



Plant hydraulic conductance measured by the high pressure flow meter in crop plants

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Abstract

A new high pressure flow meter (HPFM) method for measuring plant hydraulic conductances (K) was investigated to examine whether its results are comparable to those from a conventional evaporative flux (EF) method in crops. Hydraulic conductance (K) was measured by the two methods under quasi-steady-state conditions in six crops grown in pots: soybean (*Glycine max* L. Merr. cv. Tsurunoko daizu), sunflower (*Helianthus annuus* L. cv. Russian mammoth), kidney bean (*Phaseolus vulgaris* L. cv. Tsurunashi morocco), tomato (*Lycopersicon esculentum* Mill. cv. Sekai-ichi), green pepper (*Capsicum annuum* L. cv. shishitou), and eggplant (*Solanum melongena* L. cv. Seiguro chunaga nasu). There was a 1:1 agreement between K values measured by the two methods for K values of whole plant, root and stem, and leaf under quasi-steady-state conditions. Leaf water potential (Ψ_{leaf}) and evaporative flux density (E) in sunflower was curvilinear, indicating whole plant K estimated by the EF method increased with increase of E . Predicted Ψ_{leaf} ($=E$ divided by whole plant K measured by the HPFM method) agreed with measured Ψ_{leaf} . Diurnal changes were also found in K measured by the HPFM confirming that K changed in response to temperature and E . The HPFM revealed that variable conductance was located in all organs: roots, stems, petioles, and leaves. These observations indicated that the HPFM is valid for crops as well as for trees (as previously established by Tsuda and Tyree) and has advantages over the EF method because of the speed and ease of the HPFM method.

Key words: Evaporative flux method, high pressure flow meter method, hydraulic conductance, root, shoot, water potential, variable conductance.

Introduction

Plant growth may be limited directly by low water potential of tissue (Hsiao, 1973; Boyer, 1985) or indirectly by plant signals transported from the root under drought (Davies and Zhang, 1991; Turner, 1986). However, there is a general consensus that low tissue water potential limits photosynthesis, cell division and expansion etc. The maintenance of high crop water potential and water content may be a prerequisite to stabilize and improve crop yield. At a given evaporative flux density, leaf water potential will be higher in plants with a higher hydraulic conductance. Therefore there has been interest in measuring hydraulic conductance or hydraulic resistance (reciprocal of conductance) in crop plants (Hirasawa and Ishihara, 1991) as well as trees and shrubs (Zimmermann, 1983; Tyree and Ewers, 1991).

The conventional method of measuring plant hydraulic conductance, known as the evaporative flux method (EF method), involves the measurement of steady-state evaporative flux densities (E) and water potential of soil and leaf. E is assumed proportional to water potential difference:

$$E = K_{\text{plant}}(\Psi_{\text{soil}} - \Psi_{\text{leaf}}) \quad (1)$$

where K_{plant} is whole plant hydraulic conductance, and Ψ_{soil} and Ψ_{leaf} are water potential of soil–root boundary and leaf, respectively. The linearity between E and water potential difference, however, is not always obtained. Sometimes K_{plant} appears to increase with increase in E (Hirasawa and Ishihara, 1991; Jones *et al.*, 1982; Koide, 1985; Stoker and Weatherley, 1971). The relation of E versus $\Delta\Psi$ sometimes showed hysteresis (Moreschet *et al.*, 1996, 1998; Tomar and O'Toole, 1982). Lack of steady-state might be responsible (Jones, 1978; Jones *et al.*, 1982; Mishio and Yokoi, 1991).

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A novel method has been reported of measuring hydraulic conductances of plant roots and shoots using a high pressure flow meter (HPFM) that is independent of the EF method (Tyree *et al.*, 1994, 1995). The HPFM method differs from the EF method in several important ways. It is much faster. It allows rapid determination of linearity between pressure and flow. It measures root conductance while water flows opposite to the normal direction. It permits determination of whole-shoot conductance. It tends to reduce the effects of hydraulic capacitance in roots and shoots of small plants. It can minimize the effects of changes in osmotic potential in roots (Tyree *et al.*, 1995). Recently, it was demonstrated that the HPFM method and the EF method gave comparable results in a temperate tree species *Acer saccharinum* (Tsuda and Tyree, 1997). If the HPFM method is valid for crop plants, it will be a powerful tool for studying crop adaptation to drought-stress environments. So far, no studies in which the two methods have been compared in crop plants are known.

