

# Leaf Conductance Response to Humidity and Water Transport in Plants<sup>1</sup>

Anthony E. Hall and Glenn J. Hoffman<sup>2</sup>

## ABSTRACT

Stomatal response to humidity is a potentially important adaptive characteristic. The possibility that stomata may respond to humidity independently of changes in bulk leaf water status was tested. Also the basis for reported differences in leaf water potential response to transpiration was investigated.

Simultaneous measurements of in situ leaf water potential, transpiration, and net photosynthesis were made in controlled environments using sunflower (*Helianthus annuus* L.) and pinto bean (*Phaseolus vulgaris* L.). Responses of leaf conductance and leaf water potential to changes in ambient humidity and root medium water potential were determined.

Leaf conductance responded consistently to changes in the vapor pressure difference between leaf and air. Decreases in ambient humidity resulted in decreases in leaf conductance with constant, decreasing or increasing leaf water potentials. Leaf conductance responded to changes in leaf water potential only when manipulations of plant water supply resulted in rapid decreases in leaf water potential below a threshold level of  $-8$  bars. These data demonstrate that stomata may respond to humidity independently of changes in leaf water potential.

On occasions environmental perturbations resulted in changes in leaf water potential that were negatively correlated with changes in transpiration. On other occasions leaf water potential remained constant when transpiration rate or water potential of the root medium was changed. On one occasion an inverted water potential gradient between root medium and leaves was observed in a transpiring plant. Models of the simultaneous movement of water and solutes within plant roots provided qualitative explanations for these observations by predicting that changes in the uptake and translocation of solutes may influence leaf water potential response to transpiration.

**Additional index words:** In situ leaf psychrometer, Photosynthesis, Stomata, Ion translocation, Leaf water potential, Sunflower, Pinto bean, Transpiration.

**S**TOMATAL response to humidity has been demonstrated with epidermal strips (Lange et al., 1971) and decreases in leaf conductance have been induced by decreasing ambient humidity with constant leaf water potentials (Camacho-B et al., 1974) and with increases (Schulze et al., 1972) or decreases (Aston, 1970) in relative water content of the leaves. These data indicate that stomata may respond to humidity independently of changes in bulk leaf water status. This hypothesis was tested more completely by making simultaneous measurements of leaf conductance to water vapor and leaf water potential, while changing ambient humidity and root medium water potential.

These experiments also provided the opportunity for examining water transport in plants to try to explain the differences in leaf water potential response to transpiration that have been reported (Hailey

et al., 1973; Camacho-B et al., 1974). Effects on leaf water potential of changes in transpiration and root medium water potential were determined with intact plants and analyzed using recent models of the simultaneous uptake of water and solutes by plant roots (Dalton et al., 1975; Fiscus, 1975).

## MATERIALS AND METHODS

Sunflower (*Helianthus annuus* L. cv. Mammoth Russian) and pinto bean (*Phaseolus vulgaris* L.) were grown in 2-liter pots containing Pachappa sandy loam, coarse: loamy, mixed, thermic Mollic Haploxeralf, soil or aerated, modified Hoagland's solution (Epstein, 1972). Plants were grown in a growth chamber with a 14-hour photoperiod at a daytime air temperature of  $25 \pm 1$  C and a relative humidity of  $55 \pm 3\%$ . Nighttime air temperature and relative humidity were  $20 \pm 1$  C and  $78 \pm 3\%$ . Light was supplied by metal halide vapor and color-improved mercury lamps having a ratio of input watts of 11 to 4. Irradiance at leaf level during plant growth was between 280 and 420  $\text{Wm}^{-2}$ .

Young plants with four to six true leaves were selected for study. Older leaves comprising less than 50% of the total leaf area were removed and individual plants with 100 to 200  $\text{cm}^2$  leaf area (one side only) were placed in a stirred, controlled-environment, single-plant chamber (Hall and Kaufmann, 1975). Leaf temperature was 25.0, variation with time was within  $\pm 0.1$  C and the leaves were arranged to minimize shading and held horizontal by nylon filaments. Plants were subjected to low irradiances ( $25 \text{ Wm}^{-2}$ ) so that leaf water potentials could be determined in situ with silver-foil psychrometers attached to the lower leaf surface of unshaded leaves (Hoffman and Hall, 1976). Occasionally, these psychrometers did not function properly. Leaf necrosis was observed on some occasions with beans several hours after the psychrometers were attached. However, damage was not observed with sunflower leaves. On other occasions, sunflower leaves expanded substantially within a few hours and broke the seal between leaf and psychrometer. Therefore, after each experiment water deficits were deliberately induced in the leaves to test psychrometer functioning. Data are presented only from experiments where these tests indicated that the psychrometers were functioning properly.

