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Efficiency and regulation of water transport in some woody and herbaceous species

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To

my wife Libia and

my son Saul Orlando

ABSTRACT OF THE DISSERTATION

"Efficiency and regulation of water transport in some woody and herbaceous species"

by

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University of California, Riverside, December 1973

Professor Merrill R. Kaufmann, Chairman

Experimental verification of the assumption that water flow in the soil-plant-atmosphere continuum can be treated as a sequence of steady states is presented. The ratio of vapor pressure deficit to leaf diffusion resistance proved to be a good estimate of transpiration for citrus leaves, whenever leaf-to-air temperature differences were small. No difference in water transport characteristics was found for Valencia orange on three rootstocks in well-watered soil, but both Cleopatra mandarin and Rangpur presented greater leaf water stress than Troyer citrange at high transpiration rates and mild soil water deficits. In laboratory studies, previously unstressed seedlings had higher leaf water potentials than field trees at equivalent transpiration rates. After several drying cycles, however, leaf water potentials were similar to those observed in the field.

Studies on the efficiency of water transport of orange (Citrus sinensis var. Koethen), evergreen pear (Pyrus kawakami), sunflower

(Helianthus annuus cv. Russian Mammoth), pepper (Capsicum frutescens cv. Yolo Wonder) and sesame (Sesamum indicum cv. Glauca) seedlings were performed under controlled environmental conditions and under non-limiting soil water supply. The studies on water transport efficiency reported here were based upon a recent model that relates plant water status with soil, plant and climatic factors. The efficiency with which plants transport water is related to the water potential difference required for water flux from the soil to the leaf. Data showed contrasts in the water transport efficiency of the species tested. Woody species (citrus and pear) showed a depression of leaf water potential in response to increases in transpiration; the herbaceous species, however, had a more efficient water transport system, because no measurable response of leaf water potential to changes in transpiration were observed.

The fact that different maximum transpiration rates under the same climatic conditions were observed for the different species suggested that stomata also were somehow influenced by the climate. Studies on the regulation of water loss showed that sesame leaf diffusion resistance increased markedly as humidity was decreased, while sunflower leaf resistance responded less to humidity. Sesame appeared to respond directly to humidity because simultaneous measurements of leaf water potential showed no changes in the average water status when stomatal closure occurred. Preliminary studies on orange (Citrus sinensis var. Koethen) response to changing evaporative demands in the atmosphere are

presented. The regulation of water loss by this species due tto leaf diffusion resistance responses to humidity, temperature and radiation were partially determined.

The relationship of leaf water potential and pressure chamber values was determined by using improved methodology for citrus and evergreen pear, and results showed a curvilinear relationship between the two measurements with citrus and a linear relationship with pear.

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I. INTRODUCTION AND OBJECTIVES

Research efforts in plant water relations have focused on the measurement of plant water status, on the physiological consequences of changes in plant water status, and on the study of single cause-effect relationships between plant water status and the environment. Considerable research has been devoted to plant response to drying soils in both controlled and natural environments. In contrast, the climatic influences on the water status of plants with non-limiting water supplies have not been fully studied, although they are particularly relevant in irrigated agriculture.

Even with an adequate soil water supply plant water status is expected to be dependent on variations in climate. This dependency should be complex due to the dynamic and interacting character of climatic variables and the contrasting behavior of different ecotypes and species. Further, plant-water-status response to climate depends upon both the ability of a given species to regulate water loss and the efficiency of water transport in plants.

The studies reported here were based upon a recent model of the soil-plant-atmosphere continuum. A sound working model of the interrelationships between the plant and its soil and atmospheric environments is potentially useful in plant physiology, ecology and agriculture. Such a model could facilitate the study of the effects of specific edaphic and atmospheric conditions on plant water relations for a broad range of plants, and it could aid in understanding differences among plants adapted to contrasting environments. The first

paper describes experimental tests of basic assumptions of the model. The model was used to interpret leaf water potential response to transpiration (which depends upon the climate) by well watered citrus trees in natural and controlled environments. The second paper describes a comparative study on the efficiency of the water transport system of several contrasting species. Preliminary studies on the regulation of water loss by citrus are described in Appendix I, and observations on methods for evaluating water status are presented in Appendix II.

II. REVIEW OF LITERATURE

Water movement to roots, water transport within plants and water loss from plants are phenomena occurring in the components of a unified system: the soil-plant-atmosphere continuum (SPAC) (Philip, 1965). The flow of water in any segment of this system is dependent upon gradients in water potential and upon resistances to flow (van den Honert, 1948). Because the factors influencing water loss and uptake vary with time, and since the plant body is both plastic and elastic, the system is a dynamic one (Cowan and Milthorpe, 1968). The flow of water within the soil-plant-atmosphere continuum is particularly important since it is quantitatively much greater than the amount of water used by plants in either metabolism or growth (Kramer, 1969). Plant water status depends upon the balance between water loss and supply which depends upon the integrated functioning of the total soil-plant-atmosphere system (Slatyer, 1967).

Several reviews and detailed descriptions of the soil-plant-atmosphere continuum exist (Cowan and Milthorpe, 1968; Dainty, 1969; Kaufmann and Hall, 1973; Kramer, 1969; Philip, 1965; Slatyer, 1967; Weatherley, 1970). This review emphasizes aspects of plant water relations that are directly relevant to the work reported here.

Water loss from plants and its control.

Probably one of the major difficulties facing the evolution of plants from aquatic to terrestrial forms was the problem of water supply and retention. Land plants occupy a region bounded by the soil

which stores and holds water with variable force and the air which serves as a sink for water vapor. Apparently land plants developed two main systems by which they can satisfy water requirements and protect themselves from the desiccating power of the air (Stalfelt, 1972). One system is characterized by a high desiccation resistance of the protoplasm, water loss largely dependent on atmospheric conditions with minimal plant control and growth occurring only when water is adequately available. This system is exemplified by mosses and lichens. The second system, developed by many vascular plants is characterized by at least some degree of morphological and physiological control of water movement. Cuticle and periderm reduce water losses and stomatal movement control it. Consequently, the adaptation of plants to arid environments appears to have involved strict regulation of water loss and efficient water transport systems.

Plants require carbon dioxide for growth, and it seems that conditions favoring the most rapid exchange of carbon dioxide and oxygen also favor the loss of water. Complex stomatal regulation of gaseous transfer may represent a solution to the opposing needs of restricting water loss and fixing carbon dioxide. Selection has favored the types of stomatal regulation that can fulfill specific compromises allowing optimal growth. As an example, potato and tomato mutants with stomata locked open wilt due to their inability to control water loss (Tal, 1966; Waggoner and Simmonds, 1966). These wilting mutants grow less than those with normal stomato, even though their stomato provide more opportunity for carbon dioxide intake. Apparently the detrimental effects of

water stress predominate in this case.

Transpiration has been regarded as an inevitable but undesirable result of the construction and metabolic requirements of plants. For carbon dioxide fixation to occur, it is necessary that gaseous exchange is permitted. Consequently, evaporation occurs from the wet surfaces exposed to the atmosphere (Knight, 1965; Curtis, 1926). Transpiration has been considered as useful for leaf cooling (Gates, 1968; Knight, 1965) and for the absorption and distribution of nutrients (Russell and Barber, 1960), although the need for high transpiration rates by either of these processes probably exists in only a few situations.

Following analyses of water transport in the soil-plant-atmosphere continuum, van den Honert (1948) concluded that the main site for water flow regulation should be in the vapor phase. He suggested that stomata act as regulators of water transport by varying the diffusion resistance. The presence of the primary regulating mechanism for water flow in another part of the system, e.g. the root, would produce water stress in the whole plant. Early work failed to show the importance of stomata in regulating transpiration because boundary layer resistances were not taken into consideration (Slatyer, 1966). Bange (1953) demonstrated a direct influence of stomatal aperture on transpiration rate, when boundary-layer resistances are relatively small. Similar results were found by Milthorpe and Spencer (1957). The opposite view, that transpiration may vary independently from stomatal aperture, suggesting that other plant factors may control it directly, has been proposed (Slavik, 1958; Rawlins, 1963). However, theoretical

analyses by Slatyer (1966), suggest that it is unlikely that non-stomatal factors control transpiration under conditions of normal water supply.

With many species there is little carbon dioxide fixation during the night and stomatal closure prevents water loss (Milthorpe and Spencer, 1957). Light induces stomatal opening partially due to a potassium ion influx mediated mechanism (Fujino, 1967; Fischer, 1968; Humble and Rashke, 1971). Ion influx would alter the osmotic and pressure potentials of the guard cells. Stomata may also close during day-light, limiting both transpiration and photosynthesis. Some of this closure may be due to the classic negative feedback system, whereby, stomata close in response to increasing water deficits in the leaf. Threshold values in the water potential of the bulk leaf for stomatal closure found for several species are -7 to -9 bars for tomato (Duniway, 1971), to -12 to -16 bars for grape and greenhouse cotton leaves (Kriedemann and Smart, 1971; Jordan and Ritchie, 1971), -4 to -6 bars for corn -6 to -8 bars for sunflower (Boyer, 1970), and 2 to 4% of water deficit for Vicia faba (Stalfelt, 1955, 1961). It has also been proposed that an additional negative feedback system is operative based upon stomatal response to the carbon dioxide concentration inside the leaf (Meidner and Mansfield, 1968; Raschke, 1972). Definitive evidence has been recently obtained that demonstrates direct stomatal response to humidity. This mechanism has particular physiological significance as it may be viewed as a stomatal response that can prevent the development of water stress (Schulze et al. 1972).

Ingenious experiments with epidermal strips by Lange et al. (1971) confirmed earlier observations by showing that dry air closed stomata, while moist air opened them. They proposed that "peristomatal transpiration" could be responsible for stomatal responses to humidity. The tendency for guard cells to lose more water than adjacent cells would cause stomatal closure. In this way they are able to sense the evaporative demand of the atmosphere, adjusting leaf resistance so that no changes in water status of the whole leaf occur. Differences in stomatal response to humidity between species have been shown recently by Hall and Kaufmann, (1973). Schulze et al. (1973) studied the effects of temperature on stomatal movement of several species while maintaining a constant water vapor concentration difference between the leaf and the atmosphere, finding that the response obtained was dependent upon the water status of the plant. The possibility still exists that in some species both the leaf water status and the bulk humidity surrounding the leaf simultaneously affect the degree of stomatal regulation of transpiration.

Water uptake and tranport by plants.

Water movement in soil and from soil to roots is in the direction of decreasing free energy (Gardner, 1960a). In moist soils, a small water potential gradient is necessary to move water to and into the roots, but as the soil becomes dryer and its matric potential decreases a larger gradient is necessary, because the hydraulic conductivity of the soil also decreases (Gardner, 1960a, b). The pattern of water

extraction from the root zone is directly related to root distribution rather that to the total number of roots (Gardner, 1960b, 1964). Recently, Lang and Gardner (1970) presented theoretical and experimental evidence showing there is an upper limit to the rate at which water can be removed from the soil by plant roots as the soil dries. Upper limits for rate of water uptake under well-watered conditions have not been established.

While the greatest water absorption occurs at the terminal portions of the roots, older, suberized parts have also been reported to be active in water absorption (Kramer, 1969). Absorption of water occurs along gradients of decreasing water potential from soil to roots. The low water potentials in the roots are probably a consequence of the tension developed in the colums of water in the xylem due to evaporation from the leaves. The effects of anaerobiosis, metabolic inhibitors and temperature on water uptake by roots suggest that ion uptake and movement are also intimately involved in the total process of water uptake.

Once in the xylem water moves upwards in response to the gradient in water potential, driven primarily by the pressure potential component (Kramer, 1969; Slatyer, 1967). A mechanism for water movement in the xylem of plants was proposed by Dixon (1914). He suggested that evaporation from the cell walls in the leaves, in response to the lower vapor pressure of the air, creates a lower water potential in the cell walls and protoplasts. This lower potential is transmitted to the water columns in the xylem, pulling the columns of water which

remain intact because of the cohesion between water molecules and adhesion to cell walls. The negative water potential is further transferred to the root cells, where absorption resumes if soil water supply is adequate (Dixon, 1914; Dainty, 1969). Raschke (1970) demonstrated that plants behave like a hydraulic system, by observing stomatal responses of a detached leaf. When suction was applied to the water supply of the leaf the lag time for stomatal response was only 0.1 sec. This demonstrates that a change in the energy status of water is transmitted very rapidly throughout the plant.

