Efficiency and Regulation of Water Transport in Some Woody and Herbaceous Species[1]

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ABSTRACT

The efficiency with which plants transport water is related to the water potential differences required to drive water fluxes from the soil to the leaf. A comparative study of two woody and three herbaceous species (*Citrus sinensis* L. cv. Koethen, *Pyrus kawakami* L., *Helianthus annuus* L. cv. Mammoth Russian, *Capsicum frutescens* L. cv. Yolo Wonder, and *Sesamum indicum* L. cv. Glauca) indicated contrasts in water transport efficiency. Depression of leaf water potential in response to transpiration increases was found in the woody species; the herbaceous species, however, had more efficient water transport systems and presented no measurable response of leaf water potential to transpiration changes. Different maximum transpiration rates under the same climatic conditions were observed with different species and may be accounted for by stomatal response to humidity gradients between leaf and air. Leaf diffusion resistance in sesame increased markedly as the humidity gradient was increased, while leaf resistance of sunflower responded less to humidity. Stomata appeared to respond directly to the humidity gradient because changes in leaf water potential were not detected when leaf resistance increased or decreased.

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 are facilitated by interpreting plant responses to variations in environment using conceptual and mathematical models. Elfving et al. (4) described 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 ($r_{soil\ to\ leaf}$).

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

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 ψ_{leaf} to different steady state transpiration rates attained by changing the evaporative demand of the atmosphere. Small decreases in ψ_{leaf} resulting from large increases in flux would indicate a small $r_{soil\ to\ leaf}$ and an efficient water transport system.

Contrasting results have been reported for the relationship between ψ_{leaf} and transpiration rate with nonlimiting water supplies and steady state fluxes. Some authors have observed significant decreases in ψ_{leaf} with increasing transpiration (6, 16), others have not (17), and Barrs (1) observed both types of response with different species. These differences may be due to differences in methodology; but it is also possible that important differences exist between species in their ability to transport water. To test these possibilities we examined relationships between ψ_{leaf} and transpirational flux for woody and herbaceous species by varying the evaporative demand with optimal soil water supply in controlled environments.

Differences in water transport efficiency may be also coupled with differences in stomatal regulation of water loss from plants. Some authors (7, 10, 13) have presented evidence for stomatal responses to humidity gradients between leaf and air that are independent of average leaf water status, while others (11) have concluded that stomata are relatively unaffected by changes in external humidity. If stomata do close when the humidity gradient is increased, leaf resistance would also increase and transpirational flux would not respond linearly to changes in the humidity gradient (15). The influence of the humidity gradient on leaf resistance was investigated with two herbaceous species, since the controversy concerning stomatal response to humidity may also be due to differential behavior between species.

MATERIALS AND METHODS

Orange (*Citrus sinensis* L. cv. Koethen), evergreen pear (*Pyrus kawakami* L.), sunflower (*Helianthus annuus* 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 to 32 C and minimum temperatures of 16 to 18 C. Orange and pear were grown in 4-liter pots; sunflower, pepper, and sesame were grown in 1-liter pots. The rooting medium was UC Mix C (University of California Agriculture Extension Service, Manual 23, 1957) with an additional 25% by volume of redwood shavings. The plants were watered daily and provided with full strength Hoagland's solution once weekly.

Seedlings were placed in the growth chamber in the evening, and experiments were initiated on the following morning. Seedlings were widely spaced in the growth chamber to minimize leaf shading and to provide good air movement which was predominantly vertical at approximately 30 cm sec^{-1} velocity. Transpiration rates were determined gravimetrically by weighing pots at 20- to 60-min intervals. The pots were enclosed in plastic
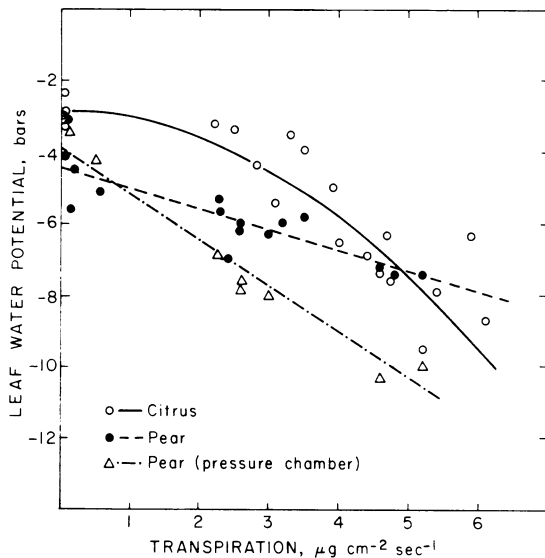
FIG. 1. Leaf water potential as a function of transpiration for citrus and evergreen pear seedlings under nonlimiting soil water conditions. Transpiration was varied by changing dew point temperature between 7 and 21 C, and air temperature between 20 and 32 C. (Each point is the mean of two to four water potential and transpiration measurements from each plant of citrus or from several plants of pear under a single set of conditions.)

