

DYNAMIC ANALYSES OF WATER RELATIONS AND LEAF GROWTH IN CUCUMBER PLANTS UNDER MIDDAY WATER DEFICIT

Kitano, Masaharu
Biotron Institute Kyushu University

Eguchi, Hiromi
Biotron Institute Kyushu University

<http://hdl.handle.net/2324/8190>

出版情報 : BIOTRONICS. 22, pp.73-85, 1993-12. Biotron Institute, Kyushu University
バージョン :
権利関係 :

DYNAMIC ANALYSES OF WATER RELATIONS AND LEAF GROWTH IN CUCUMBER PLANTS UNDER MIDDAY WATER DEFICIT

M. KITANO and H. EGUCHI

Biotron Institute, Kyushu University 12, Fukuoka 812, Japan

(Received July 28, 1993; Accepted Sept. 1, 1993)

KITANO M. and EGUCHI H. *Dynamic analyses of water Relations and leaf growth in cucumber plants under midday water deficit*. BIOTRONICS 22, 73-85, 1993. Effects of transient and mild midday water deficit on whole-plant water relations and on leaf expansive growth in cucumber plants (*Cucumis sativus* L.) were analyzed by applying on-line evaluations of evaporative demand and whole-plant water balance. Around the fair midday, the larger impact of the evaporative demand was imposed on plant water balance, and the competitive relationship between the higher evaporative demand and transpiration induced the midday water deficit, in which 10% of the shoot water content was lost. This water loss resulted in midday stomatal closure and depression in leaf expansion which were attributed to decreases in bulk leaf water potential and turgor. These responses were estimated to relate to effects of midday water deficit on diurnal variations in plant hydraulic conductance and leaf extensibility.

Key Words: *Cucumis sativus* L.; water relations; leaf growth; midday water deficit; evaporative demand.

INTRODUCTION

Midday stomatal closure has been frequently observed in plants confronted with drought stress under higher solar irradiance mainly in dry environments of arid or semi-arid (e.g. 22-24). The higher irradiance around the fair midday increases evaporative demand on transpiring plants owing to temperature rise in leaves, and stomatal closure was induced by midday water deficit (MWD), if enough water can not be supplied to transpiration sites exposed to the higher evaporative demand. Because of hydraulic resistances through plant water pathways, plants are susceptible to such MWD, even when rooting media are well-watered (23, 24).

Effects of water deficit on plant growth have been found in various events such as osmotic adjustment (1, 10, 18, 19), root ABA signal (5, 26) and change in gene expression (7, 8) under prolonged and drastic conditions of water deficits induced by soil drying or leaf excision. As compared with such severe conditions, MWD is more transient and milder in general, and effects of MWD are supposed to appear in delicate manners. Midday stomatal closure and depression in leaf gas exchange under MWD have been investigated and

discussed with special reference to water use efficiency (22-24). For better understanding of effects of MWD, dynamic analyses of whole-plant water relations and leaf expansive growth under midday higher evaporative demand are essential. Furthermore, effects of MWD on plant hydraulic and mechanical properties responsible for the water relations and the leaf growth have remained to be studied.

In previous papers, we have developed the methods for on-line evaluations of whole-plant water balance (11) and evaporative demand (13, 15). The present paper deals with analyses of effects of MWD on whole-plant water relations and leaf expansive growth in cucumber plants in reference to plant hydraulic and mechanical properties by using the developed methods.

MATERIALS AND METHODS

Plant Materials and Experimental Conditions

Cucumber plants (*Cucumis sativus* L. cv Chojitsu-ochiai) were potted in well-watered vermiculite and were grown under solar irradiance at an air temperature (T_A) of 23 ± 1 °C, a relative humidity (RH) of 70 ± 7 % and a wind velocity (U) of 25 ± 5 cm s⁻¹ in a phytotron glass room. Water potential (Ψ_s) of the well-watered vermiculite in the pots was always kept higher than -0.05 MPa. The three plants of healthy growth at the 12 leaf stage were used for measurements of diurnal variations in whole-plant water balance, leaf water status, stomatal response and leaf expansion on successive three days (Sept. 26 to 28).

Evaporative Demand per Plant

Evaporative demand on unit leaf area (ED_A) was evaluated on the basis of heat balance by using physical environmental factors as follows (13, 15)

$$ED_A = \frac{2C_p \rho G_E SD + \Delta \{aR_s - 2\sigma \epsilon_L (1 - \epsilon_A) T_A^4\}}{\{(2/n)\gamma(G_E/G_{AV}) + \Delta\}\lambda} \quad (1)$$

with

$$G_E = G_{AH} + G_R = G_{AH} + 4\epsilon_L \sigma T_E^3 / C_p \rho \quad (2)$$

where $C_p \rho$ is the volumetric heat capacity of air, SD the saturation deficit of air, Δ the slope of the saturation vapor density curve, R_s the short wave radiant flux density, a the short wave absorption coefficient of a leaf, ϵ_L and ϵ_A the respective emissivities of leaf and the environment, σ the Stephan-Boltzmann constant, T_E the equivalent temperature between leaf and the environment, G_{AH} and G_{AV} the respective boundary layer conductances for heat transfer and for vapor transfer, G_R the radiative conductance, λ the latent heat of vaporization of water, γ the thermodynamic psychrometer constant ($\gamma = C_p \rho / \lambda$) and n the constant ($n=2$ in an amphistomatous leaf and $n=1$ in a hypostomatous leaf).

