

DYNAMICS OF WHOLE-PLANT WATER BALANCE AND LEAF GROWTH IN RESPONSE TO EVAPORATIVE DEMAND. I. EFFECT OF CHANGE IN IRRADIANCE

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DYNAMICS OF WHOLE-PLANT WATER BALANCE AND
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I. EFFECT OF CHANGE IN IRRADIANCE.

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KITANO M. and EGUCHI H. *Dynamics of whole-plant water balance and leaf growth in response to evaporative demand. I. Effect of change in irradiance.* BIOTRONICS 21, 39-50, 1992. Dynamics of whole-plant water balance and leaf expansive growth were analyzed in cucumber plants (*Cucumis sativus* L.) exposed to step change in short wave irradiance (R_s). The step increase caused the rapid increase in evaporative demand (ED_A), and the oscillation in the whole-plant water balance was induced more actively under the higher R_s and the lower humidity. Leaf growth as well as stomatal movement oscillated according to the whole-plant water balance: The higher peaks of the growth rate were brought with the rapid rise of transpiration stream induced by the step increase in ED_A , and leaf shrinkage was found after the excessive water loss. The oscillations were damped immediately by the decrease in R_s . In those dynamics, the buffer action of water content in the stem and petioles was contributive to the increase in leaf growth and to the excessive transpiration even under the transient water deficit. Thus, change in ED_A caused by change in R_s affected dynamics of leaf growth and stomatal movement through the processes of whole-plant water balance.

Key words : *Cucumis sativus* L. ; whole-plant water balance ; leaf growth ; stomatal movement ; evaporative demand ; irradiance.

INTRODUCTION

Expansive growth of plant cells is attributable to increase in cellular water content, and change in leaf water content is responsible for dynamics of leaf expansive growth (e.g. 1, 2, 4). Leaf water content is directly affected by change in evaporative demand of the shoot environment through the processes of plant water balance. Therefore, the quantitative evaluation of evaporative demand and dynamic analyses of plant water balance and leaf growth as affected by the evaporative demand are essential for better understanding of environmental effects on plant water relations.

We have evaluated evaporative demand by using physical environmental factors of short wave irradiance, air temperature, humidity and wind velocity (8), and the evaluated evaporative demand has been indicated to relate closely to

transpiration (9). Leaf growth has been mainly analyzed with reference to water status and physical properties of the growing cells (e.g. 1, 2, 4, 12, 14), but dynamic relationship between leaf growth and plant water balance as affected by change in evaporative demand has remained to be studied, while stomatal movement has been analyzed and modeled on the basis of dynamic processes of plant water balance (3, 11).

Short wave irradiance is one of the environmental factors responsible for the evaporative demand (8). Therefore, the present paper deals with dynamics of whole-plant water balance and leaf expansive growth in a cucumber plant exposed to step change in short wave irradiance.

MATERIALS AND METHODS

Plant materials

Cucumber plants (*Cucumis sativus* L. cv. Chojitsu-Ochiai) were hydroponically grown at an air temperature of 23°C and a relative humidity of 70% in a phytotron glass room. The plants of healthy growth at the 4 leaf stage were used for the experiment.

Evaporative demand

By measuring environmental factors of short wave irradiance, air temperature, humidity and wind velocity near the plant, evaporative demand (ED_A) per unit leaf area was evaluated by the following equation (8, 9)

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

where the symbols are explained in APPENDIX. In the experiment, step change in ED_A was brought by step change in short wave irradiance (R_S).

Systems and measurements

Figure 1 shows a schematic diagram of the system used for the experiment. The shoot was set in the working section (0.3 × 0.3 × 2.0 m) of a wind tunnel where air temperature (T_A), saturation deficit (SD) and wind velocity (U) were controlled (7). The pot for hydroponics with a volume of 3 l was located below the working section. Nutrient solution in the pot was aerated enough before the start of the experiment, and the dissolved O_2 concentration in the solution was kept higher than 6 ppm during the experiment (15). Halogen lamps (100 W × 20 and 500 W × 4) were used for lighting through a water layer with a 2 cm depth. By selecting the number of lamps turned on, R_S was set at 540 W/m² and 135 W/m², which corresponded to 800 μmol/m²/s and 200 μmol/m²/s in $PPFD$, respectively.