Transpiration and net photosynthesis were determined simultaneously with leaf water potential using an open gas exchange system as described by Hall and Kaufmann (1975). Total leaf conductance to water vapor (including boundary layer, stomatal, and cuticular components) was calculated using the following relationship:

$$T = g_t (P_{\text{leaf}} - P_{\text{air}}) / P_{\text{atm}}$$

where  $T$  is transpiration/unit leaf area (one side),  $g_t$  is total leaf conductance (with the same units as  $T$ ),  $P_{\text{leaf}}$  and  $P_{\text{air}}$  are the partial pressures of water vapor inside the leaf and in the ambient air, and  $P_{\text{atm}}$  is atmospheric pressure.  $P_{\text{leaf}}$  was obtained from leaf temperature measurements by assuming water vapor saturation of the air at the evaporating surfaces inside the leaf.  $P_{\text{air}}$  was obtained from the air leaving the chamber, which was shown to have the same vapor pressure as the air in the chamber. The flux density units for conductance presented here are more valid than the velocity units that are commonly used, since the latter units imply that the absolute humidity difference is the driving force, whereas it is more appropriate to consider differences in relative partial pressure as the driving force (Cowan, 1972).

In some experiments the water potential of the root medium was changed by removing the solution from around the roots and replacing it within 3 sec by another solution. Tests demonstrated that exposing roots to air for periods much longer than 3 sec did not appear to stress the plants. Presumably the water film around each root was sufficient to supply the plant with

<sup>1</sup>Contribution from the Dep. of Plant Sciences, Univ. of California, Riverside, CA 92502 and from the U. S. Salinity Lab., WR, ARS, USDA, P. O. Box 672, Riverside, CA 92502. Received 21 Nov. 1975.

<sup>2</sup>Assistant plant physiologist and agricultural engineer.

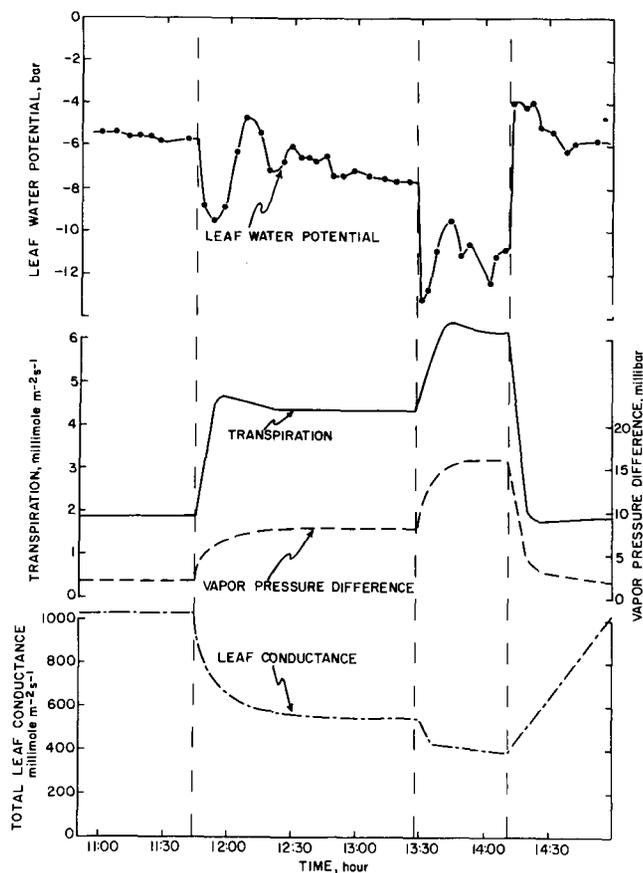


Fig. 1. Responses of a sunflower plant in full-strength nutrient solution, having a solute potential of  $-0.9$  bar, to changes in water vapor pressure difference between leaf and air. Vertical dashed lines indicate times when these changes were initiated. Leaf temperature was maintained at  $25$  C in all experiments.