Barrs (1966) reported on the occurrence of inverted water potential gradients from leaf to solutions containing polyethylene glycol in both Capsicum frutescens and Helianthus annus, and Taerum (1973) reported similar inverted gradients with bean plants when soil-matric potential was low. Barrs attributed those gradients to the effects of root pressure, but was unable to decide if there was a truly active movement and/or coupling with ion movement. More recently, Kaufmann and Eckard (1971) concluded with a similar system that pepper roots immersed in low-molecular weight polyethylene glycol solutions accumulated ions at a high rate. A great deal of literature has been published regarding the phenomena of root pressure, but relatively little is understood about the importance of root pressure in the ascent of sap in plants. Kramer (1969) suggests that it is unlikely that root pressure may supplement passive absorption, because intact plants can absorb water from much drier soil than can detopped root systems.

Limitations to water flow in the soil-plant-atmosphere continuum.

Water flow in the soil-plant-atmosphere continuum and the series of resistances it encounters can be described by an analog of Ohm's law (van den Honert, 1948). The resistances for water flow in the soil-to-root part of the system may be dependent upon the matric potential (Gardner and Ehlig, 1962). Newman (1969) made the distinction between two kind of resistances for water flow external to the root: the "pararhizal resistance" involved in water movement from one part of the soil to another, and "rhizospere resistance" for water movement from the soil to the root surface. It has been suggested that when soil matric potential is higher than -1 bar appreciable rhizosphere resistances are unlikely to occur (Newman, 1969). Macklon and Weatherley (1965) proposed that appreciable rhizosphere resistance was present with Ricinus communis when soil water potential was -9.1 atm, and high flow rates were occurring.

Roots may have a considerable resistance for water flow, because killing the roots or cutting the root system of transpiring plants has induced an immediate increase in water absorption (Camacho-B, 1972; Kramer, 1938; Ordin and Kramer, 1956). Also, recent work by Boyer (1971) has shown similarly that roots represent a considerable resistance for water flow in plants recovering from desiccation. After excising a leaf and supplying it with water, its water potential rose from -6 to -3 bars, showing the presence of a resistance below the petiole (Tinklin and Weatherley, 1966). Stems and leaves appear not to present significant resistances for water

flow in the liquid phase by the xylem pathway (Jensen et al., 1961). The pressure drop in tall trees and vines was similar to the hydrostatic gradient, also suggesting that xylem resistances are small (Scholander, 1965).

Several authors have used the van den Honert's (1948) model to evaluate indirectly whole plant resistances without disturbing the plant. The determination of the water potential gradient from soil (or solution) to leaf as a function of transpiration provides a curve whose shape and position indicate indirectly the magnitude and characteristics of the whole plant resistance for liquid flow. The shape and position of the curves published vary considerably among species and conflicts are apparent between authors as discussed in Chapter III.

Macklon and Weatherley (1965) and Tinklin and Weatherley (1966, 1968) observed no variation in the water potential gradient with varying transpiration rates in Ricinus communis. This was considered as an indication that the resistances for liquid water flow within the plant were changing as the flow rate increased. Macklon and Weatherley observed that the depression in leaf water potential when transpiration occurred was related to the depth of the water table below the roots and the type of soil used. This led them to conclude, perhaps prematurely, that all diurnal fluctuation in water potential, and therefore diurnal water deficits, are due to inadequate soil water conductivity, and that atmospheric conditions producing high rates of transpiration do not by themselves induce low water potential in the plant. Similar work with other species, such as Helianthus annuus

and Gossypium hirsutum tended to support their conclusions (Stoker and Weatherley, 1971). However, data published by Barrs (1970) show a curvilinear relationship between water potential gradient and transpiration for Gossypium barbadense and Capsicum frutescens when the plants were in nutrient solution. This suggests that these species had appreciable and fairly constant resistances for liquid water flow. Barrs also observed no influence of changes in transpiration rate on leaf water potential with Helianthus annuus and Zea mays. These results suggest that there are differences between species in the characteristics of the resistances for water flow, and consequently of the efficiency of the water transport system. However the conflict between the two species of Gossypium suggests the possibility of effects caused by differences in methodology. Studies by Elfving et al. (1972) with citrus, Millar et al. (1971) with onion, and Hailey et al. (1973) with southern pea also demonstrate the presence of appreciable resistances to water flow with some species. Pospisilova (1972) reported a variable resistance for liquid water flow in leaf tissue of Kale. The data of Barrs (1970), Elfving et al. (1972) and Millar et al. (1971) indicate that plant resistances for water flow result in increased water deficits when the evaporative demands of the atmosphere is increased even when plants are well watered. This conclusion differs from that of Macklon and Weatherley (1965).

Models of the soil-plant-atmosphere continuum.

Van den Honert (1948) assumed that the flow of water in the soil-plant-atmosphere continuum was equal throughout the system

(e.g. the system is in steady state), with the same quantity of water per unit time passing into the roots, along the xylem vessels, and through the leaf and the stomata into the atmosphere. He expressed the flow by an equation in which the flux is proportional to the gradients in water potential between parts of the system and inversely proportional to the resistances present in the segment considered. Extensions of the original idea made it possible to compare water flow in both liquid and gaseous phases. The resistances for water flow, according to this model, are not necessarily constant or independent of other flux related parameters (Dainty, 1969; Rawlins, 1963). A mathematical model for water flow from soil to root was developed by Gardner (1960a) that illustrated the importance of resistances to water flow in dry soils. Schematic and mathematical models based on van den Honert's model have been developed for the soil-plant-atmosphere system but they are not obviously useful for the solution of problems in plant water relations. Elfving et al. (1972) developed a model and demonstrated that it may be used to delineate edaphic conditions limiting for water absorption by roots. This model may also assist studies of plant response to environmental stress and comparative studies of adaptive mechanisms (Kaufmann and Hall, 1973). The basis of the model is that leaf water potential is dependent upon the transpiration rate. The transpiration rate in turn is dependent upon climate and leaf to air resistances. The water potential gradient within the plant varies to accommodate changes in transpiration. Much of the variation is in leaf water potential

because the potential of the source water in the soil is relatively constant over short time periods. The model of Elfving et al. (1972) also assumes that the dynamic water transport system may be treated as a sequence of steady-states as the rate of change in plant water content is much slower than the transpiration rate.

More complete models of the soil-plant-atmosphere continuum would provide an integrated treatment of the regulation of water loss from plants, the flow of water in plants and the flow of water in soils to plants.

III. LEAF WATER POTENTIAL RESPONSE TO TRANSPIRATION BY CITRUS

Leaf water potential is both a measure of the energy status of water in the plant and an important component of the driving force for water movement in plants. This water movement is closely coupled to the rate of water loss from leaves. The transpiration rate of a leaf is the result of the complex interaction of environmental factors such as radiation, temperature, relative humidity, and wind velocity with plant factors such as leaf diffusion resistance and leaf dimension (Elfving et al., 1972; Gates, 1968). The dependence of leaf water potential on transpirational flux and soil water supply and the dependence of physiological processes on plant water status make leaf water potential an important parameter for assessing plant-environment relationships. Recently, Elfving et al. (1972) examined the relationship of citrus leaf water potential to transpirational flux. They developed a model which describes leaf water potential as a function of water flux in the soil-plant-atmosphere continuum. In addition, they demonstrated that the model may be used to predict environmental conditions limiting water uptake from measurements of leaf water potential and estimates of water flux. Finally, they suggested that the model may be used to study how plants are suited to specific environments.

In the model of Elfving et al. (1972) leaf water potential (Ψ_{leaf}) is expressed as a function of soil water potential (Ψ_{soil}), flux rate, and resistances to flow in the liquid phase ($r_{soil\text{-}to\text{-}leaf}$):

$$\Psi_{leaf} = \Psi_{soil} - (flux)\ (r_{soil\text{-}to\text{-}leaf}).$$

The model assumes that the dynamic, diurnal changes in leaf water potential and transpiration rate may be described by a sequence of steady states because the flux of water through plants is usually much greater than the rate of change of plant water content (Cowan and Milthorpe, 1968). Rapid changes in transpiration rate with delayed changes in leaf water potential would invalidate this assumption. In this event, the relation between leaf water potential and transpirational flux would exhibit a hysteresis loop. The presence of a hysteresis loop would invalidate the model, since for a given transpiration rate there would be two distinct leaf water potential values (e.g. morning vs. afternoon). Elfving et al. (1972) also assumed that the ratio of vapor pressure deficit to leaf resistance (VPD/r_{ℓ}) is a reasonable estimate of the transpirational flux for the shaded side of citrus trees, based upon theoretical considerations. This should be tested by direct measurement as the quantitative nature of porometer data has been questioned.

This paper describes experimental tests of Elfving et al.'s model and of the assumptions on which the model is based. The model was also used to interpret field data on plant-water balance and water loss of different citrus rootstocks. Differences between rootstocks in the relationship between leaf water potential and transpirational flux would be caused by differences in the efficiency of water uptake and transport of water to leaves. The efficiency of water uptake and transport may be related to drought tolerance.

Materials and Methods

Laboratory experiments were performed with 15 greenhouse-grown seedlings (Citrus sinensis, var. Koethen) grown in 3-liter pots containing UC potting mixture. Plants were trimmed to 1 m height and had only fully-expanded leaves. The projected leaf area varied from 10 to 15 dm^2 per plant. After watering, the pots were enclosed in plastic bags and the plants were placed in a growth chamber. Environmental conditions included several temperatures (±1°C) and relative humidities (±5%), and total irradiance of up to 0.4 cal cm^{-2} min^{-1} (60 to 70% PAR). Air and dew point temperatures were monitored continuously, the latter by using a dew point hygrometer (Model 880 of EG&G Cambridge Systems). Leaf water potential was determined on 1 cm^2 discs of tissue with an isopiestic thermocouple psychrometer at 25.6°C (Boyer and Knipling, 1965). Leaf diffusion resistance measurements were made with a diffusion porometer as described previously (Elfving et al., 1972). Plants were set on a top-loading balance that could be read from outside the chamber with a precision of 0.1 g. Gravimetric transpiration measurements were taken for periods of 30 to 60 min. Repeated leaf diffusion resistance and leaf-air temperature difference measurements on similar plants showed that on occasions the citrus seedlings exhibited periodic and synchronized stomatal oscillations in all the leaves of a single plant. Similar "phase locked" oscillations have been observed by Cowan (1972), Cox (1968), Hopmans (1971), and Lang et al. (1969). Stomatal oscillations in Citrus were initiated mainly by rapid changes

in humidity. Since the seedlings proved to be very sensitive to sudden environmental changes, leaf-air temperature differences were monitored with differential thermocouples on the plant being weighed, to be certain that no stomatal oscillations occurred during the measurements reported here.

Field experiments were performed on 5-year-old trees in a rootstock experimental plot, at the Riverside Citrus Experiment Station, with 'Cutter Nucellar Valencia' (Citrus sinensis (L.) Osbeck) as scion. The three rootstocks tested were 'Troyer' citrange (Poncirus trifoliata X C. sinensis), Rangpur (Citrus limonia Osbeck), and Cleopatra mandarin (Citrus reshni Hort. ex Tan.). While field observations have suggested that Rangpur is more drought tolerant than the other two rootstocks (Dr. W. Bitters, personal communication), we are not aware of experimental tests of this possibility. Data were taken on 8 trees of each rootstock, randomly located in the orchard, at different times of the day between June and October, 1972, both shortly before and after irrigation. Soil water availability was monitored using tensiometers located at the edge of the crown and placed at depths of 46, 61 and 91 cm (Kaufmann and Elfving, 1972). Resistance blocks for measuring matric potentials lower than -0.8 bar (Cannell and Asbell, 1964), were placed at a depth of 30 cm near the tensiometers. Transpirational fluxes were estimated for the trees by the ratio VPD/r_{ℓ} as suggested by Elfving et al. (1972). Paired measurements of leaf resistance and leaf water potential were made. Leaf resistance measurements were obtained from adjacent leaves of well developed shoots of the current year's growth, located on the

north side of the trees and not exposed to direct solar radiation. The same shoot was then excised and a pressure chamber determination of leaf water status was made. Leaf water potential values were estimated from pressure chamber data using an appropriate calibration equation (see Appendix II). Wet and dry bulb psychrometer data were obtained every 10 to 15 min for calculating the vapor pressure deficit (VPD).

