was to develop a valid and simple interfronoce index for predicting the onset of interfronoce of nursery trees. The timing of interfronoce can be identified experimentally by hand defoliating plants at various stages of development (33). It was hypothesized that xylem water potential (XWP) and osmotic potential (OP) of stem sections could be used to predict interfronoce, and specifically that short days (SD) induced water status changes in red-osier dogwood. This study was designed to assess plant water relations during SD induced interfronoce development and to assess the predictive value of water changes as an interfronoce indicator.

Materials and Methods

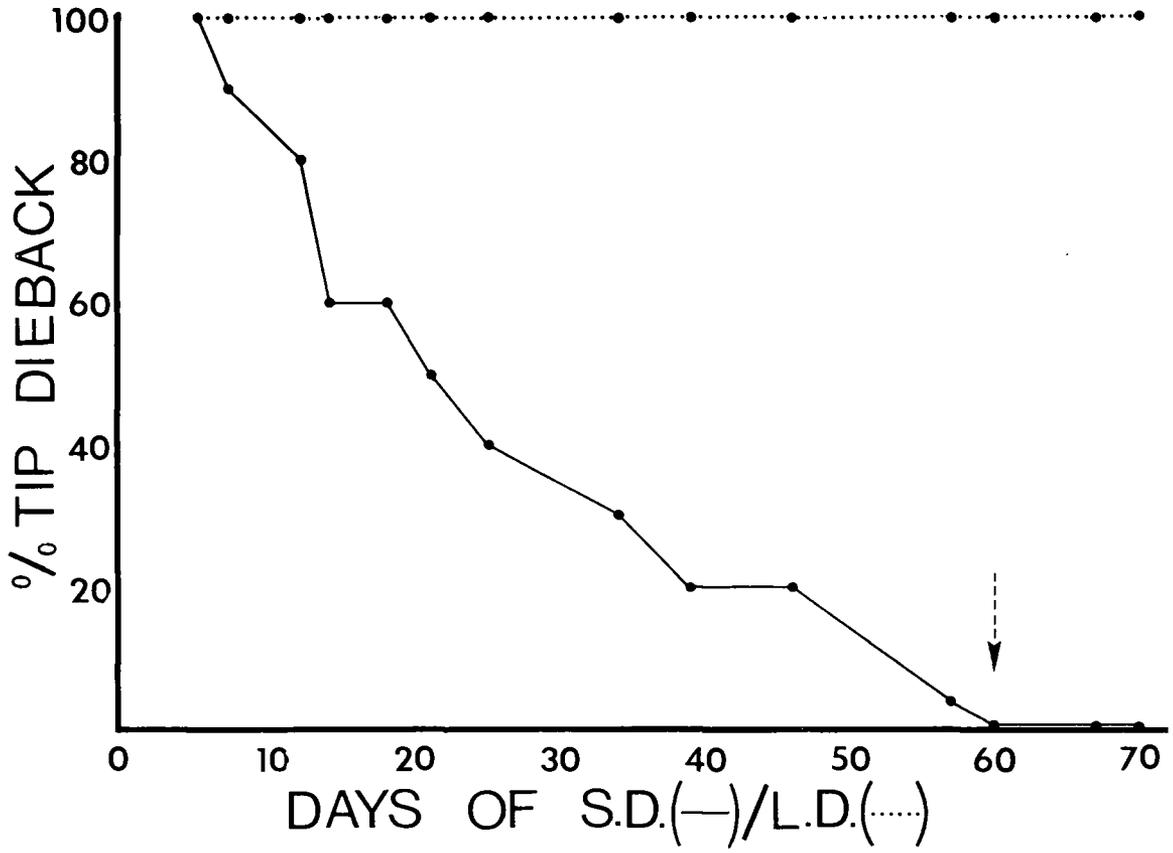
A clonal selection of red-osier dogwood, native to Wayland, Massachusetts was asexually propagated from cuttings during spring 1974. In May 1975, 200 uniform plants were placed either on a greenhouse bench under GE Lucalux lamps at a LD-16 hr photoperiod,

or in a Controlled Environment Model PGW-36 growth chamber (with an adjusted canopy having 75% input wattage of cool white fluorescent and 25% of incandescent lighting) at a SD-10 hr photoperiod. In both cases the day temp was $20 \pm 2^{\circ}\text{C}$, night temp was $15 \pm 2^{\circ}\text{C}$, relative humidity was $70 \pm 5\%$, light intensity was $3950 \mu\text{w}/\text{cm}^2$ at plant level. All plants were watered daily and fertilized weekly.

Measurements of XWP and OP were made twice a wk on 5 plants in each treatment. Pressure bomb measurements (150) of XWP were made on 2 internode stem tips. Dewpoint microvoltmeter measurements (15, 163) of OP were made on 2 internode stem tips, mid-sections, and stem bases. Turgor pressure (TP) of the stem terminal was calculated using the equation $\psi = \psi_p + \psi_s$, where ψ = water potential, ψ_p = turgor pressure, and ψ_s = osmotic potential (53). On each sampling date, 5 plants from the LD and SD treatments were hand defoliated and placed in a lathhouse for observation of overwinter survival and spring bud break and regrowth. Plants which re-foliated were defoliated daily during autumn. Plants which had been defoliated too early showed early signs of bud and stem dieback. The extent of stem dieback was measured in the spring of 1976. Tip dieback was expressed as % of the total stem: $\left(\frac{\text{length of dead stem}}{\text{total stem length}}\right)$. Each data point (Fig. 1) represents the average of 5 plants.

Data for XWP, OP, and TP were plotted and t-tests calculated (Appendix Table 1).

Fig. 1. Percent tip dieback in red-osier dogwood plants grown at long (16 hr) or short (10 hr) photoperiods and defoliated at 3 to 4 day intervals during the 70-day experimental period. Points on the graph indicate times of defoliation (5 plants in each treatment at each date). The arrow indicates onset of interfronoco.



Results

Plants under the SD treatment reached interfronocce after 60 days (Fig. 1), while the LD plants did not acquire interfronocce. SD plants which were defoliated prior to interfronocce sustained tip die-back ranging from 4 to 100% of the entire stem (Fig. 2). All defoliated LD plants died back 100% (Fig. 1). Stem sections which were not killed by premature defoliation showed varying degrees of bud break and regrowth the following spring depending upon the amount of damage incurred the previous season. Throughout the experimental period, XWP and TP was lower in the SD plants than in the LD plants (Fig. 3; Appendix Table 1) with the lowest XWP occurring after 59 days and lowest TP occurring after 25 days of SD treatment. In preliminary data of 1973 (Appendix Table 2) it was shown that red-osier dogwood plants in interfronocce had higher micromolar concentrations of N, K, P, Ca, Mg, Mn, Fe, Cu, B, Zn, Al, and soluble carbohydrates than pre-interfronocce plants. On this basis it was anticipated that OP changes might correlate well with the onset of interfronocce. This did not prove to be the case. When OP was measured separately on stem terminals, mid-sections, and stem bases in this study, there was no significant trend of OP change over time, nor any significant differences between OP in LD and SD treatments (Fig. 4, Appendix Table 1). Stem terminals generally

Fig. 2. Tip dieback on plants defoliated after 1, 2, 3, 7, 8, or 9 wks of SD treatment. (See numbers under plants.) Light stem areas are living tissue. Arrows indicate interface between living and dead portions of stems. After 60 days of SD treatment, there was no tip dieback on plants.

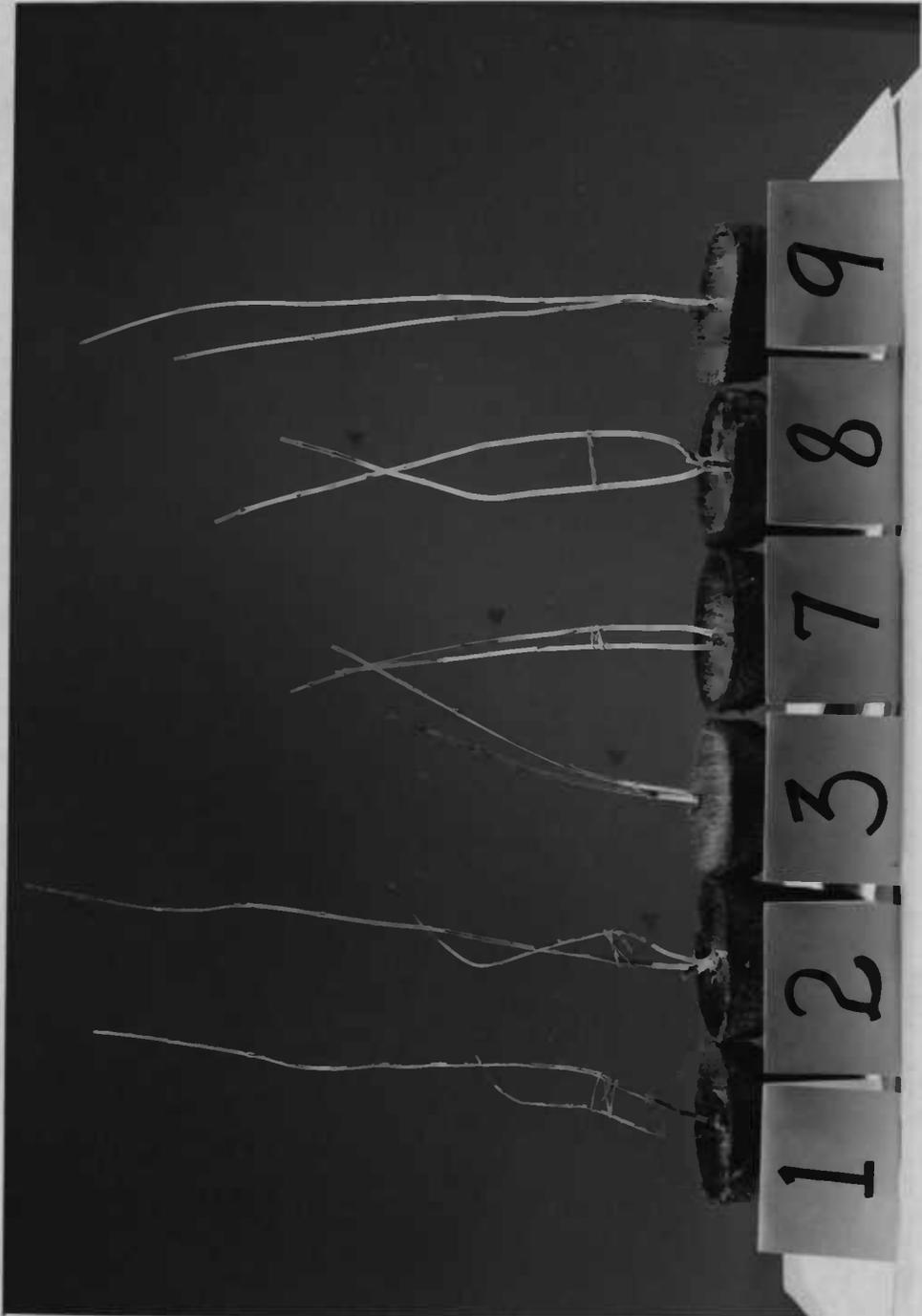


Fig. 3. XWP and TP of stem terminals (2 apical internodes) from plants grown at long (16 hr) or short (10 hr) photoperiod. Each XWP point represents 10 readings. TP was calculated. Interfronoe was reached after 60 days of SD treatment as indicated by arrow.

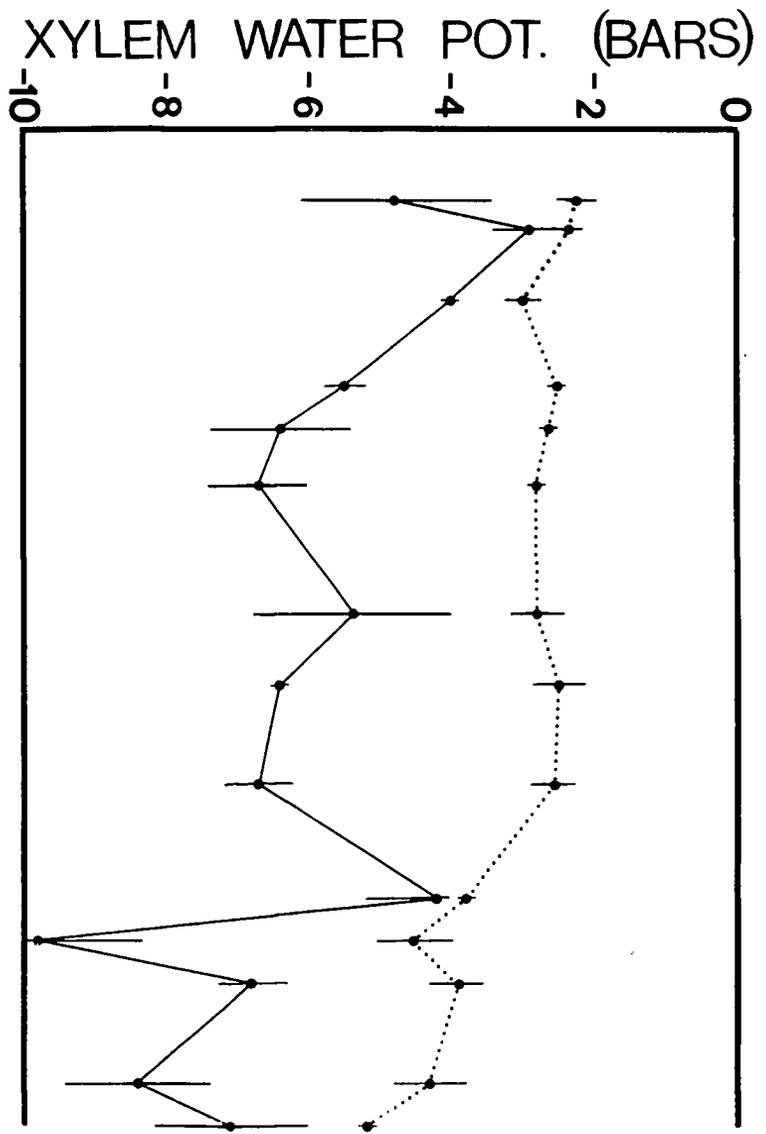
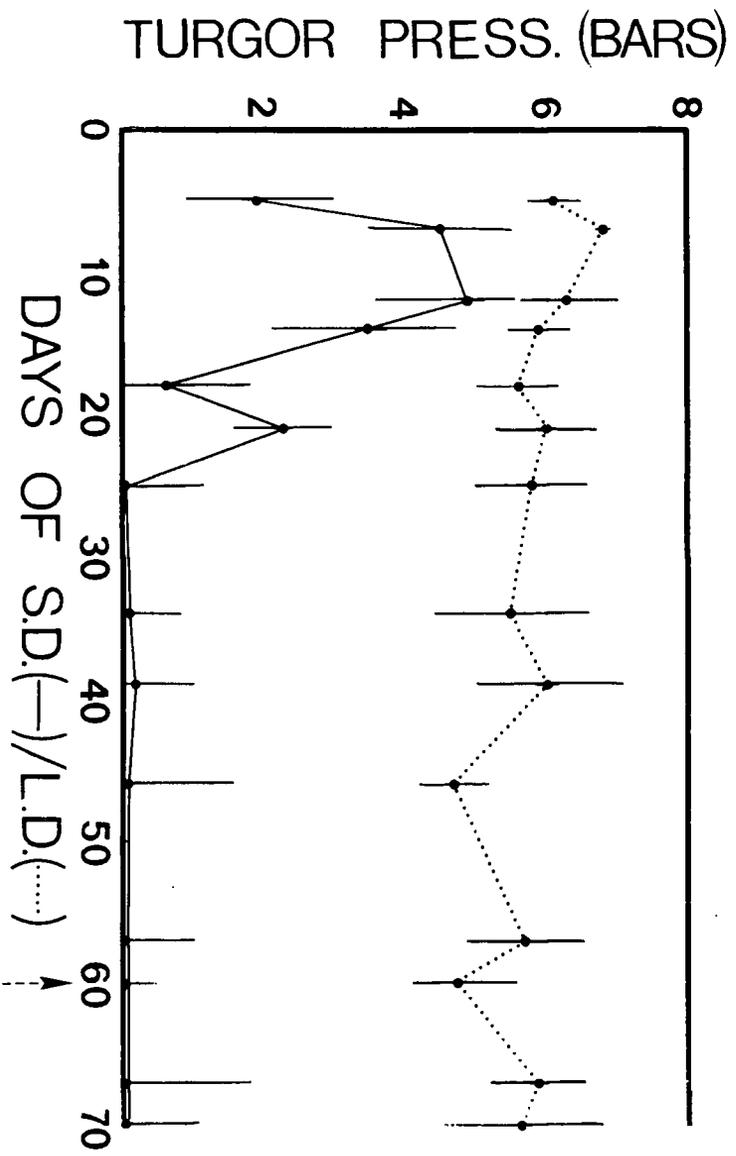
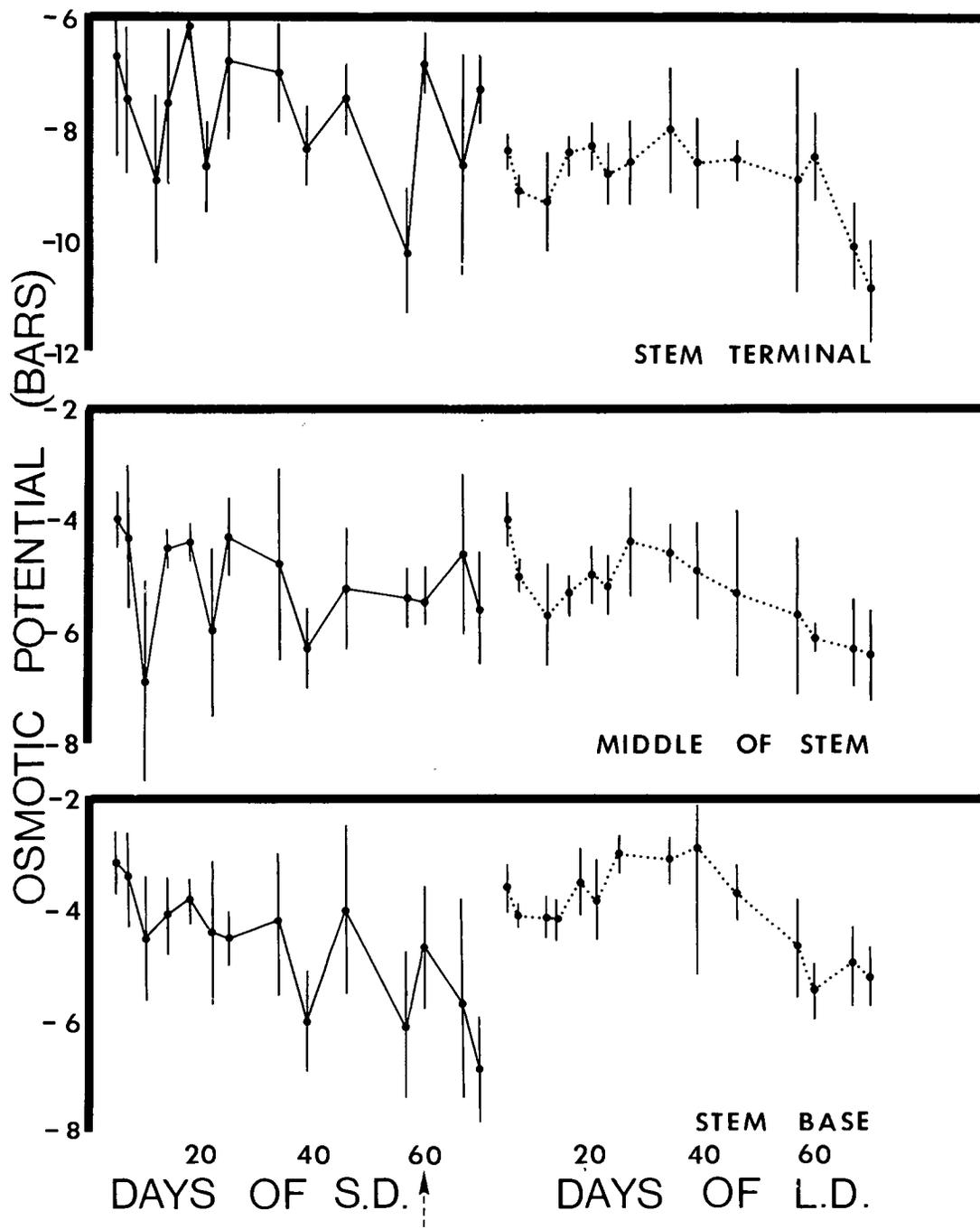