ED_A means a theoretical rate of evaporation from a wetted surface and

can be related to a theoretical transpiration rate (E_{AT}) from a real leaf with stomatal function as follows (16)

$$E_{AT} = Imp \times ED_A \quad (3)$$

where

$$Imp = C / (C + G_{AV} / G_S) = C / \{C + 1 / (G_S / G_{AV})\} \quad (4)$$

and

$$C = 1 + n \Delta G_{AV} / (2\gamma G_E) = 1 + n \Delta G_{AV} / \{2\gamma (G_{AH} + G_R)\} \quad (5)$$

E_{AT} can be considered to represent the impact of ED_A on plant water balance, and therefore, Kitano and Eguchi (16) have named *Imp* as "impact coefficient". *Imp* varies from 0 to 1 with increase in ratio (G_S / G_{AV}) of stomatal conductance (G_S) to leaf boundary layer conductance (G_{AV}). That is, the impact of ED_A on plant water balance becomes larger with increase in G_S and with decrease in G_{AV} . From Eq. (3), it can be suggested that dynamics of plant water balance is affected by changes in ED_A and *Imp* as follows

$$\Delta E_{AT} = Imp \times \Delta ED_A + ED_A \times \Delta Imp + \Delta ED_A \times \Delta Imp \quad (6)$$

Thus, ED can be considered as a physical input to plant hydraulic system, and its impact on plant water balance can be estimated by introducing *Imp*.

For evaluating ED_A , the respective environmental factors of short wave radiant flux density, air temperature, humidity and wind velocity near the plant were measured on-line at intervals of 1 min, and the leaf boundary layer conductances for heat transfer (G_{AH}) and for vapor transfer (G_{AV}) was evaluated for mixed convection (14) by using a parallel model, where the conductances for forced convection and for free convection are connected in parallel (12, 13, 15). Furthermore, other parameters involved in Eq.(1) were evaluated by the methods explained in our previous papers (13, 15).

The evaporative demand per plant (ED) was evaluated by multiplying ED_A by the total leaf area (ΣLA) of the plant as $ED = ED_A \times \Sigma LA$. The total leaf area (ΣLA) was given by suming up leaf areas (LA) of 12 leaves. LA of each leaf was evaluated from the midrib length (LL) by using a $LA-LL$ relationship obtained empirically as $LA = 1.265LL^2 - 4.784LL + 12.79$, where LL of each leaf was measured by a ruler at every 9:00 a.m.

Plant Water Balance

Water balance of the plant was evaluated by difference ($F-E$) between root water uptake rate (F) and leaf transpiration rate (E) per plant. F was evaluated as stem base water flux by using a heat flux control system (11) for on-line measurement of water flux in an intact stem with an accuracy of $\pm 5\%$, a resolution of 1 mg s^{-1} and a time constant of 1 min. Simultaneously, E was measured by weighing the plant and the pot on-line.

Leaf Water Status

For measurement of diurnal variation in leaf water status, eight leaf disks of 8 mm diameter were sampled almost every two hours from younger leaves of the 8th to the 12th of the three plants. Leaf water potential (Ψ) and osmotic potential (π) were measured by dew point psychrometry, where π was measured after freezing and thawing. The turgor pressure (P) was evaluated by difference ($\Psi - \pi$) between Ψ and π . At each sampling, four disks were used for the respective determinations of Ψ and π , and the respective mean values were used: The standard deviation in each determination was within ± 0.07 MPa.

Stomatal Response

For analysis of diurnal stomatal response, stomatal conductance (G_s) was evaluated as follows

$$G_s = 1 / \{ 2(W_L - W_A) / (E / \Sigma LA) - 1 / G_{AV} \} \quad (7)$$

$E / \Sigma LA$ is the transpiration rate per unit leaf area, and water vapor density (W_L) within leaf intercellular space was calculated from leaf temperature which was evaluated by using the mean of the voltages from 10 thermocouples inserted into the leaves. Water vapor density (W_A) in the ambient air was calculated from T_A and RH . G_{AV} was evaluated for the mixed convection mentioned above.

Leaf Growth

For evaluating growth rate of a developing younger leaf, the 12th leaf was photographed together with a scale almost every hour, and LL was measured on the photograph and converted into LA in the manner mentioned above. The increase curve of LA was fitted by smoothing with cubic spline functions. Leaf expansion rate (LER) was evaluated as dLA/dt based on the smoothed LA increase curve.

