

## DYNAMICS OF WHOLE-PLANT WATER BALANCE AND LEAF GROWTH IN RESPONSE TO EVAPORATIVE DEMAND. II. EFFECT OF CHANGE IN WIND VELOCITY

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DYNAMICS OF WHOLE-PLANT WATER BALANCE AND  
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II. EFFECT OF CHANGE IN WIND VELOCITY.

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KITANO M. and EGUCHI H. *Dynamics of whole plant water balance and leaf growth in response to evaporative demand. II. Effect of change in wind velocity.* BIOTRONICS 21, 51-60, 1992. Dynamics of whole plant water balance and leaf expansive growth were analyzed in cucumber plants (*Cucumis sativus* L.) exposed to step change in wind velocity ( $U$ ). The effect of step increase in  $U$  was caused by the hydropassive stomatal response, which appeared more active under the higher irradiance and the higher humidity conditions. Thereafter, the oscillations in whole-plant water balance and leaf growth were induced more actively under the higher irradiance in the lower humidity condition, where evaporative demand ( $ED_A$ ) and consequently leaf transpiration increased rapidly with increase in  $U$ , and then by decrease in  $U$ , the oscillations were damped immediately. On the other hand, the oscillations were not induced under the higher humidity condition where  $ED_A$  and the transpiration were scarcely affected by change in  $U$ . Thus, the effect of change in  $U$  appeared in different patterns under different conditions of irradiance and humidity through the processes of water balance affected by change in  $ED_A$ .

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

### INTRODUCTION

Wind causes heat and mass transfer by forced convection across the leaf boundary layer between the leaf surface and the ambient air, and the leaf boundary layer conductance depends on wind velocity (12, 13). Therefore, wind velocity is one of the environmental factors responsible for evaporative demand on transpiring plants as well as irradiance (7-9). It can be supposed that change in wind velocity affects plant water relations through change in the evaporative demand. The effects of wind velocity on plant water relations has been studied with reference to the effects on transpiration and stomatal response in a steady state (1-3). In the preceding paper (10), we have analyzed effects of change in irradiance on dynamics of whole-plant water balance and leaf growth.

The present paper deals with dynamics of whole-plant water balance and

leaf expansive growth in a cucumber plant exposed to step change in wind velocity.

### 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 and change in wind velocity*

By using 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 (7, 8)

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

with

$$G_E = G_R + G_{AH} \quad (2)$$

where the symbols are explained in APPENDIX. The leaf boundary layer conductances ( $G_{AH}$  and  $G_{AV}$ ) for heat and vapor transfers were evaluated for mixed convection (6), by using a parallel model where standard conductances for forced convection ( $G_{FO}$ ) and for free convection ( $G_{FR}$ ) were connected in parallel as follows (5, 7, 8)

$$G_{AH} = G_{FO} + G_{FR} \quad (3)$$

and

$$G_{AV} = G_{FO}/Le^{0.67} + G_{FR}/Le^{0.75} \quad (4)$$

with

$$G_{FO} = \frac{0.66\kappa^{0.67}}{d^{0.5}\nu^{0.17}} U^{0.5} \quad (5)$$

and

$$G_{FR} = \frac{b\beta^{0.25}g^{0.25}\kappa}{d^{0.25}\nu^{0.5}} |T_{LP} - T_A|^{0.25} \quad (6)$$

$T_{LP}$  is the temperature of an evaporating wetted surface which was estimated as

$$T_{LP} = T_A + \frac{(2/n)\gamma(G_E/G_{AV})}{(2/n)\gamma(G_E/G_{AV}) + \Delta} \times \left\{ \frac{aR_s - 2\sigma\epsilon_L(1-\epsilon_A)T_A^4}{2C_{p\rho}G_E} - \frac{SD}{(2/n)\gamma(G_E/G_{AV})} \right\} \quad (7)$$

Therefore, change in wind velocity ( $U$ ) brought change in  $ED_A$  primarily through change in  $G_{FO}$  of Eq. (5) and also through in  $T_{LP}$  which determines physical parameters such as  $T_E$ ,  $A$  and  $G_R$  responsible for  $ED_A$  of Eq. (1).