Fig. 4. OP measurements of terminal, mid, and basal stem sections of the same plants grown under long (16 hr) or short (10 hr) photoperiod. Each point represents 10 readings. Interfronoe was reached after 60 days of SD treatment as indicated by arrow.



showed the lowest OP (-6 to -10 bars) and stem bases the highest (-3 to -7 bars).

Discussion

Numerous observers have correlated periodicity of tree growth with variations in climatic factors, especially daylength and temperature (162). Red-osier dogwood plants stop growing in response to short days, but are notably unresponsive to SD induced growth cessation and cold acclimation during their spring flush of growth (32, 137). Plants in this experiment were growing rapidly on May 15 when the experiment was started so it was not surprising that 60 days of SD treatment were required to induce interfronoe. Leaves abscised after 70 days of SD treatment. SD treatment begun in mid-summer induced interfronoe in red-osier dogwood within 28 days (Fuchigami, personal communication).

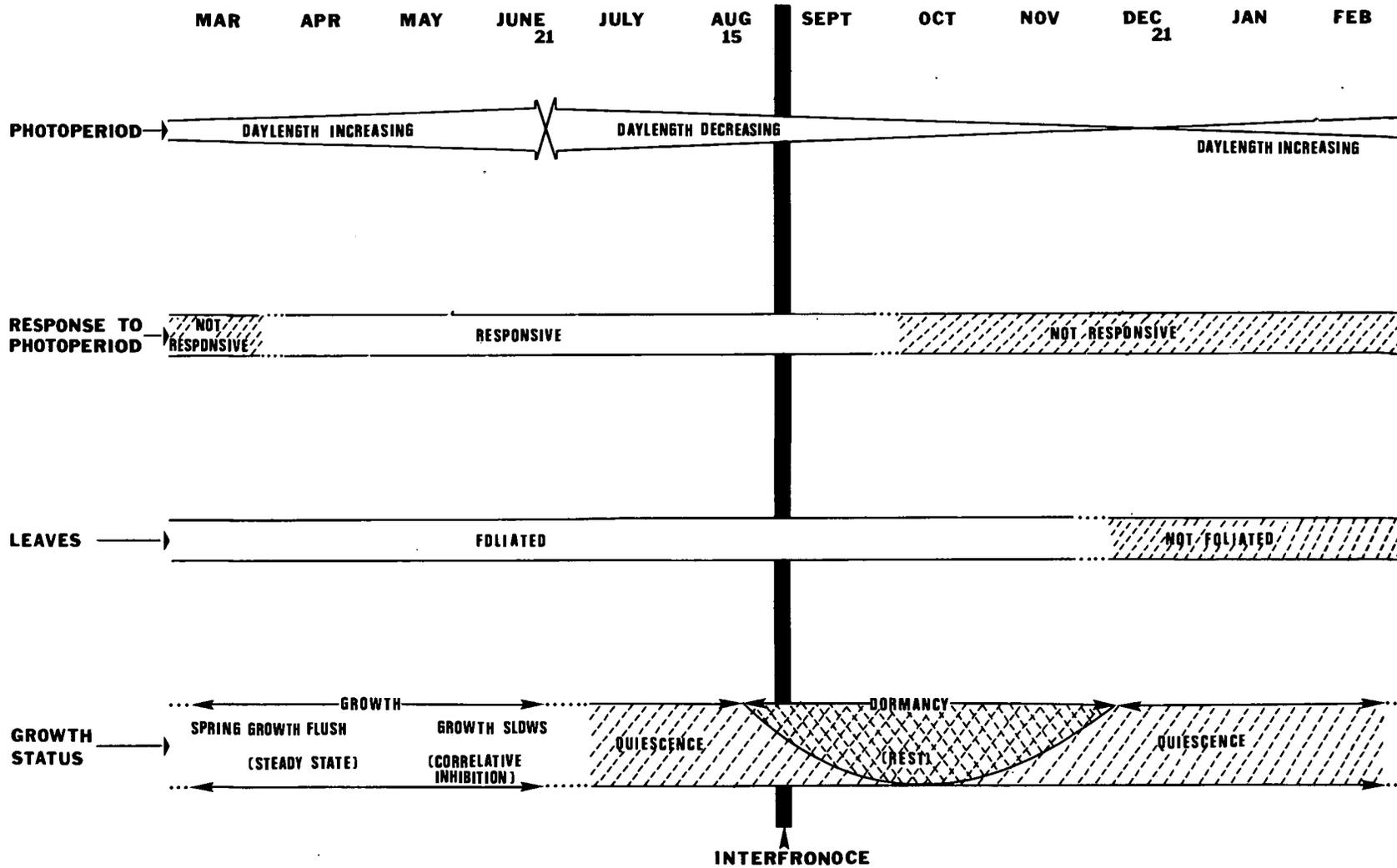
In most deciduous plants, leaves serve as perceptor sites of the photoperiodic responses leading to the development of dormancy (27) and cold acclimation (33). Leaves also synthesize photosynthates and other substances that may influence the development and survival of the other plant parts. Hence, the removal of leaves can have a pronounced influence on the fate of the plant. As reported here, defoliation during pre-interfronoe leads to tip dieback and even death of the plant. When leaves were removed biweekly, the extent of tip dieback was inversely related to duration of SD exposure up to 60 days

of treatment, after which no dieback occurred. This suggests that short days stimulate leaves to synthesize metabolites and/or other compounds vital to the survival of overwintering parts of the plant.

Although this study did not deal with cold acclimation, the timing of the first stage of acclimation seems to be closely related to interfronoe development (33), and both are distinct from rest (54, Fuchigami, personal communication). Interfronoe is a distinct stage of development that can be measured and defined. In red-osier dogwood it occurs 4 to 6 wk prior to rest. Fig. 5 is a diagrammatic representation of seasonal developmental relationships in red-osier dogwood as hypothesized by the author. Specifically, Fig. 5 summarizes relationships between interfronoe and growth, dormancy (quiescence and rest), foliation, and daylength. Rest or bud dormancy is caused by internal physiological blocks which prevent growth, even under optimum external conditions (153). Quiescence or imposed dormancy is caused by unfavorable environment (139). Rest status is established by observing bud growth, or lack thereof, on normally foliated or defoliated plants under favorable conditions for growth. "Depth of rest" can be quantitatively expressed as time required for growth (99) or amount of GA required to induce growth (141). The distinct inverse relationship between percent of tip dieback and duration of SD treatment provides a useful means for expressing "degree of interfronoe."

Fig. 5. Seasonal developmental relationships in red-osier dogwood. Interfronoe occurs 4 to 6 wk prior to deep rest and marks a distinct period during the onset of rest when the removal of foliage does not damage plants nor adversely influence their subsequent growth and development.

DEVELOPMENT OF RED-OSIER DOGWOOD



When mature leaves are removed during pre-interfronoe, plants may regrow because a source of regulatory substances has been removed which contributes to the correlative inhibition of buds. The natural autumnal decline in root cytokinin synthesis is likely accentuated by leaf removal which probably reduces the upward movement of cytokinins in the xylar sap. Hormonal balances altered by defoliation may also influence respiratory regulation.

There have been numerous reports documenting the relationship of water status to cold acclimation in plants (18, 85, 86, 87, 93). Normally there is a major reduction in stem water content in the autumn at the time of maturation of the pith cells (93). Removing leaves prior to interfronoe reduces transpiration and undoubtedly affects plant water status. Perhaps the normal reduction in stem tissue hydration is delayed. The autumnal decrease in water content is attributed in part to root suberization (93). If the roots are not fully suberized at the time of defoliation, this could further complicate interfronoe development.

This study confirms results of earlier reports which showed water status of plants is dynamic during the autumn. The time of interfronoe development in SD plants coincided with the time that XWP reached its lowest level. There were no clear relationships between interfronoe and OP and TP. The XWP correlation with interfronoe was not surprising since it has been shown (93) that

there is a 1.5-fold decrease in stomatal resistance and/or a 3.5-fold increase in root resistance to forced water flow in red-osier dogwood plants during this period of development. The increased resistance to water flow should cause a tension gradient in the plant measurable by XWP.

OP and TP changes may not have correlated with the onset of interfronoe because osmotically active solutes which increase in autumn may be present in very small quantities, or cellular contents may have been diluted by extracellular and xylar water. The OP measurement technique did not differentiate cellular sap from water in the plants. There may also have been measurement inaccuracies arising from differences in water loss between sampling and sap expression, or humidity and temperature-induced variations in microvoltmeter OP measurements. Because of erratic OP data, TP calculations gave unexpected results; e.g., TP dropping to 0 bars after 25 days of SD treatment.

In summary, interfronoe in SD-induced red-osier dogwood plants was predicted accurately by XWP measurements on stem terminal sections (Fig. 3). Decreasing values of XWP indicate alterations in the plant's internal water status which may reflect a number of physiological changes bearing a causal relationship to interfronoe development.

(TP) predicted the onset of interfronocce well in cultivars of Acer, Malus, Quercus, and Sorbus. In terms of subsequent performance (growth), interfronocce ranged from Sept 16-Nov 11.

XWP and OP measurements were made at 14-day intervals in 1975 from July to Nov. A multiple discriminant function analysis indicated that stem water status reliably predicted interfronocce in Acer, Betula, Carpinus, Crataegus, Fraxinus, Gleditsia, Malus, Platanus, Quercus, Sorbus, and Tilia.

A chemical defoliant (Ethephon with WK II surfactant), applied at interfronocce, hastened leaf abscission by 4 to 8 wks without damage. Comparatively low XWP values were used to determine the optimum timing of chemical defoliation.

Introduction

The development of trees is seasonal. Adapted native plants survive because their cycles of growth and development are well synchronized with seasonal fluctuations. They respond to relatively subtle seasonal signals in the changing environment. These environmental signals set complex patterns of development into motion (48).

The growth and development of cultivated shade tree cultivars are often not well synchronized with the photoperiod, temperature, and rainfall in major production areas such as the Willamette Valley of Oregon where nursery trees may grow 6 ft in one season. Such rapid and prolonged growth is desirable from the standpoint of production, but creates problems because harvests are delayed, ranging from Oct to Feb. In order to successfully harvest deciduous trees for storage over winter, nurserymen must wait until the trees are completely defoliated. At the present time nurserymen rely on environmental conditions to trigger natural defoliation. Chemical defoliation is possible (82). However, plants may be injured because of improper use of the defoliant. It was hypothesized that plants arrive at a stage of development when foliage no longer influences development and thus, defoliant are effective and safe to use.

Therefore, this study was designed to identify and physiologically characterize the stage of development at which the leaves could be removed from deciduous trees without affecting the plants'

survival or regrowth. This distinct phase of development does not coincide with quiescence, dormancy, or the rest period. Hence the term interfronoe was developed to identify this stage. Interfronoe is of Latin derivation: "intermissio" - interruption, cessation; "nocere" - to have a prejudicial influence; "frons" - foliage; e. g., the physiological stage of development at which leaves can be removed from deciduous trees without adversely affecting survival and regrowth after storage over winter.

The ultimate aim of the research was to develop a valid and simple interfronoe index for predicting the onset of interfronoe in nursery trees. It was hypothesized that XWP and OP of stem sections could predict interfronoe in field-grown nursery stock, and that other phenological parameters could be correlated with interfronoe. Such an interfronoe index could be used to indicate when ethylene-releasing chemical defoliant would be effective in hastening harvestability of trees.

The water status of plants is subject to internal controls. In hardy trees and shrubs water content decreases markedly in late summer and early autumn as plants cold acclimate even when soil water is at or near field capacity (93). A reduction in stem and root moisture content is associated with acclimation to low temperatures (85). The autumnal decrease in water content is attributed in part to root suberization (93).

Research on cotton (Gossypium hirsutum L. 'Stoneville 213') seedlings indicated that the amount of abscission was related to the magnitude of plant water deficit, and leaf abscission promoted by exogenous ethylene was enhanced in seedlings subjected to water stress. Water stress seemed to predispose leaves to ethylene-induced abscission (59). Nurserymen occasionally hasten the abscission of leaves of deciduous trees by subjecting the trees to various forms of water stress such as withholding irrigation water or undercutting and side pruning the root systems. Ethephon has also been used to enhance leaf abscission since it releases ethylene upon decomposing. The results of the studies reported herein indicate that these practices could be used more safely and effectively if precise measurements of water potential were used to program timing of Ethephon application.

Materials and Methods

Field data were collected at the J. Frank Schmidt & Son Wholesale Nursery, Boring, Oregon which is located at a latitude of 45°27' and an elevation of 600-650 feet. Climatological data (day-length, average air and soil temperatures, daily precipitation, and evaporation rate) were collected at weather stations nearby.