A potometer with a 2 cm diameter and a laser displacement gauge (3Z4M-J12; OMRON Co., Japan) were used for measuring root water uptake rate (F) per plant: The laser gauge detected the displacement of the water level in the potometer with a resolution of 50 μm. Leaf transpiration rate (E) per plant was

evaluated by weighing the plant and the pot with an electronic balance. Then, the whole-plant water balance was evaluated by the difference ($F-E$) and the water content loss ($WLOS$) per plant defined as

$$WLOS = -\int (F-E) dt / W_f \times 100\% \quad (2)$$

Where W_f is the fresh weight of the shoot (leaves, petioles and stem) measured after the experiment. $WLOS$ can indicate variation of whole-plant water content from the initial content; the positive $WLOS$ means that the plant water content have decreased as compared with the initial content.

Temperatures (T_{L1} , T_{L2} , T_{L3} and T_{L4}) of the respective leaves were measured by thermocouples with a 0.1 mm diameter inserted into the leaves, and the average leaf temperature (T_{L1-4}) was evaluated by $T_{L1-4} = (T_{L1} + T_{L2} + T_{L3} + T_{L4}) / 4$.

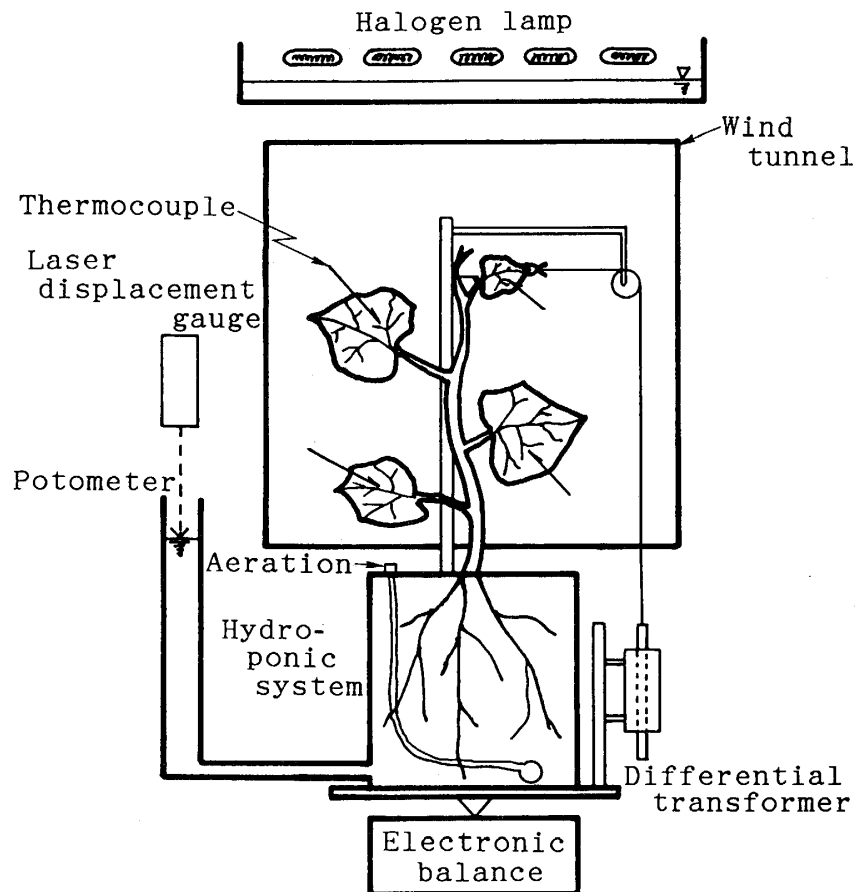


Fig. 1. A schematic diagram of the system for measuring root water uptake rate, transpiration rate, leaf growth rate and leaf temperatures.