#### *Systems and measurements*

Systems and methods used for the experiment were the same as those described in the preceding paper (10). The wind tunnel and the hydroponic system were used for controlling the respective environments of the shoot and roots.  $U$  was changed stepwise by adjusting rotational speed of a fan of the wind tunnel through a silicon controlled rectifier. The halogen lamps were used for the light source through a water layer with a 2 cm depth. The short wave irradiance was set at 540 W/m<sup>2</sup> and 135 W/m<sup>2</sup>, which corresponded to 800  $\mu\text{mol}/\text{m}^2/\text{s}$  and 200  $\mu\text{mol}/\text{m}^2/\text{s}$  in PPFD, respectively. Nutrient solution in the pot (volume of 3 l) of the hydroponic system was aerated enough before the experiment, and the dissolved O<sub>2</sub> concentration rate in the solution was kept higher than 6 ppm during the experiment.

Root water uptake rate ( $F$ ) and transpiration rate ( $E$ ) per plant were measured on-line by the potometer system and the electronic balance, respectively. The whole plant water balance were evaluated by  $F-E$  and the water content loss ( $WLOS$ ) defined as

$$WLOS = - \int (F-E) dt / W_f \times 100\% \quad (8)$$

where  $W_f$  is the fresh weight of the shoot (leaves, petioles and stem) measured after the experiment. Temperatures ( $T_{L1}$ ,  $T_{L2}$ ,  $T_{L3}$  and  $T_{L4}$ ) of the leaves were measured by the thermocouples inserted into the respective leaves, and the average leaf temperature ( $T_{L1-4}$ ) was evaluated by  $T_{L1-4} = (T_{L1} + T_{L2} + T_{L3} + T_{L4}) / 4$ . By using  $T_{L1-4}$  and  $E$  measured, stomatal conductance ( $G_s$ ) was evaluated by

$$G_s = 1 / \{ (W_L - W_A) / (E / 2 \Sigma LA) - 1 / G_{AV} \} \quad (9)$$

For evaluating growth rate of a developing younger leaf, change in  $LL$  of the 4th leaf was measured by the differential transformer, and leaf expansion rate ( $LER = dLA/dt$ ) on area basis was evaluated on the basis of the  $LA-LL$  relationship obtained empirically as  $LA = 1.265LL^2 - 4.784LL + 12.79$  (8).

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 AND DISCUSSION

$U$  was increased stepwise from 20 cm/s to 80 cm/s when  $F$  and  $E$  almost balanced with each other. The increased  $U$  was kept for 60 min, and thereafter it was decreased to 20 cm/s again. Dynamics of the whole-plant water balance and leaf growth affected by these step changes in  $U$  were analyzed under different light and humidity conditions at a constant  $T_A$  of 25°C.

Figure 1 shows time course patterns of  $ED_A$ ,  $E$ ,  $F$ ,  $F-E$ ,  $WLOS$ ,  $G_s$ ,  $LER$ ,  $T_{L1-4}$

and  $T_{L4}$  in the higher  $R_s$  of  $540 \text{ W/m}^2$  under the lower humidity condition with  $SD$  of  $20 \text{ g/m}^3$ . Before the increase in  $U$ ,  $E$  and  $F$  were kept balanced with each other at about  $4.5 \text{ mg/s}$ . The increase in  $U$  brought rise in  $ED_A$  from 145 to  $205 \text{ mg/m}^2/\text{s}$ . Following the  $ED_A$  rise,  $E$  increased immediately, but the increase in  $F$  lagged and appeared smaller as compared with that in  $E$ . This transient