1974 Studies.

Phenological Observations:

Phenological observations were made at 2 wk intervals on

59 cultivars of 25 species to establish the timing of development as it relates to the onset of interfronoco. Estimates were based on gross visual observation of several hundred trees of each cultivar at each sampling date. Observations included:

1. Leaf expansion: Estimates of time of cessation of leaf expansion expressed in percent

$$\frac{\text{(number of trees with expanding leaves)}}{\text{(total number of trees observed)}} .$$
2. Autumn leaf coloration: Visual estimate of time of leaf coloration. The percentage of leaves showing complete autumn coloration.
3. Terminal bud formation: Visual estimate of the time of terminal bud formation expressed in percent

$$\frac{\text{(number of trees with terminal buds formed)}}{\text{(total number of trees observed)}}$$

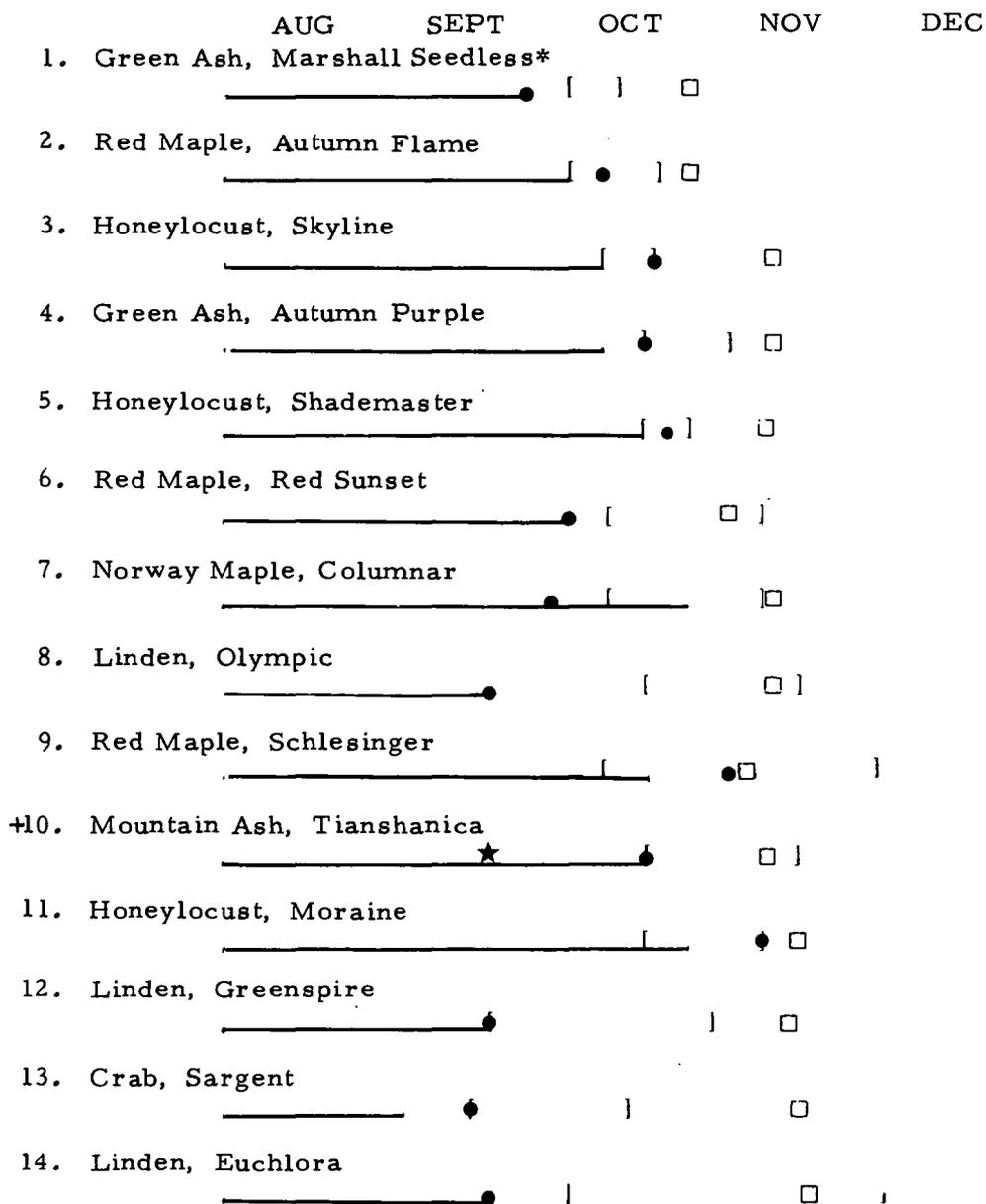
These data were compiled chronologically (Fig. 6).

Water Status Measurements:

Water status (XWP, OP, and TP) measurements were made at 2 wk intervals on 12 cultivars of 5 species.

1. XWP: Predawn pressure bomb measurements (150) were made on 5 plants, 2 readings/plant, on excised stems (terminal 2 internodes) of the first lateral branch from the apex. Measurements at other times of the day gave inconsistent readings due to varying tension on the tree's water column because of environmental fluctuations.
2. OP: Dewpoint microvoltmeter measurements (15, 163) of OP were made on the same stem terminals used for XWP measurements.
3. TP: TP of the stems was calculated (53) using the equation $\psi = \psi_p + \psi_s$, such that $\psi = \text{XWP}$, $\psi_p = \text{TP}$, and $\psi_s = \text{OP}$.

Fig. 6. Phenological observations recorded at 2 wk intervals from Aug 1, 1974 to Jan 30, 1975 on nursery stock at Boring, Oregon. Visual estimates of time of leaf expansion (—), autumn leaf coloration ([]), terminal bud formation (●), and 50% leaf abscission (□) were made. Manual defoliation responses were used in determining interfronco development (★) on 12 cultivars (+). e.g. The tendency of plants to re-foliate in the autumn after manual defoliation, their storage survival over winter, and their ability to regrow the following spring were collectively used to establish the time of interfronco development.



*Scientific name are listed on page 50.

	AUG	SEPT	OCT	NOV	DEC
+15. Norway Maple, Schwedler	_____●		★ [□] □
+16. Norway Maple, Emerald Queen	_____●			□★] □
17. Norway Maple, Cleveland	_____●		[□] □
18. Sugar Maple	_____	●		□] □
19. Red Maple, Scarlet Sentinel	_____		●] □	□
20. Red Maple, Armstrong	_____	●] □	□
+21. Crab, Royalty	_____		★	□	◆ □
22. Crab, Spring Snow	_____		●	□] □
23. London Planetree	_____	●		□] □
+24. Norway Maple, Silver Variegated	_____		●	□★] □
+25. Norway Maple, Summershade	_____		●	[□★] □
26. Norway Maple, Crimson King	_____		●	[□] □
27. Red Maple, October Glory	_____		●] □	□
+28. Oak, Pin	_____●	★] □	□
+29. Oak, Red	_____●		★] □	□
+30. Crab, Snowdrift	_____		★ ●] □	□
31. Linden, Redmond	_____		●] □	□
32. Oak, English	_____●		[] □

	AUG	SEPT	OCT	NOV	DEC
33. Oak, White,	_____●				□
34. Norway Maple, Greenlace I	_____●			□ ★	
35. Norway Maple, Globe	_____●			□ ★	
36. Mountain Ash, Cardinal Royal European	_____★			□	
37. Mountain Ash, European	_____●			□	
38. Linden, Chancellor	_____●			□	
39. Crab, Snowcloud	_____●			□	
40. Crab, Arnold	_____●			□	●
41. Crab, Selkirk	_____●			□	●
42. Crab, Klehm's Bechtel	_____●			□	●
43. Crab, Zumi	_____●			□	●
44. Crab, American Beauty	_____●			□	●
45. Crab, Pink Perfection	_____●			□	●
46. Crab, Red Jade	_____●			□	
47. Crab, Hopa	_____●			□	●
48. Crab, Royal Ruby	_____●			□	●
49. Plum, Cistena	_____●			□	
50. Crab, Scheideckeri	_____●			□	●

	AUG	SEPT	OCT	NOV	DEC
51. Cherry, Weeping	_____			□	•
52. Crab, Eleyi	_____				□ •
53. Crab, Van Eseltine	_____				□ •
54. Crab, Echtermeyer	_____				• □
55. Crab, Katherine	_____				□ •
56. Crab, Atrosanguinea	_____				□ •
57. Crab, Radiant	_____				□ •
58. Crab, Floribunda (Japanese Crab)	_____				• □
59. Goldenchain	_____				• □

1. Fraxinus pennsylvanica Marsh. lanceolata 'Marshall Seedless'
2. Acer rubrum L. 'Autumn Flame'
3. Gleditsia triacanthos L. 'Skyline'
4. Fraxinus pennsylvanica Marsh. lanceolata 'Autumn Purple'
5. Gleditsia triacanthos L. 'Shademaster'
6. Acer rubrum L. 'Red Sunset'
7. Acer platanoides L. 'Columnare'
8. Tilia cordata Mill. 'Olympic'
9. Acer rubrum L. 'Schlesingeri'
- +10. Sorbus aucuparia L. 'Tianshanica'
11. Gleditsia triacanthos L. 'Moraine'
12. Tilia cordata Mill. 'Greenspire'
- +13. Malus sargentii Rehd.
14. Tilia euchlora K. Koch (cordata x dasystyla)
- +15. Acer platanoides L. 'Schwedleri'
- +16. Acer platanoides L. 'Emerald Queen'
- +17. Acer platanoides L. 'Cleveland'
18. Acer saccharum Marsh.
19. Acer rubrum L. 'Scarlet Sentinel'
20. Acer rubrum L. 'Armstrong'
- +21. Malus 'Royalty'
22. Malus 'Spring Snow'
23. Platanus hispanica Muenchh. (acerifolia x hybrida)
- +24. Acer platanoides L. 'Silver Variegated'
- +25. Acer platanoides L. 'Summershade'
26. Acer platanoides L. 'Crimson King'
27. Acer rubrum L. 'October Glory'
28. Quercus palustris Muenchh.
29. Quercus rubra L. Sec Du Roi
30. Malus 'Snowdrift'
31. Tilia americana L. 'Redmond'
32. Quercus robur L.
33. Quercus alba L.
34. Acer platanoides L. 'Greenlace'
- +35. Acer platanoides L. 'Globosum'
- +36. Sorbus aucuparia L. 'Cardinal Royal'
37. Sorbus aucuparia L.
38. Tilia cordata Mill. 'Chancellor'
39. Malus 'Snowcloud'
40. Malus arnoldiana Rehd. (floribunda x baccata)
41. Malus 'Selkirk'
42. Malus 'Klehm's Bechtel'
43. Malus zumi Rehd. (baccata mandshurica x sieboldii) 'Calocarpa'
44. Malus 'American Beauty'
45. Malus 'Pink Perfection'

46. Malus 'Red Jade'
47. Malus 'Hopa' Rehd. (baccata x niedwetzkyana)
48. Malus 'Royal Ruby'
49. Prunus cistena N.E. Hansen
50. Malus scheideckeri Spaeth ex Zabel
51. Prunus subhirtella var. pendula (Maxim.) Tanaka
52. Malus purpurea (Barbier) Rehd. Eleyi
53. Malus 'Van Eseltine'
54. Malus 'Oekonomierat Echtermeyer'
55. Malus 'Katherine'
56. Malus atrosanguinea Schneid. (halliana x sieboldii) (Regel) Rehd.)
57. Malus 'Radiant'
58. Malus floribunda van Houtte
59. Laburnum watereri Dipp. 'Vossii'

Each XWP point in Figs. 8 and 9 represents data from 5 trees, 2 readings/tree. The following 12 cultivars of 5 species were used for water status measurements:

Acer platanoides L. 'Greenlace I', 'Schwedleri', 'Summer-shade', 'Silver Variegated', 'Emerald Queen', and 'Globosum'

Malus 'Royalty' and 'Snowdrift'

Quercus palustris Muenchh.

Q. rubra L. Sec. Du Roi.

Sorbus aucuparia L. 'Cardinal Royal' and 'Tianshanica'

Manual Defoliation Responses:

Four trees of the 12 test cultivars above were manually defoliated at 2 wk intervals through the autumn beginning on Aug 26. When previously dormant buds began growing in the autumn after defoliation, the time required for bud break and refoliation (1 cm green emerging from bud scales) was recorded in each cultivar for each defoliation date until plants were dug (from Nov 15 to Dec 15, 1974). After digging, bareroot plants were "heeled-in" sawdust piles outdoors and held until replanting in April 1975.

The following spring, observations were made of overwintering survival and of regrowth ability (April to June).

The tendency of plants to refoliate in the autumn, their storage survival, and their ability to regrow the following spring were collectively used to establish the time of interfronoco development in

each cultivar. Interfroncoce was considered to coincide with the earliest date of defoliation which did not stimulate autumn refoliation within 6 wks; which did not predispose plants to death in storage; and which did not prevent normal regrowth in the subsequent spring.

Chemical Defoliation Responses:

Forty trees of the same 12 test cultivars were sprayed with 2000 ppm (2-chloroethyl) phosphonic acid (Ethephon) and 2% Dupont-WK surfactant (WK II) using a Solo Mist Sprayer. Trees were sprayed at 2 wk intervals from Sept 16 to Nov 11. Observations of leaf abscission and plant damage were made at 2 wk intervals. Trees were dug (from Nov 15 to Dec 15) and the bareroot plants were "heeled in" sawdust piles outdoors. After replanting in April 1975, observations were made on overwintering survival and regrowth.

Analysis of Data:

Analysis of variance was used to determine whether there were significant changes in XWP, OP, and TP over time. A regression analysis was used to determine whether evaporation rate and precipitation had a modifying effect on XWP, OP, and TP. Evaporation rates and precipitation were analyzed with water status (XWP, OP, and TP) measurements as the dependent variables.

A computerized multiple discriminant function analysis was used to discriminate which phenological observations and/or water status measurements constituted the best combined index of

interfronoe. The multiple discriminant function analysis results in a linear function of interfronoe. For 2 levels of interfronoe (pre-interfronoe vs. interfronoe), 2 linear functions were developed, which differentiated the best predictors of interfronoe from among the phenological and water status variables observed. The variables were inserted into the linear function as coefficients. Since the coefficients for the linear function were selected by the computer to maximize the minimum distance between levels of interfronoe, it was possible to identify which variables were the best predictors of interfronoe by the percent of correctly classified interfronoe cases based on using those variables.

1975 Studies.

Based on the results of 1974 field studies, water status (XWP, OP, and TP) measurements were made on 38 cultivars of 22 species in 1975 to further evaluate the usefulness of these parameters for predicting interfronoe development and for timing chemical defoliation in commercial nurseries. The methods for studying water status have been described (1974 studies), and essentially the same experimental format was followed. Duplicate water status measurements were made on 5 plants of each cultivar at 2 wk intervals from July 26 to Nov 21.

Four trees of each test cultivar were manually defoliated at 2 wk intervals beginning July 26 until natural leaf abscission. The

time required for autumn bud break and refoliation following defoliation was recorded for each cultivar.

Forty trees of each of 10 test cultivars (*) were sprayed with 2000 ppm Ethephon and 2% WK II at 2 wk intervals from Sept 16 to Nov 7 using a Solo Mist Sprayer. Observations of leaf abscission and plant damage were made at 2 wk intervals.

A multiple discriminant function analysis of the water status data was conducted and comparisons drawn between 1974 and 1975 data.

The cultivars studied were (trees used for chemical defoliation analysis are marked *):

- Acer campestre L.
- A. ginnala Maxim.
- A. platanoides L. 'Cleveland', 'Columnar', 'Crimson King',
'Royal Red'*, and 'Summershade'*
- A. rubrum L. 'Autumn Flame' and 'Red Sunset'*
- A. saccharinum L.*
- Betula pendula Roth.
- Carpinus betulus L.
- Crataegus monogyna Jacq. 'Stricta'
- C. oxyacantha L. 'Crimson Cloud', emend Jacq. 'Paul's
Scarlet'*, 'Toba', and 'Winter King'
- Fraxinus holotricha Koehne. 'Moraine'*
- F. pennsylvanica Marsh. 'Kimberly Blue'* and 'Marshall
Seedless'
- Gleditsia triacanthos L. 'Skyline'
- Malus ioensis Brit. 'Plena' ('Klehm's Bechtel')*
- Malus 'Radiant', 'Royalty', and 'Snowdrift'
- Malus sargentii Rehd. ('Sargent')
- Platanus hispanica Muenchh.
- Quercus palustris Muenchh.
- Q. robur L.
- Q. rubra L. Sec. Du Roi.
- Sorbus aucuparia L. 'Cardinal Royal' and 'Tianshanica'

Tilia americana L. 'Redmond' (on T. platyphyllos Scop.) and
(on T. tomentosa Moench.)
T. cordata Mill. 'Chancellor', 'Greenspire'*, and 'Olympic'*

Results and Discussion

Comparisons of 1974 and 1975 data indicate that calendar dates cannot be used for determining the development of interfronocce (Table 1). Data collected on similar species and cultivars for 1974 and 1975 showed that interfronocce does not develop the same time each year and the degree of differences observed among the cultivars studied was quite varied. Photoperiod has been considered as one of the main environmental switches triggering dormancy development (27, 32, 41, 55, 106, 107, 145). Other environmental stimuli, however, trigger adaptive physiological responses in plants that may alter the main effects of the environment. The effect of environmental factors which regulate dormancy development is not understood for the cultivars used in this study. Controlled environmental studies of each cultivar may be required to establish cause and effect relationships.

In order to explain calendar differences in interfronocce development during 1974 and 1975, several environmental parameters (day-length, evaporation rate, precipitation, soil and air temperatures) were investigated (Appendix Fig. 1). Precipitation was notably different for the 2 years (Table 2), and this may have modified interfronocce development. Heavy precipitation in 1973-74 could have

Table 1. Comparison between calendar dates of interfronoco development during 1974 and 1975.

	<u>Sorbus aucuparia</u>		<u>Malus</u>		<u>Quercus</u>	
	'Tianshanica'	'Cardinal Royal'	'Royalty'	'Snowdrift'	<u>palustris</u>	<u>rubra</u>
1974	Sept 16	Sept 16	Oct 14	Oct 14	Sept 30	Oct 14
1975	Aug 14	Aug 14	Aug 28	Oct 10	Sept 16	Sept 26

Table 2. Precipitation from July 1973-Dec 1976 compared to 20 year average.