This study was conducted to examine whether the two techniques give comparable results under quasi-steady-state and dynamic conditions in crop plants.

Materials and methods

Crop species

Soybean (*Glycine max* L. Merr. cv. Tsurunoko daizu), sunflower (*Helianthus annuus* L. cv. Russian mammoth), kidney bean (*Phaseolus vulgaris* L. cv. Tsurunashi morocco), tomato (*Lycopersicon esculentum* Mill. cv. Sekai-ichi), green pepper (*Capsicum annuum* L. cv. shishitou), and eggplant (*Solanum melongena* L. cv. Seiguro chunaga nasu) were grown in black plastic pots for about a month in the experimental field of the Faculty of Agriculture, Okayama University. Pots were filled with 4.0 l of commercial soil for vegetables and placed in a greenhouse. The soil contained enough nutrients for the plants to grow for a month and there were no symptoms of nutrient deficiency.

Measurements under quasi-steady-state condition

Evaporative flux was measured in plants in a controlled environment room. Air temperature was 28 °C and light intensity was 1020 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the plants, but humidity was not controlled. E was estimated from weight of water lost from the plants. The pots were enclosed in plastic bags to prevent water loss from the soil and placed in the room. After an acclimation period of more than 1 h, the pot was weighed by a digital balance and, again, after about 1 h. Values of E were calculated from $\Delta W/(A\Delta t)$ where Δt was time in seconds between the two weighings, ΔW was the weight change (kg) in Δt , and A was leaf area (m^2), which was determined at the end of the experiments. E was also measured in a greenhouse, in which environmental conditions were not controlled. The procedures in the greenhouse were the same as in the room, except that measurements were taken between 10.00 h and 14.00 h on sunny days, which allowed measurement under relatively stable conditions. Thus, they are referred to as quasi-steady-state conditions.

One leaf per plant was covered with aluminium foil to

prevent transpiration before the plant was subjected to evaporative flux measurements and is referred to as a bagged leaf. A bagged leaf and a leaf that was allowed to transpire were excised at the petioles at the end of the evaporative flux measurements. The xylem pressure potentials of the bagged and transpiring leaf were determined in a pressure bomb. The pressure potentials of the bagged leaf and a transpiring leaf were assumed to provide estimates of stem water potential (Ψ_{stem}) and leaf water potential (Ψ_{leaf}), respectively. Four to five plants were covered with black plastic bags and kept dark in a laboratory for 6–8 h. Xylem pressure potential of a leaf was measured in a pressure bomb and assumed to equal soil water potential (Ψ_{soil}). K_{plant} was calculated as $E/(\Psi_{\text{soil}} - \Psi_{\text{leaf}})$ and conductance from root to stem ($K_{\text{root} + \text{stem}}$) and that from stem to leaf (K_{leaf}) were $E/(\Psi_{\text{soil}} - \Psi_{\text{stem}})$ and $E/(\Psi_{\text{stem}} - \Psi_{\text{leaf}})$, respectively.

HPFM measurements were made on similar plants adjacent to the plants for EF measurement. Plants were taken to a room next to the controlled environment room or the greenhouse and the hydraulic conductances were measured with the HPFM at similar ambient temperatures as the EF measurements. Methods are described in detail elsewhere (Tyree *et al.*, 1995). Briefly, the stem was cut 30–50 mm above the soil surface, while the whole shoot was held under water. The stump was connected to the HPFM with a water-tight seal. The root conductance (k_{root}) was measured by a few transient measurements. Water flow into root (F) and applied pressure (P) were measured every 3 s while ramping the applied pressure increasing at the constant rate of 3–7 kPa s^{-1} . k_{root} was calculated as the slope of the plot of F versus P :

$$k_{\text{root}} = dF/dP \quad (2)$$

where dF/dP was computed from the regression line. Then the HPFM was connected to the stem base and the shoot was perfused with water at a pressure of *c.* 0.5 MPa for up to 15 min until the flow rate or shoot conductance became stable. Then shoot conductance (k_{shoot}) was measured by a transient measurement. The next transient measurement was made after leaf (lamina and petiole) were removed and gave conductance of stem and petioles (k_{stem}). k_{plant} was calculated as a reciprocal of $(1/k_{\text{shoot}} + 1/k_{\text{root}})$, leaf conductance (k_{leaf}) as a reciprocal of $(1/k_{\text{shoot}} - 1/k_{\text{stem}})$. All conductance values measured with the HPFM were normalized (made leaf specific) by dividing k_{root} , k_{shoot} , k_{leaf} , and k_{plant} by the total plant leaf area to yield K_{shoot} , K_{root} , K_{leaf} , and K_{plant} , respectively.