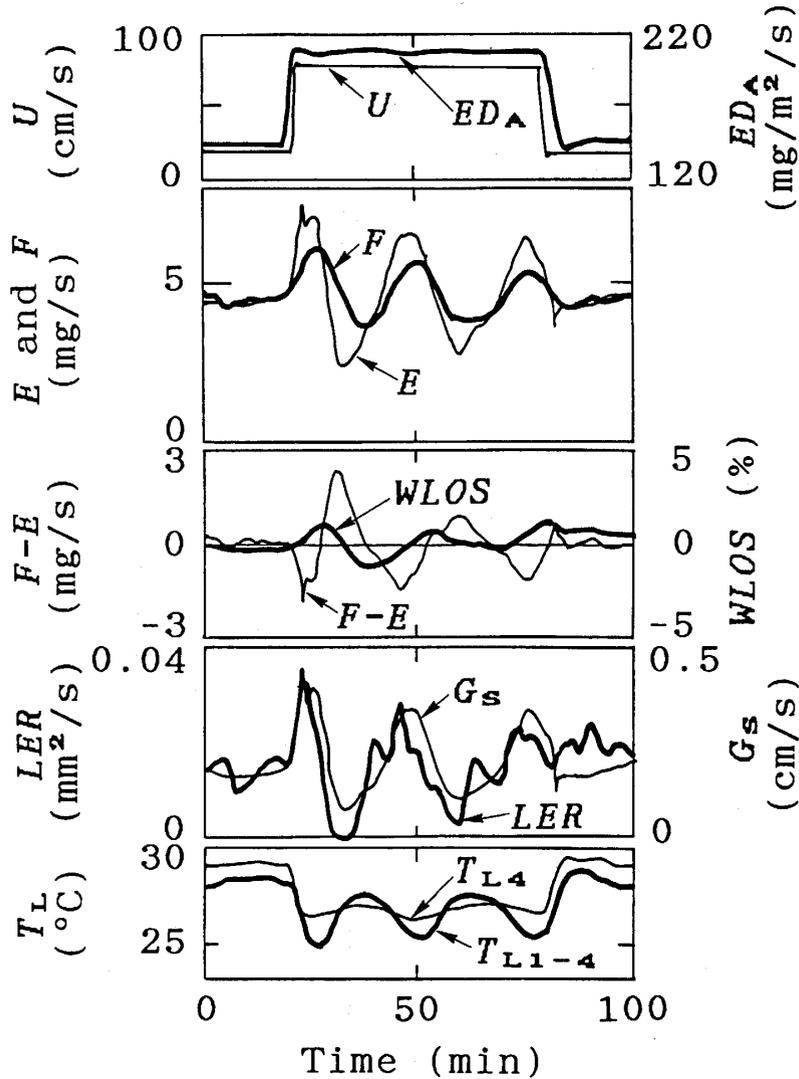


Fig. 1 Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to step changes in  $U$  under the higher  $R_s$  of  $540 \text{ W/m}^2$  in the lower humidity condition with  $SD$  of  $20 \text{ g/m}^3$  at  $T_A$  of  $25^\circ\text{C}$ :  $U$ , wind velocity;  $ED_A$ , evaporative demand evaluated by Eq. (1);  $F$ , root water uptake rate;  $E$ , transpiration rate per plant;  $WLOS$ , water content loss evaluated by Eq.(8);  $LER$ , 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;  $SD$ , saturation deficit;  $T_A$ , air temperature.

unbalance ( $E > F$ ) between  $E$  and  $F$  resulted in the oscillation in the whole plant water balance with a period of about 30 min, where the oscillation in  $F$  showed the phase lag of about 5 min and the damped amplitude in comparison with that of  $E$ . Therefore,  $F-E$  and  $WLOS$  also oscillated.  $G_s$  and  $LER$  rose immediately just after the increase in  $U$ . Thereafter, according to the whole-plant water balance,  $G_s$  and  $LER$  oscillated and synchronized with each other: The troughs of  $G_s$  and  $LER$  appeared about 8 min behind the peaks of  $WLOS$ .