bags to prevent evaporation from the soil surface. Every 3 hr the water lost was added to the pots to ensure adequate water supply to roots. This was particularly important with the sunflower plants which rapidly depleted soil water under high evaporative demands. Moisture release curves indicate that the change in soil matric potential was less than 10 centibars. Leaf area (one side only) 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 $\pm 3\%$, and specific humidity was measured with a dew point hygrometer and was varied between 6 and 29 C dew point (Cambridge Systems Model 880). Ambient temperatures were varied between 20 to 35 C, were controlled to ± 0.5 C and were 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, radiation between 400 and 700 nm) was supplied by metal halide vapor and color-improved mercury lamps having a ratio of input watts of 11 to 4, respectively. Leaf water potentials were determined with an isopiestic thermocouple psychrometer (2) using 1 cm^2 leaf discs excised shortly before the second pot weighing. Very young leaves, very old leaves, major veins, and leaf margins were not sampled. A pressure chamber was used for measuring leaf water status in some experiments. Leaf resistances were determined for the abaxial side of leaves using a diffusion porometer (4).

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. 1). The response of pear was linear, with ψ_{leaf} decreasing from -4.5 to -7.5 bars as transpiration increased. Responses obtained with citrus were curvilinear

with maximum ψ_{leaf} of -3 bars and a substantial decrease in ψ_{leaf} to -9 bars at high transpiration rates. Pressure chamber values obtained with pear responded more to changes in transpirational flux than did ψ_{leaf} values obtained from the same plants.

Similar studies were conducted with 20 sunflower, 17 sesame, and 12 pepper plants. These herbaceous species did not show a measurable depression of ψ_{leaf} as transpiration was increased (Fig. 2). Sunflower mean water potential values varied between -1.9 and -3.2 bars with no apparent decreases when transpiration rates as great as 15 μg cm^{-2} sec^{-1} were maintained for several hours. Similar results were obtained with sesame and pepper, although transpiration rates of these species were slower. Lack of water potential change in the herbaceous plants and the distinct decrease in water potential of the woody species as transpiration increased were established using both an isopiestic psychrometer and a pressure chamber. Differences in the regulation of water loss may also be present since 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 was examined by comparing the transpiration rates of all species tested with the absolute humidity deficits imposed when obtaining data for Figures 1 and 2. The absolute humidity deficit is only an approximation of the driving force for water loss but variability in differences between leaf and air temperatures prevented a more detailed analysis. Transpirational flux was greater for sunflower than for the other species at equivalent large evaporative demands (Fig. 3). It was not clear, however, whether the slow transpiration of the other species was due to large minimal leaf resistances or to partial stomatal closure at large humidity gradients between leaf and air.

Possible differences in stomatal responses to humidity were tested with sesame and sunflower. Leaf resistances (obtained with a diffusion porometer) and ψ_{leaf} 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
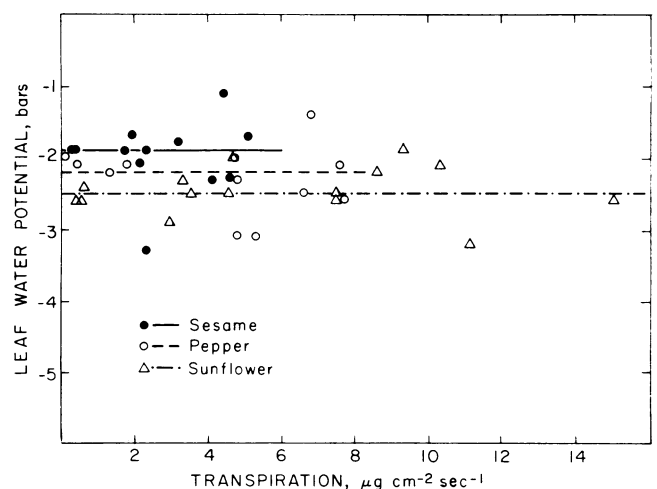

FIG. 2. Leaf water potential as a function of transpiration for three herbaceous species under nonlimiting soil water conditions. Transpiration was varied by changing dew point temperature between 7 and 26 C, and air temperature between 20 and 33 C. (Most points are the means of six water potential and transpiration measurements obtained from different plants under a single set of conditions.)