Hydraulic and Mechanical Properties of Plant

Hydraulic conductance (L_p) through plant water pathways was evaluated from F and $\Psi_s - \Psi$ (soil-to-leaves water potential difference) as $L_p = F / (\Psi_s - \Psi)$. Hydraulic resistance ($R_T = 1/L_p$) was also evaluated for analyzing more clearly the small change in the lower L_p . Diurnal variations in L_p and R_T were analyzed in relation to F and π . Furthermore, an extensibility (m) of the developing younger leaf (the 12th leaf) was evaluated on the basis of the relationship between P and LER . That is, m was given by $m = LER / (P - Y)$, where the yield threshold (Y) of turgor was estimated as a value of P at $LER = 0$ on the P - LER regression line obtained.

RESULTS

Diurnal variations in solar irradiance on the successive three days (Sept. 26

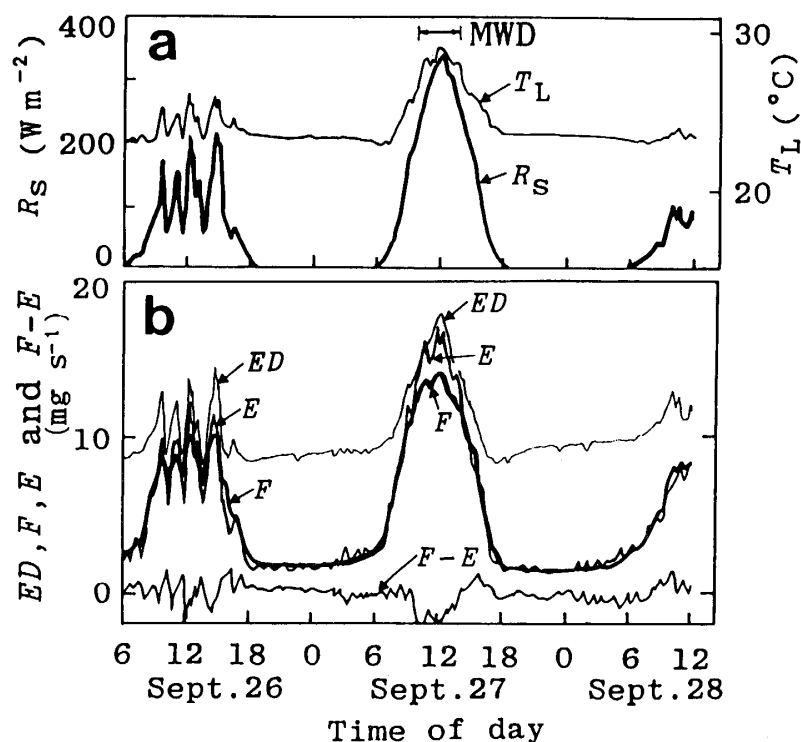


Fig. 1 Diurnal variations in evaporative demand and water balance of a cucumber plant in an air-controlled phytotron glass room: (a), solar irradiance (R_s) and leaf temperature (T_L): (b), evaporative demand (ED), root water uptake rate (F), leaf transpiration rate (E) per plant and difference ($F-E$) between F and E : MWD is the midday water deficit.

to 28) appeared in different patterns, depending on the weather condition (Fig. 1a). R_s became remarkably higher in the fair daytime (Sept. 27) than in the cloudy daytime (Sept. 26 and 28). T_L around the fair midday rose $6^{\circ}C$ higher than T_A . In the air-controlled phytotron glass room, ED varied with R_s and increased to the higher level around the fair midday as compared with that in the cloudy daytime (Fig 1b). Under the condition of lower ED , E remained distinctly lower than ED . Under higher ED condition around the fair midday, however, E approached the higher level of ED . Under such condition, the appreciable unbalance between F and E was found around the fair midday. This unbalance appeared in water deficit as $F < E$ for about four hours (10:00–14:00, Sept. 27), and the amount of water ($\int (E-F) dt$) transpired excessively during this MWD corresponded to about 10 % of water content in the shoot (leaves, petioles and stem). That is, the plants were confronted with transient water deficit around the fair midday even in the case of the well-watered rooting media.