Results

Data were collected to test the validity of the assumption that VPD/r_ℓ provides a good estimate of actual transpiration. To make the units of transpiration comparable, the humidity gradient from leaf to air was expressed as an absolute humidity difference. In this case, the water vapor concentration difference between leaf and air was determined rather than VPD because leaf-to-air temperature differences were larger in the growth chamber than in the field. The ratio of absolute humidity difference to leaf resistance provided a reasonable estimate of transpirational flux in these conditions (Fig. 1).

Leaf water potential, leaf resistance, and the vapor pressure deficit were determined every 60 to 90 min in the field through four diurnal cycles on six trees to test the assumed sequence of steady states. Representative data (Fig. 2) show a close linkage of leaf water potential and transpiration as estimated by the ratio VPD/r_ℓ. Rapid changes in transpiration rate were accompanied by rapid changes in potential, so that for a given transpiration rate in the morning and in the afternoon the same water potential occurred. These results

Figure 1. The ratio of leaf to air water vapor concentration difference to leaf diffusion resistance as an estimate of transpiration rate for citrus leaves.

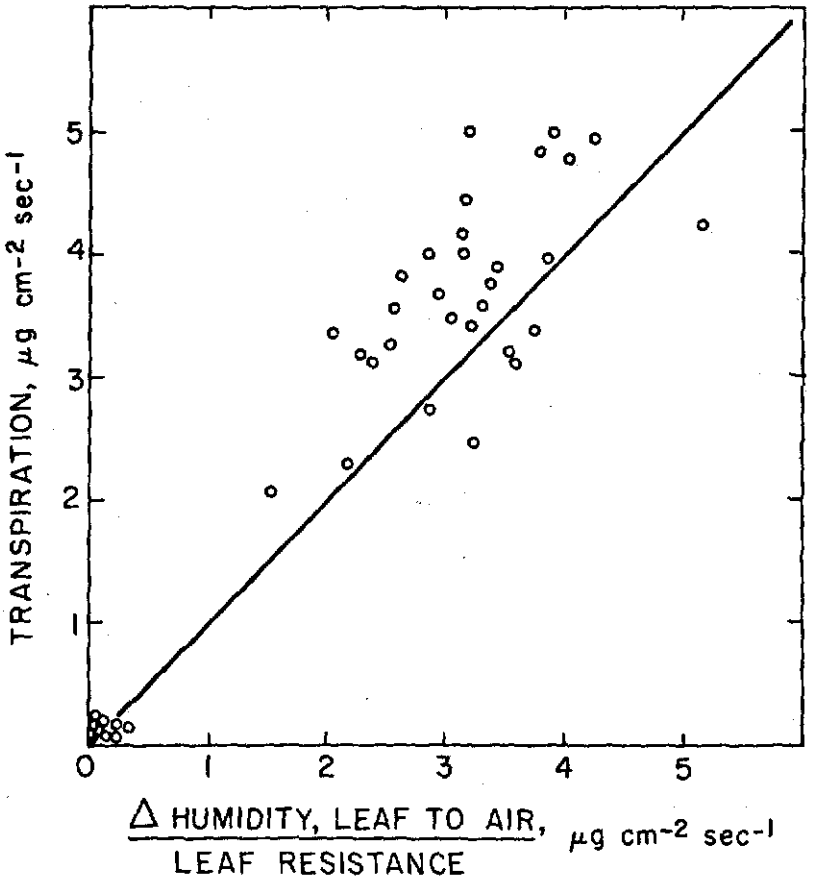
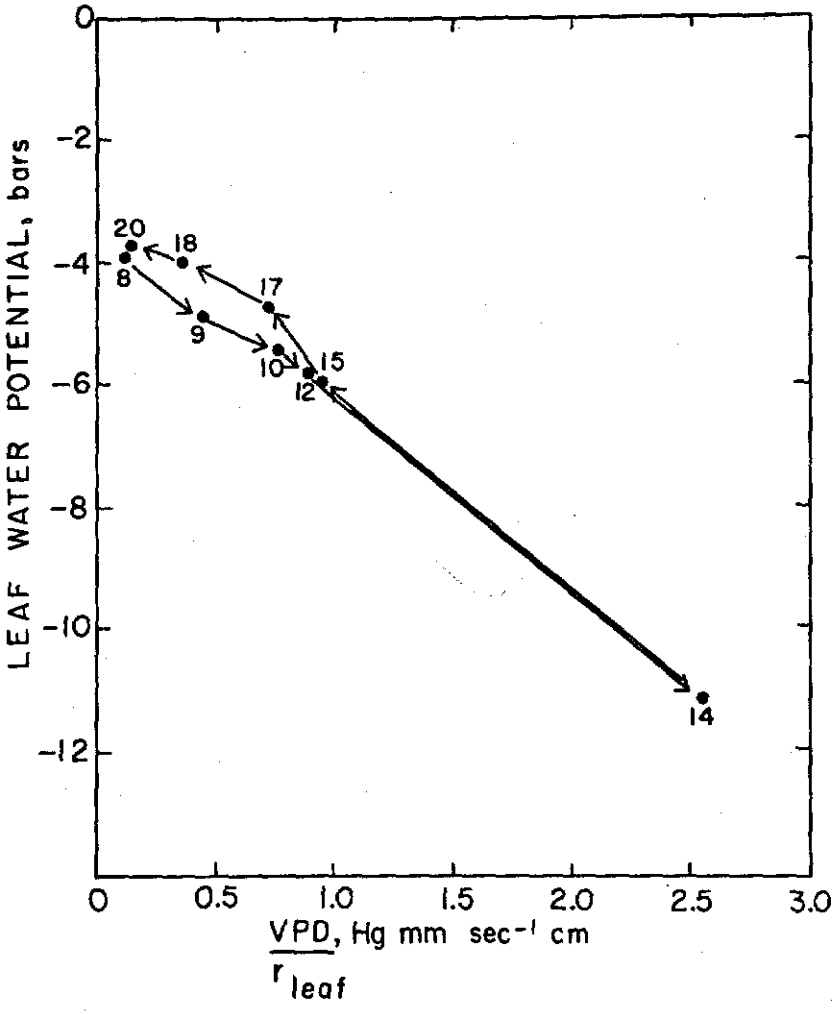

TRANSPIRATION, μg cm-2 sec-1
0
1
2
3
4
5
Δ HUMIDITY, LEAF TO AIR, μg cm-2 sec-1
LEAF RESISTANCE

Figure 2. Diurnal changes in the relationship between citrus leaf water potential and transpiration rate, estimated by pressure chamber and by the ratio of vapor pressure deficit to leaf diffusion resistance respectively. Numbers indicate hour of sampling.


0
-2
-4
-6
-8
-10
-12
LEAF WATER POTENTIAL, bars
20
18
8
17
9
10
15
12
14
0
0.5
1.0
1.5
2.0
2.5
3.0
VPD, Hg mm sec⁻¹ cm
r leaf

support the assumption of Elfving et al. (1972) that changes in transpirational flux and water potential in the plant could be described by a sequence of steady states.

The relationship between leaf water potential and transpiration was determined in the field both before and after irrigation for Valencia orange trees grafted on three rootstocks (Fig. 3). No difference between rootstocks was observed for well watered trees and leaf water potential was linearly correlated with VPD/r_ℓ ($\Psi_\ell = -4 - 1.94 \frac{VPD}{r_\ell}$). Data obtained before irrigation did show some differences between rootstocks. Because of very large sample size, Cleopatra mandarin and Rangpur grafted trees showed a significantly (1% level) greater depression of leaf water potential as transpiration increased, than they did when trees were well watered. Troyer citrange did not exhibit differences in response before and after irrigation. Prior to irrigation mean tensiometers readings for the three depths were between -0.3 and -0.5 bar for all of the trees compared with -0.1 to -0.2 bar after irrigation. Lower leaf water potentials would be expected in dryer soil (Elfving et al., 1972). Further studies will be needed to confirm the differences observed among rootstocks.

The relationship between leaf water potential and transpirational flux was investigated with citrus seedlings in controlled environments by direct measurments. Transpiration rates were determined by pot weighing, and leaf water potential was measured using isopiestic thermocouple psychrometers. Water potential values were higher for an equivalent transpirational flux with the seedlings than had been observed in the field (Fig. 4). Since trees in the field were subjected

Figure 3. Leaf water potential as a function of estimated transpiration (VPD/r_ℓ) for Valencia orange trees on three rootstocks under non-limiting conditions (.....) and for each rootstock (Cleopatra mandarin O, Rangpur ● and Troyer Citrange Δ) before irrigation. For convenience of presentation, each point is the mean of leaf water potential values found in intervals in VPD/r_ℓ formed by one tenth increments. Regression analyses were performed on approximately 140 data points for each rootstock. The regression line for after irrigation was based on 420 samples.

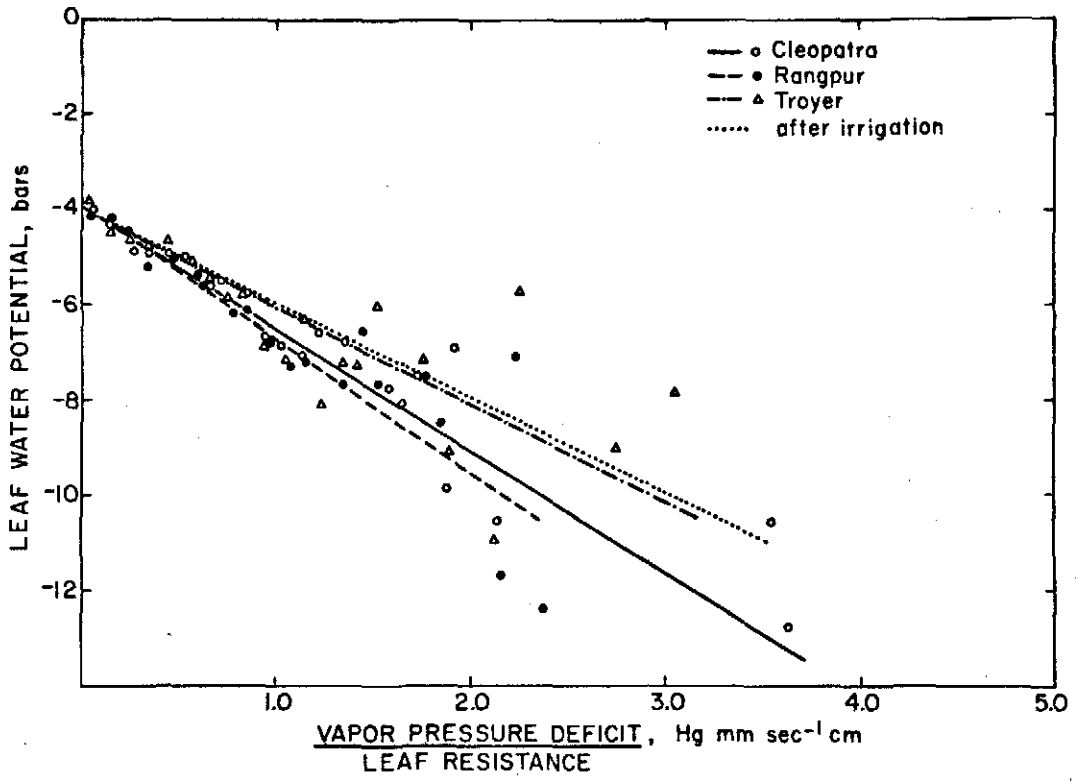
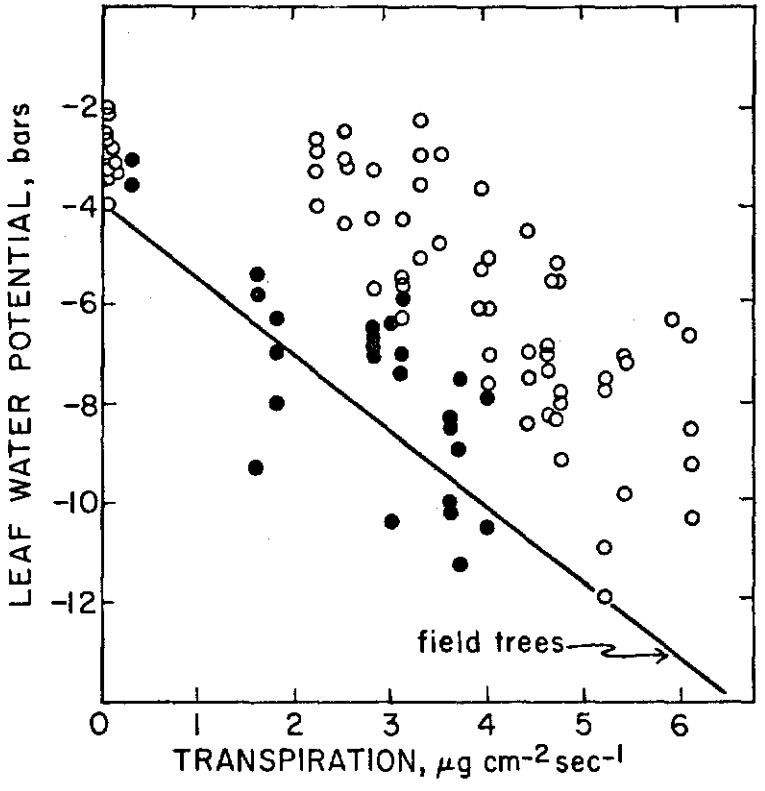

o Cleopatra
• Rangpur
△ Troyer
..... after irrigation
LEAF WATER POTENTIAL, bars
0
-2
-4
-6
-8
-10
-12
1.0
2.0
3.0
4.0
5.0
VAPOR PRESSURE DEFICIT, Hg mm sec⁻¹ cm
LEAF RESISTANCE