	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
20 yr avg												
Monthly precip.	0.75	1.38	2.64	6.15	9.75	10.67	10.33	6.37	7.78	5.12	3.68	2.65
Accumulation	0.75	2.14	4.83	10.99	20.75	31.42	39.90	46.05	53.55	58.01	61.58	64.12
1973												
Monthly precip.	0.20	1.41	4.53	5.03	15.87	12.97	12.43	8.67	8.52	4.36	4.63	1.39
Accumulation	0.20	1.61	6.14	11.17	27.04	40.01	52.44	61.11	69.63	73.99	78.62	80.01
1974												
Monthly precip.	2.44	0.14	0.32	3.41	8.92	10.28	10.23	6.46	6.77	3.62	2.86	2.18
Accumulation	2.44	2.58	2.90	6.31	15.23	25.51	35.74	42.20	48.97	52.59	55.45	57.63
1975												
Monthly precip.	0.41	4.24	0.01	8.93	8.50	10.48						
Accumulation	0.41	4.65	4.66	13.59	22.09	32.57						

delayed interfronocoe by the following: 1) leaching of nutrients from the soil (Nov 1973) likely slowed development the subsequent year (Table 2); 2) unseasonally cool temperatures and evaporative cooling of buds during the rainy season (1973-74) likely delayed spring growth; 3) moisture stress during certain phases of the plant's development may have inhibited or slowed down metabolic processes essential to interfronocoe development (Aug 1974), whereas moisture stress applied at other times may have enhanced its development (Sept 1975) (18, 87); 4) leaching of nutrients and growth substances from the plant (134) during the time of abundant summer rain (Aug 1975) may have hastened removal of substances inhibiting interfronocoe development.

Evaporation rates and precipitation did not have a modifying effect on XWP, OP, and TP in this study as determined by simple regression analysis on the 1974 data. Values for r^2 were less than 0.50. Differences in the water status during the summer and fall apparently occurred as a result of internal physiological alterations in the plant. Endogenous regulation (lowering) of water potential appears to provide a mechanism by which vulnerable processes are checked preparatory to unfavorable environmental conditions (93, 151).

Phenological parameters provided a chronology of developmental stages (Fig. 6). Of the plants studied, Fraxinus pennsylvanica

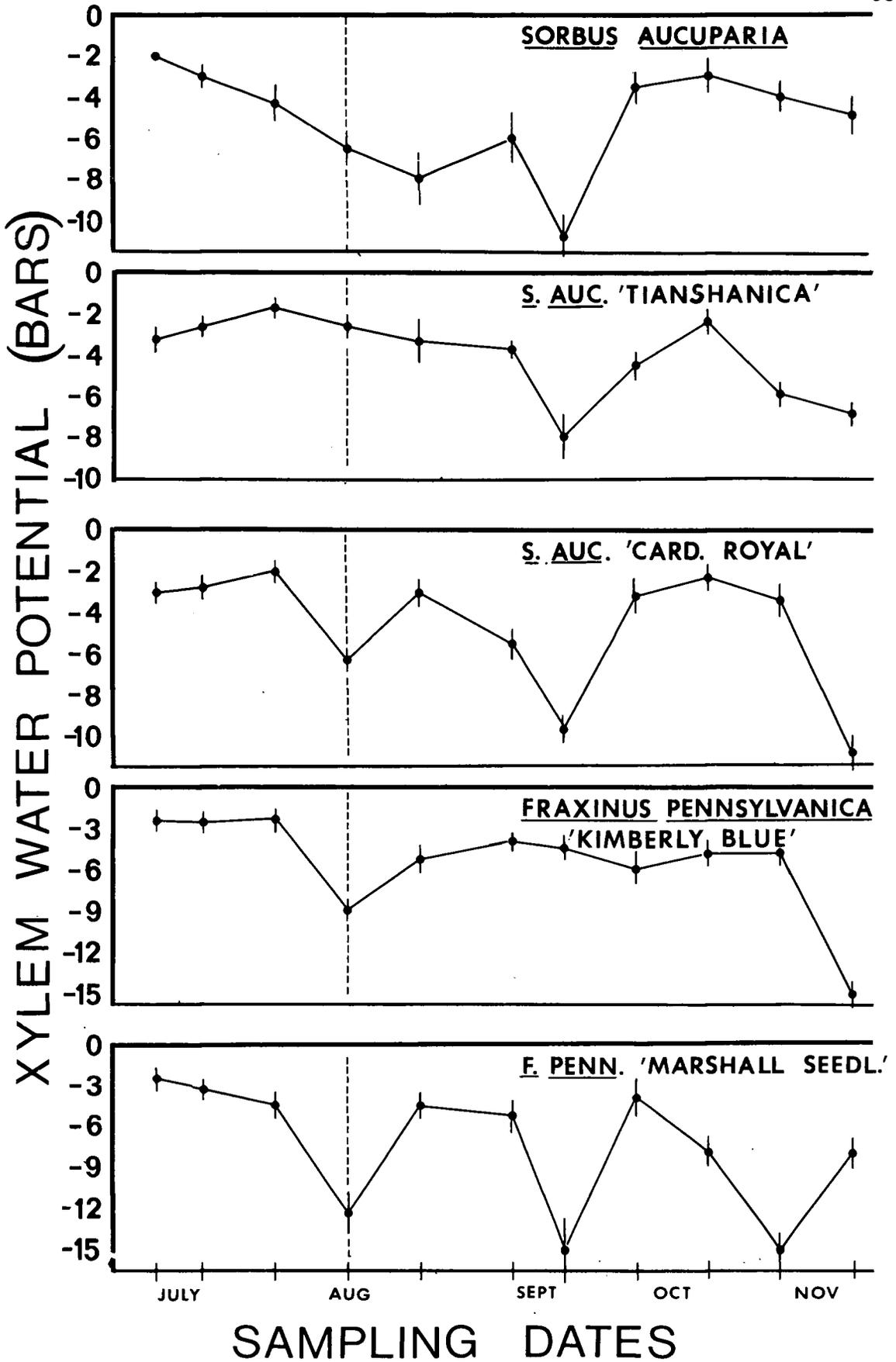
'Marshall Seedless' (green ash) showed the earliest natural leaf abscission (Sept 20) and Laburnum watereri 'Vossi' (goldenchain tree) the latest (Jan 20). Phenological observations (Fig. 6) were used as variables in the multiple discriminant function analysis but, unfortunately, failed to show correlation to interfronoc and pre-interfronoc. In mountain ash 'Tianshanica' interfronoc occurred before the formation of the terminal bud, in mountain ash 'Cardinal Royal', interfronoc occurred at the time of terminal bud formation, and in pin oak and red oak, interfronoc occurred after terminal bud formation. It was impossible to choose any one of the phenological parameters as indicative of interfronoc development in setting up the chronological listing (Fig. 6).

Appendix 4 and 5 contain a summary of XWP, OP, and TP values and dates of interfronoc based on manual defoliation test for 1974 and 1975. In a few cases, (1974: A. platanoides 'Emerald Queen', S. aucuparia 'Tianshanica', Malus 'Snowdrift'; 1975: M. ioensis 'Klehm's Bechtel') interfronoc corresponded with lowest XWP. However, in many cultivars studied, interfronoc corresponded with a trend toward low XWP readings (Table 3). In several cases (Quercus palustris, Q. robur, and Q. rubra) a lowering of 0.4 to 1.0 bar is sufficient to signal the development of interfronoc (Appendix Table 4). Fig. 7 and 8 contain examples (cultivars of Tilia, Sorbus, and Fraxinus) of XWP values collected during 1975.

Table 3. Trend of lowering XWP at the onset of interfronoe (+). Date of interfronoe based on manual defoliation. Data collected in 1975.

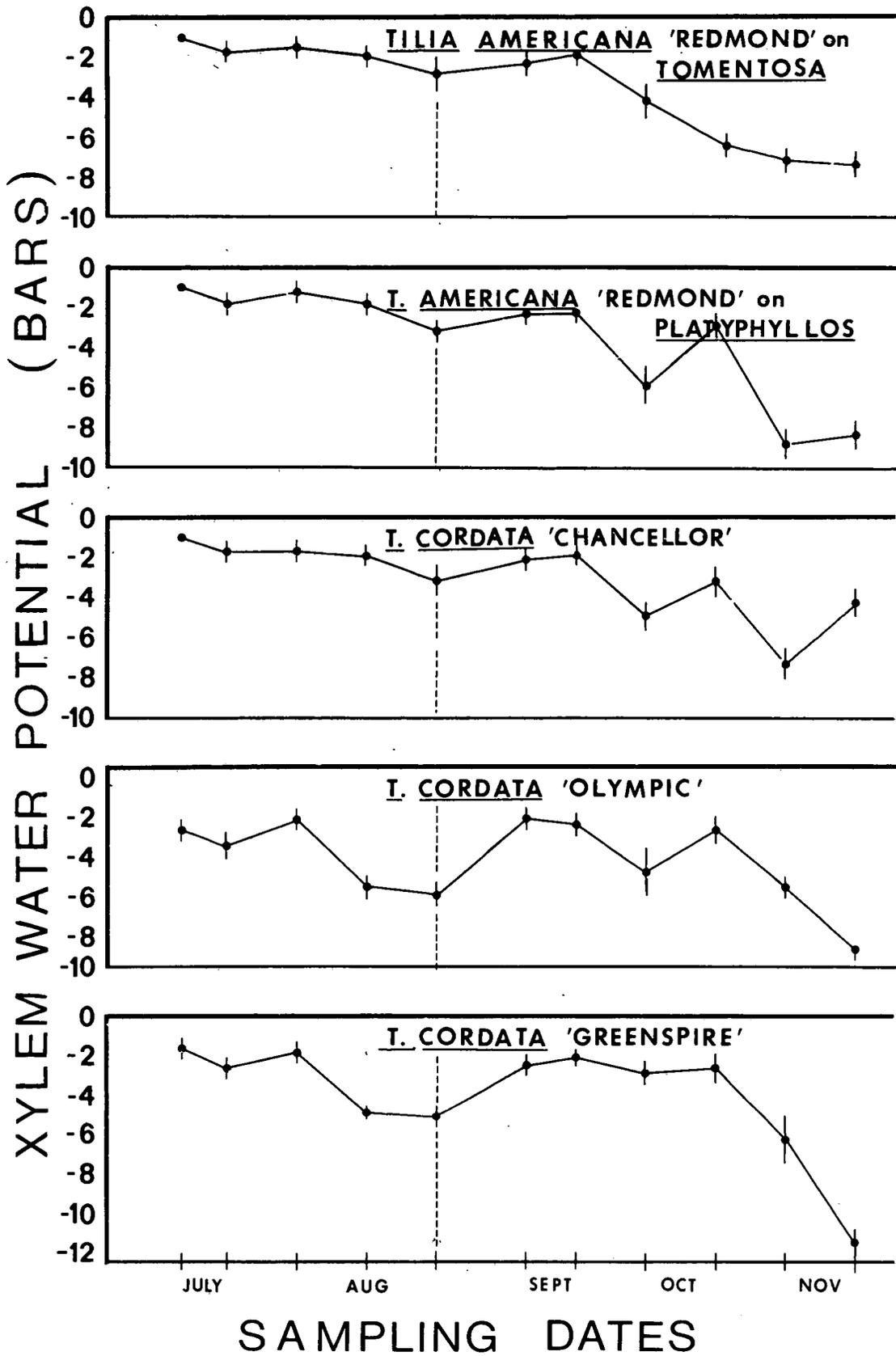
	Dates of XWP measurements										
	July		Aug			Sept		Oct		Nov	
	9	18	1	14	28	16	26	10	24	7	21
<u>Acer platanoides</u> 'Cleveland'	-2.0	-3.2	-5.4	-5.0	-5.7	-2.8	-6.7	-6.2	-3.5	-11.9	- 9.9
							(+)				
<u>A. rubrum</u> 'Red Sunset'	-1.9	-1.8	-1.6	-2.5	-3.5	-3.0	-4.1	-4.3	-2.3	- 7.6	- 7.5
								(+)			
<u>A. saccharinum</u>	-1.9	-2.5	-2.4	-2.5	-3.5	-2.8	-3.2	-3.9	-4.5	- 7.1	-11.0
									(+)		
<u>Fraxinus holotricha</u> 'Moraine'	-1.7	-2.0	-2.2	-3.3	-3.4	-3.8	-4.0	-6.2	-7.8	- 8.5	-13.7
							(+)				
<u>Gleditsia triacanthos</u> 'Skyline'	-3.0	-2.3	-3.5	-4.7	-4.4	-7.3	-9.0	-8.4	-9.4	-12.2	- 4.8
						(+)					

Fig. 7. Relationship between XWP and time of interfronoe development in 3 Sorbus and 2 Fraxinus cultivars. Interfronoe based on manual defoliation data occurred on Aug 14.



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Fig. 8. Relationships between XWP and time of interfronoe development in 5 Tilia cultivars. Interfronoe based on manual defoliation data, occurred on Aug 28.



When water status measurements from 1974 were used as variables in a multiple discriminant function analysis, pre-interfronoe and interfronoe were predicted accurately (Table 4). In Acer cultivars tested in 1974, using XWP, OP, and TP as predictors, there was 63.7% correlation between water status data in predicting pre-interfronoe cases and manual defoliation data in predicting pre-interfronoe cases; and 71.9% of the cases classed as interfronoe based on water status data were also classed as interfronoe based on manual defoliation data. In other words, 65.5% of all pre-interfronoe and interfronoe cases were correctly classed using water status data as predictors. For this reason, water status data were collected on 38 cultivars in 1975. A multiple discriminant function analysis of 1975 data (Table 4) showed generally, the percent of correctly classified cases of interfronoe and pre-interfronoe was higher.

In every cultivar, for both years of data, XWP, OP, and TP were eligible variables for predicting pre-interfronoe and interfronoe. The computer determines which variable best fits in predicting pre-interfronoe and interfronoe, and enters this variable into step 1 of the analysis. Other variables are entered in subsequent steps. In 1974, TP was entered in setp 1 in Acer, Malus, and Sorbus, while XWP was entered in setp 1 for Quercus. In 1975, XWP was entered in step 1 in all 11 genera analyzed. The combination of

Table 4. Predictability of interfronoe based on multiple discriminant function analysis of XWP, OP, and TP measurements.

	Variable entered in step #1	Percent correct classification of		
		All cases	Pre-interfronoe	Interfronoe
<u>1974 data</u>				
<u>Acer</u>	TP	65.5	63.7	71.9
<u>Malus</u>	TP	69.8	50.0	89.6
<u>Quercus</u>	XWP	86.5	82.5	89.3
<u>Sorbus</u>	TP	99.0	94.1	100.0
<u>1975 data</u>				
<u>Acer</u>	XWP	78.1	90.7	62.9
<u>Betula</u>	XWP	98.2	100.0	96.0
<u>Carpinus</u>	XWP	77.3	94.0	63.3
<u>Crataegus</u>	XWP	73.3	76.8	66.1
<u>Fraxinus</u>	XWP	79.1	100.0	67.1
<u>Gleditsia</u>	XWP	90.9	100.0	83.3
<u>Malus</u>	XWP	80.0	90.7	67.6
<u>Platanus</u>	XWP	74.5	72.0	76.7
<u>Quercus</u>	XWP	80.6	100.0	62.4
<u>Sorbus</u>	XWP	74.5	93.3	67.5
<u>Tilia</u>	XWP	67.1	87.0	55.7

XWP, OP, and TP variables was a better predictor of pre-interfronoce and interfronoce than any one variable alone. However, because XWP in 1975 proved to be the best variable for distinguishing between pre-interfronoce and interfronoce, it could be used alone as an interfronoce index.

Water content in tree trunks decreases during summer to a minimum in fall but increases by the following spring (84). It seems that vessels which become drained do not refill that same season even though soil moisture is adequate. A slight lowering of XWP appears to signal the onset of interfronoce. In cases where XWP does not continue dropping in autumn, the adaptive mechanisms of these trees are considered to be different from those where XWP continues to drop; e.g., 1) during the autumn, characterized by humidity and abundant precipitation, a slight tension gradient may be re-established even though the leaves have abscised; 2) in shifting from one phase to another (Hotze, first manuscript of thesis), the process is very gradual and some trees may develop higher tensions required for water flow to proceed again before others (84); 3) some trees' roots may absorb ions faster or break down starch and other storage materials in the roots and stem faster than other plants. The result would be some adjustment of osmotic potential with attendant effects on water movement (84). The activities of degradative enzymes such as RNase, polyphenol oxidase, and proteases were found to increase

during senescence of apple leaves in the autumn (127). The enzymes reached their highest specific activities after first frost. It is not known how much of an adjustment of osmotic potential would be required for attendant effects on water movement, but it would be worth investigating.

It appears that endogenously controlled changes in internal water status may be a primary physiological response of plants to the environment. Decreases in water permeability of root cells may be significant in the reduction of plant water potential initially (75, 76, 77, 93). With alterations in the plant's water status, many vulnerable processes may be shut down (93, 151).

Several hormones are known to be related to resistance to water flow. Kinetin added to root media decreased the exudation rate from tomato stumps (130). ABA and cytokinins are instrumental in the regulation of stomatal function via changes in ionic flux. This suggests a tight coupling between permeability and hormonal status (84). Mizrahi (101) suggested that ABA through its influence on stomata, is a major factor facilitating the adaptive response of plants to root stress that impede water balance. They imply that the ratio of cytokinins and ABA direct the extent of this response. Itai and Vaadia (56) have speculated that the signal for the synthesis of cytokinins in the roots may be a change in water potential which is transmitted through the plant.