Leaf water status appeared to be influenced by the MWD (Fig. 2a): In the nighttime (16:00, Sept. 26 to 8:00, Sept. 27) before MWD, π remained almost constant at about -0.85 MPa, while Ψ and P continued to increase, which reached about -0.5 MPa and 0.3 MPa at the respective maximums in the early

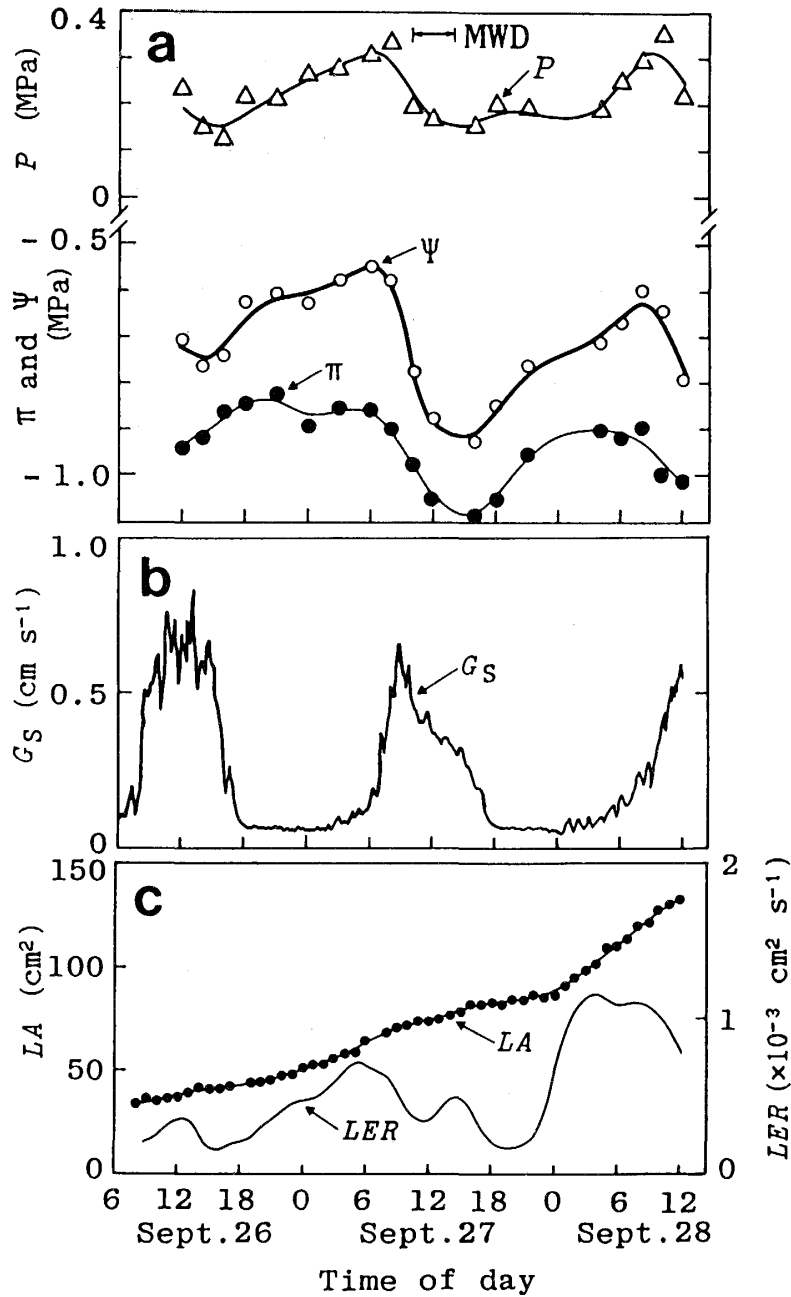


Fig. 2 Diurnal variations in leaf water status, stomatal conductance and leaf growth in the cucumber plant under the condition of Fig. 1 : (a), leaf water potential (Ψ), osmotic potential (π) and turgor pressure (P); (b), stomatal conductance (G_s) ; (c) area (LA) and expansion rate (LER) of an developing younger leaf : MWD is the midday water deficit, and solid lines for Ψ , π , P and LA are smoothed by cubic spline functions.

morning. In the fair daytime around MWD, remarkable decrease in π , Ψ and P were found : The decreases in π and P were 0.2 MPa, and consequently Ψ decreased by 0.4 MPa to the minimum lower than -0.9 MPa, In the

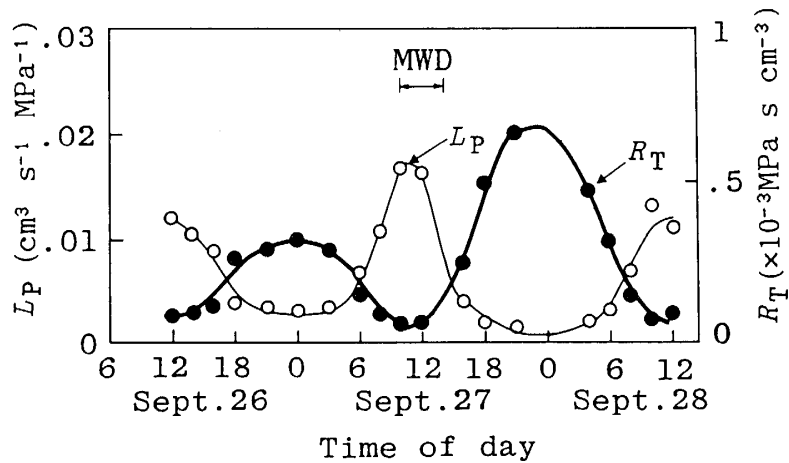


Fig. 3 Diurnal variations of hydraulic conductance (L_P) and resistance (R_T): MWD is the midday water deficit, and solid lines for L_P and R_T are smoothed by cubic spline functions.

nighttime (18:00, Sept. 27 to 6:00, Sept. 28) after MWD, π and Ψ appeared in increase patterns, but the levels of these recovered π and Ψ remained lower than those before MWD. On the other hand, P remained at the lower level around 0.15 MPa and did not recover before the sunrise.