In these oscillations, the buffer action of water content in the stem and petioles was contributive to the increase in  $LER$  as well as to the excessive  $E$  under the transient water deficit, as observed under the step change in  $R_s$  in the preceding paper (10): The increase pattern was found in  $LER$  even under the negative  $F-E$  and the increasing  $WLOS$ .  $T_{L1-4}$  and  $T_{L4}$  dropped by about 3°C and approached to  $T_A$  just after the increase in  $U$ . Thereafter,  $T_{L1-4}$  oscillated according to the latent heat loss with  $E$ , while  $T_{L4}$  of the developing 4th leaf did not oscillate because of the undeveloped function of stomatal movement (11). When  $U$  was decreased to 20 cm/s again,  $E$  and  $F$  balanced again with each other, and the oscillations in  $E$ ,  $F$ ,  $F-E$ ,  $WLOS$ ,  $G_s$ ,  $LER$  and  $T_{L1-4}$  were damped immediately.

Figure 2 shows the time course patterns in the lower  $R_s$  of 135 W/m<sup>2</sup> under the lower humidity condition with  $SD$  of 20 g/m<sup>3</sup>. By the step increase in  $U$ ,  $ED_A$  was increased from 100 to 160 mg/m<sup>2</sup>/s, and the oscillations were induced in  $E$ ,  $F$ ,  $F-E$ ,  $WLOS$ ,  $G_s$ ,  $LER$  and  $T_{L1-4}$  as observed under the higher  $R_s$  of 540 W/m<sup>2</sup>. Those amplitudes, however, were smaller than those under the higher  $R_s$ . Furthermore the elevations of  $E$ ,  $F$ ,  $G_s$  and  $LER$  were lower as compared with those under the higher  $R_s$ .

Figure 3 shows the time course patterns in the dark under the lower humidity condition with  $SD$  of 20 g/m<sup>3</sup>.  $ED_A$  increased from 80 to 140 mg/m<sup>2</sup>/s by the step increase in  $U$ . In the dark with the closed stomata,  $E$ ,  $F$ ,  $G_s$  and  $LER$  were kept remarkably lower than those under the light and were scarcely affected by the changes in  $U$ .

Figure 4 shows the time course patterns in the higher  $R_s$  of 540 W/m<sup>2</sup> under the lower humidity condition with the lower  $SD$  of 5 g/m<sup>3</sup>. The step increase in  $U$  from 20 to 80 cm/s brought small increase in  $ED_A$  of only 10 mg/m<sup>2</sup>/s, although the increase in  $ED_A$  under the lower humidity condition reached 60 mg/m<sup>2</sup>/s. This smaller increase in  $ED_A$  under the higher humidity was attributed to the lower sensitivity of  $ED_A$  to  $U$  under the higher humidity condition (9). Therefore,  $E$ ,  $F$ ,  $F-E$  and  $WLOS$  were scarcely affected by the changes in  $U$  under the lower  $SD$  of 5 g/m<sup>3</sup>. On the other hand,  $G_s$  increased stepwise with the increase in  $U$  to the level higher than that observed under the lower humidity condition (Fig. 1). This increase in  $G_s$  did not bring the increase in  $E$ , because  $T_{L1-4}$ , that is  $W_L - W_A$ , decreased by the leaf-to-air sensible heat transfer enhanced by the increased  $U$ . Thereafter,  $G_s$  was kept at the higher level until  $U$  was decreased again.  $LER$  showed a small decrease pattern under the increased  $U$ .