Figure 4. Leaf water potential as a function of measured transpiration rate for unstressed (0) and previously stressed (●) citrus seedlings, compared with the relationship for field trees under non-limiting soil water conditions. For previously unstressed seedlings, $\Psi_\ell = -2.82 - 0.18(\text{FLUX})^2$.


LEAF WATER POTENTIAL, bars
-2
-4
-6
-8
-10
-12
field trees
0
1
2
3
4
5
6
TRANSPIRATION, μg cm⁻² sec⁻¹

to a series of irrigation and drying cycles during the summer, it was hypothesized that the difference in the relationship between field-grown trees and greenhouse non-stressed seedlings was due to the effect of the drying cycles. Citrus seedlings were subjected to a series of three drying cycles severe enough to result in wilting of leaves to test this hypothesis. At the end of the third drying cycle plants were rewatered to field capacity and the relationship between leaf water potential and transpiration was determined. Leaf water potentials were more negative after the drying cycles than before at equivalent transpirational fluxes, and these plants behaved more like field trees than the seedlings which had not been subjected to drying cycles (Fig. 4). In the field, however, the drying cycles were not severe enough to cause wilting of leaves.

Discussion

Direct measurement of transpiration confirmed the assumption of Elfving et al. (1972) that VPD/r_{ℓ} provides a reasonable estimate of transpirational flux by citrus when leaf-to-air temperature differences are small (Fig. 1). Thus, transpirational flux may be estimated in the field for citrus using a diffusion porometer and a wet and dry bulb psychrometer within the constraints described by Elfving et al. (1972). Determination of the relationship between leaf water potential and flux through several diurnal cycle gave a unique response curve (Fig. 2). These data support the assumption that the dynamic system of water flow in the soil-plant-atmosphere continuum may be described by a sequence of steady states with this species. Substantial non-steady state events would have resulted in a hysteresis loop in

the relationship between leaf water potential and transpirational flux, but this was not evident.

Citrus leaf water potential was dependent upon the transpirational flux, confirming the model proposed by Elfving et al. (1972). The shape of the response curve relating leaf water potential to transpirational flux is still uncertain (Barrs, 1970; Elfving et al., 1972; Hailey et al., 1973; Tinklin and Weatherley, 1968; Stocker and Weatherley, 1971). Direct measurements of leaf water potential and transpiration with citrus seedlings in controlled environments produced a curvilinear relationship (Fig. 4) that contrasted with the linear relationship observed in the field (Figs. 2 and 3). After soil-drying cycles, however, greenhouse-grown trees behaved more like field trees. The lower water potentials at equivalent water fluxes in trees that have been subjected to drying cycles, in comparison with continuously well-watered trees may be due to changes in root morphology of the type described by Kaufmann (1968c). The slope of the relationship is an estimation of the resistance for water flow between soil and leaf (Eq. 1). It is not clear whether increased resistance for water flow is an unavoidable consequence of drying cycles or whether it represents an adaptive mechanism to arid environments. Larger resistances to flow result in greater leaf water stress which can be considered either as being detrimental to the plant or as being a necessary component of the system by which shoot-root ratios are controlled (Wit and Brouwer, 1968) and by which roots contribute to stomatal control of water loss.

Elfving et al. (1972) reported a curvilinear response of leaf water

potential to water flux for field citrus. Their pressure chamber values were, however, similar to those obtained in this experiment at equivalent flux rates. Differences in procedures used for converting pressure chamber values to leaf water potential may account for the differences between the linear response reported here for field conditions and the curvilinear response reported by Elfving et al. (1972). A detailed discussion of the relationship between leaf water potential and pressure chamber values for citrus is presented elsewhere (see Appendix II).

Few authors have attempted to study drought tolerance of citrus rootstocks by comparing their physiological responses to changing climate within narrow ranges in soil water availability. Some authors have proposed that certain citrus rootstocks have greater drought tolerance than others based upon field observations under extreme conditions, and explain the tolerance in terms of root system size (Ford, 1954; Mendel, 1951). Mendel (1951) made visual observations of wilting, and measured stomatal aperture, transpiration of detached leaves, and relative leaf water contents while comparing trees on sour orange, sweet lime, and rough lemon rootstocks both with and without irrigation during a summer. While there were no differences in recently irrigated trees, rough lemon appeared to be the most drought resistant, due probably to its large root system. Our data suggest that Valencia orange on Citrange Troyer roootstock appeared not to suffer leaf water stress, other than the normal stress levels experienced in well-watered conditions, when mild soil-water deficit occurred. In contrast, trees on Cleopatra mandarin and Rangpur did show a greater leaf water stress

under those conditions than when they were well watered. The differences, however, were significant only when high transpiration rates occurred. Leaf water potentials were similar at low transpirational fluxes both before and after irrigation, indicating that the soil water supply was not limiting plant recovery overnight (Elfving et al., 1972). Under drier soil conditions leaf water potential may have been lower than reported here for low transpirational fluxes. Differences between rootstocks in leaf water potential response to transpiration may also be larger with drier soils.

IV. EFFICIENCY AND REGULATION OF WATER TRANSPORT IN SOME WOODY AND HERBACEOUS SPECIES

The extent to which climatic, plant, and edaphic factors influence plant-water balance and plant water use is both complex and of considerable adaptive significance. Analyses of water movement in the soil-plant-atmosphere continuum and of the development of plant-water stress is facilitated by interpreting plant responses to variations in environment using conceptual and mathematical models. The model of Elfving et al. (1972) describes leaf water potential (Ψ_{leaf}) as being dependent upon three elements: soil water potential (Ψ_{soil}), flux of water through the system, and resistance to flow between the soil and the leaf ($r_{soil\text{-}to\text{-}leaf}$).

$$\Psi_{leaf} = \Psi_{soil} - (flux)(r_{soil\ to\ leaf}) \qquad (1)$$

When the soil water supply is optimal, Ψ_{soil} is approximately zero and the resistance for water flow from soil to root is negligible. The efficiency of water transport to leaves may be elucidated by measuring the response of leaf water potential to different steady-state transpiration rates attained by changing the evaporative demand of the atmosphere. If the resistance to flow from root to leaf is constant and of sufficient magnitude, the leaf water potential should decrease linearly with increases in transpiration rate and approach zero when the flow of water is negligible and the system approaches equilibrium. Curvilinear responses would indicate variable resistance to flow within

the plant.

Contrasting results have been reported for the relationship between leaf water potential and transpiration rate with non-limiting water supplies and steady-state fluxes. Tinklin and Weatherley (1966, 1968) observed no effects of transpiration changes on Ψ_{leaf} of castor bean. Stoker and Weatherley (1971) reported sharp decreases in leaf water potential in response to small increases in transpiration which were followed by a plateau where leaf water potential was not influenced by further increases in transpiration with both Helianthus annus and Gossypium hirsutum. In contrast, Barrs (1970) observed no influence of changes in transpiration rate on leaf water potential with sunflower and maize. He obtained a curvilinear relationship between leaf water potential and transpiration rate with both Capsicum frutescens and Gossypium barbadense; however, these curvilinear responses were radically different in shape from responses reported by Stoker and Weatherley (1971). A linear relationship was reported for the influence of transpiration rate on pressure chamber values with Vigna sinensis (southern pea) (Hailey et al., 1973). Apparently these contrasting results are due partially to differences in methodology; but it is also possible that important differences exist between species in their ability to transport water. In this paper, relationships between leaf water potential and transpirational flux were determined for woody and herbaceous species in controlled environments where the soil water supply was optimal. Uniform methodology was applied so that species contrasts in efficiency of water transport could be ascertained.

Differences in water transport efficiency may be coupled with differences in regulation of water flow by plants. Stomata are considered to be the principal agents controlling water flow through plants (Slatyer and Bierhuizen, 1964). Some authors (Hall and Kaufmann, 1973; Lange et al., 1971; Schulze et al., 1972) have proposed that stomata respond to external humidity gradients independent of the average internal leaf water status, while others (Meidner and Mandsfield, 1968) have concluded that stomata are relatively unaffected by changes in external humidity. Transpirational flux is often described as being dependent upon the absolute humidity difference between leaf and air and resistances to flow in the vapor phase.

$$T = \frac{[H_2O]_{leaf} - [H_2O]_{air}}{r_{leaf} + r_{air}} \qquad (2)$$

If stomata do close when the humidity gradient is increased, leaf resistance (r_{leaf}) would increase and transpirational flux would not increase linearly with increases in the humidity gradient when the boundary layer resistance (r_{air}) is small. The influence of the humidity gradient on leaf resistance was investigated for two herbaceous species, since the controversy concerning stomatal response to humidity may also be due to differential behavior between species.

Material and Methods

Orange (Citrus sinensis L., cv. Koethen), evergreen pear (Pyrus kawakami L.), sunflower (Helianthus annus L., cv. Mammoth Russian), bell pepper (Capsicum frutescens L., cv. Yolo Wonder), and sesame (Sesamum

indicum L., cv. Glauca) were grown in a greenhouse with maximum temperatures of 29-32 C and minimum temperatures of 16-18 C. Orange and pear were grown in 4 liter pots; sunflower, pepper, and sesame were grown in 1 liter pots containing UC potting mixture. The plants were watered daily and provided with full strength Hoagland's solution once weekly.

Seedlings were widely spaced in the growth chamber to minimize leaf shading and to provide good air movement. Transpiration rates were determined gravimetrically by weighing pots at 20 to 60 min intervals. Every 3 hr the water lost was added to the pots to insure adequate water supply to roots. This was particularly important with the sunflower plants which rapidly depleted soil water under high evaporative demands. The pots were enclosed in plastic bags to prevent evaporation from the soil surface. Projected leaf area was measured at the conclusion of the experiments and used as a basis for determining transpiration rates. Different transpiration rates were obtained by varying ambient humidity and temperature. Relative humidity was controlled to ±3% and specific humidity was measured with a dew point hygrometer (Cambridge Systems Model 880). Ambient temperatures were controlled to ±0.5 C and measured with a shielded thermistor (YSI Tele-thermometer Model 73). Total irradiance of up to 0.4 cal cm^{-2} min^{-1} (60-70% PAR) was supplied by metal halide vapor and color-improved mercury lamps having a ratio of input watts of 11 to 4. Leaf water potentials were determined with an isopiestic thermocouple psychrometer (Boyer and Knipling, 1965) using small leaf disks excised shortly before the second pot weighing. A pressure

chamber was used for measuring leaf water status in some experiments. Leaf resistances were determined for the abaxial side of leaves by using a diffusion porometer. The construction, calibration, and measuring procedure used with the diffusion porometer have been described previously (Elfving et al., 1972).