Diurnal changes in evaporative flux, leaf water potential and hydraulic conductances

Sunflower (*Helianthus annuus* L. cv. Russian mammoth) plants were grown in pots for about a month with the same procedure described above. Measurements were conducted on a sunny day, 4 August 1998. Sixty plants were placed in the field. Three pots were enclosed in plastic bags to prevent water loss from the soils. The pots were weighed at about hourly intervals. At the end of the experiment their leaf areas were measured. Between the weighing times xylem pressure potential was determined on three leaves from different plants selected at random with the pressure bomb. Three plants selected at random each hour were used for HPFM measurements as described above. Calculations of evaporative flux density and conductances were the same as those under quasi-steady-state conditions. Several plants were covered with black plastic bags and kept dark in a laboratory for 6 h. Leaf water potential was determined at the end of the dark period as Ψ_{soil} .

Results

Under quasi-steady-state conditions

Leaf area per plant ranged between 0.03 m^2 and 0.09 m^2 . Evaporative flux density was from $0.7 \text{ kg m}^{-2} \text{ s}^{-1}$ to $15 \text{ kg m}^{-2} \text{ s}^{-1}$ and leaf water potential was from -0.3 MPa to -1.02 MPa . Stem water potential was from -0.2 MPa to -0.74 MPa , thus the differences of water potentials between leaf and stem were relatively small between 0.1 MPa and 0.28 MPa . Water potentials at $E=0$ or Ψ_{soil} were not significantly different between leaves and stems. There were, however, small differences of Ψ_{soil} among the crops, which ranged from -0.02 MPa (soybean) to -0.16 MPa (eggplant).

Hydraulic conductances calculated from the EF method ($K(\text{EF})$) were regressed versus those from the HPFM method ($K(\text{HPFM})$) (Fig. 1), which compares values of K_{plant} , $K_{\text{root+stem}}$ and K_{leaf} . K_{leaf} was much larger than $K_{\text{root+stem}}$. When the three sets of data were included, there was a significant relationship between $K(\text{EF})$ and $K(\text{HPFM})$ although considerable scatter in data. The slope of the regression was not different from one.

Diurnal changes in sunflower

The minimum air temperature was 28.3°C and the maximum 36.3°C , the difference was 8°C . E showed a diurnal trend; it increased to $1.7 \times 10^4 \text{ kg m}^{-2} \text{ s}^{-1}$ at noon from

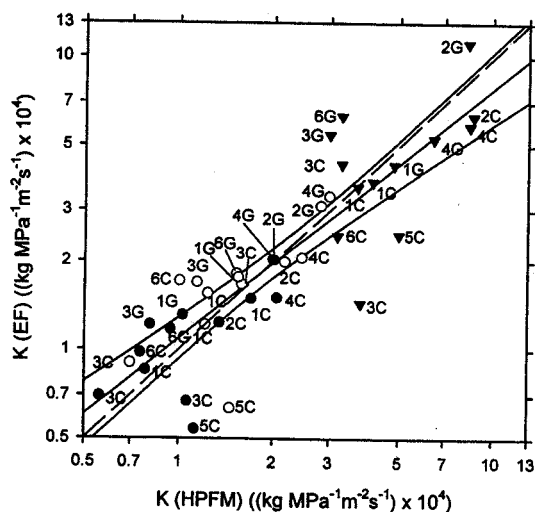


Fig. 1. Hydraulic conductances measured by the high pressure flow meter (HPFM) method ($K(\text{HPFM})$) versus those by the evaporative flux (EF) method ($K(\text{EF})$) under quasi-steady-state conditions in soybean, sunflower, kidney bean, tomato, green pepper, and eggplant. Symbols are hydraulic conductances of whole plant (●), root and stem (○) and leaf (▼). Straight line is the regression of $K(\text{EF})$ versus $K(\text{HPFM})$ and curved lines are 95% confidence interval. The regression line applies to all data in the plot and the slope is not significantly different from one. $\log K(\text{EF}) = -0.536 + 0.857 \log K(\text{HPFM})$, $r^2 = 0.567$, $P < 0.01$. Numbers indicate 1: soybean, 2: sunflower, 3: kidney bean, 4: tomato, 5: green pepper, and 6: egg plant, and C and G indicate measurements in controlled environments and greenhouse, respectively.