We have measured water vapor profile in the leaf boundary layer under different conditions of  $U$  and have indicated that under the higher  $U$  condition the outer surface of epidermis is exposed to the larger vapor difference between

the leaf and the leaf boundary sublayer (4). This larger vapor difference brought by the increase in  $U$  could be estimated to decrease the epidermal turgor exerted to the guard cells and to cause the hydropassive stomatal response. From the fact that the rapid increase in  $G_s$  just after the step increase in  $U$  were larger under the higher light and higher humidity conditions, it can be suggested that the more active hydropassive stomatal response is brought by the higher guard cell turgor under the higher light and higher humidity conditions.

This hydropassive rapid increase in  $G_s$  caused the oscillations in whole-plant water balance, stomatal movement and leaf growth, when the rapid increase in  $E$  was brought according to the rapid rise in  $ED_A$  by the step increase in  $U$  as observed under the lower humidity condition (Figs. 1 and 2). In the oscillations caused by the increase in  $U$ , the dynamic relationships among the whole-plant water balance, stomatal movement and leaf growth were the same as those found under the increase in  $R_s$  in the preceding paper (10): The buffer action of

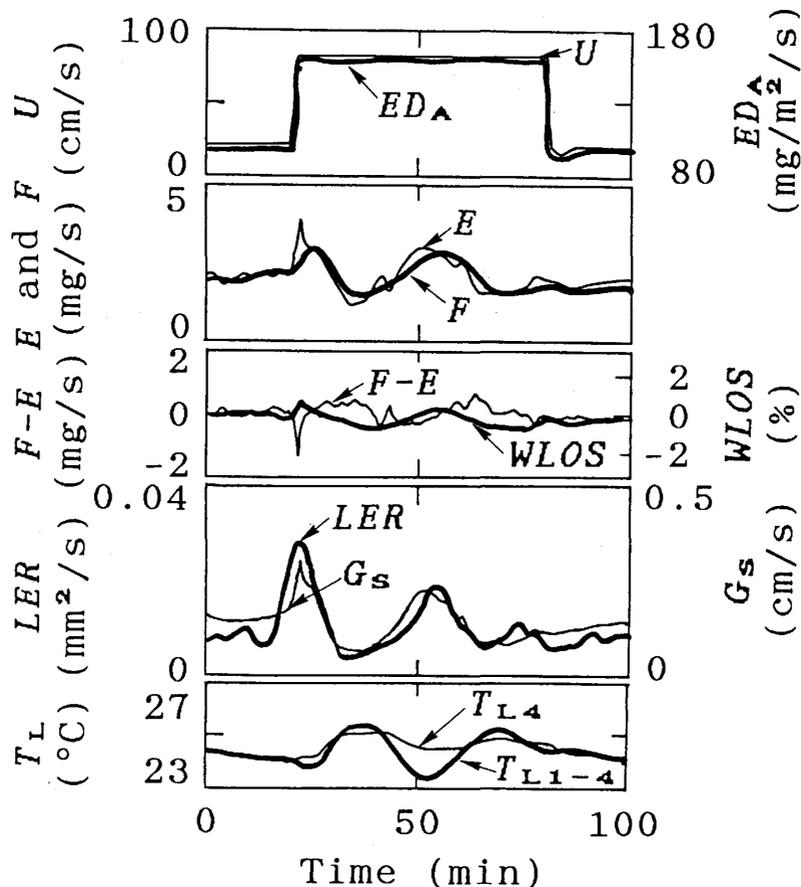


Fig. 2 Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to step changes in  $U$  under the lower  $R_s$  of  $135 \text{ W/m}^2$  in the lower humidity condition with  $SD$  of  $20 \text{ g/m}^3$  at  $T_A$  of  $25^\circ\text{C}$ : The symbols are explained in Fig. 1.

water content in the stem and petioles was found under the transient water deficit, and  $LER$  was dependent on the transpiration stream into the leaf. On the other hand, under the higher humidity condition the oscillations were not induced, because  $ED_A$  and  $E$  were scarcely increased by the step increase in  $U$ .