Results

The influence of transpiration rate on leaf water potential was studied with 11 pear seedlings and 15 citrus seedlings. Sudden decreases in humidity around the citrus plants resulted in stomatal oscillations which were detected by a sensitive thermocouple clamp measuring leaf-to-air temperature differences. Data were obtained on single plants when oscillations were not apparent. Leaf water potential decreased as transpiration rate increased with both pear and citrus (Fig. 5). Pear response was linear, with leaf water potential decreasing from -4.5 to -7.5 bars as transpiration increased. The citrus data were curvilinear with maximum leaf water potentials of -3 bars and a substantial decrease in leaf water potential to -9 bars at high transpiration rates. Pear pressure chamber values were more sensitive to changes in transpirational flux than were leaf water potential measurements.

Similar studies were conducted with 20 sunflower, 17 sesame, and 12 pepper plants. These herbaceous species did not show a measurable depression of leaf water potential as transpiration was increased (Fig. 6). Sunflower mean water potential values varied between -1.9 and -3.2 bars with no apparent decreases in potential when transpiration

Figure 5. Leaf water potential as a function of transpiration for citrus and evergreen pear seedlings under non-limiting soil water conditions. Each point is the mean of two to five water potential and transpiration measurements from each plant of citrus or from several plants of pear under a single set of conditions.

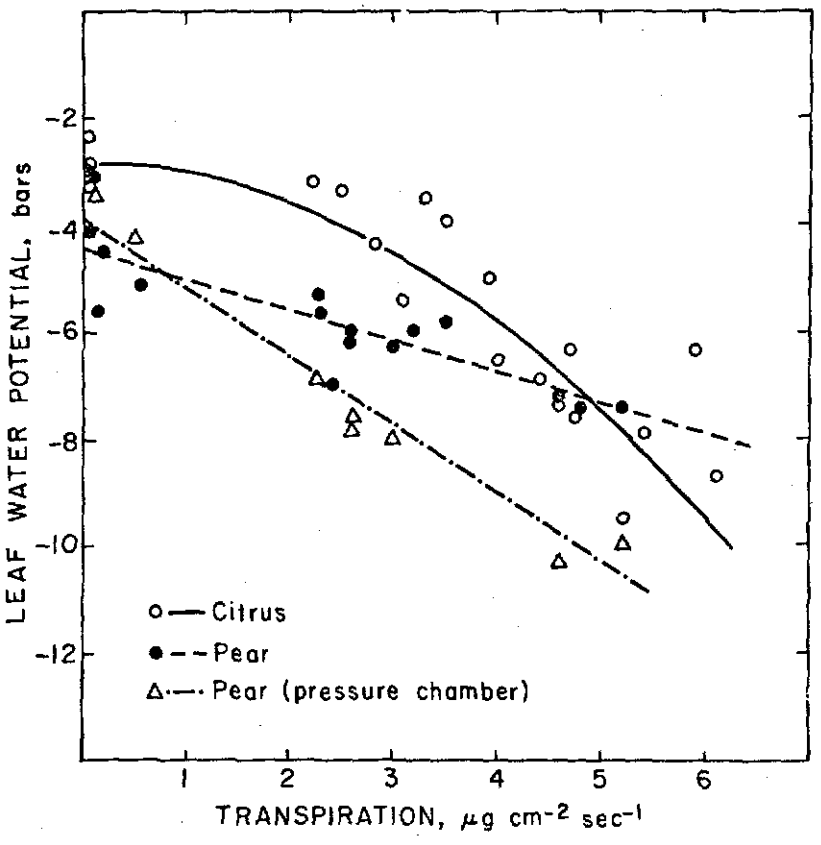
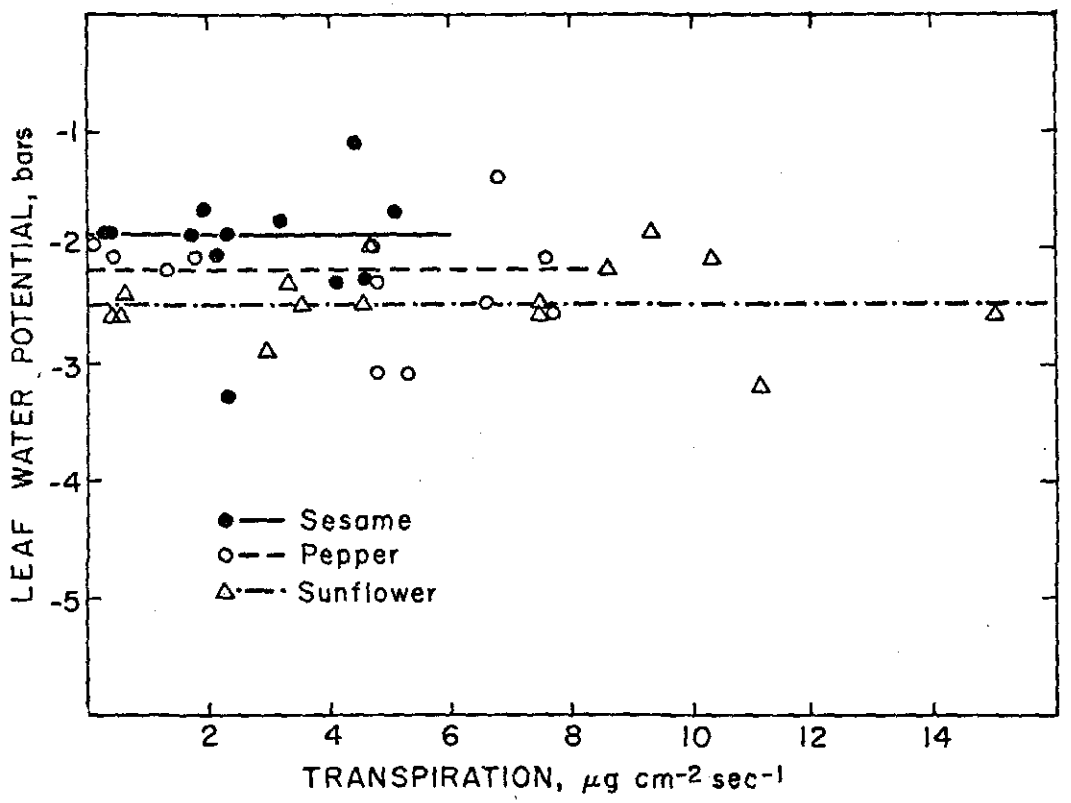

LEAF WATER POTENTIAL, bars
-2
-4
-6
-8
-10
-12
1
2
3
4
5
6
TRANSPIRATION, μg cm⁻² sec⁻¹
Citrus
Pear
Pear (pressure chamber)

Figure 6. Leaf water potential as a function of transpiration for three herbaceous species under non-limiting soil water conditions. Most points are the mean of six water potential and transpiration measurements obtained from different plants under a single set of conditions.

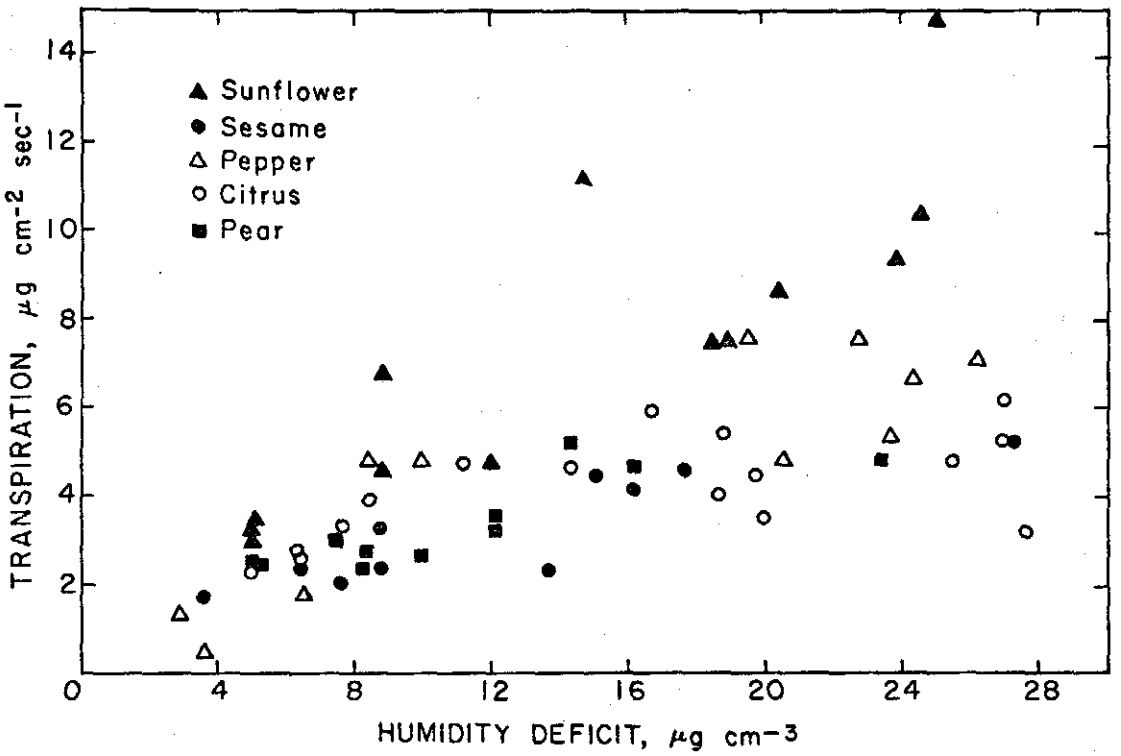

LEAF WATER POTENTIAL, bars
-1
-2
-3
-4
-5
2
4
6
8
10
12
14
TRANSPIRATION, μg cm-2 sec-1
Sesame
Pepper
Sunflower

rates of as fast of 15 μg cm^{-2} sec^{-1} were obtained. Similar results were obtained with sesame and pepper, although transpiration rates of these species were slower. A comparison of Figures 5 and 6 shows that the woody species required larger water potential gradients than the herbaceous species for equivalent water fluxes in the soil-to-leaf system. Lack of water potential change in herbaceous plants and the distinct decrease in water potential of the woody species were observed with both an isopiestic psychrometer and a pressure chamber. Differences in the regulation of water flow may also be present as sunflower achieved transpiration rates that were far greater than the maximum transpiration rates of the other species at high evaporative demands.

Regulation of water transport in the vapor phase (Fig. 7) was examined by comparing the transpiration rates of all species tested with the absolute humidity deficits imposed when obtaining data for Figures 5 and 6. The absolute humidity deficit is an approximation of the absolute humidity gradient between the leaf and the air in equation (2) obtained by assuming leaf temperature equal to air temperature. Transpirational flux was greater for sunflower than for the other species at large evaporative demands. It is not clear whether the low transpirational fluxes of the other species were due to large minimal leaf resistances or to partial stomatal closure at large humidity gradients between leaf and air.

The presence of differences in stomatal responses to humidity was tested with sesame and sunflower. Leaf resistances (obtained with a

Figure 7. Transpiration per unit leaf area as a function of absolute humidity deficit for several herbaceous and woody species.


▲ Sunflower
● Sesame
△ Pepper
○ Citrus
■ Pear
TRANSPIRATION, μg cm⁻² sec⁻¹
HUMIDITY DEFICIT, μg cm⁻³
0
2
4
6
8
10
12
14
4
8
12
16
20
24
28

diffusion porometer) and leaf water potentials were determined for well-watered plants subjected to different steady-state evaporative demands in a controlled environment chamber. Leaf-to-air temperature differences were measured with a thermocouple clamp. Leaf resistances of sesame and sunflower were similar at small humidity gradients (Fig. 8 and 9); however, at large humidity gradients leaf resistances of sesame were twice those of sunflower. No changes in leaf water potential were detected with either of these species when leaf resistances increased in response to larger evaporative demands. In addition, no changes in pressure chamber values were detected with sesame as evaporative demand was increased.