By using T_{L1-4} , leaf-to-air vapor density difference ($W_L - W_A$) was calculated, and stomatal conductance (G_S) was evaluated on the basis of the measured E by

$$G_S = 1 / \{ (W_L - W_A) / (E / 2 \Sigma LA) - 1 / G_{AV} \} \quad (3)$$

where leaf boundary layer conductance (G_{AV}) was evaluated for mixed convection (5, 7). The total leaf area (ΣLA) of the plant was given by summing up LA 's of all leaves. LA of each leaf was evaluated from the midrib length (LL) by using a $LA-LL$ relationship obtained empirically as $LA = 1.265 LL^2 - 4.784 LL + 12.79$ (9), where LL of each leaf was measured by a ruler at the start of the experiment.

For evaluating growth rate of a developing younger leaf, change in LL of the 4th leaf was measured by a differential transformer (DCP-25L; Shinko Denki Co, Ltd., Japan): Both ends of the midrib of the leaf were held by small clips which were connected to the transformer through stretched threads. The LL change measured was converted into the LA change by using the $LA-LL$ relationship mentioned above, and leaf expansion rate (LER) on area basis was evaluated by $LER = dLA/dt$.

Signals from all the sensors were transmitted to CPU at an interval of 4 s through interfaces and smoothed by moving average for 1 min.

RESULTS

ED_A was kept at the levels higher than $140 \text{ mg/m}^2/\text{s}$ under T_A of 25°C , SD of 20 g/m^3 and U of 80 cm/s , and dynamics of whole-plant water balance, stomatal movement and leaf growth responding to change in ED_A were measured under step changes in R_S . Figure 2 shows time course patterns of ED_A , E , F , $F-E$, $WLOS$, G_S , LER , T_{L1-4} and T_{L4} when the plant was irradiated with the higher R_S of 540 W/m^2 under the higher ED_A condition. After the step input of the higher R_S , ED_A rose from 140 to $220 \text{ mg/m}^2/\text{s}$. Following the ED_A rise, E and F increased, but the increase in F lagged behind that in E . Thereafter, E and F appeared in oscillation patterns with a period of 30 min, where the oscillation of F showed the phase lag of about 5 min and the damped amplitude in comparison with that of E . Eventually, $F-E$ remarkably oscillated from -4 to 3.5 mg/s , and $WLOS$ also oscillated under the condition of water deficit of 2 to 8%.

G_S and LER just after irradiating rose rapidly in spite of the excessive water loss caused by the unbalance ($E > F$) between E and F . Thereafter, G_S and LER oscillated with a period of 30 min according to dynamics of the whole-plant water balance. The troughs of G_S and LER appeared about 8 min behind the peaks of $WLOS$. In the oscillation of LER , LER increased even under increasing $WLOS$, and the elevation of LER in the light became higher than that in the dark, although the shoot under the higher R_S was confronted with the water deficit under the positive $WLOS$ of 2 to 8%. Furthermore, around the troughs of LER after the higher peaks of LER and $WLOS$, LER decreased to negative values, that is, the leaf continued to shrink for 5 to 15 min like an elastic body.

T_{L1-4} oscillated with a period of 30 min according to latent heat loss with E . On the other hand, the oscillation pattern was not found in temperature (T_{L4}) of the developing 4th leaf, in which LER showed the oscillation pattern.