G_S started to increase in the early morning, and thereafter the increased G_S was depressed around the fair midday (10:00 to 15:00, Sept. 27) when Ψ dropped to the level lower than -0.8 MPa. That is, midday stomatal closure was induced (Fig. 2b). On the other hand, such depression in G_S was not found around the cloudy midday when Ψ was kept higher than -0.8 MPa.

LER started to decline in the fair morning (6:00, Sept. 27) and reached to the minimum in the evening (18:00 to 21:00, Sept. 27) subsequent to MWD (Fig. 2c). In particular, LER after MWD remained depressed until the midnight, while LER before MWD appeared in increase pattern from the afternoon (15:00, Sept. 26) to the sunrise (6:00, Sept. 27). The LER depressed after MWD recovered rapidly at the midnight before the start (4:00, Sept. 28) of increase in P and LER reached to its maximum around the sunrise.

L_P and R_T also varied diurnally (Fig. 3): L_P became maximum at the fair midday and was kept higher in the daytime than in the nighttime. That is, R_T became higher in the nighttime. In particular, remarkable decrease in L_P (i.e. increase in R_T) was found in the evening subsequent to MWD. These hydraulic properties varied with F , and any influence of MWD was not found in relationships between L_P or R_T and F (Fig. 4): R_T dropped abruptly at around $F=1$ mgs^{-1} and L_P increased linearly with F . The correlation between L_P and π (Fig. 5) was not significant ($r=-0.41$). However, in the case that L_P 's in the evening after MWD (16:00–21:00, Sept. 27) were excluded, a negative correlation between L_P and π was found significant ($r=-0.78^{***}$).

Turgor dependence of leaf expansion before MWD (Fig. 6) was found in positive correlation between P and LER ($r=0.91^{***}$). After MWD, however,

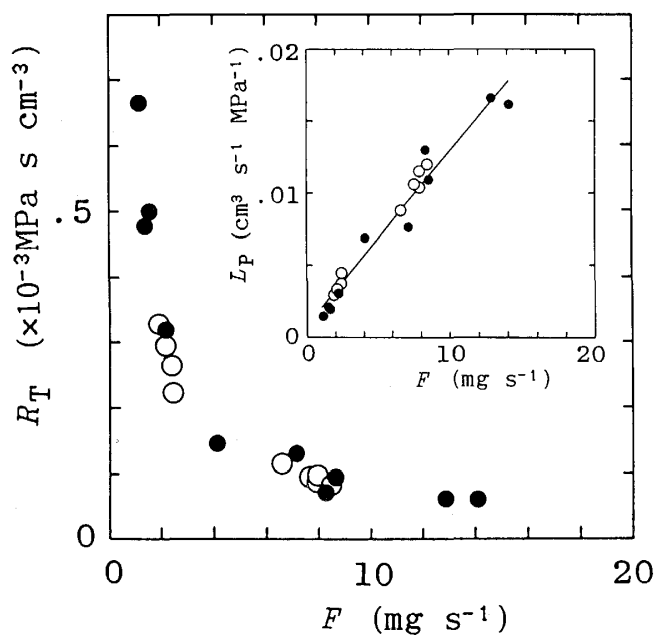


Fig. 4 Changes in hydraulic conductance (L_P) and resistance (R_T) with change in root water uptake rate (F): \circ , L_P and R_T before midday water deficit; \bullet , L_P and R_T after midday water deficit.