$0.1 \times 10^4 \text{ kg m}^{-2} \text{ s}^{-1}$ in the morning and decreased to about zero in the evening (Fig. 2a). A corresponding trend was observed in Ψ_{leaf} , which showed the maximum values in the morning and in the evening and the minimum value around noon (Fig. 2d). The relation between E and Ψ_{leaf} was curvilinear (Fig. 2b). When E was $< 0.5 \times 10^4 \text{ kg m}^{-2} \text{ s}^{-1}$, Ψ_{leaf} decreased quickly due to a small change in E . The slope of Ψ_{leaf} versus E was less when E was $> 0.5 \times 10^4 \text{ kg m}^{-2} \text{ s}^{-1}$. The whole plant hydraulic conductance ($= -\text{inverse slope}$) increased with an increase of E , but there was no hysteresis in the curvilinear relationship.

Whole plant hydraulic conductance measured by the HPFM, $K_{\text{plant}}(\text{HPFM})$ also fluctuated diurnally (Fig. 2c). $K_{\text{plant}}(\text{HPFM})$ was $1.5 \times 10^4 \text{ kg MPa}^{-1} \text{ m}^{-2} \text{ s}^{-1}$ in the morning and increased to $2.3 \times 10^4 \text{ kg MPa}^{-1} \text{ m}^{-2} \text{ s}^{-1}$ around noon. Ψ_{leaf} was predicted from $E \times K_{\text{plant}}(\text{HPFM}) - \Psi_{\text{soil}}$, where Ψ_{soil} was -0.12 MPa (Fig. 2d, open circles). The predicted Ψ_{leaf} was comparable to measured Ψ_{leaf} by a pressure bomb (compare open and filled circles in Fig. 2d). When the value of $K_{\text{plant}}(\text{HPFM})$ measured early in the morning was used for the prediction of Ψ_{leaf} , predicted Ψ_{leaf} was much lower than measured Ψ_{leaf} (compare filled circles and triangles in Fig. 2d).

Root conductance changed diurnally, being lower in the dark period than in the light period (Fig. 3). Whole shoot conductance was also higher in the light period. Both changes of K_{stem} and K_{leaf} were responsible for diurnal fluctuation of K_{shoot} . Consequently, the HPFM confirmed the conclusion of the EF method, i.e. that K_{plant} was variable and that it was due to independent changes in K_{root} and K_{shoot} .

Discussion

The HPFM method and the conventional EF method yielded consistent values of plant hydraulic conductance under quasi-steady-state conditions (Fig. 1). The predicted Ψ_{leaf} from the HPFM measurement and E agreed with Ψ_{leaf} measured by a pressure chamber under dynamic conditions (Fig. 2). These data verify the HPFM method for measuring hydraulic conductances of crop plants. Nevertheless, there is a large scatter of data in Fig. 1, where the $K(\text{HPFM})$ values are sometimes larger than $K(\text{EF})$ values or vice versa. A full explanation for the reason for the deviations would require a detailed analysis of the hydraulic architecture of each species, which was beyond the scope of this preliminary study. However, some insight can be gained from a detailed analysis of the hydraulic architecture of maize plants (Wei *et al.*, 1999). After measuring hydraulic conductance of maize roots, stems, leaf sheaths, and leaf blades, the theoretical plot of pressure potential versus position in a mature maize plant was given (Wei *et al.*, 1999; see Fig. 10c). In

