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

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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

M. KITANO and H. EGUCHI

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-waterd 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 envitonmental factors as follows (13, 15)

$$ED_{\rm A} = \frac{2C_p \rho G_{\rm E} SD + \Delta \{aR_{\rm S} - 2\sigma \varepsilon_{\rm L} (1 - \varepsilon_{\rm A})T_{\rm A}^{4}\}}{\{(2/n)\gamma (G_{\rm E}/G_{\rm AV}) + \Delta\}\lambda}$$
(1)

with

$$G_{\rm E} = G_{\rm AH} + G_{\rm R} = G_{\rm AH} + 4\varepsilon_{\rm L}\sigma T_{\rm E}^{3}/C_{\rm p}\rho \tag{2}$$

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, $R_{\rm S}$ the sort wave radiant flux density, a the short wave absorption coefficient of a leaf, $\varepsilon_{\rm L}$ and $\varepsilon_{\rm A}$ the respective emissivities of leaf and the environment, σ the Stephan-Boltzmann constant, $T_{\rm E}$ the equivalent temperature between leaf and the environment, $G_{\rm AH}$ and $G_{\rm AV}$ the respective boundary layer conductances for heat transfer and for vapor transfer, $G_{\rm R}$ 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)

$$E_{\rm AT} = Imp \times ED_{\rm A} \tag{3}$$

where

$$Imp = C/(C + G_{\rm AV}/G_{\rm S}) = C/\{C + 1/(G_{\rm S}/G_{\rm AV})\}$$
(4)

and

$$C = 1 + n \varDelta G_{\rm AV} / (2\gamma G_{\rm E}) = 1 + n \varDelta G_{\rm AV} / \{2\gamma (G_{\rm AH} + G_{\rm R})\}$$
(5)

 $E_{\rm AT}$ can be considered to represent the impact of $ED_{\rm A}$ 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 $(G_{\rm S}/G_{\rm AV})$ of stomatal conductance $(G_{\rm S})$ to leaf boundary layer conductance $(G_{\rm AV})$. That is, the impact of $ED_{\rm A}$ on plant water balance becomes larger with increase in $G_{\rm S}$ and with decrease in $G_{\rm AV}$. From Eq. (3), it can be suggested that dynamics of plant water balance is affected by changes in $ED_{\rm A}$ and Imp as follows

$$\Delta E_{\rm AT} = Imp \times \Delta ED_{\rm A} + ED_{\rm A} \times \Delta Imp + \Delta ED_{\rm A} \times \Delta Imp \tag{6}$$

Thus, *ED* can be considered as a physical input to plant hydraulic system, and it's 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 ± 5 %, a resolution of 1 mg s⁻¹ and a time constant of 1 min. Simultaneously, Ewas measured by weighing the plant and the pot on-line.

M. KITANO and H. EGUCHI

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

$$G_{\rm S} = 1/\{2(W_{\rm L} - W_{\rm A})/(E/\Sigma LA) - 1/G_{\rm AV}\}$$
(7)

 $E/\Sigma LA$ is the transpiration rate per unit leaf area, and water vapor density $(W_{\rm L})$ 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 $(W_{\rm A})$ in the ambient air was calculated from $T_{\rm A}$ and RH. $G_{\rm AV}$ 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

BIOTRONICS

76



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. la). $R_{\rm S}$ became remarkably higher in the fair daytime (Sept. 27) than in the cloudy daytime (Sept. 26 and 28). $T_{\rm L}$ around the fair midday rose 6°C higher than $T_{\rm A}$. In the air-controlled phytotron glass room, *ED* varied with $R_{\rm S}$ 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 $(L_{\rm P})$ and resistance $(R_{\rm T})$: MWD is the midday water deficit, and solid lines for $L_{\rm P}$ and $R_{\rm T}$ 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 loweer level around 0.15 MPa and did not recover before the sunrise.

 $G_{\rm S}$ started to increase in the early morning, and thereafter the increased $G_{\rm S}$ 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 $G_{\rm S}$ 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. 2 c). 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 recoverred rapidly at the midnight before the start (4:00, Sept. 28) of increase in P and LER reached to its maximum around the sunrise.

 $L_{\rm P}$ and $R_{\rm T}$ also varied diurnally (Fig. 3) : $L_{\rm P}$ became maximum at the fair midday and was kept higher in the daytime than in the nighttime. That is, $R_{\rm T}$ became higher in the nighttime. In particular, remarkable decrease in $L_{\rm P}$ (i.e. increase in $R_{\rm T}$) 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 $L_{\rm P}$ or $R_{\rm T}$ and F (Fig. 4) : $R_{\rm T}$ dropped abruptly at around F=1 mgs,⁻¹ and $L_{\rm P}$ increased linearly with F. The correlation between $L_{\rm P}$ and π (Fig, 5) was not significant (r=-0.41). However, in the case that $L_{\rm P}$'s in the evening after MWD (16:00-21:00, Sept. 27) were excluded, a negative correlation between $L_{\rm P}$ 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 $(L_{\rm P})$ and resistance $(R_{\rm T})$ with change in root water uptake rate (F): \bigcirc , $L_{\rm P}$ and $R_{\rm T}$ before midday water deficit; \bigcirc , $L_{\rm P}$ and $R_{\rm T}$ after midday water deficit.



Fig. 5 Changes in hydraulic conductance (L_P) with change in osmotic potential (π): ○,
 L_P before midday water deficit ; ●, L_P after midday water deficit ; ● 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 chage in leaf turgor pressure (*P*): \bigcirc , *LER* before midday water deficit; \bigcirc , *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 eatimated from Eqs. (1–5), increse in G_S and consequently increse in *Imp* were brought together with the higher *ED* by increase in R_S in the fair morning. When the incressed *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 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 $L_{\rm P}$ in this experiment (Fig. 4) can support the consideration that $L_{\rm P}$ 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-tosymplast 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 dependece of $L_{\rm P}$ on π was found significant in the negative correlation except $L_{\rm P}$'s in the evening subsequent to MWD (Fig. 5) : $L_{\rm P}$'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 $L_{\rm P}$ after MWD, it could be suggested that MWD induces $L_{\rm P}$ depression (i.e. $R_{\rm T}$ increase) through some drastic process of which manners differ from π dependence of $L_{\rm p.}$ This $L_{\rm p}$ 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 $L_{\rm P}$ (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.

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M. KITANO and H. EGUCHI

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