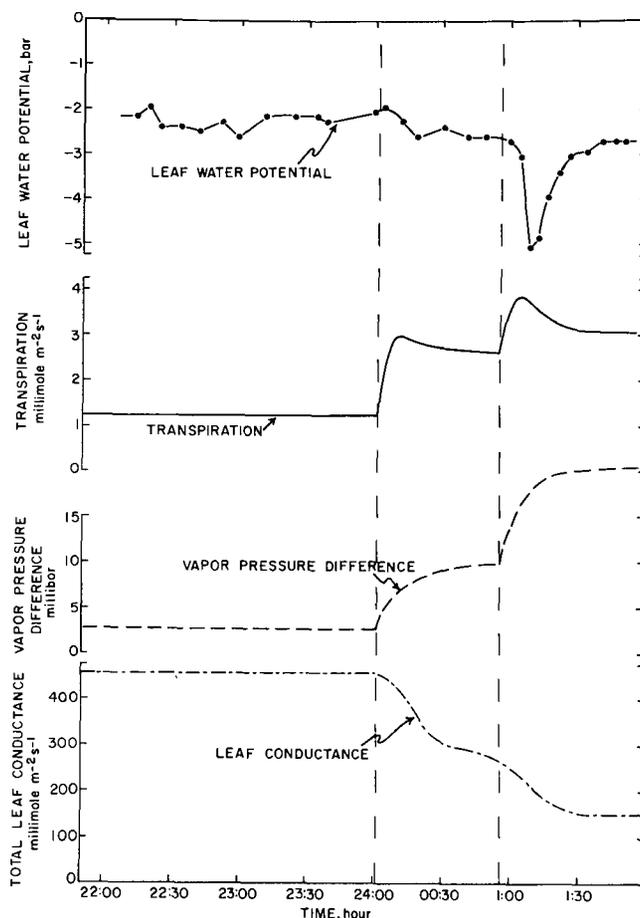


Fig. 2. Responses of a sunflower plant to changes in water vapor pressure difference between leaf and air. Vertical dashed lines indicate times when these changes were initiated. In this experiment the root-zone nutrient solution was changed from full- to  $1/100$ -strength at 1610 hours, at which it remained for the rest of the experiment. Other experiments indicate, however, that this treatment was not responsible for the difference in response from that described in Fig. 1.

water for several seconds. Root solutions were aerated during experimentation and stirred with a magnetic stirrer. Different root-media water potentials were obtained by adding mannitol to nutrient solutions. Water potential of these solutions was determined with a wet-loop thermocouple psychrometer (Richards and Ogata, 1958). In other experiments ambient humidity was changed by either changing the flow rate of air through the single-plant chamber or by changing the humidity of the air entering the chamber.

**RESULTS**

Two types of experiments are described: those where ambient humidity was changed; and those where root-medium water potential was changed. One example is presented of the different types of responses that were observed. At this time we are not able to describe the conditions under which these different types of responses are most likely to occur.

**Humidity Effects on Transpiration, Leaf Conductance, and Leaf Water Potential**

On all occasions leaf conductance was negatively correlated with the vapor pressure difference between leaf and air. On some occasions sunflower exhibited more negative leaf water potentials with increasing

transpiration (Fig. 1). Leaf water potential tended to oscillate before reaching a steady value. In this case it was not possible to determine whether the decreases in leaf conductance were due to the lower leaf water potentials or to the larger vapor pressure differences between leaf and air. These responses of leaf water potential to transpiration and leaf conductance to humidity were reversible.

On other occasions decreasing ambient humidity had little effect on leaf water potential of sunflower even though transpiration increased substantially (Fig. 2). The second change in humidity did cause a transitory decrease in leaf water potential but within 20 min the leaf water potential had recovered to the original value. At the conclusion of this experiment the leaves were stressed by cutting the stem and leaf water potential dropped rapidly indicating that the psychrometer was functioning. Leaf conductance decreased as vapor pressure difference increased even though leaf water potential remained constant.

In another experiment both types of leaf water potential response were observed with the same sun-