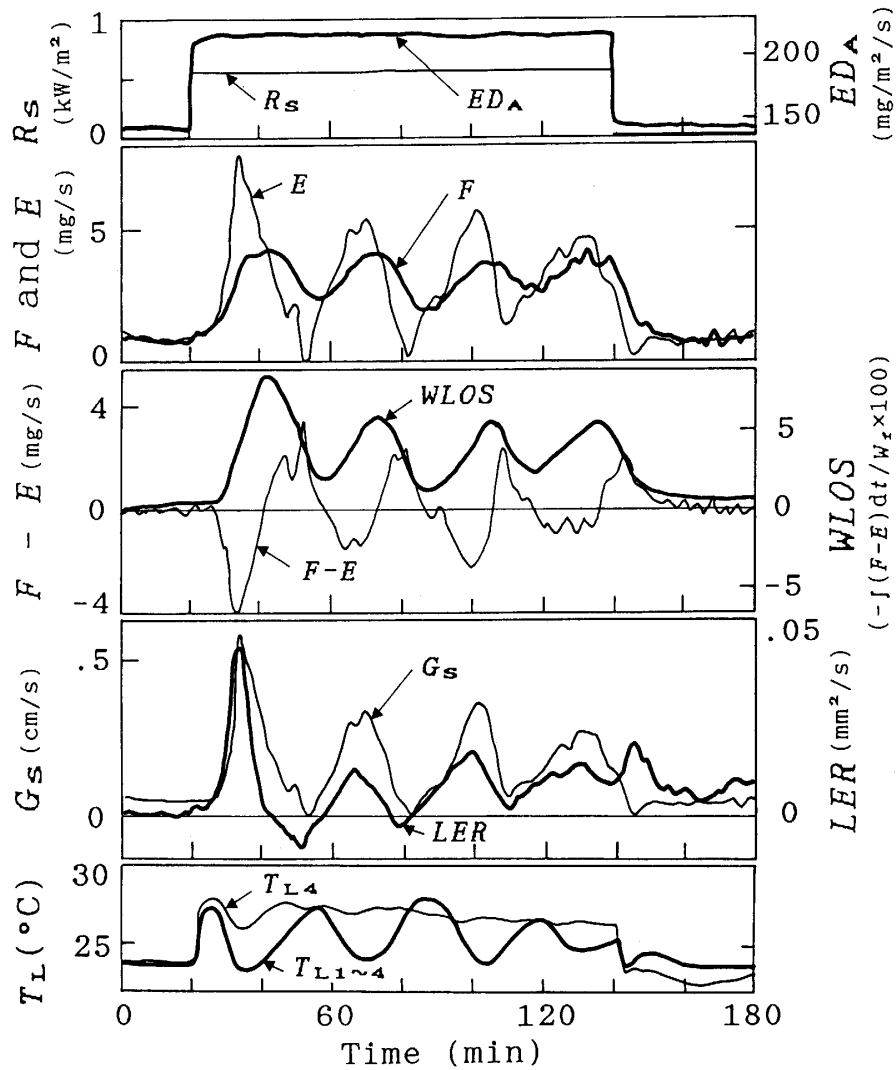


Fig. 2. Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to step input of the higher R_s of 540 W/m^2 under the higher ED_A condition with T_A of 25°C , SD of 20 g/m^3 and U of 80 cm/s : R_s , short wave irradiance; ED_A , evaporative demand evaluated by Eq(1); F , root water uptake rate per plant; E , transpiration rate per plant; $WLOS$, water content loss per plant evaluated by Eq (2); LER , growth rate of the developing 4th leaf; G_s , stomatal conductance; T_{L1-4} , average leaf temperature of the 1st to the 4th leaves; T_{L4} , temperature of the 4th leaf; T_A , air temperature; SD , saturation deficit; U , wind velocity.