Discussion

It is widely accepted that the development of water deficits in plants depends upon interactions between factors influencing the water supply to and the water loss from plants. Equations (1) and (2) describe some of these factors. The development of plant water deficits due to decreases in soil water availability is well documented (Ehlig and Gardner, 1964; Gardner and Nieman, 1964; Kaufmann and Elfving, 1972; Slatyer, 1957), but climatic effects on the development of water deficits have not been adequately described. In our studies, the woody species (citrus and pear) exhibited progressive decreases in leaf water potential as transpiration increased in response to changes in evaporative demand even though soil water supply was optimal (Fig. 5). In contrast, the herbaceous species (sunflower, pepper, and sesame), which

Figure 8. Leaf diffusion resistance, measured with a diffusion porometer, leaf water potential (●) and pressure chamber values (○) for sesame as a function of the absolute humidity gradient from leaf to air. Each point is the mean of four measurements ± standard error.

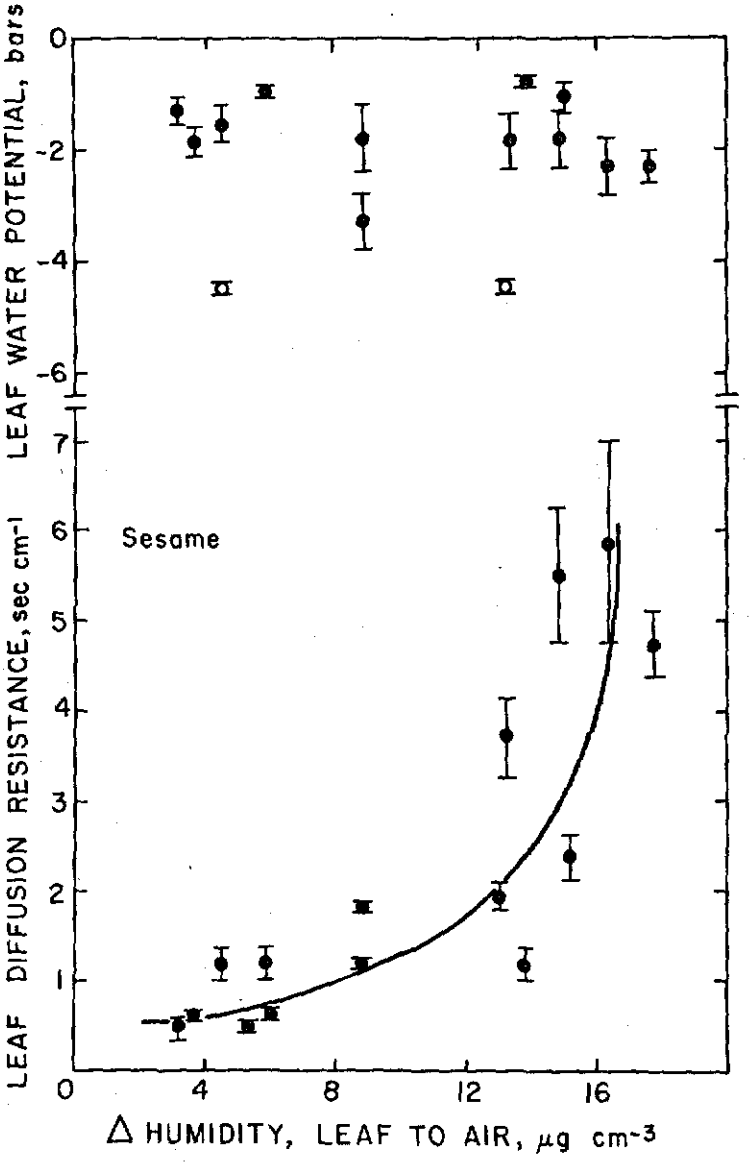
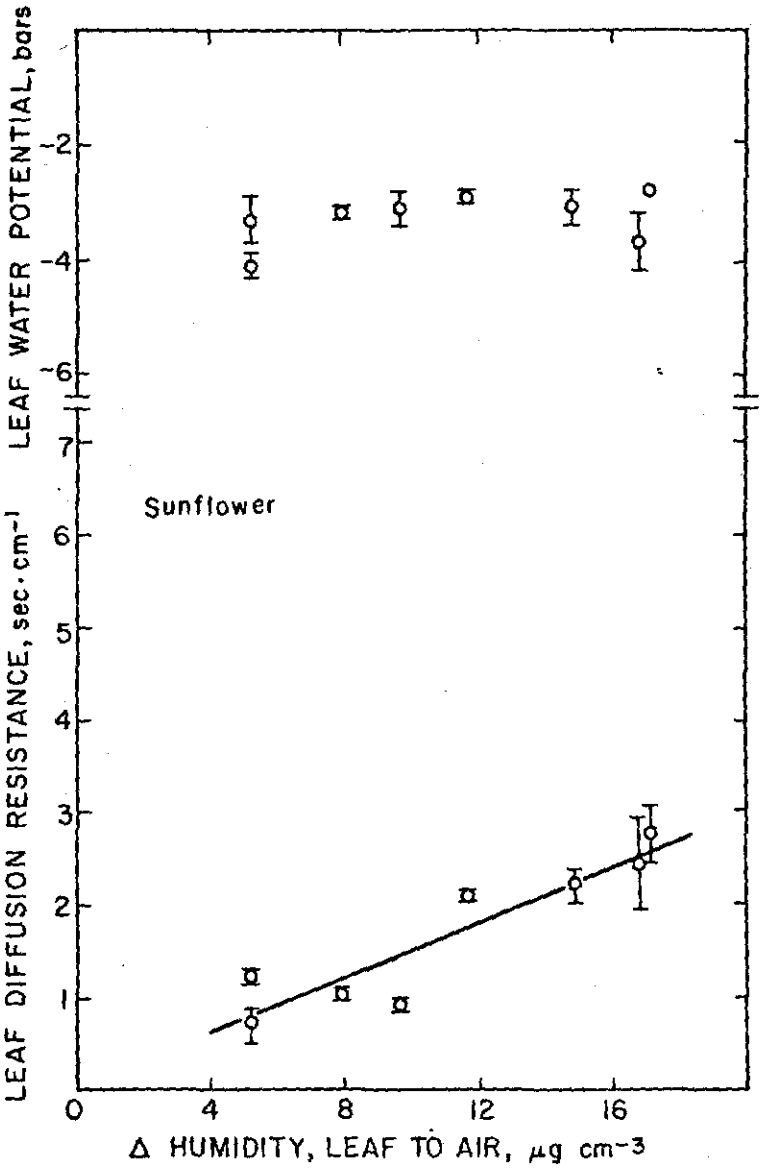

LEAF WATER POTENTIAL, bars
0
-2
-4
-6
LEAF DIFFUSION RESISTANCE, sec cm⁻¹
7
6
5
4
3
2
1
Sesame
0
4
8
12
16
Δ HUMIDITY, LEAF TO AIR, μg cm⁻³

Figure 9. Leaf diffusion resistance, measured with a diffusion porometer, and leaf water potential of sunflower as a function of the absolute humidity gradient from leaf to air. Each point is the mean of four measurements ± standard error.


LEAF WATER POTENTIAL, bars
-2
-4
-6
7
6
5
4
3
2
1
0
LEAF DIFFUSION RESISTANCE, sec·cm⁻¹
Sunflower
4
8
12
16
Δ HUMIDITY, LEAF TO AIR, μg cm⁻³

were also under optimal water supply conditions, exhibited constant leaf-water potentials over a wider range of transpirational fluxes (Fig. 6). It is apparent that these herbaceous species have an efficient water transport system capable of maintaining a range of transpiration rates with a small and constant water potential gradient (the driving force). This also indicates that their resistance to water flow from root to leaf is very small or decreases as flux increases (equation 1). Variable resistances for water flow in plants have been discussed by several authors (Barrs, 1970; Elfving et al., 1972; Millar et al., 1971; Stocker and Weatherley, 1971). In these experiments sunflower had the most efficient water transport system as it sustained very high fluxes without measurable decreases in leaf water potential. An increased water potential gradient from root to leaf with increases in transpirational flux indicates the presence of a substantial resistance to water flow in citrus and pear. In addition, the curve relating leaf water potential to transpiration for citrus seedlings (Fig. 5) may be moved downward by subjecting seedlings to drying cycles even though measurements are made with non-limiting water supplies (Fig. 4).

Some of Barrs' data (1970) are in agreement with our observations. He reported constant leaf water potentials for sunflower and maize over a range of transpirational fluxes. He also observed decreases in leaf water potential as transpiration increased with the woody shrub Gossypium barbadense; the shape of the response curve was similar to that reported for citrus in this paper. Stoker and Weatherley (1971) observed decreases in sunflower leaf water potential as transpiration

increased at low transpiration rates. Like Barrs (1970), we did not observe responses of this type. Also, Stoker and Weatherley (1971) reported responses of leaf water potential to transpiration with Gossypium hirsutum that were different from the responses observed by Barrs with G. barbadense. In our experiments, pepper leaf water potential was constant over a range of transpiration rates, whereas Barrs (1970) reported that leaf water potential decreased in this species as transpiration increased. Differences in plant age, environmental conditions prior to the experiment, rates at which climatic conditions were varied, and sampling techniques for leaf water potential measurements may account for these conflicting responses. The pressure chamber technique provided a more sensitive indicator of changes in plant water status with pear (Fig. 5) and these data illustrate that different response curves may result if different techniques are used for determining plant water status. The plant water status characteristic determined by the pressure chamber is not clearly understood at this time however.

Sunflower attained higher transpiration rates per unit leaf area than the other species tested at equivalent large humidity gradients between leaf and air (Fig. 7). The variability in the data probably resulted from gradients of irradiance, leaf temperature, and transpirational flux in the intact plants used in these experiments. Leaf resistances of sesame and sunflower were similar at small humidity gradients but leaf resistance of sesame increased exponentially as humidity gradients were increased (Fig. 8). With increases in humidity gradient (Fig. 9) leaf resistance of sunflower responded much less

and linearly. Changes in the average leaf water potential were not detected as leaf resistance increased in response to increases in the humidity gradient with sesame or sunflower, even though the small leaf resistances of the latter resulted in large transpiration rates. Unpublished observations by A. E. Hall indicated a threshold value of leaf water potential in sunflower of -8 bars. Stomata only responded to leaf water potential at leaf water potentials more negative than this threshold value. Similar observations by other workers were reviewed previously by Hsiao (1973). Differences between sesame and sunflower in the regulation of water loss have also been observed by Hall and Kaufmann (1973) using more accurate but less direct gas-exchange methods.

The response of leaf resistance to the humidity gradient may be interpreted as a control system by which stomata regulate water loss and prevent the development of water deficits. The classical negative feedback system whereby stomata respond to changes in water status of the bulk leaf may be regarded as another control system that prevents further desiccation after substantial water deficits have already developed. Lange et al. (1971) proposed that "peristomatal transpiration" could provide a mechanism for stomatal response to humidity. Schulze et al. (1972) demonstrated that increases in leaf resistance as the humidity gradient from leaf to air increased resulted in higher relative leaf water content. This supports our contention that with some species stomata may respond to humidity and prevent the development of leaf water stress. The contrasting behavior of different species described

in this paper and by Hall and Kaufmann (1973) may account for some of the controversy concerning stomatal responses to humidity (Lange, et al., 1971; Meidner and Mansfield, 1968).

There appear to be two physiological characteristics important to plant adaptation in the water relations of plants: the efficiency of the water transport system, and the regulatory mechanisms for water transport. The combination of those characteristics provide species with different capabilities for responding to the environment. The responses observed are placed in three categories: (a) species that combine moderate restriction of water loss by stomata with low efficiency of their water transport system and which are unable to prevent depression of leaf water potential as transpiration increases (i.e. pear, citrus); (b) species that moderately restrict water loss by stomata and have a more efficient water transport system than the previous case (i.e. sesame, pepper); (c) species with little stomatal restriction of transpiration and a highly efficient water transport system (i.e. sunflower). Sunflower exhibited rapid sap exudation after leaves were removed even though plants had been in a high evaporative demand climate.

Strong regulation of water transport via stomatal responses to humidity would provide an adaptive advantage to plants in desert environments where evaporative demands are large and water supplies are limited. Sesame is grown in arid areas without irrigation (Weiss, 1971). Stomata that do not close in dry air would provide an adaptive advantage for colonizing species such as sunflower, in areas where soil water is abundant and evaporative demands are large because growth has priority

over conservation of water. In this case, an efficient water transport system would also be needed to minimize the development of water deficits at large transpiration rates. Effects of stomatal response to humidity on photosynthesis, water use efficiencies, and leaf temperature were described by Hall and Kaufmann (1973). The tendency for woody species to exhibit lower leaf water potentials than herbaceous species at large evaporative demands may be a consequence of the physical constraints set by the structure of these woody species. High resistances between root and leaf may also be essential components of a feedback system for controlling root/shoot ratios (Wit and Brouwer, 1968).