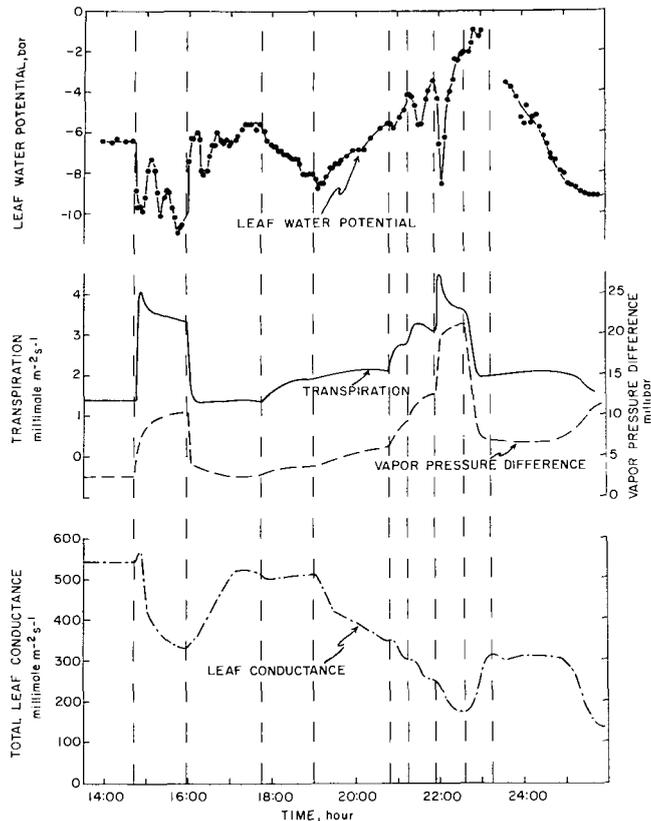


Fig. 3. Responses of a sunflower plant growing in well-watered Pachappa sandy loam soil. The plant was subjected to changes in water vapor pressure difference between leaf and air until 2315 hours, when reductions in soil temperature were begun. Vertical dashed lines indicate the times when these changes were initiated.

flower plant (Fig. 3). Initially, leaf water potentials responded to changes in the rate of transpiration. Subsequently, leaf water potential increased apparently independent of increases in transpiration which were obtained by increasing the vapor pressure difference. As before, leaf conductance was consistently and negatively correlated with vapor pressure difference between leaf and air. Finally, the plant was stressed by cooling its roots, and leaf conductance decreased rapidly when leaf water potential decreased as low as  $-8$  bars. In this instance vapor pressure difference increased due to reduced humidification of the plant chamber caused by stomatal closure. This response of leaf conductance to leaf water potential has been consistently observed with sunflower when leaf water potential has decreased rapidly below  $-8$  bars due to manipulation of water supply to the leaves. At the conclusion of this experiment the psychrometer reading was  $-9.2$  bar. The plant chamber was opened and xylem potentials of the leaves were measured with a pressure chamber. The leaf with the psychrometer attached had a value of  $-9.5$  bar and the adjacent leaf had a value of  $-10.5$  bar.

Pinto bean responded to changes in humidity somewhat differently than sunflower. When humidity was decreased gradually, leaf water potential changed very little even though transpiration increased substan-

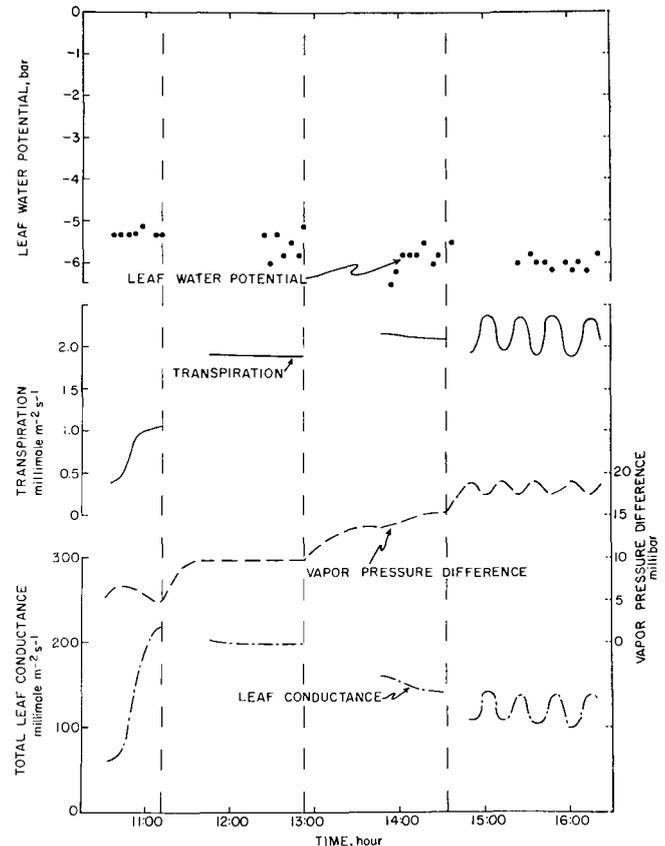


Fig. 4. Responses of a pinto bean plant in full-strength nutrient solution, having a solute potential of  $-0.9$  bar. Lights were turned on at 1035 hours. The water vapor pressure difference between leaf and air was increased at 1112 hours and subsequently as indicated by vertical dashed lines.

tially (Fig. 4). Leaf conductance was, however, negatively correlated with vapor pressure difference. Further decreases in humidity caused mild stomatal oscillations with no detectable change in leaf water potential. The oscillations in vapor pressure difference were due to oscillations in chamber humidification by the plants. In this particular series of experiments, humidity was decreased even further and leaf water potential and leaf conductance both oscillated (refer to Fig. 4 in Hoffman and Hall, 1976). Oscillations of this type were easily induced by reductions in ambient humidity with pinto bean, kidney bean, *Gossypium hirsutum* L., and *Citrus sinensis* L., but not with sunflower. With *Sesamum indicum* L. rapid decreases in humidity resulted in such large decreases in leaf conductance that transpiration did not increase.