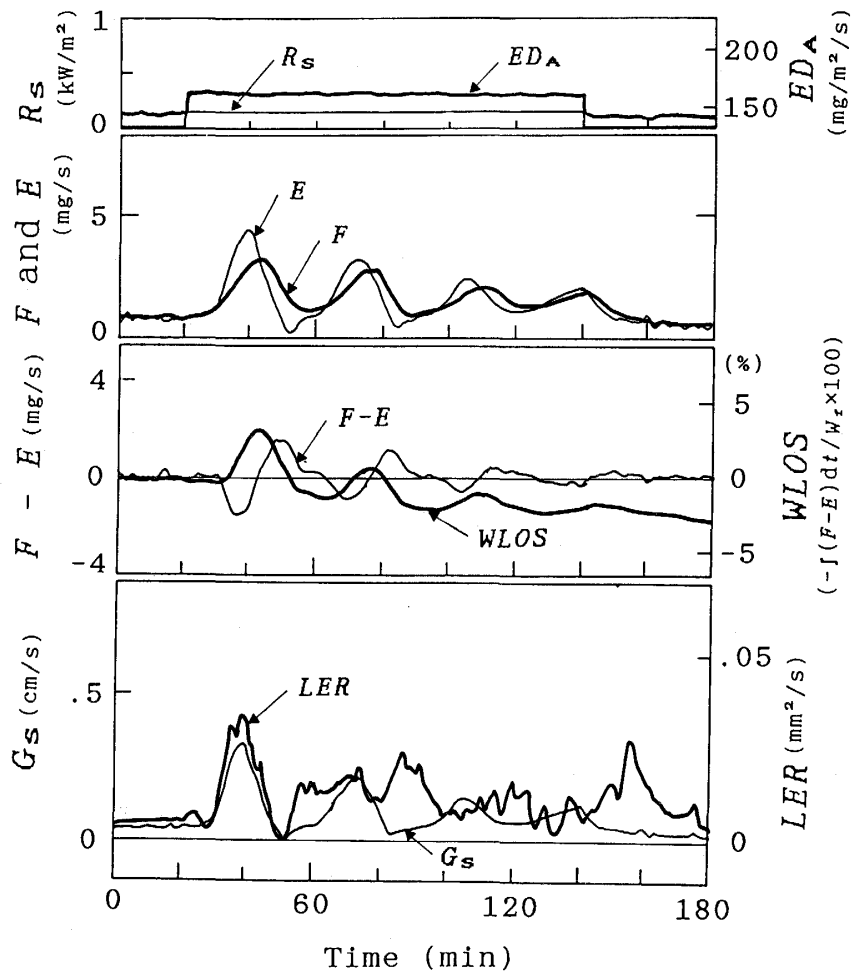


Fig. 3. Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to step input of the lower R_s of 135 W/m^2 under the higher ED_A condition with T_A of 25°C , SD of 20 g/m^3 and U of 80 cm/s : The symbols are explained in Fig. 2.

Figure 3 shows time course patterns of ED_A , E , F , $F-E$, $WLOS$, G_s and LER when the shoot was irradiated with the lower R_s of 135 W/m^2 under the higher ED_A condition. Step increase in ED_A after irradiating was only $20 \text{ mg/m}^2/\text{s}$, which induced small rise in E . Therefore, the oscillations of E , F , $F-E$, G_s and LER were found to be damped much more as compared with those after step input of the higher R_s . Furthermore, the peak of LER just after irradiating became lower than that caused by the higher R_s .

Figure 4 shows time course patterns of ED_A , E , F , $F-E$, $WLOS$, G_s and LER when the shoot was alternately irradiated with the lower R_s of 135 W/m^2