small humidity gradients (Figs. 4 and 5); however, at large humidity gradients leaf resistances of sesame were twice those of sunflower. No changes in ψ_{leaf} 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.
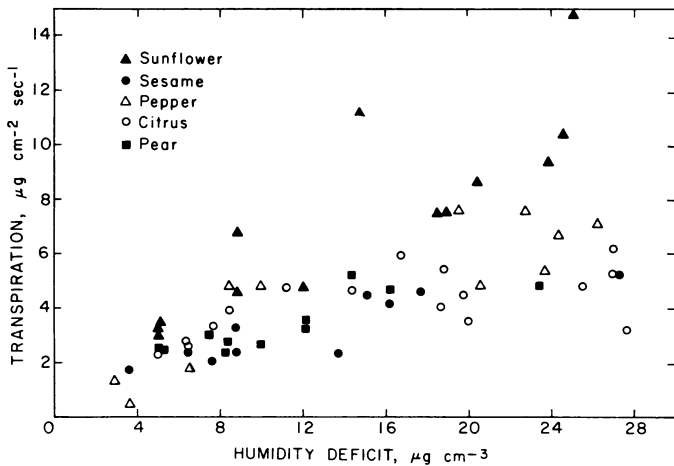

FIG. 3. Transpiration per unit leaf area as a function of absolute humidity deficit for several herbaceous and woody species. Data are from the same experiments as Figures 1 and 2.

FIG. 4. Leaf diffusion resistance, measured with a diffusion porometer, leaf water potential (●) and pressure chamber values (○) for sesame as a function of the absolute humidity difference between leaf and air, calculated by assuming water vapor saturation of the air inside the leaf. The humidity difference was varied by changing dew point temperature between 6 and 25 C, and air temperature between 20 and 30 C. (Each point is the mean of four measurements ± SE.)
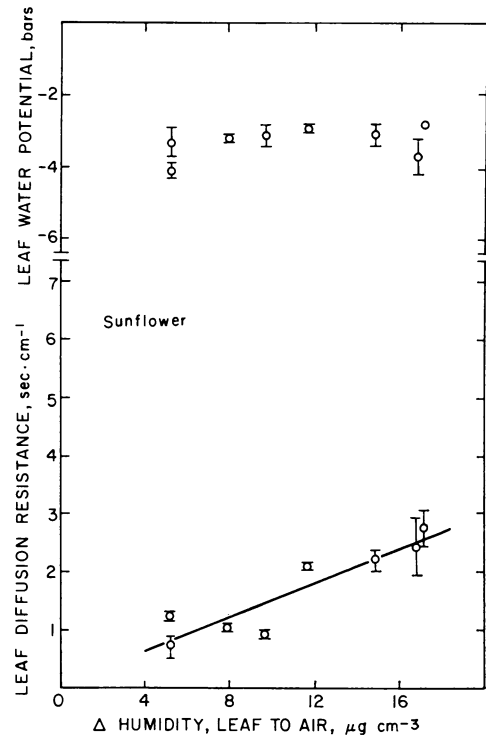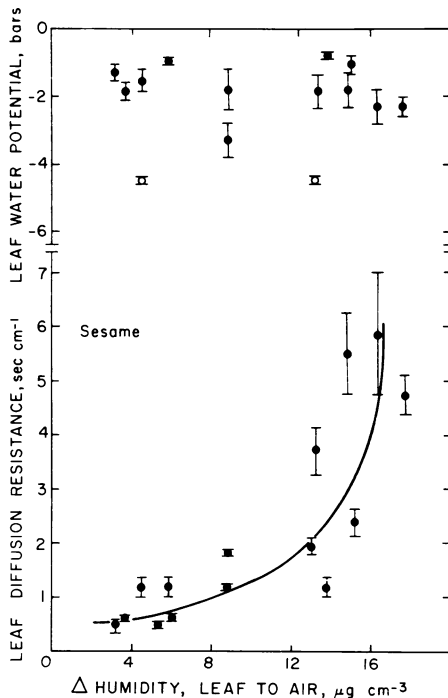

FIG. 5. Leaf diffusion resistance, measured with a diffusion porometer, and leaf water potential of sunflower as a function of the absolute humidity difference between leaf and air, calculated by assuming water vapor saturation of the air inside the leaf. The humidity difference was varied by changing dew point temperature between 17 and 29 C, and air temperature between 29 and 35 C. (Each point is the mean of four measurements ± SE.)