#### Effects of Root-medium Water Potential on Leaf Water Potential and Leaf Conductance

On some occasions a step change in root-medium water potential resulted in step changes in leaf water potential (Fig. 5). However, leaf conductance did not decrease until leaf water potential rapidly decreased below  $-8$  bars. Net photosynthesis increased gradually throughout much of the experiment but decreased after leaf conductance and leaf water potential

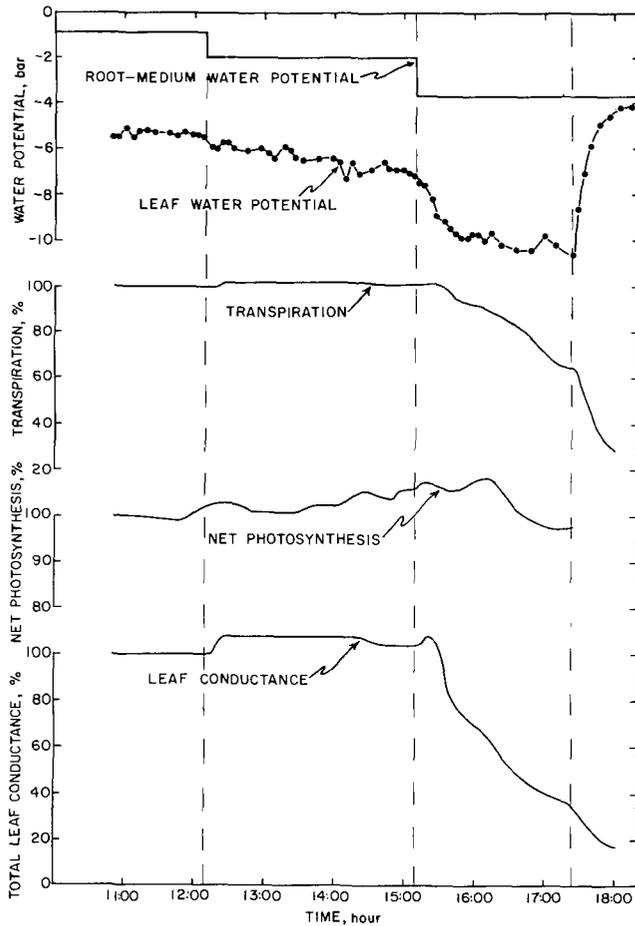


Fig. 5. Responses of a pinto bean plant to changes in root medium water potential. The first nutrient solution was full-strength; subsequent solutions had increasing quantities of mannitol. The water vapor pressure difference between leaf and air was maintained at  $5.2 \pm 0.2$  mbar until 1530 hours, after which it increased due to decreases in transpiration, to 10 mbar by 1724 hours when the lights were turned off.

had already decreased substantially. When the chamber lights were switched off at 1724 hours the stomata closed further and decrease in transpiration resulted in a recovery in leaf water potential approaching the value of the root solution.

On other occasions, with sunflower, leaf water potential remained relatively constant even though root medium water potential was decreased. In one experiment root-medium water potential was substantially more negative than leaf water potential for more than 2 hours with substantial and relatively constant rates of transpiration (Fig. 6). Further reductions in root-medium water potential resulted in drastic decreases in leaf water potential and leaf conductance. Net photosynthesis increased throughout much of the experiment but decreased when leaf conductance and leaf water potential decreased.

## DISCUSSION

Leaf conductance responded consistently to changes in the vapor pressure difference between leaf and air. Decreases in leaf conductance occurred, presumably