Thus, effects of change in  $U$  were not so large as those of change in  $R_S$  (10), but it can be suggested that effects of the increase in  $U$  are caused by the hydropassive stomatal response and appear in different patterns under the different conditions of light and humidity through the processes of water balance directly affected by change in  $ED_A$ .

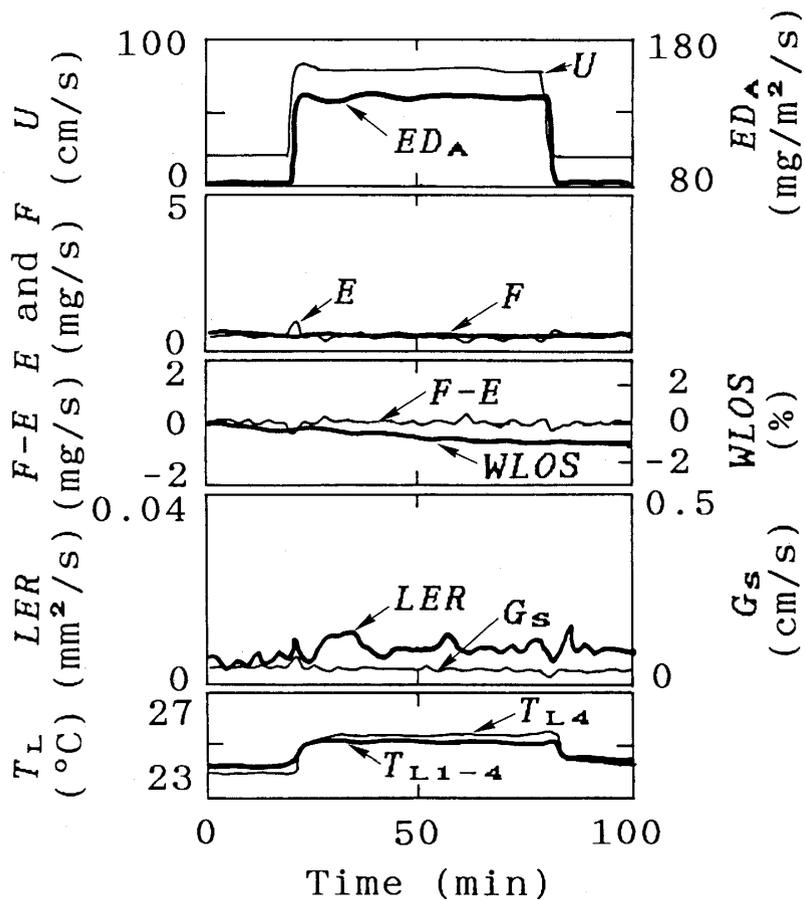


Fig. 3 Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to step changes in  $U$  under the dark in the lower humidity condition with  $SD$  of  $20 \text{ g/m}^3$  at  $T_A$  of  $25^\circ\text{C}$ : The symbols are explained in Fig. 1.