DISCUSSION

The development of water deficits in plants depends upon interactions between factors influencing the water supply to, and the water loss from, plants. The development of plant water deficits due to decreases in soil water availability is well documented (3, 5, 9, 14), but climatic effects on the development of water deficits have not been so extensively described. The progressive decreases in ψ_{leaf} as transpiration increased with the woody species (Fig. 1) indicate the presence of a substantial resistance to water flow in citrus and pear. In addition, unpublished observations by S. E. Camacho-B indicate that this resistance to water flow may be increased by subjecting citrus seedlings to drying cycles before measurements made with nonlimiting water supplies. In contrast, the herbaceous species, which were also under optimal water supply conditions, exhibited constant ψ_{leaf} over a wider range of transpirational fluxes (Fig. 2). 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 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 (1, 4, 12, 16).

Some of Barrs's data (1) are in agreement with our observations. He reported constant ψ_{leaf} for sunflower and maize over a range of transpirational fluxes. He also observed decreases in ψ_{leaf} as transpiration increased with the woody shrub *Gossypium barbadense* and the shape of the response curve was similar to our citrus curve. In contrast Stoker and Weatherley (16) observed decreases in sunflower ψ_{leaf} as transpiration increased at low transpiration rates. Also, Stoker and Weatherley (16) re-

ported responses of ψ_{leaf} to transpiration with *Gossypium hirsutum* that were different from the responses observed by Barrs with *G. barbadense*. In our experiments, pepper ψ_{leaf} was constant over a range of transpiration rates, whereas Barrs (1) reported that ψ_{leaf} decreased in this species as transpiration increased. Differences in plant age, environmental conditions before the experiment, rates at which climatic conditions were varied, and sampling techniques for ψ_{leaf} measurements may account for these conflicting responses. The pressure chamber data (Fig. 1) illustrate that different response curves may result if different techniques are used for determining plant water status.

The higher transpiration rates per unit leaf area of sunflower in comparison with the other species (Fig. 3) may be explained by the following observations. 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. 4), whereas, leaf resistance of sunflower responded much less and linearly (Fig. 5). Similar differences between sesame and sunflower in the regulation of water loss have also been observed by Hall and Kaufmann (7) using more accurate but less direct gas-exchange methods. They also reported that leaf resistance was more responsive to humidity gradients at lower than at higher leaf temperatures.

Changes in average ψ_{leaf} 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. As suggested by Lange *et al.* (10), 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. Also, Schulze *et al.* (13) reported that increases in leaf resistance as the humidity gradient from leaf to air increased could result in higher relative leaf water content. Lange *et al.* (10) proposed that "peristomatal transpiration" could provide a mechanism for stomatal response to humidity. 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. Unpublished observations by A. E. Hall indicated that stomata of sunflower only respond to ψ_{leaf} at leaf water potentials more negative than a threshold value of −8 bars. Similar observations by other workers were reviewed previously by Hsiao (8). The contrasting behavior of different species described in this paper and by Hall and Kaufmann (7), and the influence of temperature upon stomatal responses to humidity gradients (7) may explain some of the controversy concerning stomatal responses to humidity (10, 11).

There appear to be two physiological characteristics important to plant adaptation with respect to water relations: the efficiency of the water transport system and the regulatory mechanisms for water loss. The combination of those characteristics provides species with different capabilities for responding to the environment. The responses observed are placed in three categories: (*a*) species that combine strong regulation of water loss by stomata with low efficiency of their water transport system and which are unable to prevent depression of ψ_{leaf} as transpiration increases (*i.e.*, pear, citrus); (*b*) species that strongly regulate 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 regulation of transpiration and a highly efficient water transport system (*i.e.*, sunflower). Sunflower sustained very high rates of transpiration without measurable decreases in ψ_{leaf} and exhibited rapid sap exudation after leaves were removed even with plants in soil in a high evaporative demand climate.

Strong regulation of water loss via stomatal responses to hu-

midity could provide an adaptive advantage to plants in desert environments where evaporative demands are large and water supplies are limited as it may improve water use efficiency (7). Sesame is grown in arid areas without irrigation (19). 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, and stomatal closure in dry air would decrease photosynthesis (7). In this case, an efficient water transport system would also be needed to minimize the development of water deficits at large transpiration rates. The tendency for woody species to exhibit lower ψ_{leaf} 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 (20). The negligible influence of changes in evaporative demand on ψ_{leaf} of the adequately watered herbaceous species indicates, as suggested by Weatherley (18), the primary importance of edaphic conditions in determining plant-water status with some species.

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