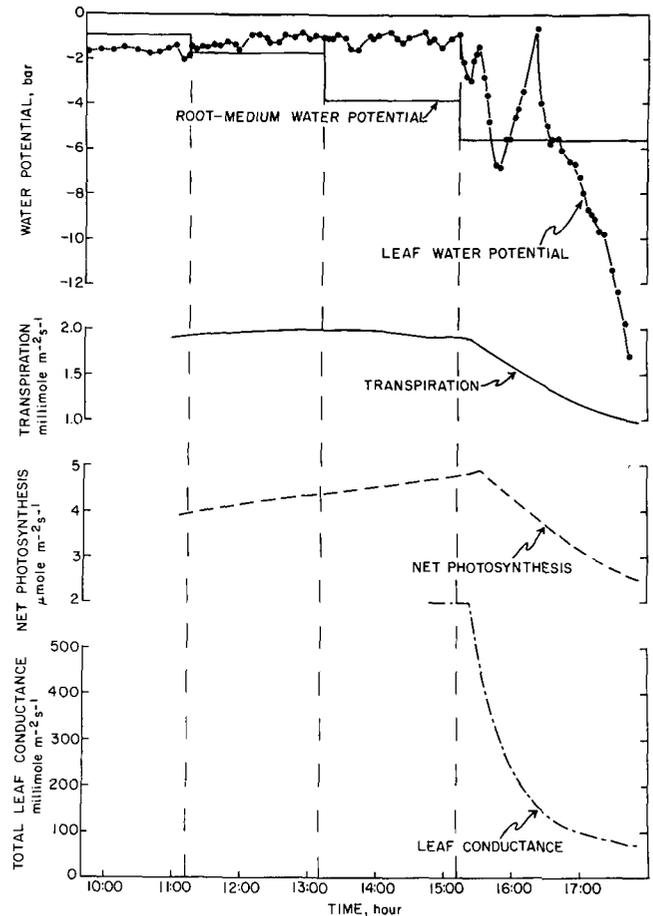


Fig. 6. Responses of a sunflower plant to changes in root medium water potential achieved as described in Fig. 5. Water vapor pressure difference between leaf and air was  $2.7 \pm 0.5$  mbar until 1522 hours, after which it increased, due to decreases in transpiration, to 14 mbar by 1758 hours.

due to partial stomatal closure, when ambient humidity was decreased with decreasing leaf water potential (Fig. 1), constant leaf water potential (Fig. 2 and 4), and with increasing leaf water potential (Fig. 3). This demonstrates that leaf conductance may respond to the vapor pressure difference between leaf and air independently of changes in bulk leaf water potential confirming earlier work by Schulze et al. (1972) and Camacho-B et al. (1974). The adaptive advantage of this mechanism in preventing development of bulk leaf water deficits has been discussed by Lange et al. (1971) and possible mechanisms for stomatal response to the vapor pressure difference were discussed by Hall et al. (1976).<sup>3</sup>

Leaf conductance only appeared to respond to changes in leaf water potential when manipulations of the water supply system resulted in rapid decreases in leaf water potential or in decreases in leaf water potential below a threshold level of  $-8$  bars. It is possible that the effects on stomata of changes in leaf water potential that were induced in these experi-

<sup>3</sup> Hall, A. E., E.-D. Schulze, and O. L. Lange. 1976. Current perspectives of steady-state stomatal response to environment. In O. L. Lange, L. Kappen, and E.-D. Schulze (eds.) Ecological studies. Springer Verlag, New York. (in press).

ments may not occur in field conditions where the availability of water to the roots changes more slowly with time resulting in slower changes in leaf water potential and occasionally osmotic adjustment in the leaves.

Different relationships between leaf water potential, transpiration, and root-medium water potential were observed with similar plants on different days and in a few instances with the same plant on the same day. One may argue that these differences in leaf water potential response are artifacts due to the method for measuring leaf water potential. Earlier work described conditions during which the *in situ* leaf psychrometer appeared to perform adequately (Hoffman and Hall, 1976) and these conditions were used in this study. Measurements of leaf water potential made on a small area may not be representative of the total leaf area, however, occasional measurements with a pressure chamber gave similar values. The major uncertainty with this method of measurement concerns the seal between psychrometer and leaf. In this work it was assumed that if a perfect seal is present at the end of the experiment, as demonstrated by an appropriate psychrometer response to deliberately induced leaf water stress, then the psychrometer has functioned adequately during the experiment. It would not appear likely that a psychrometer could reseal itself once the original seal is broken.

The ability of the model of Dalton et al. (1975) to predict the observed responses of leaf water potential to environment was tested. A model for leaf water potential response to environment was obtained by assuming that the single membrane model applies to whole plants and that steady state conditions prevail. Leaf water potential ( $\psi_{\text{leaf}}$ ) was related to root medium water potential ( $\psi_{\text{soil}}$ ), pressure potential difference ( $\Delta P$ ) and osmotic pressure difference ( $\Delta\pi$ ), root minus leaf, by the following equation.

$$\psi_{\text{leaf}} = \psi_{\text{soil}} - \Delta P + \Delta\pi \quad [1]$$

Substituting equations 8, 10, and 11 of Dalton et al. (1975) into this equation gives a model for leaf water potential response to environment that considers  $\psi_{\text{leaf}}$  as the dependent variable, as was justified by Elfving et al. (1972).