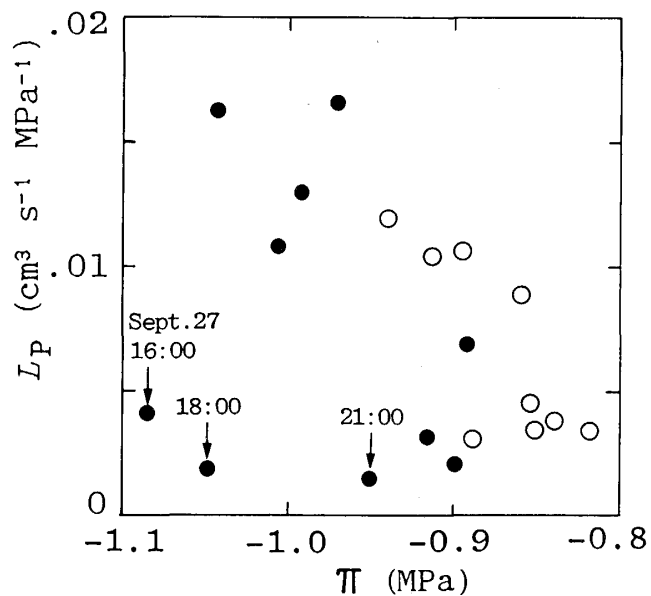


Fig. 5 Changes in hydraulic conductance (L_P) with change in osmotic potential (π): \circ , L_P before midday water deficit; \bullet , L_P after midday water deficit; \bullet arrowed, L_P at 16:00, 18:00 and 21:00 on Sept. 27 subsequent to midday water deficit.

the positive correlation was disturbed ($r=0.64^*$). Y at $LER=0$ was estimated to be about 0.06 MPa and not to be affected by MWD. On the other hand, m was found to be much affected by MWD (Fig. 7). Before MWD, m remained

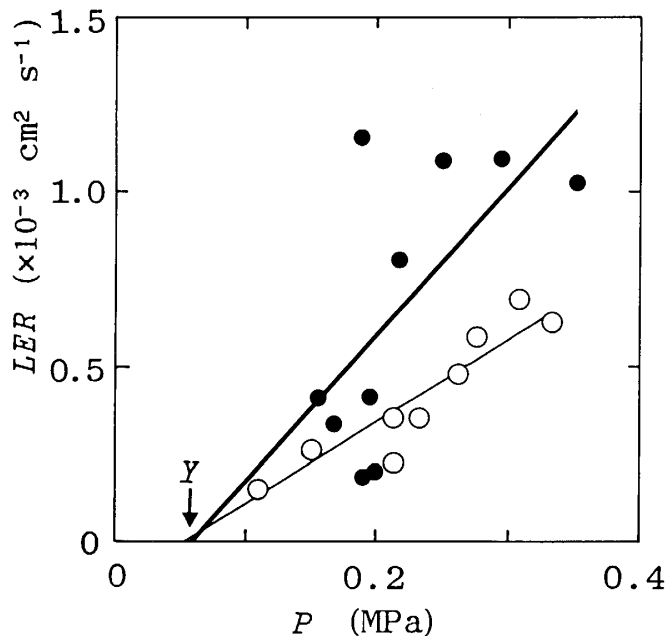


Fig. 6 Changes in leaf expansion rate (LER) with change in leaf turgor pressure (P): \circ , LER before midday water deficit; \bullet , LER after midday water deficit.

almost constant, but m after MWD varied remarkably: m clearly decreased in the evening subsequent to MWD (18:00 to 21:00, Sept. 27) and thereafter recovered before the sunrise.

DISCUSSION

As estimated from Eqs. (1-5), increase in G_s and consequently increase in Imp were brought together with the higher ED by increase in R_s in the fair morning. When the increased Imp closed to 1 around the fair midday, the impact of ED_A , i.e. E_{AT} of Eq. (3), approached the higher level of ED_A . Subsequently, E approached ED (i.e. $ED_A \times \Sigma LA$), and MWD was induced. As indicated by Eq. (6), this increase in Imp under the higher evaporative demand imposed the larger ΔE_{AT} on plant water balance. These facts suggest that plants are susceptible to water deficit when the larger impact of the evaporative demand is imposed on their water balance. Thus, on-line measurement of transpirational water flux with simultaneous evaluation of the evaporative demand could be contributive to reliable estimation of MWD in analyses of plant hydraulic system.

In the daytime, decrease in π with increase of solute concentration in leaves can be supposed to contribute to osmoregulation for turgor maintenance when water loss from leaves is not large (1, 19). During MWD, however, root water uptake was not sufficient to compensate the excessive water loss by leaf transpiration (Fig. 1b), and the water loss of 10% of the shoot water content caused turgor drop by 0.2 MPa in spite of the osmoregulation by 0.2 MPa,

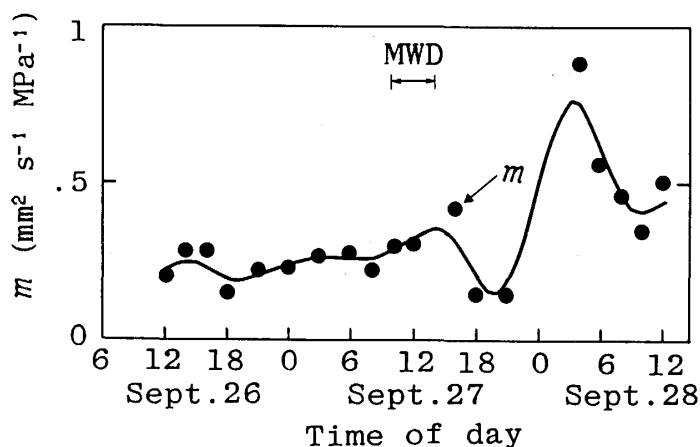


Fig. 7 Diurnal variation of leaf extensibility (m): MWD is the midday water deficit, and solid line for m is smoothed by cubic spline functions.