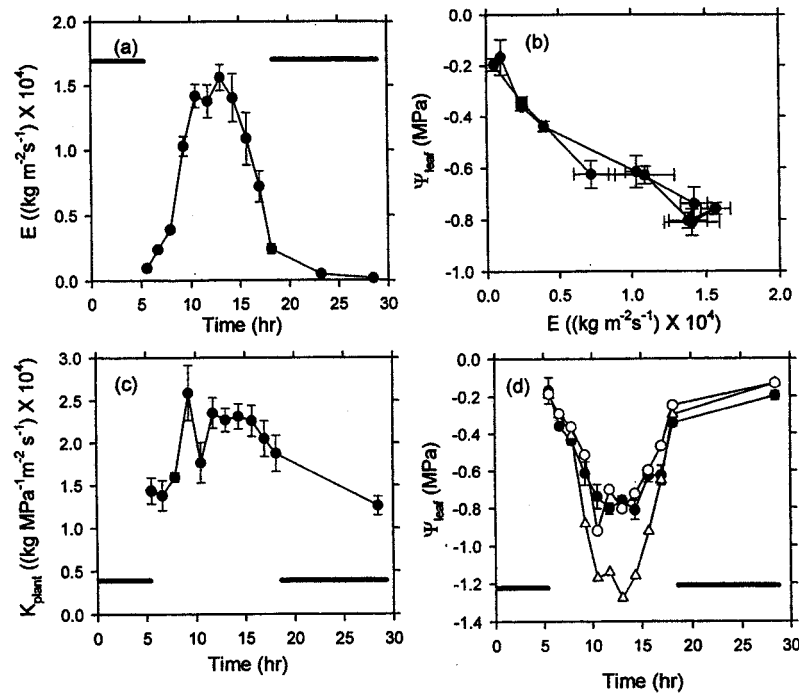


Fig. 2. Diurnal changes of evaporative flux density (E) (a), whole plant hydraulic conductance measured by the high pressure flow meter (K_{plant}) (c) and leaf water potential (Ψ_{leaf}) versus E (d) in sunflower. (b) E versus Ψ_{leaf} measured by a pressure chamber. Horizontal lines indicate dark period. Error bars are standard error $n=3$. Open circles in (d) indicate predicted Ψ_{leaf} from corresponding K_{plant} of (c) and E of (a), and triangles those from K_{plant} in dark period and E .

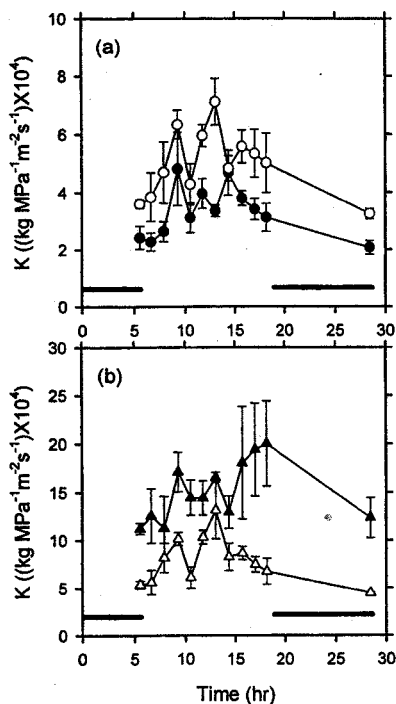


Fig. 3. Diurnal changes of hydraulic conductance (K) measured by the high pressure flow meter in sunflower: (a) shoot (open symbols) and root (closed symbols), (b) stem (closed) and leaves (open). Horizontal lines indicate dark period and vertical bars standard error, $n=3$.

full sunlight maize-leaf pressure potentials can vary from -0.9 to -1.5 MPa. So in the EF method errors will result from selection of non-representative leaves for pressure-chamber determination of pressure potential. In the HPFM method, the pattern of water flow through a whole maize plant is not the same as during transpiration (Fig. 10d; Wei *et al.*, 1999). Consequently, the value of K (HPFM) will be weighted by the altered pattern of water flow which tends to favour the pathways near the base of the plant. For other architectures, the pattern may be different.

The goal of many research projects has been to determine a single value of K to represent the 'average' hydraulic conductance of a plant. A single value makes it easier to compare plants within or between species. Nevertheless, it must not be forgotten that plants are more accurately represented by a branched catena of K s and that a single value never will be fully representative of the real case. The scatter of data seen in Fig. 1 is the necessary consequence of trying to represent a complex hydraulic structure by a single number.

A curvilinear relationship between E and Ψ_{leaf} was found in sunflower under dynamic conditions, indicating K_{plant} varied as a function of E (Fig. 2). This observation agreed with other studies (Hirasawa and Ishihara, 1991; Koide, 1985; Jones *et al.*, 1982), although hysteresis was observed in other studies (Moreshet *et al.*, 1996, 1998; Tomar and O'Toole, 1982). The apparent E dependence

of K_{plant} in some species may be caused by an increase in resistance at the soil-root interface due to soil water depletion, which might occur under limited soil water conditions (Moreschet *et al.*, 1996, 1998; Reid and Huck, 1990). This possibility can be eliminated in this study because the soil was well watered and because the change in K_{plant} was in the wrong direction, i.e. increasing with E . So the cause of apparent E dependence of K_{plant} may be events in the plant.