$$\psi_{\text{leaf}} = \psi_{\text{soil}} - \frac{J_v}{L} + (1 - \sigma) \frac{(\sigma\pi_1 J_v - nRTk)}{(J_v + nRT\omega)} \quad [2]$$

where  $J_v$  is transpiration,  $L$  is the filtration coefficient of the membrane,  $\sigma$  is the reflection coefficient of the membrane,  $\pi_1$  is the osmotic pressure of the root medium,  $n$  is the sum of cation and anion valencies,  $R$  is the gas constant,  $T$  is absolute temperature,  $k$  is the active flux of solutes across the membrane, and  $\omega$  is the osmotic permeability. According to this equation,  $\psi_{\text{leaf}}$  will be linearly related to  $J_v$  when  $\sigma$  approaches unity or zero (in which case  $k$  approaches zero), or when  $J_v$  is large. The responses observed by Hailey et al. (1973), Neumann et al. (1974), and in Fig. 1 are of this type. Small responses of leaf water potential to transpiration (Barrs, 1973; Camacho-B et al., 1974; and Fig. 2) or curvilinear responses (Weatherley, 1970) are predicted when  $\sigma$  is less than unity but greater than zero and when  $J_v$  is small as was shown by Fiscus (1975). Time dependent in-

creases in  $\psi_{\text{leaf}}$  with constant or increasing  $J_v$  (Fig. 3) could be due to time dependent increases in  $L$  or  $\sigma$ , or decreases in  $\omega$  or  $k$ . The equation predicts that changes in  $\psi_{\text{soil}}$  due to changes in  $\pi_1$  will result in smaller changes in  $\psi_{\text{leaf}}$ . It also predicts that increases in  $\pi_1$  and decreases in  $k$  (or  $\omega$ ) could result in leaf water potentials that are less negative than the soil water potential, even though steady-state water uptake and transpiration are occurring [Fig. 6 and as may have been observed by Rawlins (1964), Barrs (1966), and Taerum (1973)]. The model of Fiscus (1975) gives similar predictions but differs in that  $\omega$  is assumed to be insignificantly small. Numerous workers have observed that leaf water potential is more negative than soil water potential when water uptake and transpiration are very small. This apparent deviation from equilibrium is predicted by the model because as  $J_v$  approaches zero, leaf water potential approaches  $\psi_{\text{soil}} - (k/\omega)(1 - \sigma)$ . This states that with very low rates of water uptake, leaf water potential could be more negative than soil water potential if ions are being actively pumped into the stele across a membrane that is not ideal.

A rigorous test of the extent to which these models can account for small or curvilinear responses of  $\psi_{\text{leaf}}$  to changes in  $J_v$  requires a knowledge of the values  $L$ ,  $\sigma$ ,  $k$ , and  $\omega$ . Unfortunately these values are not known at this time for whole root systems, although Dalton et al. (1975) propose methods by which these values may be obtained with detopped plants.

The model may be extended by considering the uptake of solutes from the solution in the xylem vessels into surrounding parenchyma cells (Lauchli, 1972; Rains, 1972). The effects of this process on  $\psi_{\text{leaf}}$  were modeled by determining the change in osmotic pressure in the xylem solution ( $\Delta\pi_2$ ) due to a solute flux from xylem vessels to xylem parenchyma of  $U$  with a transpirational flux  $J_v$ :

$$\Delta\pi_2 = - (nRTU/J_v) \quad [3]$$

where  $n$ ,  $R$ , and  $T$  were defined previously. The region of  $U$  is probably located far enough from the root tip that it has minimal influence on ion uptake into the stele. Consequently the effect of  $\Delta\pi_2$  on  $\psi_{\text{leaf}}$  can be obtained by subtraction from Eq. 2, which results in

$$\psi_{\text{leaf}} = \psi_{\text{soil}} - \frac{J_v}{L} + (1 - \sigma) \frac{(\sigma\pi_1 J_v - nRTk)}{(J_v + nRT\omega)} + \frac{nRTU}{J_v} \quad [4]$$

The equation predicts that the uptake of ions from the xylem solution could also result in curvilinear responses of  $\psi_{\text{leaf}}$  to changes in  $J_v$  and in the occurrence of transpiration with  $\psi_{\text{leaf}}$  less negative than  $\psi_{\text{soil}}$  as was proposed by Barrs (1966) and Taerum (1973). These effects of  $U$  would decrease with increases in  $J_v$  and would depend upon the magnitude of  $U$ . Values for  $U$  have not been reported. According to Eq. 4, the direct effect of an increase in  $k$  would be a decrease in  $\psi_{\text{leaf}}$ . However in steady state conditions  $U$  cannot exceed the flux of ions the xylem, consequently an increase in  $k$  may also tend to increase  $\psi_{\text{leaf}}$  if it results in an increase in  $U$ .