This paper illustrates that studies of the water tranport system and of the control mechanisms for water flow in plants may provide a partial basis for an ecological classification of species. Such studies could be aided by appropriate mathematical models, as the system involves complex interactions between soil, plant and atmosphere. Further studies of the efficiency of water transport and the regulation of water loss from plants may be particularly appropriate in the selection of plants for agricultural use in desert environments. The negligible influence of changes in evaporative demand on leaf water potential of the adequately watered herbaceous species indicates, as suggested by Weatherley (1970), the primary importance of edaphic conditions in determining plant water status with some species.

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APPENDIX I

Climatic influences on transpiration by Citrus seedlings.

The regulation of water loss by citrus was studied by determining the influence of climate on transpiration of sweet orange seedlings (Citrus sinensis var. Koethen).

Greenhouse grown seedlings were pruned back and the remaining, uppermost three to five leaves were enclosed in a ventilated, controlled environment chamber (Hoeffer Scientific Instr., San Francisco). Leaf temperature, humidity, wind speed and incident radiation (supplied by quartz-iodine lamps, Dicrolite Company Inc.) were controlled within the chamber. Sixty-two percent of the incident radiation was between 400 and 700 nm wavelength. Transpiration rates per unit projected leaf area were determined by an open flow, gas-exchange system that measured specific humidity with a dew point hygrometer (Cambridge Systems Inc., Model 880). The absolute humidity difference between the leaf and the air was determined from leaf temperature and external humidity data by assuming that the air within the leaf was saturated with moisture. The intrinsic resistance of the leaves to loss of water vapor was estimated from the ratio, absolute humidity deficit/ transpiration rate. This should provide a reasonable estimate of leaf resistance as the boundary layer resistance was small due to the use of a high speed fan to stir the air inside the chamber. Also, the leaves were not large. Climatic changes within the chamber were made slowly to prevent stomatal oscillations. All measurements were made after steady-state conditions had been achieved.

The influence of irradiance of total leaf resistance to water loss was determined at a leaf temperature of 25°C, and a constant absolute humidity difference (leaf to air) of 4 to 5 $\mu g\ cm^{-3}$ (Fig. 10). The responses were similar to those reported by Kriedeman (1971) for mature orange leaves. Leaf resistance increased markedly when irradiances were decreased below 7×10^4 erg cm^{-2} sec^{-1}. Subsequent experiments were conducted at irradiances greater than that value.

Leaf resistance responses to temperature were examined. When leaf temperature was raised with a constant absolute humidity of $18.0 \pm 0.5\ \mu g\ cm^{-3}$ in the chamber, the leaf to air humidity difference increased and leaf resistance increased (Fig. 11). In contrast, temperatures between 20 and 30°C did not influence leaf resistance with constant humidity differences (leaf to air) . As suggested by Schulze et al. (1973), conflicts in stomatal response to temperature reported in the literature may be due to variations in humidity conditions, stomatal closure at high temperatures being primarily due to increasing humidity gradients. In subsequent experiments, leaf temperature were maintained constant or varied between 20 and 30°C and it was assumed that the variations in temperature were not directly influencing leaf resistance.

The humidity gradient between the leaf and the air was increased in steps by either decreasing the humidity of the air around the leaf or increasing the leaf temperature while maintaining a constant absolute humidity in the chamber. In both cases, leaf resistance increased in the same manner when the humidity gradient was increased

Figure 10. Total leaf diffusion resistance as a function of irradiance (●), at a leaf temperature of 25 ± 0.1°C, and a fairly constant absolute humidity difference from leaf to air (○).

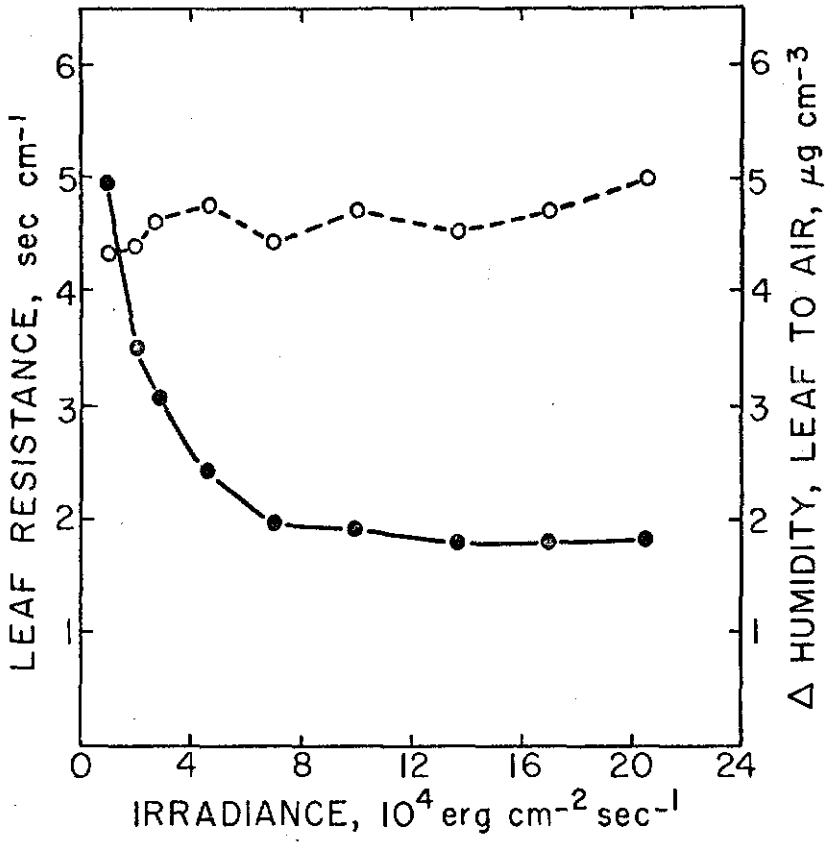
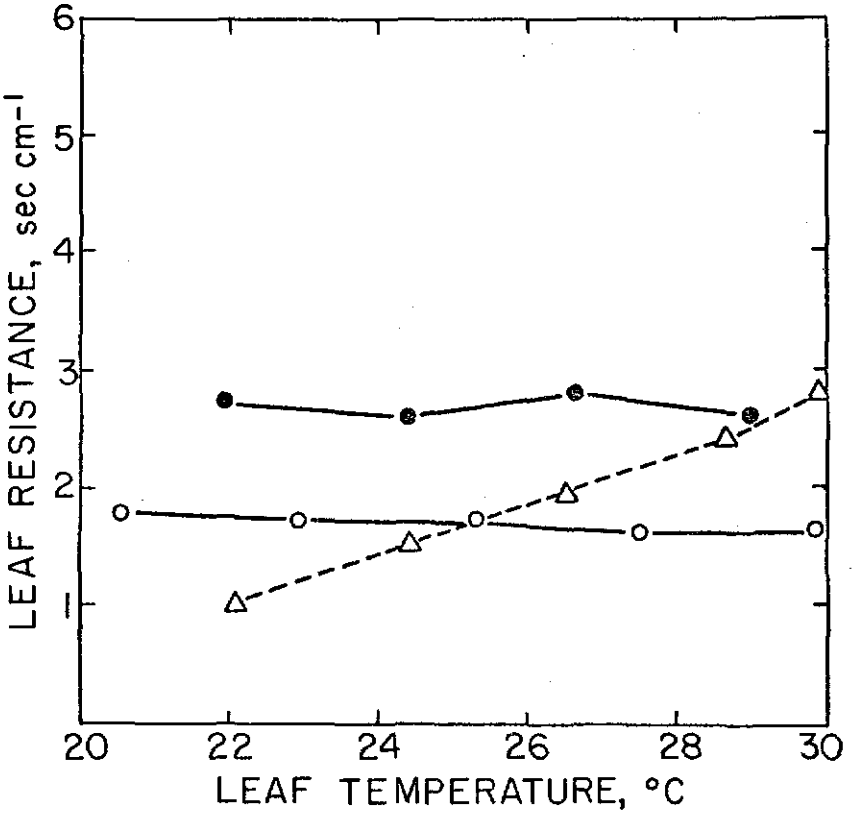

LEAF RESISTANCE, sec cm⁻¹
Δ HUMIDITY, LEAF TO AIR, μg cm⁻³
IRRADIANCE, 10⁴ erg cm⁻² sec⁻¹
0
4
8
12
16
20
24
1
2
3
4
5
6

Figure 11. Total leaf diffusion resistance as a function of leaf temperature at low (3.9 ± 0.1 μg cm^{-3}, 0) and moderate (7.4 ± 0.1 μg cm^{-3}, ●) constant humidity gradients from leaf to air, and at constant external absolute humidity (Δ), with an irradiance of 20×10^4 erg cm^{-2} sec^{-1} in all experiments.


LEAF RESISTANCE, sec cm-1
6
5
4
3
2
1
20
22
24
26
28
30
LEAF TEMPERATURE, °C

and plant response was greater during the first days that the plants were in the chamber (Fig. 12). After five days in the chamber the response of leaf resistance to the humidity gradient became consistent from day to day whether the humidity gradient was achieved by increasing temperature or decreasing the external humidity. The influence of the humidity gradient on leaf resistance may be due to stomatal responses to humidity as has been reported by Lange et al. 1971; Schulze et al., 1972; Hall and Kaufmann, 1973; and in this thesis for sesame and sunflower. Leaf resistance may also have increased due to effects of leaf water stress on stomata, although this could not explain all of the responses observed. Transpiration rates changed very little in some instances where increases in the absolute humidity difference from leaf to air resulted in increased leaf resistance (Fig. 13), and it is unlikely that leaf water status would change with a constant transpiration rate. No explanation is available for the decrease of humidity effects on leaf resistance with time. Pruning of the seedlings prior to experimentation did stimulate axillary bud break that was observed at the conclusion of the experiment. Lenz et al. (1972) have reported enhanced photosynthesis by lemon cuttings having emerging axillary shoots in comparison with the rates observed when these shoots were removed. Another explanation could be that the plants were acclimating to some aspect of the experimental treatments.