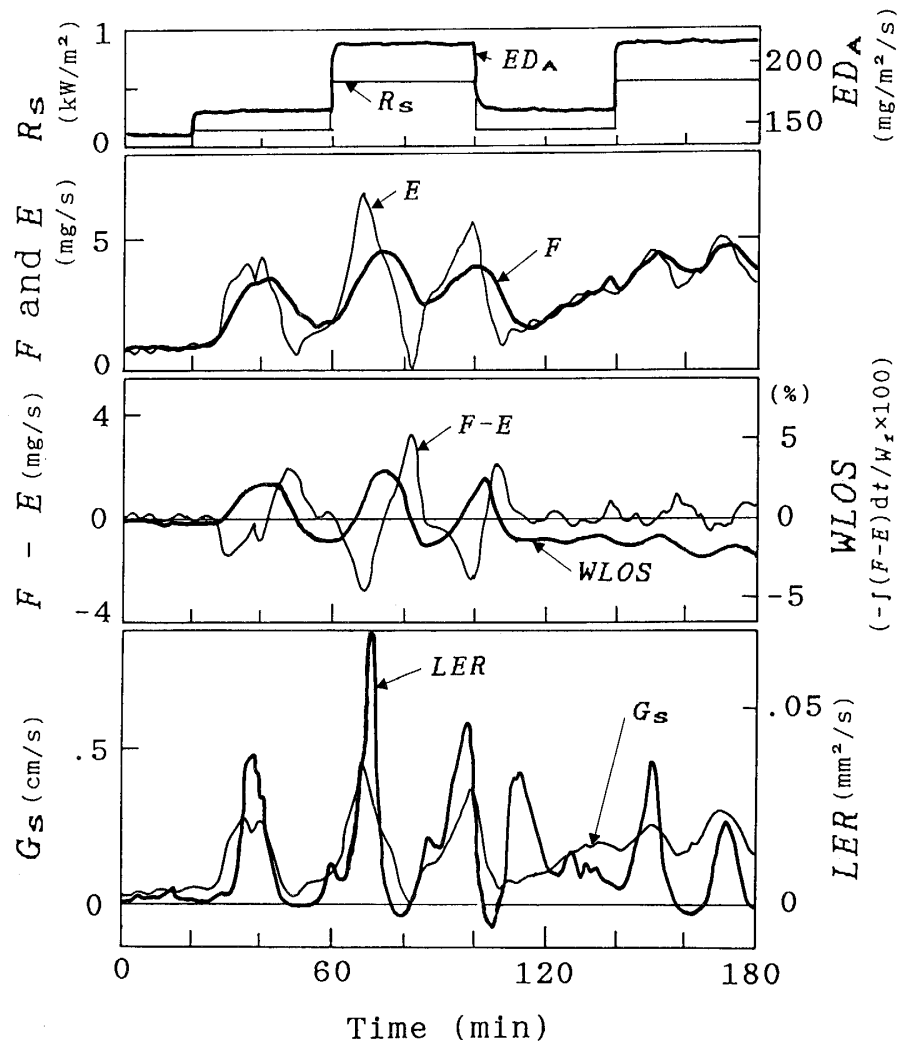


Fig. 4. Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to alternate step inputs of the lower R_s of 135 W/m^2 and the higher R_s of 540 W/m^2 under the higher ED_A condition with T_A of 25°C, SD of 20 g/m^3 and U of 80 cm/s : The symbols are explained in Fig. 2.

and the higher R_s of 540 W/m^2 under the higher ED_A condition. When ED_A rose from 160 to 220 $mg/m^2/s$ by increasing R_s from 135 to 540 W/m^2 , the unbalance between E and F appeared remarkable, and amplitudes of the oscillations of E , F , $F-E$, $WLOS$, G_s and LER became larger. In particular, the peaks of LER induced by the rise in R_s under the negative $WLOS$ became higher than those observed under the water deficit with positive $WLOS$ shown in Fig. 2. After the higher peaks of LER , LER dropped to negative troughs, that is, the leaf shrank. On the other hand, when ED_A dropped from 220 to 160 $mg/m^2/s$ by decreasing R_s