which resulted in drop of Ψ from -0.5 to -0.9 MPa (Fig. 2a): The Ψ drop by 0.4 MPa around MWD corresponded to small drop of leaf relative water content from 92 to 89% because of lower hydraulic capacitance of the cucumber leaf (unpublished data). Therefore, the excessive water loss during MWD can be considered to be buffered by water content stored in the herbaceous stem and petioles (11). This hydraulic buffer action by the stem and petioles could contribute to stable leaf water status under rapid and small fluctuations in evaporative demand of the environment.

Whole-plant water balance was affected by diurnal variations in hydraulic properties (Fig. 3). Water transport through a plant consists of symplastic water flow with lower hydraulic conductance and apoplastic water flow with the higher conductance. The positive correlation between F and L_p in this experiment (Fig. 4) can support the consideration that L_p becomes lower at lower F because of higher ratio of symplastic water flux to apoplastic water flux (2, 3). Water flux into symplast depends on water permeability across cell membranes (plasmalemma and tonoplast) as well as on apoplast-to-symplast water potential gradient. The membrane permeability has been reported to depend on π (17). Furthermore, the water valves of which hydraulic conductance depends on π have been implied to locate in plasmodesmata (20). These π dependences can be supported by the fact that the dependence of L_p on π was found significant in the negative correlation except L_p 's in the evening subsequent to MWD (Fig. 5): L_p 's for 5h in the evening subsequent to MWD was drastically depressed deviating from the π dependence observed. From the drastic and transient depression in L_p after MWD, it could be suggested that MWD induces L_p depression (i.e. R_T increase) through some drastic process of which manners differ from π dependence of L_p . This L_p depression caused by MWD was reversible in several hours under lower evaporative demand. Further studies are necessary for understanding reason why the F - L_p relationship (Fig. 4) can not be influenced by MWD,

while the π dependence of L_p (Fig. 5) is clearly disturbed by MWD.

Dynamics of leaf water status affected stomatal movement and leaf expansion. The water status (Ψ , π and P) determined in this experiment could be considered to represent bulk leaf water status which mainly reflects water status of mesophyll occupying more than 80% of the total volume of the cucumber leaf. Water potential gradients within a leaf are the driving forces regulating respective water fluxes from xylem to mesophyll, epidermal and guard cells (21, 22). Therefore, from the midday stomatal closure accompanied with remarkable decrease in Ψ (Fig. 2), it could be supposed that the reduced mesophyll water potential lower than -0.8 MPa cut the water flux to guard cells by breaking the water potential gradient from xylem to guard cells. On the other hand, in the cloudy daytime Ψ was kept higher than -0.8 MPa because of smaller water loss under lower ED , and water flux to guard cells was able to maintain guard cell turgor. Midday stomatal closure has been reported to appear with little change in bulk leaf water potential in sclerophyll species (24). The observed midday stomatal closure accompanied with Ψ decrease might be attributed to small hydraulic capacitance and to low hydraulic resistance of xylem-to-guard cells in the cucumber leaves.

Leaf expansion is regulated by the respective properties of cell wall extensibility, yield threshold and hydraulic conductivity as well as by water status of the growing tissue (3, 4, 9, 18). Change in leaf expansion can be attributed primarily to turgor change, while the hydraulic and mechanical properties might be changed by water deficit (4, 9). In this experiment, LER before MWD increased with increase in P under lower ED in the nighttime (Fig. 2c), and the linear turgor dependence was found in the constant m (Figs. 6 and 7). After MWD, however, change in LER was caused by drastic change in m , which was reversible under lower ED as well as change in L_p after MWD. Leaf extensibility has been reported to change in sunflower (18) and maize (25) under prolonged water deficit by soil drying, and this change can be brought by physiological effects of the water deficit on cell wall metabolism (4, 9, 18, 25). From the m change caused by MWD in this experiment, it could be suggested that transient and mild MWD can trigger physiological changes in cell walls responsible for leaf extensibility.

Thus, the applied methods for on-line evaluations of whole-plant water balance and evaporative demand were estimated to be useful for dynamic analyses of whole-plant water relations and leaf growth: The quantitative information brought by the on-line evaluations was contributive to elucidate the delicate effects of midday water deficit, and it was demonstrated that drastic and reversible changes in plant hydraulic and mechanical properties can be induced even under transient and mild midday water deficit.

ACKNOWLEDGEMENTS

We would like to thank Mr. M. Hamakoga for his technical assistance, and the financial support by the Japanese Ministry of Education (No. 05454105) is

gratefully acknowledged.