It is tempting to speculate that hormonal balance functions in a causal manner in controlling the hydration of plants, thereby initiating development of interfronoe. The possibility also exists that short days and other environmental parameters alter transpiration in a way that causes water status changes which, in turn, initiate changes in hormonal balance to initiate interfronoe. Cultivar differences in environmental response compound the problem further. In short, it would require years of controlled studies on each cultivar to determine causes and effects of growth responses.

Interfronoe is a distinct developmental phase (Hotze, first manuscript of thesis) which occurs 4 to 6 wks prior to rest in red-osier dogwood (Fuchigami, personal communication). This study was not concerned with analyzing rest period, but it is assumed that other species behave similarly. Leaves are the perceptor sites of SD stimulus and are required for the development of interfronoe. When leaves were manually removed during pre-interfronoe, plants refoliated (Fig. 9). The tendency to refoliate proved to be a good index of interfronoe in itself. Pre-interfronoe plants refoliated rapidly (within 2 wk) and did not store nor grow as well as interfronoe plants which did not refoliate in 6 or more wks. Leaf removal eliminates photosynthetic capacity (27, 32, 33, 68, 74, 162), a source of phytohormones (27, 32, 33), and the major transpirational surface of plants (84, 123, 124). Defoliation likely alters a sequential

Fig. 9. Refoliation of A. platanoides 'Globosum', 1) hand defoliated on Sept 30, 1974; 2) hand defoliated on Nov 11. Photo was taken on Nov 25. Plants defoliated Nov 11 were in interfroncoce and did not refoliate after that date.



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and interrelated series of metabolic adjustments. Physiological and biophysical changes involved in the numerous adaptive responses which occur in the autumn are almost certainly involved in interfronoe development (151), particularly those influenced by food reserves, hormones synthesized in the leaves, and water status in different parts of the plant (Hotze, first manuscript of thesis).

Trees defoliated with 2000 ppm Ethephon and 2% WK II did not refoilate regardless of the date of treatment. If applied too early, Ethephon and WK II caused tip dieback and bud mortality (1975: A. rubrum 'Red Sunset', A. saccharinum, Malus ioensis 'Klehm's Bechtel'); death and abscission of entire branches (A. rubrum 'Red Sunset'); and peeling of the cuticle from branches (M. ioensis 'Klehm's Bechtel'). Apparently, high concentrations of ethylene can do extensive damage to plants prior to interfronoe. The literature indicates that Ethephon must be applied at specific developmental stages to be effective (17, 82). There are many defoliants on the market (82), but optimum times of application and possible undesirable side-effects are not well established (83). This study indicates that XWP can predict when chemical defoliants can be applied both safely and with maximum effectiveness in causing defoliation (Table 5). A trend toward low XWP was characteristic of several species in which defoliation was fast and safe (Table 3, check A. rubrum 'Red Sunset', A. saccharinum, Fraxinus holotricha

Table 5. Number of weeks required for 100% defoliation after application of 2000 ppm Ethephon and 2% WK II. Dates of interfronoe are marked (+). Notes concerning damage to trees from defoliant are included for species which were affected. Data were collected in 1975.

	Spray dates					Date of natural defoliation
	Sept		Oct		Nov	
	16	26	10	24	7	
<u>Acer platanoides</u> 'Summershade'	8	4 (+)	2	2	2	Nov 21
<u>A. platanoides</u> 'Royal Red'	8	4 (+)	4	2	2	Nov 21
<u>A. rubrum</u> 'Red Sunset'	8 Death and abscission of branches.	6 Tip dieback. Bud mortality.	2 (+)	2	2	Nov 28
<u>A. saccharinum</u>	9 Tip dieback. Bud mortality.	7 Tip dieback. Bud mortality.	4	2 (+)	2	Nov 28
<u>Fraxinus holotricha</u> 'Moraine'	7	4 (+)	3	2	2	Nov 7
<u>Malus ioensis</u> 'Klehm's Bechtel'	11 Tip dieback. Bud mortality. Peeling of cuticle from branches.	8 Tip dieback. Bud mortality. Peeling of cuticle from branches.	2 (+)	2	2	Dec 12

'Moraine'). Applying chemical defoliants after interfronoe was equally effective (Table 5). Fig. 10 demonstrates effective defoliation on Quercus palustris 2 wks after application of Ethephon and WK II on Oct 10. Interfronoe occurred on Sept 16 at XWP of -1.4 bars. On Oct 10, XWP was -4.9 bars and proved to be prime time for defoliation with chemicals.

Ethylene has long been known for its ability to induce abscission (119). Abscission occurs in response to water stress in some plants. In cotton (95) abscission of bolls or leaves was more or less proportional to the daily minimal water deficit as indicated by predawn leaf water potential. Some evidence suggests that abscission induced by water stress may be mediated through ethylene production (59). Ethylene production by petioles on intact cotton plants tended to increase within hours after water deficits developed, and declined quickly on rewatering in many cases (95). When exogenous ethylene and CO₂ were applied to cotton (59), ethylene did not induce abscission at high water potential but greatly enhanced abscission in stressed plants. The threshold water deficit required to induce abscission was reduced by exogenous ethylene. Thus water stress seemed to predispose leaves to ethylene-induced abscission.

The results of these studies support the evidence that water status alterations predispose plants to ethylene-induced abscission.

Fig. 10. Results of chemical defoliation on Q. palustris 3 wks after development of interfronoe. Trees in center row were sprayed Oct 10. Untreated rows are on left and right. Photo taken Oct 24.



XWP measurements can be useful in programming Ethephon applications.

There are probably other physiological criteria to use for predicting interfronoe but based on these data, water potential was a good predictor of interfronoe. It has several limitations in nursery practice. XWP follows a trend, varying from one cultivar to another, and from one year to another. Regular and fairly frequent sampling is necessary to establish trends and timing of low XWP values. Because of this and since the measurements must be done predawn at the time of minimum tension, it is not likely that XWP measurements will become a nursery practice for determining defoliation timing.

Conclusion

Interfronoe occurred at different calendar dates during 1974 and 1975. The degree of differences observed among the cultivars studied was varied. Environmental differences and the sensitivity of each cultivar to these differences is believed to be the cause of alterations in timing of interfronoe development. Phenological parameters failed to show consistent correlations to pre-interfronoe and interfronoe, while good correlations were observed between interfronoe development and water status of stem terminal sections over time as determined by multiple discriminant function analysis.

A trend toward low xylem water potential can be used to indicate when ethylene-releasing chemical defoliants are effective in hastening harvestability of trees without detrimental effects.

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APPENDIX

Appendix Table 1. *Cornus stolonifera* were subjected to short-day (10 hr) treatment in the growth chamber at 20°C days and 15°C nights. The plants were watered daily. Moderate differences in moisture content of the soil did not account for decreased xylem water potential of the short-day-treated stem terminals after 21 days of short-day treatment.

Days short-day treatment		Xylem water potential-stem terminal				Turgor pressure-stem terminal				Moisture content of container soil (% dry wt)			
		\bar{x}	SD	c. v.	t-test	\bar{x}	SD	c. v.	t-test	\bar{x} (%)	SD	c. v.	t-test
5	SD	-4.8	1.4	0.3	5.88**	1.9	1.1	0.6	-11.79**	26	4.1	0.1	3.75**
	LD	-2.3	0.3	0.1		6.1	0.4	0.1		31	2.2	0.0	
7	SD	-2.9	0.6	0.2	2.80*	4.5	1.0	0.2	- 6.38**	32	9.3	0.1	-0.80
	LD	-2.4	0.2	0.1		6.8	0.2	0.0		30	1.3	0.0	
12	SD	-4.1	0.3	0.1	7.58**	4.9	1.4	0.3	- 2.84*	25	4.4	0.1	2.39*
	LD	-3.0	0.3	0.1		6.3	0.7	0.1		30	5.0	0.1	
14	SD	-4.1	0.3	0.1	12.83**	3.5	1.4	0.4	-5.34**	26	2.8	0.0	2.65*
	LD	-2.5	0.2	0.1		5.9	0.4	0.1		30	3.6	0.1	
18	SD	-5.5	1.0	0.2	8.76**	0.7	1.1	1.7	-12.61**	30	8.4	0.1	-0.18
	LD	-2.7	0.2	0.1		5.6	0.6	0.1		29	6.1	0.1	
21	SD	-6.4	0.7	0.1	14.45**	2.3	0.6	0.3	-13.22**	26	3.1	0.0	0.91
	LD	-2.8	0.3	0.1		6.0	0.7	0.1		28	6.3	0.1	
25	SD	-6.7	1.4	0.2	8.23**	0.1	1.1	14.2	-13.16**	30	5.1	0.1	3.12*
	LD	-2.8	0.4	0.2		5.8	0.8	0.1		35	2.0	0.0	
34	SD	-5.4	0.2	0.1	17.02**	1.7	0.7	0.4	- 9.03**	17	5.0	0.1	2.91**
	LD	-2.5	0.5	0.2		5.5	1.2	0.2		23	4.5	0.1	
39	SD	-6.4	0.4	0.1	22.54**	2.0	0.9	0.4	- 9.48**	27	4.0	0.1	0.82
	LD	-2.6	0.4	0.1		6.1	1.1	0.2		29	4.7	0.1	

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Appendix Table 1. (Continued)

Days short-day treatment		Xylem water potential- stem terminal				Turgor pressure- stem terminal				Moisture content of container soil (% dry wt)			
		\bar{x}	SD	c. v.	t-test	\bar{x}	SD	c. v.	t-test	\bar{x} (%)	SD	c. v.	t-test
46	SD	-6.7	0.8	0.1	11.04**	0.7	1.4	1.9	- 8.56**	30	2.2	0.0	0.49
	LD	-3.8	0.3	0.1		4.7	0.5	0.1		31	4.7	0.1	
57	SD	-9.8	1.6	0.2	9.80**	-0.9	1.0	-1.1	-16.56**	28	3.6	0.1	-0.09
	LD	-4.6	0.7	0.2		5.7	0.8	0.1		28	6.5	0.1	
60	SD	-6.8	0.6	0.1	12.97**	0.1	0.4	7.2	-16.48**	30	3.4	0.1	0.76
	LD	-3.9	0.4	0.1		4.8	0.8	0.2		31	4.7	0.1	
67	SD	-8.4	1.1	0.1	10.41**	0.3	1.9	4.3	-10.15**	24	3.8	0.1	-1.46
	LD	-4.3	0.6	0.1		5.9	0.7	0.1		21	5.8	0.1	
70	SD	-7.1	1.1	0.2	5.37**	0.3	1.1	4.4	-11.32**	39	5.1	0.1	-5.66**
	LD	-5.2	0.2	0.0		5.6	1.0	0.2		25	6.0	0.1	
		Osmotic potential stem terminal				Osmotic potential middle of stem				Osmotic potential stem base			
		\bar{x}	SD	c. v.	t-test	\bar{x}	SD	c. v.	t-test	\bar{x}	SD	c. v.	t-test
5	SD	-6.8	1.8	0.3	- 2.77*	-4.0	0.5	0.1	- 0.04	-3.2	0.6	0.2	-1.83
	LD	-8.4	0.3	0.0		-4.0	0.5	0.1		-3.6	0.5	0.1	
7	SD	-7.4	1.3	0.2	- 4.00**	-4.3	1.3	0.3	- 1.80	-3.4	0.8	0.2	-3.00**
	LD	-9.1	0.3	0.3		-5.0	0.4	0.1		-4.1	0.2	0.1	
12	SD	-8.9	1.5	0.2	- 0.64	-6.9	1.8	0.3	1.84	-4.5	1.1	0.2	0.88
	LD	-9.3	0.9	0.1		-5.7	1.0	0.2		-4.2	0.4	0.1	
14	SD	-7.6	1.3	0.2	- 1.92	-4.5	0.3	0.1	- 5.72**	-4.1	0.7	0.2	-0.38
	LD	-8.4	0.5	0.1		-5.4	0.4	0.1		-4.2	0.4	0.1	

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Appendix Table 1. (Continued)

Days short-day treatment		Osmotic potential- stem terminal				Osmotic potential- middle of stem				Osmotic potential- stem base			
		\bar{x}	SD	c. v.	t-test	\bar{x}	SD	c. v.	t-test	\bar{x}	SD	c. v.	t-test
18	SD	-6.2	0.2	0.0	-12.16**	-4.4	0.3	0.1	-3.08*	-3.8	0.4	0.1	1.30
	LD	-8.3	0.5	0.1		-5.0	0.5	0.1		-3.5	0.6	0.2	
21	SD	-8.7	0.8	0.1	- 0.47	-6.0	1.5	0.3	1.50	-4.4	1.3	0.3	1.17
	LD	-8.8	0.6	0.1		-5.2	0.5	0.1		-3.9	0.7	0.2	
25	SD	-6.8	1.4	0.2	- 3.52**	-4.3	0.7	0.2	-0.25	-4.5	0.5	0.1	8.11**
	LD	-8.6	0.8	0.1		-4.4	0.9	0.2		-3.0	0.4	0.1	
34	SD	-7.0	0.9	0.1	- 2.17*	-4.8	1.7	0.4	0.32	-4.2	1.3	0.3	2.47*
	LD	-8.0	1.2	0.2		-4.6	0.4	0.1		-3.1	0.4	0.1	
39	SD	-8.4	0.7	0.1	- 0.64	-6.3	0.6	0.1	5.26**	-6.0	0.9	0.2	3.95**
	LD	-8.6	0.8	0.1		-4.9	0.9	0.2		-2.9	2.3	0.8	
46	SD	-7.4	0.6	0.1	- 4.69**	-5.3	1.1	0.2	-0.16	-4.1	1.5	0.4	0.79
	LD	-8.5	0.4	0.1		-5.3	1.5	0.3		-3.7	0.6	0.2	
57	SD	-8.9	2.0	0.2	- 1.83	-5.4	0.6	0.1	-0.67	-6.1	1.3	0.2	2.97*
	LD	-10.2	1.1	0.1		-5.7	1.4	0.2		-4.7	0.9	0.2	
60	SD	-6.9	0.5	0.1	- 6.07**	-5.5	0.6	0.1	-3.36**	-4.7	1.2	0.3	-2.06
	LD	-8.7	0.8	0.1		-6.1	0.3	0.1		-5.5	0.4	0.1	
67	SD	-8.7	2.1	0.2	- 2.05	-4.6	1.5	0.3	-3.16*	-5.7	1.9	0.3	1.16
	LD	-10.1	0.8	0.1		-6.3	0.8	0.1		-4.9	0.7	0.1	
70	SD	-7.3	0.7	0.1	-10.09**	-5.7	1.1	0.2	-1.86	-6.9	0.9	0.1	5.12**
	LD	-10.9	0.9	0.1		-6.4	0.8	0.1		-5.2	0.5	0.1	

Appendix Table 2. Micromolar concentrations of various elements and soluble carbohydrates in tissues of *C. stolonifera* which reached the stage of being safe to defoliate (+) vs. *C. stolonifera* which was actively growing and did not survive after hand defoliation (-). Atomic weights of each element and molecular weight of glucose were used to determine micromolarity. Total N of the 4 plant parts was determined by a Technicon Kjeldahl Autoanalyzer (Ferrari, 1960); K, P, Ca, Mg, Mn, Fe, Cu, B, Zn and Al were determined on a Jarrell-Ash 3/4 Meter Direct Reading Photoelectric Spark Emission Spectrometer. The anthrone method was used to estimate soluble carbohydrates in the aqueous fraction of water extracts (Yemne and Willis, 1954).

	Micromolar concentrations							
	Stem terminal		Root tips		Root bases		Stem bases	
	+	-	+	-	+	-	+	-
N	446.62	237.34	212.96	163.71	380.54	291.63	448.51	249.31
K	78.83	64.04	88.96	49.36	61.41	71.79	65.33	61.49
P	53.98	23.30	23.31	15.57	43.57	32.93	48.06	32.53
Ca	197.75	129.76	47.34	31.10	101.10	106.11	193.84	156.75
Mg	39.85	23.77	50.17	31.42	37.04	27.99	35.02	25.52
Mn	0.87	0.32	5.33	4.24	1.94	1.08	1.18	0.54
Fe	1.23	0.25	11.58	10.05	4.73	4.95	1.30	1.08
Cu	0.08	0.05	0.04	0.01	0.06	0.04	0.07	0.05
B	2.12	1.07	0.79	0.48	1.67	1.42	1.97	1.44
Zn	1.09	0.70	1.66	1.14	1.95	1.90	1.42	0.96
Al	1.80	0.50	28.68	25.98	18.75	14.16	1.66	1.75
Soluble carbohydrates	359.60	101.66	449.53	245.17	387.17	148.85	354.75	131.96

Appendix Table 3. Deciduous shade trees, 2-2 in age, were used for pre-dawn field measurements of xylem water potential (XWP). Stem terminals used for XWP were transported to the laboratory for measurement of osmotic potential (OP). Turgor pressure (TP) was calculated based on $\psi = \psi_p + \psi_s$. (+) indicates date of 0% reflushing of leaves from terminal and lateral buds. Data were collected in 1974. All measurements are expressed in bars.