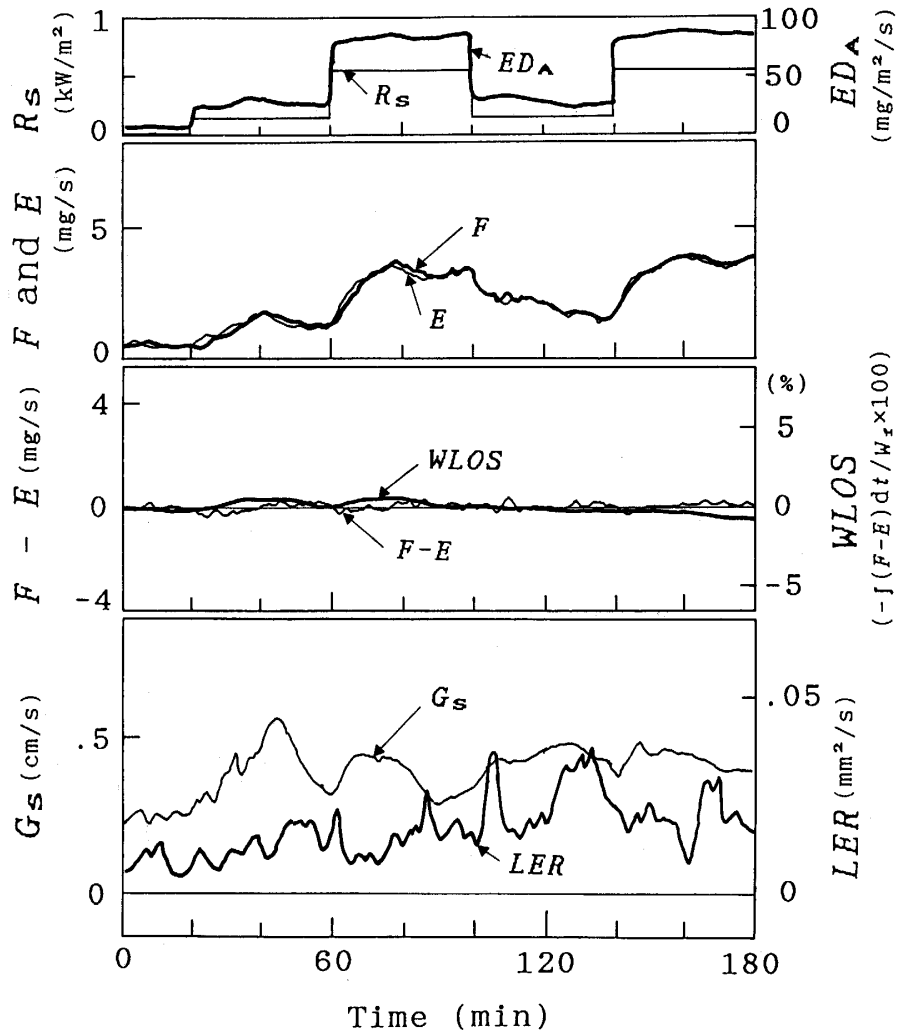


Fig. 5. Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to alternate step inputs of the lower R_s of 135 W/m^2 and the higher R_s of 540 W/m^2 under the lower ED_A condition with T_A of 25°C , SD of 5 g/m^3 and U of 20 cm/s : The symbols are explained in Fig. 2.

from 540 to 135 W/m^2 , E and F balanced again with each other, and the oscillations were damped. When ED_A rose again by irradiating with the higher R_s , the oscillations were caused again by the unbalance between E and F .

Furthermore, ED_A was set at the lower level of $10 \text{ mg/m}^2/\text{s}$ by decreasing SD and U to 5 g/m^3 and to 20 cm/s , respectively, and the dynamics under the alternate changes in R_s were analyzed. Figure 5 shows time course patterns of ED_A , E , F , $F-E$, $WLOS$, G_s and LER responding to the changes in R_s under the lower ED_A condition. The rise in E caused by the R_s increase was smaller than

that found under the higher ED_A condition, and consequently the oscillations caused by the unbalance between E and F were not appreciable. The elevations of G_s and LER became higher as compared with those under the higher ED_A condition, but the peak of LER just after the R_s increase did not appear because of the smaller rise in E .

DISCUSSION

From the results, it was conceivable that LER as well as G_s oscillates according to dynamics of whole-plant water balance which is directly affected by ED_A of the shoot environment. The whole-plant water balance was characterized by dynamics of F lagged behind E directly responding to rapid change in ED_A . In particular, the damping in F was appeared more remarkable as compared with that in the petiole water flux which has been measured in a single leaf water balance by Lange *et al.* (11) and Cowan (3). Furthermore, hydraulic capacitance of cucumber leaves is small because of those thinness. These facts suggest that water content stored in the stem and petioles can be applied compensatingly for excessive transpiration from leaves during the transient unbalance ($E > F$) between E and F (6).

From the oscillation of LER in the 4th leaf with the non-oscillatory T_{L4} , it was estimated that transpiration stream into the 4th leaf synchronized with dynamics of the whole-plant water balance although transpiration rate in the 4th leaf did not oscillate because of the undeveloped function of stomatal movement (10).