REFERENCES

1. Acevedo E., Fereres E., Hsiao T.C. and Henderson D.W. (1979) Diurnal growth trends, water potential and osmotic adjustment of maize and sorghum leaves in the field. *Plant Physiol.* **64**, 476-480.
2. Boyer J.S. (1974) Water transport in plants: Mechanism of apparent changes in resistance during absorption. *Planta* **117**, 187-207.
3. Boyer J.S. (1985) Water transport. *Ann. Rev. Plant Physiol.* **36**, 473-516.
4. Bradford K.J. and Hsiao T.C. (1982) Physiological responses to moderate water stress. pages 263-324 in O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler (eds) *Physiological Plant Ecology II, Encyclopedia of Plant Physiology, 12B*. Springer-Verlag, Berlin.
5. Davies W.J. and Zhang J. (1991) Root signals and the regulation of growth and development of plants in drying soil. *Ann. Rev. Plant Physiol. Mol. Biol.* **42**, 55-76.
6. Gates D.M. (1980) *Biophysical Ecology*. Springer-Verlag, New York.
7. Guerrero F.D. and Mullet J.E. (1988) Reduction of turgor induces rapid changes in leaf translatable RNA. *Plant Physiol.* **88**, 401-408.
8. Ho T-Y. and Mishkind M. L. (1991) The influence of water deficits on mRNA levels in tomato. *Plant Cell Environ.* **14**, 67-75.
9. Hsiao T.C. and Bradford K.J. (1983) Physiological consequence of cellular water deficit. Pages 227-265 in H.M. Taylor, W.R. Jordan and T.R. Sinclair (eds) *Limitations to Efficient Water Use in Crop Production*. Ame. Soc. Agon., Inc., Madison.
10. Jones M.M. and Turner N.C. (1978) Osmotic adjustment in leaves of sorghum in response to water deficits. *Plant Physiol.* **61**, 122-126.
11. Kitano M. and Eguchi H. (1989) Quantitative analysis of transpiration stream dynamics in an intact cucumber stem by a heat flux control method. *Plant Physiol.* **89**, 643-647.
12. Kitano M. and Eguchi H. (1989) Dynamic analysis of stomatal responses by an improved method of leaf heat balance. *Environ. Exp. Bot.* **29**, 175-185.
13. Kitano M. and Eguchi H. (1990) Physical evaluation of effective evaporative demand with reference to plant water relations. *Biotronics* **19**, 109-119.
14. Kitano M. and Eguchi H. (1990) Buoyancy effect on forced convection in the leaf boundary layer. *Plant Cell Environ.* **13**, 965-970.
15. Kitano M. and Eguchi H. (1991) Dynamics of plant water relations as affected by evaporative demand. Pages 367-372 in Y. Hashimoto and W. Day (eds) *Mathematical and Control Applications in Agriculture and Horticulture*. Pergamon Press, Oxford.
16. Kitano M. and Eguchi H. (1993) An impact coefficient of evaporative demand on plant water balance. *Biotronics* **22**, 61-72.
17. Kiyosawa K. and Tazawa M. (1972) Influence of intracellular and extracellular tonicities on water permeability in characean cells. *Protoplasma* **74**, 257-270.
18. Matthews M.A., Van Volkenburgh E. and Boyer J.S. (1984) Acclimation of leaf growth to low water potentials in sunflower. *Plant Cell Environ.* **7**, 199-206.
19. Morgan J.M. (1984) Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.* **35**, 299-319.
20. Passioura J.B. and Munns R. (1984) Hydraulic resistance of plants. II. Effects of rooting medium, and time of day, in barley and lupin. *Aust. J. Plant Physiol.* **11**, 341-350.
21. Shackel K.A. and Brinckmann E. (1985) *In situ* measurement of epidermal cell turgor, leaf water potential, and gas exchange in *Tradescantia virginiana* L. *Plant Physiol.* **78**, 66-70.

22. Schulze E-D. and Hall A.E. (1982) Stomatal responses, water loss and C O₂ assimilation rates of plants in contrasting environments. Pages 181-230 in O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler (eds) *Physiological Plant Ecology II, Encyclopedia of Plant Physiology, 12B*. Springer-Verlag, Berlin.
23. Schulze E-D. (1986) Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. *Ann. Rev. Plant Physiol.* **37**, 247-274
24. Tenhunen J.D., Pearcy R.W. and Lange O.L. (1987) Diurnal variations in leaf conductance and gas exchange in natural environments. Pages 323-351 in E. Zeiger, G.D. Farquhar and I. R. Cowan (eds) *Stomatal Function*. Stanford University Press, Stanford.
25. Van Volkenburgh E. and Boyer J.S. (1985) Inhibitory effects of water deficit on maize leaf elongation. *Plant Physiol.* **77**, 190-194.
26. Zhang J. and Davies W.J. (1990) Does ABA in the xylem control the rate of leaf growth in soil-dried maize and sunflower plants? *J. Exp. Bot.* **41**, 1125-1132.