Some researchers presented explanations for the apparent dependence of K_{plant} on E , e.g. water capacitance of plants (Jones, 1978; Mishio and Yokoi, 1991), osmotic changes in root (Fiscus, 1975), and changes in distribution of water flow between transpiration and growth (Boyer, 1985; Fiscus *et al.*, 1983). In this study the HPFM detected substantial diurnal variation in K_{plant} (Fig. 2). The HPFM eliminates the effects of water capacitance (Tyree *et al.*, 1995) and osmotic changes in the root, which may be induced in the time period required for approaching steady-state flow (Tyree *et al.*, 1994). The distribution of water between evaporative and growth flux usually changes due to changes in E or volume of growing tissues (Boyer, 1985; Fiscus *et al.*, 1983). If some water is diverted to growing tissues during the transient method of measuring K_{root} and K_{shoot} , then such diversion could cause changes in the measured conductances. K_{root} and K_{shoot} was measured by a transient method, while pressure changed linearly with time from 0 to 0.5 MPa in 60–90 s. Under these conditions it is more likely that flow to growing points would remain more or less constant causing an offset on the plot of F versus P rather than growth being a linear function of P which would cause a change of slope (= conductance). A more likely alternative is that K_{plant} actually changed during the day resulting in the E dependence of K_{plant} . The diurnal change of whole plant conductance in lupin has also been demonstrated with an elegant pressure-chamber technique (Passioura and Munns, 1984).

Past studies have considered that the cause of variable K_{plant} is located in the root (Koide, 1985; Stoker and Weatherley, 1971). This study demonstrated that conductances of shoot including stem, petioles and leaf lamina were also variable like that of the root (Fig. 3). What made the conductances change in such a wide array of organs? The changes of conductances may be caused by the changes of water viscosity due to fluctuation of temperature. The values in Fig. 2 and Fig. 3 were not corrected by temperature. Temperature will increase conductance $2.25\% ^\circ\text{C}^{-1}$ (Tyree *et al.*, 1995) in both the HPFM and the object being measured. When the object being measured is a plastic capillary tube, the uncorrected conductance is approximately independent of temperature because the calibration factor of the HPFM and the conductance of the tube are influenced equally by temper-

ature. Hence making no temperature correction on a plant root or shoot is effectively equivalent to reporting the conductance of that plant at the calibration temperature of the HPFM after correction for viscosity effects. The maximum difference of temperature in this study was 8°C , equivalent to an increase of 18% of conductance due to viscosity, whereas the observed increase of conductance was as much as 53% (without a viscosity correction) or 71% ($= 53 + 18\%$ with a temperature correction for viscosity). Hence changes of viscosity would not reasonably explain the observed variable conductances.

Although the temperature dependence of water viscosity would not explain the diurnal changes of plant hydraulic conductances, effects of temperature should not be eliminated. There are several reports which demonstrated that hydraulic conductances increased with higher temperature at a degree more than that expected from the increase of water viscosity (Jensen and Taylor, 1961; Ramos and Kaufmann, 1979). More recently Zhang and Tyree (unpublished results) have measured the temperature dependence of K_{root} and K_{shoot} from 0 – 40°C on nine species of trees and crop plants using the HPFM and found they were all $< 2.3\% ^\circ\text{C}^{-1}$.

So plant hydraulic conductances may directly respond to E . This possibility requires a mechanism which is responsible for changes of hydraulic conductance at the cell level since structures such as xylem vessels can not quickly change in a reversible way. A tentative hypothesis might involve membrane water channels (Steudle and Henzler, 1995). It is suggested that water channels regulate water flow in response to temperature and pressure induced by evaporative flux. Alternatively, there may be rapidly reversible changes in the percentage of embolized vessels during the day by an unknown mechanism as recently documented (Tyree *et al.*, 1999). The plant gains an advantage by increasing K_{plant} as E increases. The net effect is to decrease water stress. This advantage can be seen by comparing the predicted Ψ_{leaf} with variable K_{plant} versus what Ψ_{leaf} would have been if K_{plant} had remained at the night-time level (Fig. 2d).

This study revealed that plant hydraulic conductance changed quickly under dynamic conditions. It seems important to know hydraulic conductance under low E as well as those under high E (Hirasawa and Ishihara, 1991). The EF method is not accurate under low E because the water potential difference and E are small and difficult to measure accurately, suggesting large error in estimating hydraulic conductance. In contrast to the EF method, the HPFM measures hydraulic conductance at such times in small plants without serious error arising from water capacitance, osmotic change etc, although the method has the disadvantage of being destructive. The HPFM may be a powerful tool for studies on crop adaptation to various environments.

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