	Aug. 26	Sept. 16	Sept. 30	Oct. 14	Oct. 28	Nov. 11	ANOVA F value
<u>Acer platanoides</u> 'Greenlace I'							
XWP	- 2.50	- 5.29	- 3.88	- 8.56	- 3.56	- 6.06 ⁺	162.74**
OP	-11.80	-13.00	-11.51	-11.30	-10.61	-10.02	1.66
TP	9.25	5.49	7.63	2.55	7.05	3.96	51.50**
<u>Acer platanoides</u> 'Schwedleri'							
XWP	- 2.43	- 7.00	- 7.81	- 5.06 ⁺	- 4.12	- 4.60	235.45**
OP	-10.81	-13.66	-11.17	-12.32	-10.33	- 9.63	1.01
TP	8.23	6.61	3.36	7.20	6.21	5.10	20.51**
<u>Acer platanoides</u> 'Summershade'							
XWP	- 3.31	- 7.50	- 9.75	- 6.88	- 5.56	- 5.25 ⁺	154.03**
OP	-11.01	-10.68	-10.66	-10.33	-12.07	-13.00	1.00
TP	7.78	3.90	0.91	3.43	6.26	7.69	43.96**
<u>Acer platanoides</u> 'Silver Variegated'							
XWP	- 4.06	- 7.00	- 7.88	- 8.31	- 4.88	- 6.75 ⁺	169.30**
OP	-11.42	-11.47	-11.54	- 9.90	-11.11	-10.05	5.80**
TP	7.36	4.10	3.66	1.59	6.23	3.30	59.53**
<u>Acer platanoides</u> 'Emerald Queen'							
XWP	- 3.62	- 8.00	- 8.37	- 9.25	- 5.00	- 9.43 ⁺	324.36**
OP	-11.17	-13.91	14.20	-12.21	-11.03	- 8.14	26.79**
TP	7.76	5.72	5.82	2.96	5.95	- 1.30	86.53**
<u>Acer platanoides</u> 'Globosum'							
XWP	- 2.37	- 9.25	- 9.94	- 8.81	- 4.88	- 9.94 ⁺	287.21**
OP	-13.86	-13.34	-16.34	-13.54	-11.48	-10.21	14.37**
TP	11.49	4.31	6.41	4.73	6.60	0.28	59.93**
<u>Sorbus aucuparia</u> 'Tianshanica'							
XWP	- 3.50	-10.50 ⁺	- 7.38	- 8.81	- 5.06	- 3.00	218.97**
OP	-24.28	-14.95	-16.28	-17.49	-13.58	-11.49	53.94**
TP	20.78	4.64	8.91	9.01	8.51	8.49	158.38**
<u>Sorbus aucuparia</u> 'Cardinal Royal'							
XWP	- 4.22	-12.78 ⁺	-11.50	-13.38	- 5.63	- 2.00	608.33**
OP	-21.83	-17.10	-16.85	-20.51	-14.45	-13.91	40.40**
TP	17.84	4.11	5.35	7.14	8.82	11.91	139.04**

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Appendix Table 3. (Continued)

	Aug. 26	Sept. 16	Sept. 30	Oct. 14	Oct. 28	Nov. 11	ANOVA F value
<u>Malus 'Royalty'</u>							
XWP	- 2.21	- 5.19	- 4.50	- 6.38 ⁺	- 3.75	- 8.25	219.89**
OP	-23.51	-15.70	-14.16	-15.45	-13.58	-11.73	94.41**
TP	20.86	10.51	9.66	9.07	9.86	3.48	314.78**
<u>Malus 'Snowdrift'</u>							
XWP	- 2.44	- 4.44	- 7.56	- 9.12 ⁺	- 3.75	- 1.81	403.78**
OP	-21.44	-12.54	-12.49	-15.07	-13.07	-10.76	95.83**
TP	19.00	8.10	4.93	5.93	9.33	8.95	311.16**
<u>Quercus palustris</u>							
XWP	- 2.00	- 1.94	- 1.81 ⁺	- 1.50	- 1.19	- 1.19	10.90**
OP	-17.24	-11.78	-11.35	-12.88	-12.45	-11.58	27.81**
TP	15.24	9.83	9.54	11.38	11.25	10.39	35.17**
<u>Quercus rubra</u>							
XWP	- 2.00	- 2.75	- 2.25	- 1.94 ⁺	- 1.38	- 1.25	22.68**
OP	-16.60	-13.79	- 9.73	-13.01	-12.24	-11.83	20.08**
TP	14.60	11.03	7.48	10.93	10.89	10.58	26.86**

Appendix Table 4. Deciduous shade trees, 2-2 in age, were used for pre-dawn field measurements of xylem water potential (XWP). Stem terminals used for XWP were transported to the laboratory for measurement of osmotic potential (OP). Turgor pressure (TP) was calculated based on $\psi = \psi_p + \psi_s$. (+) indicates date of 0% refushing of leaves from terminal and lateral buds. Data were collected in 1975. Mean measurements are expressed in bars.

Date	Xylem water potential			Osmotic potential			Turgor pressure			
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	
<u>Acer campestre</u>										
July	9	- 2.8	0.3	9.2	- 9.1	0.8	8.9	6.3	0.6	10.7
	18	- 2.9	0.3	10.9	- 9.8	0.4	4.5	6.8	0.4	6.3
Aug.	1	- 2.8	0.4	12.5	-10.5	0.4	3.3	7.7	0.5	5.9
	14	- 1.8	0.4	23.4	-11.4	0.8	6.8	9.6	0.8	8.6
	28	- 2.4	0.4	16.4	- 7.9	0.7	8.5	5.6	0.9	16.1
Sept.	16	- 2.4	0.4	16.4	- 8.9	0.5	5.3	6.5	0.4	6.2
	26+	- 2.6	0.6	23.6	- 7.5	0.7	8.9	4.9	1.0	20.9
Oct.	10	- 3.6	0.4	10.9	- 8.7	0.4	4.0	5.1	0.3	6.2
	24	- 3.8	0.5	14.1	- 8.9	0.3	3.4	5.1	0.7	13.8
Nov.	7	- 4.1	0.4	9.6	- 9.5	0.6	6.4	5.4	0.7	12.1
	21	- 9.5	0.5	5.0	-13.8	0.7	4.9	4.3	0.8	18.1
<u>Acer ginnala</u>										
July	9	- 1.3	0.3	19.9	-10.0	0.3	3.3	8.7	0.3	3.7
	18	- 1.3	0.4	26.9	-10.8	0.6	5.4	9.5	0.6	6.7
Aug.	1	- 1.8	0.3	15.1	-11.2	0.3	3.1	9.3	0.6	6.5
	14	- 1.7	0.3	15.2	-11.4	0.4	3.7	9.7	0.4	3.9
	28	- 2.3	0.4	15.7	- 8.5	1.0	11.7	6.3	1.1	18.0
Sept.	16	- 2.9	0.2	7.3	- 9.0	0.3	3.1	6.1	0.3	4.2
	26+	- 4.4	0.6	14.0	- 9.3	0.6	6.4	4.9	0.5	10.7
Oct.	10	- 2.6	0.4	15.2	- 9.8	0.3	3.2	7.2	0.6	7.7
	24	- 4.6	0.4	8.6	-12.1	0.4	3.6	7.5	0.6	8.4
Nov.	7	- 9.0	0.3	3.7	-15.1	0.4	2.6	6.1	0.5	7.8
<u>Acer platanoides 'Cleveland'</u>										
July	9	- 2.0	∅	∅	- 7.8	0.8	10.6	5.8	0.8	14.2
	18	- 3.2	0.3	8.1	- 8.0	0.8	10.2	4.8	0.8	17.3
Aug.	1	- 5.4	0.4	7.3	- 9.6	0.3	2.7	4.1	0.4	8.9
	14	- 5.0	0.3	5.1	-10.2	0.9	9.1	5.2	0.9	18.0
	28	- 5.7	0.5	8.5	- 8.0	0.6	6.9	2.3	1.0	42.0

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure		
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)
Sept. 16	- 2.8	0.3	9.2	- 9.2	0.5	5.3	6.4	0.2	3.4
26 +	- 6.7	0.4	6.3	- 8.6	0.5	6.0	1.9	0.9	44.8
Oct. 10	- 6.2	0.4	6.8	- 6.0	0.6	10.1	-0.2	0.8	14.6
24	- 3.5	0.5	13.5	- 7.9	0.6	7.9	4.4	0.8	17.5
Nov. 7	-11.9	0.4	3.3	-10.2	0.4	4.2	1.7	0.5	29.5
21	- 9.9	0.7	7.1	-10.6	0.5	4.3	0.7	0.8	108.3

Acer platanoides 'Columnare'

July 8	- 4.2	0.4	10.0	- 7.9	0.5	5.8	3.7	0.4	11.8
18	- 3.3	0.4	12.8	- 8.0	0.4	5.1	4.7	0.3	6.0
Aug. 1	- 4.6	0.4	8.6	- 9.4	0.2	2.2	5.0	0.5	10.5
14	- 3.0	0.9	29.4	-10.8	1.7	15.9	7.6	2.0	25.9
28	- 4.1	0.5	11.2	- 7.2	0.4	4.9	3.1	0.4	12.9
Sept. 16	- 3.5	0.5	13.5	- 8.5	0.7	8.0	5.0	0.8	15.1
26 +	- 6.9	0.7	10.1	-10.5	1.0	10.0	3.5	1.2	33.1
Oct. 10	- 5.6	0.6	11.0	- 9.8	0.6	6.0	4.2	1.0	23.4
24	- 3.5	0.5	13.5	-11.8	0.7	5.9	8.3	0.7	8.2
Nov. 7	- 6.3	0.4	6.7	-12.5	0.8	6.3	6.2	0.8	13.4
21	- 8.7	0.4	4.8	-14.7	0.5	3.5	6.0	0.5	8.6

Acer platanoides 'Crimson King'

July 9	- 4.0	∅	∅	- 8.3	0.8	9.7	4.3	0.8	18.7
18	- 5.3	0.4	8.0	- 7.6	0.4	5.5	2.3	0.3	11.3
Aug. 1	- 5.6	0.4	7.0	-10.2	0.3	3.2	4.6	0.5	10.4
14	- 3.0	1.1	36.9	-12.1	0.3	2.0	9.1	1.3	14.4
28	- 3.9	0.5	12.3	-10.7	0.5	5.0	6.9	0.6	8.9
Sept. 16	- 3.0	0.3	11.1	-11.5	0.5	4.0	8.5	0.6	6.5
26 +	- 6.5	0.7	10.3	- 8.3	0.7	8.2	1.8	1.0	56.4
Oct. 10	- 5.3	0.4	8.0	- 6.3	1.1	17.0	1.0	1.2	31.4
24	- 3.6	0.8	21.5	-10.2	0.4	3.8	6.6	0.5	7.9
Nov. 7	-10.3	0.4	4.1	-13.2	0.8	6.2	2.9	1.2	42.4
21	-15.3	0.4	2.8	-11.1	0.5	4.8	4.6	1.0	22.0

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Appendix T table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure		
	\bar{x}	SD	c.v.(%)	\bar{x}	SD	c.v.(%)	\bar{x}	SD	c.v.(%)
<u>Acer platanoides 'Royal Red'</u>									
July 9	-4.0	0	0	-7.9	0.2	3.0	4.0	0.4	9.2
18	-6.5	0.3	5.1	-8.1	0.6	7.5	1.6	0.3	20.4
Aug. 1	-4.3	0.3	6.2	-11.7	0.5	4.0	7.4	0.5	6.9
14	-4.2	0.3	6.1	-13.0	0.3	2.5	8.8	0.3	3.8
28	-4.8	0.5	10.1	-7.7	0.7	8.8	2.9	1.1	38.7
Sept. 16	-3.0	0.3	11.1	-8.1	0.5	6.3	5.1	0.6	11.2
26+	-6.3	0.5	8.5	-7.7	1.2	15.8	1.4	1.5	106.3
Oct. 10	-6.0	0.3	5.6	-8.6	0.5	6.0	2.6	0.5	18.6
24	-4.0	0.3	8.3	-10.8	0.5	4.3	6.8	0.7	10.6
Nov. 7	-12.0	0.6	4.8	-9.5	0.9	9.4	2.5	1.3	52.5
<u>Acer platanoides 'Summershade'</u>									
July 9	-4.8	0.4	8.8	-8.9	0.4	4.0	4.1	0.6	12.3
18	-7.0	0.3	4.8	8.7	0.4	4.4	1.7	0.1	7.1
Aug. 1	-4.4	0.4	9.4	-10.5	1.1	10.0	6.2	0.7	10.7
14	-3.2	0.4	13.2	-11.5	1.7	15.2	8.3	1.3	16.1
28	-4.2	0.5	11.5	-5.1	0.3	5.6	0.9	0.5	58.6
Sept. 16	-3.6	0.4	10.9	-8.7	0.2	2.7	5.1	0.3	6.3
26+	-8.4	0.6	7.3	-7.8	1.4	17.7	-0.6	0.9	56.8
Oct. 10	-7.7	0.5	7.0	-6.7	1.2	17.9	-1.0	1.2	19.5
24	-5.5	0.5	8.6	-8.0	0.7	8.7	3.5	1.0	28.8
Nov. 7	-8.8	0.3	2.9	-10.6	0.4	4.1	1.8	0.6	34.3
21	-7.3	0.4	5.8	-13.0	0.5	3.9	5.7	0.8	13.6
<u>Acer rubrum 'Autumn Flame'</u>									
July 9	-1.6	0.2	13.2	-6.9	0.4	5.3	5.3	0.3	5.4
18	-3.4	0.4	11.6	-9.0	0.5	5.0	5.6	0.4	6.7
Aug. 1	-2.7	0.3	12.7	-12.4	1.3	10.3	9.7	1.4	14.5
14	-5.0	0.2	3.0	-7.6	0.8	10.9	2.7	0.9	31.8
28	-5.1	0.7	12.9	-8.2	1.2	13.9	3.1	1.7	53.9
Sept. 16	-4.2	0.3	6.2	-10.2	0.2	2.1	6.0	0.4	6.9
26	-3.0	0.3	11.1	-8.2	1.0	11.6	5.3	0.9	16.6
Oct. 10+	-4.3	0.4	9.8	-10.0	0.5	4.6	5.7	0.9	15.1
24	-2.6	0.4	14.5	-13.3	0.4	2.8	10.8	0.5	4.6
Nov. 7	-15.7	0.8	5.0	-11.7	0.6	5.3	-4.0	0.7	17.9
21	-11.5	0.5	4.1	-10.6	0.8	7.1	-0.9	0.9	101.0
<u>Acer rubrum 'Red Sunset'</u>									
July 9	-1.9	0.2	11.1	-9.1	0.2	1.8	7.2	0.5	6.3
18	-1.8	0.3	14.3	-9.8	0.4	4.2	8.0	0.4	4.6
Aug. 1	-1.6	0.2	13.2	-11.5	0.3	2.4	9.9	0.2	1.7
14	-2.5	0.1	3.2	-9.6	0.2	2.4	7.1	0.2	3.0
28	-3.5	0.5	15.1	-7.1	0.9	12.2	3.6	0.9	26.1

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure		
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)
Sept. 16	- 3.0	0.3	11.1	- 8.4	0.3	3.3	5.4	0.4	7.6
26	- 4.1	0.4	9.6	- 8.1	0.6	7.7	4.0	0.8	19.8
Oct. 10+	- 4.3	0.4	9.8	- 9.2	0.8	8.7	4.9	0.9	17.5
24	- 2.3	0.4	18.3	-11.4	0.3	2.4	9.1	0.6	6.4
Nov. 7	- 7.6	0.4	5.2	-13.6	0.6	4.4	6.0	0.9	15.2
21	- 7.5	0.5	6.3	-13.1	0.5	3.5	5.7	0.8	13.7
<u>Acer saccharinum</u>									
July 9	- 1.9	0.2	11.1	- 7.5	0.3	3.6	5.6	0.3	5.8
18	- 2.5	0.3	13.3	- 9.8	0.7	7.2	7.3	0.6	8.0
Aug. 1	- 2.4	0.4	16.4	- 9.3	0.2	1.7	6.9	0.3	4.8
14	- 2.5	0.2	6.7	-13.5	0.7	5.2	11.0	0.5	4.9
28	- 3.5	0.3	9.5	- 8.6	1.3	14.6	5.1	1.4	27.1
Sept. 16	- 2.8	0.3	9.2	- 9.1	0.1	1.4	6.3	0.4	5.6
26	- 3.2	0.5	16.8	- 8.9	0.8	9.4	5.7	1.3	22.0
Oct. 10	- 3.9	0.4	10.0	-11.9	0.4	3.3	8.0	0.5	6.7
24+	- 4.5	0.5	10.5	-13.3	0.8	6.1	8.8	0.8	9.5
Nov. 7	- 7.1	0.4	5.5	- 9.3	0.7	7.6	2.2	0.5	23.9
21	-11.0	0.8	6.8	- 9.8	0.4	4.4	-1.2	0.9	75.8
<u>Betula pendula</u>									
July 9	- 1.0	∅	∅	- 8.1	0.5	6.1	7.1	0.5	7.0
18	- 1.8	0.4	19.4	- 9.3	1.1	11.8	7.5	1.1	14.7
Aug. 1	- 1.9	0.4	20.8	- 9.8	0.9	8.8	7.9	0.1	8.6
14	- 2.0	0.3	16.6	- 8.2	0.2	2.9	6.3	0.4	6.3
28	- 2.5	0.4	15.1	- 8.4	0.4	4.8	5.9	0.5	81.5
Sept. 16	- 2.3	0.3	11.2	- 8.4	0.5	5.8	6.1	0.5	8.4
26+	- 7.0	0.3	4.8	- 7.9	0.4	4.8	-0.9	0.3	3.7
Oct. 10	- 6.1	1.0	15.8	- 8.9	0.3	3.6	2.8	0.8	28.2
24	- 7.2	0.5	7.5	-10.1	0.3	3.4	2.9	0.8	27.3
Nov. 7	- 4.1	0.7	17.0	- 8.7	0.6	7.0	4.6	1.1	24.1
21	- 5.6	0.4	7.0	-10.2	0.6	6.3	4.6	0.6	13.6
<u>Carpinus betulus</u>									
July 9	- 1.5	0.1	4.2	- 8.5	0.6	7.4	6.8	0.4	5.3
18	- 1.8	0.3	14.3	- 8.3	0.5	5.9	6.5	0.5	7.8
Aug. 1	- 2.1	0.4	18.8	-13.7	0.5	3.3	11.6	0.8	6.7
14	- 3.0	0.3	11.0	-11.3	0.9	7.8	8.3	0.9	10.5
28	- 2.4	0.4	17.5	- 8.8	0.9	9.8	6.5	1.2	18.9
Sept. 16+	- 2.2	0.3	11.7	- 9.0	0.3	3.4	6.8	0.5	8.0
26	- 2.8	0.5	19.2	- 8.3	0.5	5.9	5.5	0.7	12.2
Oct. 10	- 4.4	0.8	17.6	- 5.5	0.5	8.8	1.3	0.7	53.8
24	- 3.8	0.5	14.1	- 7.7	0.3	3.8	3.9	0.4	9.6
Nov. 7	- 2.4	0.4	16.4	-12.0	0.4	3.4	9.6	0.4	4.4
21	- 9.5	0.5	5.0	-19.6	2.2	11.8	9.8	0.6	6.3