These models predict that it is not prudent to evaluate water transport in plants without considering the uptake and translocation of solutes. A more com-

plete model of steady-state water flow in plants would also include effects of physical resistances to flow in the shoot and the branched character of the flow pathway (Richter, 1973; Boyer, 1974).

#### ACKNOWLEDGMENTS

The authors acknowledge the helpful comments of Drs. P. A. C. Raats and G. D. Farquhar in the preparation of this manuscript.

#### LITERATURE CITED

- Aston, M. J. 1973. Changes in internal water status and the gas exchange of leaves in response to ambient evaporative demand. p. 243-247. *In* R. O. Slayter (ed.) Plant response to climatic factors. Proc. Uppsala Symp. (1970) UNESCO.
- Barrs, H. D. 1966. Root pressure and leaf water potential. *Science* 152:1266-1268.
- . 1973. Controlled environment studies of the effect of variable atmospheric water stress on photosynthesis, transpiration and water status of *Zea mays* L. and other species. p. 249-258. *In* R. O. Slayter (ed.) Plant response to climatic factors. Proc. Uppsala Symp. (1970) UNESCO.
- Boyer, J. 1974. Water transport in plants: mechanism of apparent changes in resistance during absorption. *Planta (Berlin)* 117:187-207.
- Camacho-B, S. E., A. E. Hall, and M. R. Kaufmann. 1974. Efficiency and regulation of water transport in some woody and herbaceous species. *Plant Physiol.* 54:169-172.
- Cowan, I. R. 1972. An electrical analogue of evaporation from, and flow of water in plants. *Planta (Berlin)* 106:221-226.
- Dalton, F. N., P. A. C. Raats, and W. R. Gardner. 1975. Simultaneous uptake of water and solutes by plant roots. *Agron. J.* 67:334-339.
- Elfving, D. C., M. R. Kaufmann, and A. E. Hall. 1972. Interpreting leaf water potential measurements with a model of the soil-plant-atmosphere continuum. *Physiol. Plant.* 27:161-168.
- Epstein, E. 1972. Mineral nutrition of plants: principles and perspectives. John Wiley and Sons, Inc., New York. p. 39.
- Fiscus, E. L. 1975. The interaction between osmotic- and pressure-induced water flow in plant roots. *Plant Physiol.* 55:917-922.
- Hailey, J. L., E. A. Hiler, W. R. Jordan, and C. H. M. van Bavel. 1973. Resistance to water flow in *Vigna sinensis* L. (End.) at high rates of transpiration. *Crop Sci.* 13:264-267.
- Hall, A. E., and M. R. Kaufmann. 1975. The regulation of water transport in the soil-plant-atmosphere continuum. p. 187-202. *In* D. M. Gates and R. B. Schmerl (eds.) Perspectives of biophysical ecology. Ecological studies. Vol. 12. Springer Verlag, New York.
- Hoffman, G. J., and A. E. Hall. 1976. Performance of silver-foil psychrometer for measuring leaf water potential *in situ*. *Agron J.* 68:872-875.
- Lange, O. L., R. Losch, E.-D. Schulze, and L. Kappen. 1971. Responses of stomata to changes in humidity. *Planta (Berlin)* 100:76-78.
- Lauchli, A. 1972. Translocation of inorganic solutes. *Ann. Rev. Plant Physiol.* 23:197-218.
- Neumann, H. H., G. W. Thurtell, and K. R. Stevenson. 1974. *In situ* measurements of leaf water potential and resistance to water flow in corn, soybean, and sunflower at several transpiration rates. *Can. J. Plant Sci.* 54:175-184.
- Rains, D. W. 1972. Salt transport by plants in relation to salinity. *Ann. Rev. Plant Physiol.* 23:367-388.
- Rawlins, S. L. 1964. Systematic error in leaf water potential measurements with a thermocouple psychrometer. *Science* 146:644-646.
- Richards, L. A., and G. Ogata. 1958. Thermocouple for vapour pressure measurement in biological and soil systems at high humidity. *Science* 128:1089-1090.
- Richter, H. 1973. Frictional potential losses and total water potential in plants: a re-evaluation. *J. Exp. Bot.* 24:983-994.
- Schulze, E.-D., O. L. Lange, U. Buschbom, L. Kappen, and M. Evenari. 1972. Stomatal responses to changes in humidity in plants growing in the desert. *Planta (Berlin)* 108:259-270.
- Taerum, R. 1973. Occurrence of inverted water potential gradients between soil and bean roots. *Physiol. Plant.* 28:471-475.
- Weatherley, P. E. 1970. Some aspects of water relations. *Adv. Bot. Res.* 3:171-206.