LER increasing with $WLOS$ and the higher elevation of LER in the water deficit (positive $WLOS$) under the higher R_s and ED_A (Figs. 2 and 4) indicate that the water content stored in the stem and the petioles can be also applied for leaf expansive growth even under the condition of transient water deficit. This buffer action of water content in the stem and petioles was contributive to the higher peaks of LER with the rapid rise in E just after the R_s increase under the higher ED_A condition. The peak of LER became higher when the stem and petioles were more turgid with negative $WLOS$ (Fig. 4). On the other hand, the peak of LER was not induced by the smaller rise in E under the condition of lower ED_A (Fig. 5). These results suggest that rapid rise in E , i.e. rapid increase in transpiration stream into the leaf, can supply the water flux available for the rapid growth even in the case of transient water deficit in the whole-plant after increase in R_s .

The respective properties of extensibility, yield threshold and hydraulic conductivity in the growing cells responsible for leaf expansive growth could be influenced by lighting (13) and water deficit (2, 4, 12, 14). In this experiment, the relationship between LER and the transpiration stream can be attributed to increase in water potential gradient ($\Psi_0 - \Psi_L$) from the stem to the leaf. The drop in leaf water potential (Ψ_L) caused by the increased R_s is enhanced by water loss by the rapid rise in E under the condition of higher ED_A , and the stem and the petioles can be more turgid with higher Ψ_0 under negative $WLOS$. Then, the

increase in $\Psi_O - \Psi_L$ can be estimated to supply much more water available for leaf expansive growth through the transpiration stream into the leaf. On the other hand, when the excessive water deficit reduces the water flux into the leaf by breaking $\Psi_O - \Psi_L$, leaf turgor drops to the level lower than the yield threshold, and the leaf shrinks like an elastic body as shown in Figs. 2 and 4. Thus, dynamics of leaf expansive growth was closely related to the whole-plant water balance directly affected by change in evaporative demand.

APPENDIX : List of symbols

a	short wave absorption coefficient of a leaf.
C_P	specific heat of air at a constant pressure.
E	transpiration rate per plant.
ED_A	evaporative demand per unit leaf area.
F	water uptake rate per plant.
G_{AH}	leaf boundary layer conductance for heat transfer by mixed convection ($G_{AH} = G_{FO} + G_{FR}$) (5, 7).
G_{AV}	leaf boundary layer conductance for vapor transfer by mixed convection ($G_{AV} = G_{FO}/Le^{0.67} + G_{FR}/Le^{0.75}$).
G_E	parallel conductance of G_{AH} and G_R .
G_{FO}	leaf boundary layer conductance for forced convection which depends on U .
G_{FR}	leaf boundary layer conductance for free convection which depends on $T_L - T_A$.
G_R	radiative transfer conductance ($4\epsilon_L \sigma T_E^3 / C_P \rho$).
G_S	stomatal conductance.
LA	leaf area.
Le	Lewis number.
LER	leaf expansion rate (dL_A/dt).
LL	midrib length of a leaf.
n	constant ($n=2$ in an amphistomatous leaf and $n=1$ in a hypostomatous leaf).
RH	relative humidity of ambient air.
R_S	short wave irradiance.

SAV	saturation vapor density of air.
SD	saturation deficit of ambient air $(1-RH/100) \times SAV$.
T_A	temperature of ambient air.
T_E	$(T_A + T_{LP}) / 2$.
T_L	leaf temperature.
T_{L1-4}	average temperature of the 1st to the 4th leaves.
T_{L4}	temperature of the 4th leaf.
T_{LP}	estimated temperature of a wetted surface (8, 9).
U	wind velocity of ambient air.
W_A	water vapor density of ambient air.
W_f	fresh weight of the shoot (leaves, petioles and a stem).
W_L	saturated water vapor density in leaf intercellular space.
$WLOS$	water content loss of a whole plant $(-\int (F-E) dt / W_f \times 100\%)$.
γ	thermodynamic psychrometer constant $(C_p \rho / \lambda)$.
Δ	slope of the saturation vapor density curve at T_E .
ε_A	emissivity of environment.
ε_L	emissivity of a leaf.
λ	latent heat of vaporization of water.
ρ	density of air.
σ	Stefan-Boltzmann constant $(5.67 \times 10^{-8} \text{ W/m}^2/\text{K}^4)$.
Ψ_L	leaf water potential.
Ψ_O	water potential outside of the growing leaf (i.e. water potential of the stem).

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