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure			
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	(c. v. (%))	
<u>Crataegus monogyna 'Stricta'</u>										
July	9	- 1.4	0.2	15.1	- 9.6	0.4	3.9	8.2	0.7	7.6
	18	- 1.7	0.3	15.2	- 8.4	0.4	5.2	6.7	0.4	6.0
Aug.	1	- 1.8	0.3	15.1	-11.2	0.2	1.5	9.5	0.3	2.9
	14	- 7.1	0.4	5.8	-15.9	0.7	4.5	8.8	0.9	10.5
	28	- 6.6	0.5	7.0	-13.2	1.5	11.2	6.6	1.6	23.6
Sept.	16	- 2.0	0.3	16.7	-12.8	0.4	2.9	10.8	0.6	5.5
	26	- 2.3	0.3	11.2	-11.6	0.3	2.9	9.2	0.4	4.1
Oct.	10	- 5.7	0.6	9.4	-14.4	0.5	3.3	8.5	0.9	10.7
	24	- 3.4	0.4	11.6	-15.6	1.0	6.3	12.1	1.3	10.8
Nov.	7+	- 6.0	0.3	5.5	-14.6	0.4	2.9	8.6	0.4	4.7
	21	-13.8	0.5	3.9	-23.6	0.7	2.8	9.8	0.9	9.5
<u>Crataegus oxyacantha 'Crimson Cloud'</u>										
July	9	- 1.1	0.2	19.0	-10.8	0.2	1.9	9.7	0.3	3.2
	18	- 3.4	0.4	11.6	-11.5	0.4	3.5	8.1	0.4	4.4
Aug.	1	- 2.1	0.4	18.0	-11.4	0.7	6.0	9.3	0.5	5.0
	14	- 2.3	0.4	18.6	-10.3	0.3	2.7	8.0	0.2	2.7
	28	- 2.4	0.5	21.5	- 8.1	1.1	12.9	5.7	1.1	18.8
Sept.	16	- 3.0	0.5	15.7	- 8.6	0.6	7.2	5.6	1.1	19.1
	26	- 1.8	0.3	14.3	- 7.7	1.2	14.9	5.9	1.2	19.9
Oct.	10+	- 6.0	0.3	5.6	-12.5	0.4	2.9	6.5	0.6	9.4
	24	- 3.0	0.3	11.1	-10.5	0.6	6.0	7.5	0.6	8.4
Nov.	7	- 6.8	0.3	3.8	-14.9	0.5	3.6	8.1	0.6	7.5
	21	-12.6	0.4	3.1	-18.5	0.6	3.3	5.9	0.5	8.0
<u>Crataegus oxyacantha 'Paul's Scarlet'</u>										
July	9	- 2.0	∅	∅	-11.0	0.8	6.8	9.0	0.8	9.0
	18	- 3.7	0.3	7.0	- 9.5	1.2	12.1	5.8	1.0	17.9
Aug.	1	- 1.8	0.3	15.1	-13.6	0.8	5.6	11.8	0.7	5.6
	14	- 7.1	0.8	10.9	-13.5	0.2	1.7	6.2	0.9	14.2
	28	- 6.2	0.5	8.7	-11.8	0.6	4.8	5.6	0.6	10.4
Sept.	16	- 3.4	0.4	11.6	-11.7	0.6	5.1	8.3	0.8	9.1
	26	- 3.5	0.3	9.5	- 9.7	0.4	4.0	6.2	0.3	4.9
Oct.	10+	- 5.2	0.5	10.3	- 7.1	0.5	7.3	1.9	0.8	41.4
	24	- 3.2	0.4	13.2	- 9.6	0.6	6.6	6.4	0.5	8.1
Nov.	7	- 5.7	0.5	9.4	-14.4	0.5	3.8	8.7	0.9	10.0
	21	- 3.4	0.3	11.6	-18.2	0.5	2.9	14.8	0.7	5.0
<u>Crataegus oxyacantha 'Toba'</u>										
July	9	- 1.6	0.2	13.2	-11.3	0.6	5.6	9.7	0.8	8.3
	18	- 2.1	0.2	10.0	- 9.9	0.2	2.9	7.8	0.3	4.0
Aug.	1	- 2.0	0.3	16.7	-12.6	1.3	10.5	10.6	1.3	12.6
	14	- 7.4	1.3	17.9	-16.7	1.9	11.2	9.4	2.1	22.9
	28	- 5.7	0.5	8.5	-13.7	1.4	9.5	8.1	1.2	14.3

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure		
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)
Sept. 16	- 2.7	0.3	9.6	-13.6	0.3	2.1	10.9	0.4	4.1
26	- 1.8	0.3	14.3	- 9.7	0.8	8.1	7.9	0.9	10.8
Oct. 10+	- 5.4	0.4	7.3	- 6.7	0.5	7.0	1.3	0.7	54.9
24	- 1.8	0.5	29.9	-10.8	0.4	3.8	8.9	0.8	9.5
Nov. 7	- 3.6	0.6	17.0	- 9.5	0.4	4.1	5.9	0.8	12.7
21	- 4.0	0.3	8.3	- 9.1	0.6	6.3	5.1	0.7	14.4
<u>Crataegus oxyacantha</u> 'Winter King'									
July 9	- 1.0	∅	∅	- 9.3	0.3	3.0	8.3	0.6	6.7
18	- 1.8	0.3	14.3	- 8.8	1.3	15.2	6.9	1.4	19.7
Aug. 1	- 1.3	0.3	19.9	-13.7	0.3	2.3	12.5	0.5	4.0
14	- 5.4	0.6	10.9	-12.5	0.0	8.3	7.0	0.6	8.0
28	- 5.0	0.5	10.0	-12.2	1.3	11.0	7.2	1.3	18.1
Sept. 16	- 1.9	0.2	11.0	-12.2	0.1	5.6	10.3	0.6	6.0
26	- 1.9	0.2	11.0	- 9.1	0.4	3.9	7.2	0.4	5.1
Oct. 10+	- 5.6	0.4	6.9	-13.3	0.7	5.1	7.7	0.7	9.6
24	- 3.1	0.4	12.7	-14.8	1.0	6.7	11.7	1.0	8.5
Nov. 7	- 6.9	0.5	7.5	-13.4	0.4	2.9	6.5	0.9	13.0
21	- 9.6	0.4	4.1	-15.9	0.4	2.8	6.4	0.8	12.7
<u>Fraxinus holotricha</u> 'Moraine'									
July 9	- 1.7	0.4	24.8	- 8.8	1.1	12.4	7.1	1.0	13.2
18	- 2.0	0.3	16.6	-10.6	0.9	8.2	8.6	0.7	8.0
Aug. 1	- 2.2	0.4	19.2	-12.4	0.6	5.0	10.2	0.8	7.7
14	- 3.3	0.2	6.7	-13.7	0.3	2.3	10.5	0.3	3.3
28	- 3.4	0.5	15.2	- 9.0	0.8	9.3	5.6	1.1	19.3
Sept. 16	- 3.8	0.3	6.8	- 8.5	0.6	6.7	4.7	0.6	13.6
26+	- 4.0	0.3	8.3	- 6.7	0.4	5.7	2.7	0.6	23.4
Oct. 10	- 6.2	0.5	8.7	-10.1	0.2	2.1	4.0	0.8	18.8
24	- 7.8	0.5	6.9	-10.8	0.5	5.0	3.0	0.7	24.1
Nov. 7	- 8.5	0.5	5.5	-11.0	0.3	2.6	2.5	0.6	22.9
21	-13.7	0.4	3.1	-15.8	0.7	4.6	2.1	0.6	27.4
<u>Fraxinus pennsylvanica</u> 'Kimberly Blue'									
July 9	- 2.2	0.3	11.7	-9.3	0.4	4.5	7.1	0.5	7.4
18	- 2.3	0.3	11.2	- 6.6	0.6	9.8	4.3	0.5	11.3
Aug. 1	- 1.9	0.3	16.6	-10.5	0.7	7.0	8.6	0.9	10.1
14+	- 8.9	0.3	2.8	-14.0	0.4	3.0	5.1	0.2	3.6
28	- 5.2	0.5	9.2	-10.5	0.7	7.0	5.2	0.7	14.0
Sept. 16	- 3.8	0.3	6.8	- 9.8	0.6	5.8	6.0	0.4	7.0
26	- 4.6	0.4	8.6	- 8.5	0.3	3.4	3.9	0.7	17.7
Oct. 10	- 6.0	0.8	12.4	- 5.7	0.5	9.2	-0.5	1.3	24.4
24	- 5.2	0.7	13.7	-15.0	1.3	8.6	9.8	1.4	3.9
Nov. 7	- 5.1	0.4	7.7	-16.2	0.5	2.8	11.1	0.8	6.9
21	-15.3	0.5	3.5	-15.4	0.5	3.2	-0.4	0.3	46.6

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure		
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)
<u>Fraxinus pennsylvanica</u> 'Marshall Seedless'									
July 9	- 2.3	0.4	18.3	- 9.6	0.5	5.3	7.3	0.4	5.6
18	- 3.3	0.3	8.0	-13.1	0.9	6.8	9.8	0.8	8.5
Aug. 1	- 4.5	0.4	12.4	-14.1	1.5	10.3	10.0	1.7	17.6
14+	-12.7	0.8	6.2	-13.0	1.1	8.5	0.1	1.4	23.2
28	- 4.6	0.4	8.1	- 9.5	0.4	3.7	4.9	0.6	12.5
Sept. 16	- 5.2	0.4	8.1	-12.6	0.5	3.9	7.4	0.9	11.5
26	-15.2	1.4	9.2	-13.2	1.5	11.2	-2.3	1.9	83.2
Oct. 10	- 4.0	0.8	18.6	- 6.8	0.9	13.0	2.8	1.0	36.5
24	- 7.8	0.5	6.9	-16.7	0.4	2.3	9.3	1.1	11.9
Nov. 7	-15.2	0.5	3.5	-15.0	0.4	2.5	-0.2	0.8	16.0
21	- 7.9	0.5	6.5	-20.0	0.7	3.3	12.0	0.9	7.2
<u>Gleditsia triacanthos</u> 'Skyline'									
July 9	- 3.0	∅	∅	- 9.9	0.4	3.5	6.9	0.4	5.0
18	- 2.3	0.3	11.7	- 8.7	0.2	1.9	5.4	0.2	3.8
Aug. 1	- 3.5	0.4	10.7	-13.8	0.1	0.9	10.4	0.4	4.1
14	- 4.7	0.3	5.5	-13.3	1.5	11.5	8.6	1.5	17.2
28	- 4.4	0.4	9.5	-11.9	1.5	12.8	7.6	1.6	20.5
Sept. 16+	- 7.3	1.0	14.1	- 9.1	0.3	2.8	2.1	0.9	44.1
26	- 9.0	0.7	7.4	-11.1	0.7	6.4	2.9	0.7	27.2
Oct. 10	- 8.4	0.8	9.2	-11.4	0.4	3.8	12.5	0.8	6.7
24	- 9.4	0.6	6.5	-21.8	0.4	1.8	4.4	0.8	9.6
Nov. 7	-12.2	0.5	4.4	-16.6	0.2	1.4	8.3	0.4	11.8
21	- 4.8	0.5	11.2	-13.1	0.7	5.0	8.3	1.0	11.8
<u>Malus</u> 'Klehm's Bechtel'									
July 9	- 1.0	∅	∅	- 9.2	0.3	3.3	8.2	0.2	2.7
18	- 1.8	0.3	14.3	-11.5	0.5	4.5	9.7	0.4	4.0
Aug. 1	- 1.7	0.2	14.6	-12.9	0.4	3.4	11.3	0.3	2.8
14	- 3.0	0.3	11.1	-14.4	1.4	9.7	11.4	1.7	14.6
28	- 5.7	0.4	7.3	-11.2	0.5	4.0	5.6	0.6	9.9
Sept. 16	- 1.9	0.2	11.0	-12.8	0.3	2.4	10.9	0.4	3.6
26	- 2.2	0.3	11.7	-10.7	0.4	4.0	8.5	0.5	6.0
Oct. 10+	- 7.4	0.3	5.3	-10.0	0.6	6.4	2.6	0.8	29.5
24	- 4.8	0.5	11.2	-17.0	0.7	4.4	12.1	1.2	9.9
Nov. 7	- 3.3	0.4	12.8	-12.1	0.4	3.0	8.8	0.6	7.1
21	- 4.5	0.3	7.4	-14.9	0.7	5.1	10.4	0.7	6.8
<u>Malus</u> 'Radiant'									
July 8	- 1.2	0.2	21.0	- 8.9	0.4	4.3	7.7	0.4	4.7
18	- 1.8	0.3	14.3	-11.9	0.5	4.4	10.1	0.4	3.4
Aug. 1	- 1.8	0.3	15.0	-13.2	0.7	5.5	11.4	0.6	5.2
14	- 3.9	0.4	10.1	-13.8	0.3	1.9	9.9	0.6	5.6

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Appendix Table 4. (Continued)

Date	<u>Xylem water potential</u>			<u>Osmotic potential</u>			<u>Turgor pressure</u>			
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	
Aug. 28	- 4.1	0.5	11.2	-13.3	0.4	2.7	9.2	0.4	3.9	
Sept. 16	- 2.0	0.3	16.6	-13.1	0.4	3.0	11.2	0.5	4.2	
26	- 2.8	0.3	9.2	-10.8	0.4	3.9	8.1	0.3	3.5	
Oct. 10 +	- 7.2	0.5	7.5	- 6.8	0.5	7.8	-0.5	0.8	14.6	
24	- 5.1	0.6	12.0	- 7.8	0.5	5.9	2.7	0.9	31.6	
Nov. 7	- 5.9	0.4	6.7	-12.7	0.5	4.1	6.8	0.4	5.8	
21	- 8.7	0.3	3.0	-11.7	0.7	6.0	3.0	0.7	23.8	
<u>Malus 'Royalty'</u>										
July 8	- 1.0	∅	∅	-10.2	0.2	1.6	9.2	0.2	1.7	
18	- 2.3	0.3	11.2	-11.9	0.3	2.4	9.6	0.4	4.1	
Aug. 1	- 1.7	0.3	15.2	-11.9	0.4	3.1	10.2	0.3	3.3	
14	- 4.4	0.6	14.0	-11.4	1.1	9.5	6.8	1.4	20.2	
28 +	- 4.8	0.4	8.8	- 8.4	0.6	7.5	3.6	0.9	24.9	
Sept. 16	- 1.8	0.3	14.3	-10.0	0.4	4.2	8.1	0.6	7.7	
26	- 1.6	0.2	13.2	-10.9	0.4	3.4	9.3	0.4	4.4	
Oct. 10	- 7.4	0.6	8.3	-10.9	0.7	6.7	3.5	1.1	32.1	
24	- 4.2	0.5	12.8	-10.6	0.4	3.6	6.4	0.6	9.1	
Nov. 7	- 3.4	0.4	11.6	-14.8	0.5	3.2	11.4	0.4	3.6	
21	- 4.9	0.4	8.0	-20.4	0.5	2.2	15.5	0.6	4.0	
<u>Malus sargentii</u>										
July 9	- 1.0	∅	∅	- 9.8	0.4	3.6	8.8	0.4	4.2	
18	- 1.7	0.3	15.2	-11.6	0.3	2.8	9.9	0.2	1.8	
Aug. 1	- 1.1	0.2	14.4	-10.4	0.5	4.7	9.3	0.6	6.4	
14	- 1.5	∅	∅	-10.8	0.6	5.1	9.3	0.6	5.9	
28 +	- 3.1	0.4	12.7	- 8.9	0.6	6.7	5.3	1.3	23.0	
Sept. 16	- 1.7	0.3	15.2	- 9.0	0.3	2.9	7.3	0.4	5.6	
26	- 1.6	0.2	13.2	- 8.3	0.4	4.8	6.7	0.4	6.0	
Oct. 10	- 9.6	0.8	8.0	-12.9	0.9	7.0	3.2	1.1	34.4	
24	- 5.7	0.5	9.4	-10.1	0.3	2.9	4.3	0.7	17.3	
Nov. 7	- 4.2	0.4	10.0	- 7.3	0.6	7.6	3.1	0.5	16.7	
<u>Malus 'Snowdrift'</u>										
July 9	- 1.0	∅	∅	- 9.1	0.3	3.1	8.1	0.3	3.4	
18	- 1.7	0.2	14.6	-11.7	0.8	6.8	10.1	0.6	6.2	
Aug. 1	- 3.0	0.3	11.0	-11.3	0.1	1.1	8.3	0.4	4.3	
14	- 2.1	0.2	10.0	-14.6	0.2	1.6	12.5	0.4	3.2	
28	- 3.3	0.5	14.6	-12.3	0.2	1.6	9.0	0.6	6.5	
Sept. 16	- 1.8	0.3	14.3	-11.6	0.5	4.2	9.8	0.4	5.1	
26	- 2.2	0.3	11.7	-10.5	0.5	4.8	8.3	0.7	8.1	
Oct. 10 +	- 8.2	0.5	6.6	- 7.6	0.7	8.6	-0.8	0.2	30.0	
24	- 4.8	0.5	11.2	- 9.9	0.4	3.5	5.1	0.9	16.9	
Nov. 7	- 6.0	0.3	5.5	-12.5	0.5	4.2	6.5	0.7	11.3	
21	- 9.6	0.4	4.1	-13.1	0.5	3.8	3.5	0.6	15.8	