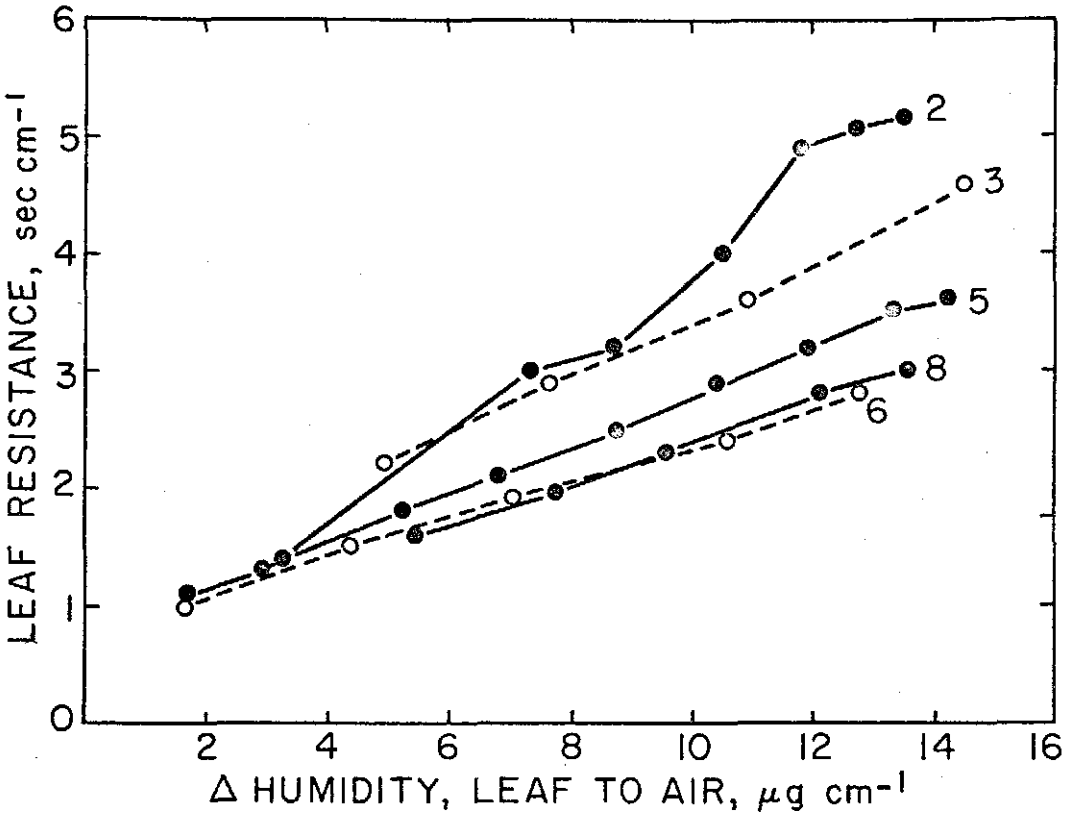
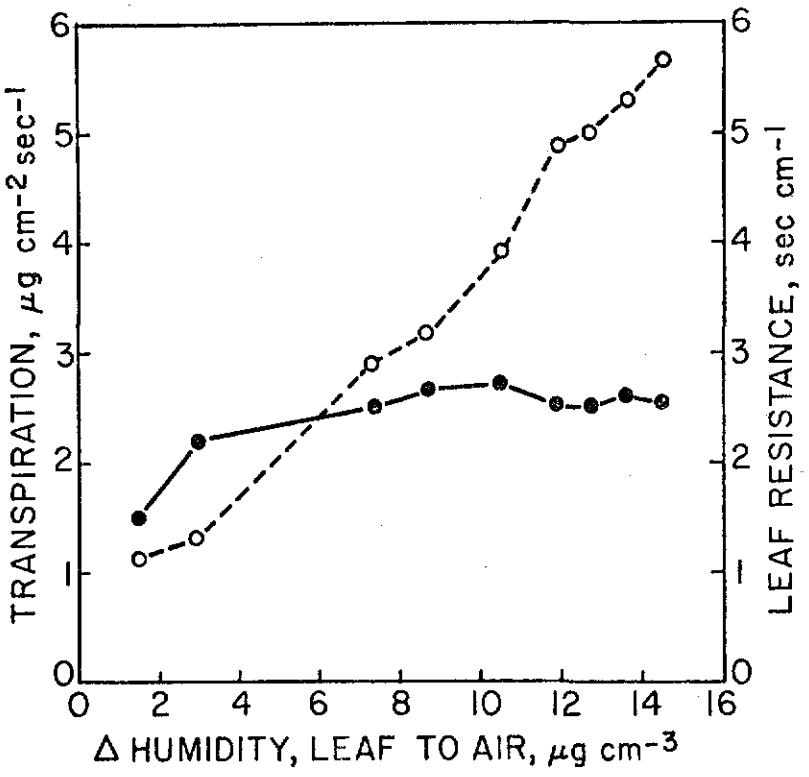

LEAF RESISTANCE, sec cm⁻¹
Δ HUMIDITY, LEAF TO AIR, μg cm⁻¹
0
1
2
3
4
5
6
2
4
6
8
10
12
14
16
2
3
5
8
6

Figure 13. The influence of the absolute humidity difference from leaf to air on transpiration (●) and leaf resistance (○). Data from day six of Figure 3.


TRANSPIRATION, μg cm-2 sec-1
LEAF RESISTANCE, sec cm-1
Δ HUMIDITY, LEAF TO AIR, μg cm-3
0
1
2
3
4
5
6
0
2
4
6
8
10
12
14
16

APPENDIX II

Relationship between pressure chamber and psychrometric determinations of leaf water status for citrus and pear.

The pressure chamber, developed by Scholander et al. (1964), has facilitated the determination of plant water status in the field. Since psychrometers are the most accurate instruments for measuring the leaf water status expressed as water potential (Barrs, 1968), curves relating the two methods are desirable. Relationships between pressure chamber values and psychrometrically determined leaf water potential have been reported for different species and the response curves exhibit differences that may be due to the species or methods used (Barrs et al., 1970; Boyer, 1967; Kaufmann 1968a, b; Klepper and Ceccato, 1969; West and Gaff, 1971).

Relationships between pressure chamber values and leaf water potential for citrus were obtained for branches (Kaufmann, 1968a) and leaves (Klepper and Ceccato, 1969) but variations in water status were obtained by tissue dehydration after excision from the tree. In addition Klepper and Ceccato (1969) sampled for the psychrometer from the same leaf used for obtaining the pressure chamber after the latter determination had been made, while Kaufmann (1968a) obtained psychrometer samples from a neighboring branch that supposedly was in equilibrium with the one used in the pressure chamber determination. In addition, artifacts have been reported for the pressure chamber vs. water potential relationship when water stress is induced after detaching material from the plant (West and Gaff, 1971).

Experimentation with seedlings and small trees makes it desirable to have a curve relating pressure chamber values and psychrometer determinations for single leaves so that less plant material is used in the measurements.

Potted and greenhouse grown seedlings of orange (Citrus sinensis var. Koethen) and evergreen pear (Pyrus kawakami) were used for the experiments. Paired samples were obtained from the same leaf by first cutting a 1 cm^2 disc of tissue with a circular knife for the psychrometer and then rapidly severing the leaf for the pressure chamber determination. Psychrometric determinations were made by the isopiestic method (Boyer and Knipling, 1965) at a temperature of 25.6°C, using a smaller psychrometer chamber than described by Boyer and Knipling. A range of plant water stress was attained by withholding irrigation. Also, by changing evaporative demand of the atmosphere surrounding the plants leaf water potential values as low as -10 bars were obtained for both species.

The relationships between pressure chamber value and leaf water potential for pear and citrus are shown in Figures 14 and 15 respectively. A quadratic equation describes the relationship for citrus, where the pressure chamber values are lower than the water potential throughout most of the range, except at water potentials around -2 to -6 bars, when the two measurements are very similar in value. For pear, on the other hand, a straight line describes well the relationship over the range of -2 to -26 bars; data shows that the pressure chamber overestimates the water stress, so that differences as great as -8 bars may

Figure 14. Relationship between pressure chamber and psychrometric determinations of leaf water status for mature leaves of orange seedlings. $\Psi_{\ell} = -3.69 - 0.02(PC)^2$. Dashed line indicates a 1:1 relationship.

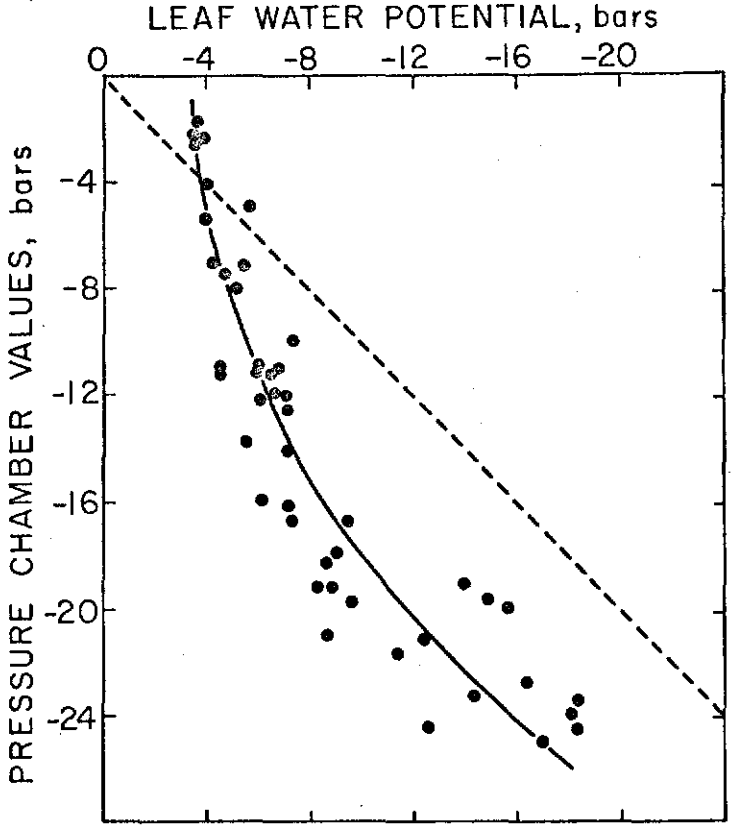
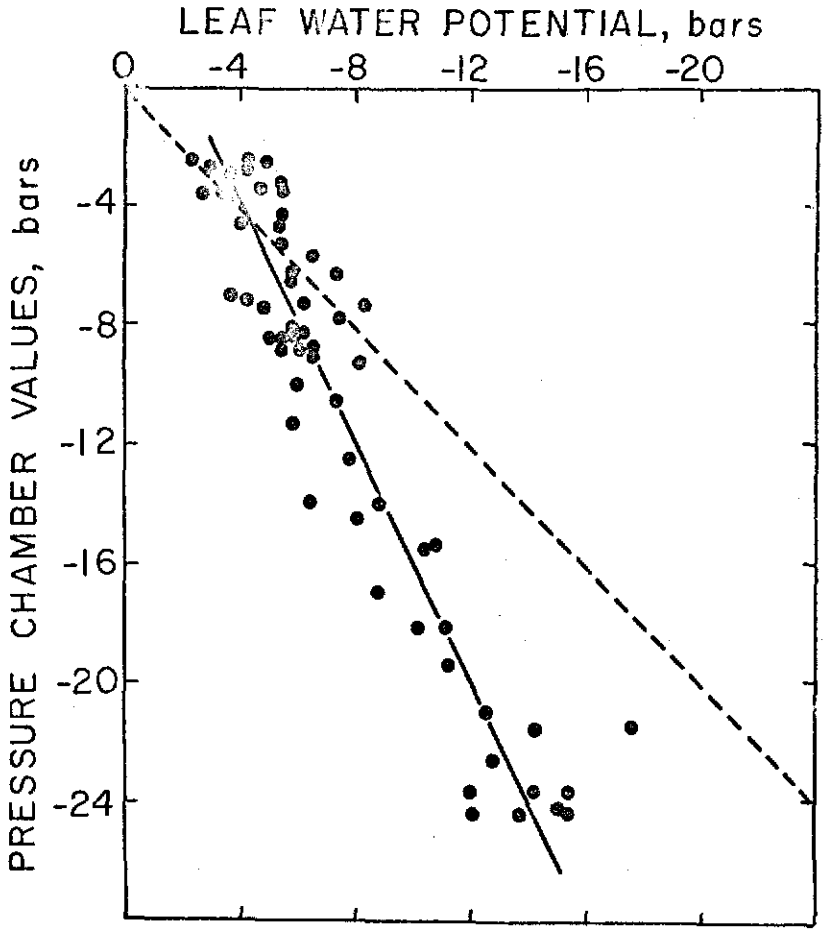

LEAF WATER POTENTIAL, bars
0
-4
-8
-12
-16
-20
PRESSURE CHAMBER VALUES, bars
-4
-8
-12
-16
-20
-24

Figure 15. Relationship between pressure chamber and psychrometric determination of leaf water status for mature leaves of evergreen pear seedlings. $\Psi_{\ell} = -2.39 + 0.48(PC)$. Dashed line indicates a 1:1 relationship.


LEAF WATER POTENTIAL, bars
0
-4
-8
-12
-16
-20
PRESSURE CHAMBER VALUES, bars
-4
-8
-12
-16
-20
-24

be found between the two measurements in the lower part of the range studied. In both species, the pressure chamber appears to be more sensitive to changes in the water status of the plants.

The reason for the difference in the citrus relationship with those already reported is not clear at this time. Both, the sampling procedure and the methods of inducing water stress may have influenced the results. A detailed analyses of the experimental techniques in curves reported is still in progress and results are to be published later. The two curves reported here, however, are in general terms similar to curves published for other species. With few exceptions, most of the relationships show a tendency for the pressure chamber to overestimate plant water stress in comparison with the psychrometer (Barrs et al., 1970; Boyer, 1967; Kaufmann 1968a, b; Klepper and Ceccato, 1969).

West and Gaff (1971) reported that with apple used here to stress plants should give relationship where pressure chamber values were less negative than the psychrometric values. Our data failed to show that tendency and in fact displacement in the opposite direction occurred.