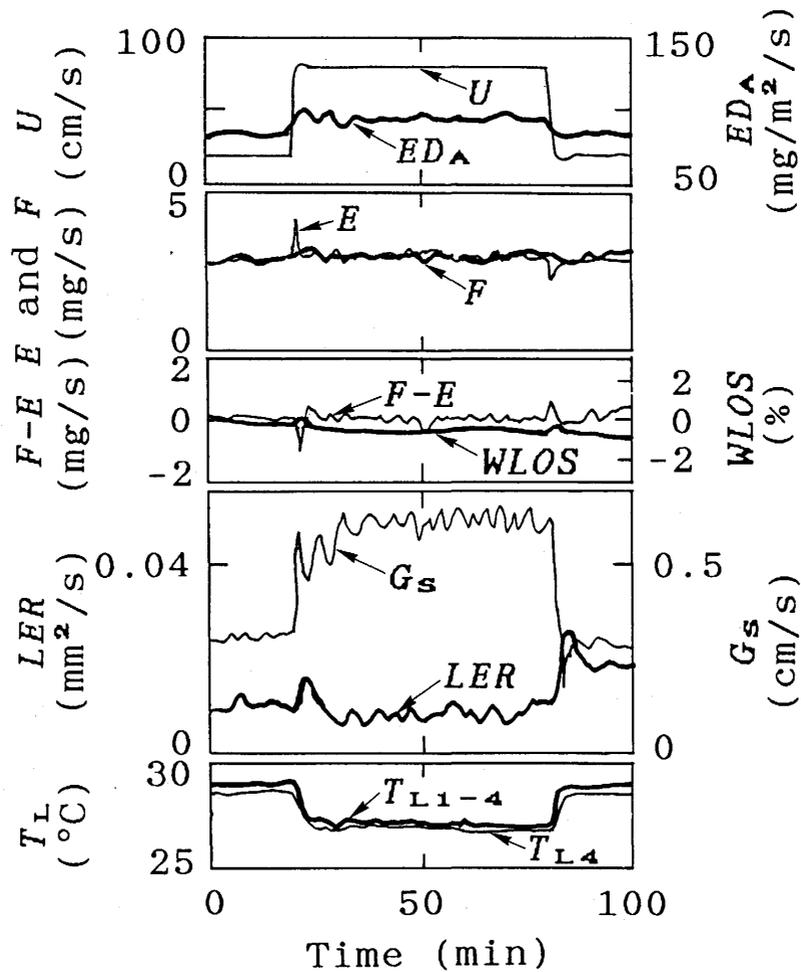


Fig. 4 Time course patterns of whole-plant water balance, stomatal movement and leaf expansive growth in the 4 leaf stage cucumber plant exposed to step changes in  $U$  under the higher  $R_s$  of  $540 \text{ W/m}^2$  in the higher humidity condition with  $SD$  of  $5 \text{ g/m}^3$  at  $T_A$  of  $25^\circ\text{C}$ : The symbols are explained in Fig. 1.

#### APPENDIX : List of symbols

- $a$  short wave absorption coefficient of a leaf.
- $b$  constant ( $b=0.50$  on upper leaf surface and  $b=0.23$  on lower leaf surface)
- $C_p$  specific heat of air at a constant pressure.
- $d$  leaf characteristic dimension by chord basis, which was evaluated by using an empirical equation of  $d=0.852LL-1.27$ .
- $E$  transpiration rate per plant.
- $ED_A$  evaporative demand per unit leaf area.

$F$	water uptake rate per plant.
$g$	acceleration of gravity.
$G_{AH}$	leaf boundary layer conductance for heat transfer by mixed convection.
$G_{AV}$	leaf boundary layer conductance for vapor transfer by mixed convection.
$G_E$	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 ( $dLA/dt$ ).
$LL$	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.
$T_{L1-4}$	average temperature of the 1st to the 4th leaves.
$T_{L4}$	temperature of the 4th leaf.
$T_{LP}$	temperature of a wetted surface estimated by Eq. (7).
$T_E$	$(T_A + T_{LP})/2$
$U$	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 $(-\int (F-E)dt / W_f \times 100\%)$ .
$\beta$	coefficient of thermal expansion of air.
$\gamma$	thermodynamic psychrometer constant ( $C_p \rho / \lambda$ ).

$\Delta$	slope of the saturation vapor density curve at $T_E$ .
$\varepsilon_A$	emissivity of environment.
$\varepsilon_L$	emissivity of a leaf.
$\kappa$	thermal diffusivity of air.
$\lambda$	latent heat of vaporization of water.
$\nu$	coefficient of kinematic viscosity of air.
$\rho$	density of air.
$\sigma$	Stefan-Boltzmann constant ( $5.67 \times 10^{-8} \text{ W/m}^2/\text{K}^4$ ).

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