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Appendix Table 4. (Continued)

Date	<u>Xylem water potential</u>			<u>Osmotic potential</u>			<u>Turgor pressure</u>			
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	
<u>Platanus hispanica</u>										
July	9	- 1.0	∅	∅	- 5.9	0.4	6.3	4.9	0.4	7.6
	18	- 2.1	0.5	24.6	- 8.9	0.7	7.3	6.8	0.4	6.3
Aug.	1	- 1.9	0.2	11.1	- 8.3	0.4	4.6	6.5	0.4	6.6
	14	- 3.5	0.5	13.5	-10.6	1.1	10.5	7.1	1.2	16.8
	28	- 3.7	0.4	11.3	- 9.5	1.3	13.6	5.8	1.3	21.3
Sept.	16 +	- 2.4	0.2	8.8	- 9.2	0.3	2.8	6.8	0.5	6.7
	26	- 4.6	0.4	8.6	- 8.6	1.0	11.1	4.0	0.6	15.3
Oct.	10	- 5.0	0.8	14.9	- 5.2	0.5	8.5	0.2	1.2	24.9
	24	- 3.2	0.3	8.1	- 8.1	0.7	9.0	4.7	1.0	20.8
Nov.	7	- 4.1	0.2	5.1	-13.4	0.6	4.5	9.3	0.5	5.8
	21	- 5.7	0.4	7.4	- 9.3	0.6	6.4	3.6	0.8	22.5
<u>Quercus palustris</u>										
July	9	- 1.0	∅	∅	- 6.5	0.4	6.0	5.5	0.4	7.1
	18	- 1.2	0.2	21.0	- 8.0	0.8	9.8	6.8	0.6	8.5
Aug.	1	- 1.1	0.2	19.2	- 9.9	1.6	16.2	8.8	1.5	17.3
	14	- 1.2	0.3	21.5	- 8.5	0.6	6.2	7.3	0.3	4.0
	28	- 1.2	0.2	21.0	- 8.1	0.4	5.4	6.9	0.6	8.4
Sept.	16 +	- 1.4	0.2	15.1	- 8.4	0.3	3.2	7.0	0.4	5.8
	26	- 1.7	0.3	15.2	- 8.7	0.8	9.7	7.0	0.9	13.2
Oct.	10	- 4.9	0.4	8.0	-11.9	0.3	2.5	7.0	0.5	7.7
	24	- 1.8	0.4	23.4	- 9.5	0.5	5.7	7.7	0.9	11.4
Nov.	7	- 2.5	0.3	13.3	- 9.2	0.7	7.4	6.7	0.6	9.6
	21	- 5.6	0.4	7.0	-16.1	0.5	3.1	10.5	0.8	7.2
<u>Quercus robur</u>										
July	9	- 1.0	∅	∅	- 5.7	0.5	8.0	4.7	0.5	9.7
	18	- 1.2	0.2	21.0	- 7.3	0.6	8.2	6.2	0.5	7.8
Aug.	1	- 1.4	0.2	15.1	- 8.9	0.4	4.3	7.4	0.4	5.4
	14	- 1.2	0.3	21.5	- 9.7	0.3	3.4	8.5	0.5	6.2
	28	- 1.2	0.3	22.0	- 7.2	0.3	3.9	6.0	0.5	7.6
Sept.	16 +	- 1.8	0.3	14.3	- 8.8	0.2	2.1	7.1	0.4	6.1
	26	- 1.9	0.2	11.1	- 9.3	0.5	5.6	7.4	0.6	8.6
Oct.	10	- 5.4	0.4	7.3	-11.0	0.2	2.0	5.6	0.6	10.4
	24	- 1.9	0.4	20.8	-11.4	0.6	5.2	9.5	0.6	6.4
Nov.	7	- 3.2	0.3	8.1	- 8.9	0.5	6.0	5.7	0.6	10.1
	21	- 5.9	0.4	6.7	-15.0	0.8	5.3	9.2	1.0	11.0
<u>Quercus rubra</u>										
July	9	- 1.0	∅	∅	- 8.7	0.5	5.8	7.7	0.5	6.5
	18	- 1.2	0.2	21.0	- 8.6	0.6	6.9	7.5	0.7	8.8
Aug.	1	- 1.3	0.3	19.9	- 8.5	0.5	6.2	7.2	0.5	7.0
	14	- 1.3	0.3	19.9	- 8.8	0.3	2.9	7.5	0.4	5.0
	28	- 1.6	0.3	19.8	- 9.7	0.7	7.3	8.1	0.6	7.6

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure			
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	
Sept. 16	- 1.9	0.2	11.1	- 9.4	0.3	3.0	7.5	0.3	4.2	
26 +	- 3.0	0.3	11.1	- 8.6	0.4	4.0	5.6	0.6	10.8	
Oct. 10	- 3.0	0.3	11.1	- 9.7	0.4	3.8	6.7	0.6	8.6	
24	- 2.1	0.4	18.8	-10.8	0.5	4.6	8.7	0.6	6.8	
Nov. 7	- 4.9	0.5	10.5	-11.8	0.5	3.8	6.9	0.8	11.8	
21	- 5.7	0.6	11.1	-15.7	0.8	4.9	10.0	1.1	10.9	
<u>Sorbus aucuparia</u>										
July 8	- 2.0	∅	∅	- 9.3	0.5	5.3	7.3	0.5	6.7	
18	- 3.0	0.3	9.6	- 9.5	0.5	5.5	6.6	0.4	6.7	
Aug. 1	- 4.3	0.5	12.7	-10.5	0.6	5.8	6.2	0.3	4.8	
14 +	- 6.5	0.5	7.2	-10.1	0.5	4.9	3.6	0.7	18.5	
28	- 7.9	0.8	10.6	- 8.7	0.5	6.1	0.8	1.0	24.7	
Sept. 16	- 6.0	1.0	15.7	- 8.7	0.5	5.8	2.7	0.8	0.3	
26	-10.8	0.8	7.3	- 9.3	0.9	9.2	-1.8	0.5	54.6	
Oct. 10	- 3.6	0.6	0.7	-10.0	0.4	4.4	6.5	0.6	9.1	
24	- 3.1	0.4	12.7	-12.6	0.5	4.2	9.5	0.4	4.1	
Nov. 7	- 4.0	0.3	8.3	-13.3	0.4	3.2	9.4	0.5	4.9	
21	- 4.9	0.4	8.0	-14.5	0.7	0.5	9.6	0.9	9.4	
<u>Sorbus aucuparia 'Cardinal Royal'</u>										
July 9	- 3.1	0.2	6.8	- 9.8	0.4	4.2	6.7	0.5	6.9	
18	- 2.8	0.4	12.9	-10.2	0.6	5.9	7.5	0.4	4.9	
Aug. 1	- 2.2	0.2	11.2	-10.3	0.4	4.0	8.3	0.5	5.7	
14 +	- 6.3	0.3	4.1	-11.3	1.3	11.6	5.0	1.3	26.0	
28	- 3.1	0.4	12.1	- 8.5	0.6	6.9	5.5	0.5	9.2	
Sept. 16	- 5.5	0.5	8.6	-12.0	0.1	8.4	6.5	1.5	23.3	
26	- 9.7	0.4	4.3	-10.5	1.0	9.3	0.8	1.2	23.8	
Oct. 10	- 3.2	0.5	16.8	-10.4	0.4	4.1	7.2	0.7	9.4	
24	- 2.4	0.4	16.4	- 8.8	0.3	3.2	6.4	0.5	7.1	
Nov. 7	- 3.5	0.5	13.5	-13.0	0.5	4.0	9.5	0.7	7.7	
21	-10.9	0.7	6.4	-15.3	1.2	7.6	4.4	1.5	33.7	
<u>Sorbus aucuparia 'Tianshanica'</u>										
July 9	- 3.3	0.4	12.8	- 7.8	0.3	4.1	4.5	0.6	12.3	
18	- 2.7	0.3	12.7	- 8.8	0.4	5.0	6.1	0.3	5.2	
Aug. 1	- 1.7	0.3	15.0	- 9.6	0.3	3.1	7.9	0.5	6.2	
14 +	- 2.6	0.4	15.2	-11.1	1.7	14.9	8.5	1.7	19.5	
28	- 3.3	0.7	21.7	- 8.4	0.6	6.8	5.1	1.0	20.6	
Sept. 16	- 3.7	0.3	7.0	-11.1	0.5	4.2	7.4	0.6	83.1	
26	- 8.0	0.9	11.8	-10.1	0.5	5.1	2.1	1.2	58.8	
Oct. 10	- 4.5	0.5	10.5	- 7.4	0.6	8.2	2.9	0.8	26.9	
24	- 2.4	0.4	16.4	-10.9	0.4	3.6	8.5	0.5	6.4	
Nov. 7	- 5.9	0.4	6.7	-14.2	0.4	3.0	8.1	0.3	3.6	
21	- 6.9	0.4	5.7	- 8.8	0.5	5.6	1.9	0.6	30.2	

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure			
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	
<u>Tilia americana 'Redmond' (on T. platyphyllos)</u>										
July	9	- 1.0	∅	∅	- 8.8	0.7	7.6	7.8	0.7	8.6
	18	- 1.8	0.3	14.3	- 9.3	0.2	2.6	7.5	0.2	2.9
Aug.	1	- 1.3	0.3	21.0	- 8.3	0.4	4.7	7.1	0.5	6.6
	14	- 1.8	0.3	14.3	- 7.8	0.2	2.6	6.2	0.3	5.4
	28 +	- 3.2	0.3	8.1	- 7.2	0.4	5.6	4.0	0.5	11.6
Sept.	16	- 2.3	0.3	11.2	- 8.8	0.7	8.0	6.5	0.6	9.5
	26	- 2.2	0.3	11.7	- 8.8	0.5	5.4	6.3	0.7	10.8
Oct.	10	- 5.9	0.7	11.9	- 6.7	0.3	4.0	0.7	1.0	22.0
	24	- 2.9	0.4	13.6	- 8.2	0.8	9.9	5.3	0.8	14.8
Nov.	7	- 8.8	0.5	6.1	-13.3	0.3	2.5	4.5	0.5	10.7
	21	- 8.4	0.4	4.7	-10.3	0.5	4.4	1.9	0.7	36.4
<u>Tilia americana 'Redmond' (on T. tomentosa)</u>										
July	9	- 1.0	∅	∅	- 9.6	0.3	3.1	8.6	0.3	3.5
	18	- 1.7	0.3	15.1	- 5.9	0.1	2.1	4.1	0.2	4.5
Aug.	1	- 1.5	0.3	19.6	- 9.9	0.5	5.2	8.5	0.6	7.6
	14	- 1.8	0.3	14.3	-10.0	0.6	6.4	8.2	0.7	8.0
	28 +	- 2.8	0.6	21.4	- 8.8	1.2	13.0	6.1	0.9	15.2
Sept.	16	- 2.3	0.4	18.3	- 8.3	0.4	4.4	6.0	0.3	5.5
	26	- 1.8	0.3	14.3	- 6.7	0.4	5.4	4.9	0.6	13.3
Oct.	10	- 4.2	0.5	12.8	- 5.9	1.3	22.3	1.5	1.6	46.0
	24	- 6.4	0.4	6.7	-11.4	0.5	4.1	5.0	0.4	7.8
Nov.	7	- 7.1	0.4	5.5	-10.9	0.7	6.5	3.8	0.5	14.1
	21	- 7.3	0.4	5.8	-12.6	0.6	4.4	5.4	0.7	12.5
<u>Tilia cordata 'Chancellor'</u>										
July	9	- 1.0	∅	∅	- 7.1	0.1	1.7	6.1	0.1	2.0
	18	- 1.6	0.2	13.2	- 7.6	1.1	14.0	6.0	0.9	14.3
Aug.	1	- 1.7	0.3	15.2	-10.1	0.4	3.8	8.4	0.4	4.7
	14	- 1.9	0.2	11.1	- 9.5	0.4	4.3	7.6	0.2	3.2
	28 +	- 3.2	0.6	18.4	- 8.5	0.5	5.8	5.4	0.8	15.4
Sept.	16	- 2.0	0.3	16.7	- 9.1	0.4	4.5	7.1	0.7	10.0
	26	- 1.9	0.2	11.1	- 6.7	0.3	5.0	4.6	0.2	5.0
Oct.	10	- 4.9	0.4	8.0	- 8.7	0.3	3.9	3.8	0.6	16.5
	24	- 3.2	0.5	16.8	- 9.9	0.5	5.0	6.7	0.8	12.4
Nov.	7	- 7.4	0.5	6.9	- 9.2	0.5	5.2	1.8	0.9	4.9
	21	- 4.3	0.4	9.8	- 6.0	0.7	11.4	1.7	0.5	28.4
<u>Tilia cordata 'Greenspire'</u>										
July	9	- 1.7	0.3	15.2	- 7.2	0.4	5.9	5.5	0.7	13.4
	18	- 2.7	0.3	9.6	- 9.9	0.6	5.8	7.2	0.7	9.1
Aug.	1	- 1.8	0.3	14.3	- 8.7	0.5	6.2	6.9	0.7	9.7
	14	- 4.9	0.2	3.2	-10.7	1.6	14.5	5.7	1.5	26.6
	28 +	- 5.2	0.4	6.9	-10.5	1.0	9.5	5.3	1.0	18.2

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Appendix Table 4. (Continued)

Date	Xylem water potential			Osmotic potential			Turgor pressure		
	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)	\bar{x}	SD	c. v. (%)
Sept. 16	- 2.5	0.3	13.3	- 9.0	0.4	4.9	6.5	0.5	7.6
26	- 2.1	0.2	10.0	- 8.1	0.8	9.3	6.0	0.9	14.3
Oct. 10	- 2.9	0.4	13.6	- 9.8	0.3	3.1	6.9	0.2	3.0
24	- 2.7	0.5	19.9	-10.7	0.3	3.0	8.0	0.6	8.0
Nov. 7	- 6.3	1.0	16.4	- 9.0	0.7	7.9	2.7	0.9	32.6
21	-11.7	0.5	4.6	-10.7	0.9	8.4	1.0	1.0	74.4
<u>Tilia cordata 'Olympic'</u>									
July 9	- 2.6	0.3	9.6	- 7.5	0.8	10.6	4.8	1.1	23.6
18	- 3.4	0.4	11.6	- 9.2	0.5	5.6	5.8	0.3	4.6
Aug. 1	- 2.1	0.2	10.0	- 9.9	0.5	4.9	7.8	0.6	7.2
14	- 5.5	0.3	6.0	- 7.1	0.6	8.0	1.6	0.6	40.5
28 +	- 5.9	0.4	6.7	- 7.8	0.5	5.8	1.9	0.5	27.8
Sept. 16	- 2.0	0.3	16.7	- 9.5	0.5	4.7	7.5	0.3	3.4
26	- 2.5	0.3	13.3	- 6.5	0.5	7.0	3.9	0.6	14.3
Oct. 10	- 4.8	0.9	17.8	- 8.8	0.6	6.7	4.0	1.3	33.1
24	- 2.7	0.5	18.7	-11.9	0.5	3.8	9.2	0.3	2.9
Nov. 7	- 5.5	0.3	6.0	-12.0	0.4	3.3	6.5	0.7	9.9
21	- 8.7	0.3	3.0	-14.5	0.7	4.7	5.9	0.8	12.9

Appendix Fig. 1. 1974 Air temperature and precipitation records from 10 miles south of experimental site at an elevation of 450 feet (Estacada 2SE weather station), and soil temperatures and evaporation rates measured 40 miles south of site at an elevation of 150 feet. The elevation of the experimental site is 600-650 feet. Daylength plot based on Oregon State University, Corvallis records. Temperature data points indicate the mean of daily maximum and minimum temperatures. The average temperature data are based on monthly means during 1969-1973.

