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# CONTROL OF EVAPORATIVE DEMAND ON TRANSPIRING PLANTS III. TRANSPIRATION AND GROWTH OF CUCUMBER UNDER CONTROLLED EVAPORATIVE DEMAND

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KITANO M., HAMAKOGA M. and EGUCHI H. *Control of evaporative demand on transpiring plants III. Transpiration and growth of cucumber under controlled evaporative demand.* BIOTRONICS 23, 105-111, 1994. The Control of evaporative demand on transpiring plants was performed in natural light growth chambers, and transpiration, stomatal conductance and dry matter production of cucumber seedling (*Cucumis sativus* L.) were analyzed under different conditions of the controlled evaporative demand. Under the lower evaporative demand, transpiration was extremely depressed, and stomatal conductance and turgor-driven leaf expansion were enhanced. These effects of the lower evaporative demand brought the higher photosynthetic dry matter production with the higher water use efficiency. From the results, it is suggested that the control of evaporative demand can be a reliable measure to manipulate water use and dry matter production of plants.

**Key words:** *Cucumis sativus* L.; water relations; evaporative demand; transpiration; dry matter production.

## INTRODUCTION

Evaporative demand on transpiring plants directly affects plant water relations through dynamics such as water balance, stomatal movement and leaf expansion (7, 9, 11, 12). Evaporative demand largely depends on air humidity as well as irradiance (8), and effects of evaporative demand on horticultural crops have been studied with special reference to humidity effects on yield, quality and nutrients accumulation (e.g. 1-6, 13). In the preceding paper (10), the control of evaporative demand was performed in a growth chamber by adjusting air humidity according to variation in solar irradiance.

The present paper deals with effects of the controlled evaporative demand on water use, stomatal conductance and dry matter production in cucumber plants.

## MATERIAL AND METHODS

### *Control of evaporative demand*

Evaporative demand ( $ED_A$ ) on unit area of an amphistomatous leaf can be

evaluated on-line by using physical environmental factors of short wave irradiance, air temperature, humidity and wind velocity as follows (7, 8)

$$ED_A = \frac{2C_{P\rho}G_E(1-RH/100)SAV + \Delta\{\alpha R_S - 2\sigma\epsilon_L(1-\epsilon_A)T_A^4\}}{(\gamma G_E/G_{AV} + \Delta)\lambda}$$

with

$$G_E = G_{AH} + 4\sigma\epsilon_L T_E^3 / C_{P\rho}$$

where  $G_{AH}$  and  $G_{AV}$  are the leaf boundary layer conductances for the respective transfers of heat and water vapor,  $C_{P\rho}$  the volumetric heat capacity of air,  $RH$  the relative humidity of air,  $SAV$  the saturation water vapor density of air,  $\Delta$  the slope of the saturation vapor density curve,  $R_S$  the short wave radiant flux density,  $\alpha$  the short wave absorption coefficient of a leaf,  $\sigma$  the Stefan-Boltzmann constant,  $\epsilon_L$  and  $\epsilon_A$  the respective emissivities of a leaf and the environment,  $T_A$  the air temperature,  $T_E$  the equivalent temperature between a leaf and the environment,  $\lambda$  the latent heat of vaporization of water and  $\gamma$  the thermodynamic psychrometer constant ( $\gamma = C_{P\rho}/\lambda$ ).

$ED_A$  is highly sensitive to respective changes in  $R_S$  and  $RH$  (8), and the reliable control of  $ED_A$  was performed in a natural light growth chamber, where  $RH$  was adjusted to diurnal variation in solar  $R_S$  by using the sensitivity ( $\partial ED_A / \partial RH$ ) of  $ED_A$  to change in  $RH$  as follows (10)

$$\Delta RH = (SED_A - ED_A) / (\partial ED_A / \partial RH)$$

where  $\Delta RH$  is the  $RH$  deviation to be adjusted and  $SED_A$  the desired value of  $ED_A$ . Thus, by applying the on-line system for  $ED_A$  evaluation and  $RH$  adjustment in a growth chamber,  $ED_A$  was able to be controlled at a desired value even under  $R_S$  variation.

#### *Plant material and experimental procedures*

Cucumber plants (*Cucumis sativus* L. cv. Chojitsu-Ochiai) were potted in vermiculite moistened with nutrient solution and grown at  $T_A$  of 23°C and  $RH$  of 70% in a phytotron glass room. The seedlings of healthy growth at the 1st leaf stage were transferred to three adjacent growth chambers and grown under the same natural light condition. In the respective growth chambers,  $ED_A$  was controlled at different conditions (high, medium and low  $ED_A$ ) under diurnal variation in solar  $R_S$  by adjusting  $RH$  as mentioned above, where  $SED_A$  was set at each value of 140, 80 and 20 mg/m<sup>2</sup>/s at  $T_A$  of 23°C.

Transpiration rate per unit leaf area ( $E_A$ ) was evaluated by dividing transpiration rate per plant ( $E$ ) by the total leaf area ( $LA = \Sigma LA_i$ ):  $E$  was measured on-line by weighing the plant and pot, and each leaf area ( $LA_i$ ) was evaluated from the midrib length ( $LL_i$ ) on the basis of a  $LA_i$ - $LL_i$  relationship obtained as  $LA_i = 1.265 LL_i^2 - 4.784 LL_i + 12.79$ , where  $LL_i$  of each leaf was measured by a rule at every 9:00 a.m. Stomatal conductance ( $G_S$ ) was evaluated from  $E_A$  and leaf temperature ( $T_L$ ) measured by fine thermocouples inserted into

leaves (7, 9). After the 10 days cultivations under the respective  $ED_A$  conditions, dry weight of leaves ( $DW(L)$ ), dry weight of stems with petioles ( $DW(S)$ ) and shoot length ( $SL$ ) were measured, and water use efficiency ( $WUE$ ) was evaluated by  $\{DW(L)+DW(S)\}/\Sigma E$ , where  $\Sigma E$  was the integrated  $E$  during the 10 days cultivation.

### RESULTS AND DISCUSSION

In the respective three growth chambers with  $SED_A$  of 140, 80 and 20  $\text{mg/m}^2/\text{s}$ ,  $RH$ ,  $ED_A$ ,  $E_A$ ,  $G_S$  and  $T_L$  appeared in different diurnal variations. Figures 1 and 2 show diurnal variations of  $R_S$ ,  $RH$ ,  $ED_A$ ,  $E_A$ ,  $G_S$  and  $T_L$  on successive cloudy day (Feb. 2, 1993) and fair day (Feb. 3, 1993). In two growth chambers with the higher  $SED_A$  of 140 and 80  $\text{mg/m}^2/\text{s}$  (i.e. lower humidity conditions),  $RH$  was adjusted to 45% and 75% at the fair midday respectively, and  $ED_A$  was kept constant at each  $SED_A$  of 140 and 80  $\text{mg/m}^2/\text{s}$  independent of  $R_S$  variation. In the growth chamber with the lowest  $SED_A$  of 20  $\text{mg/m}^2/\text{s}$  (i.e. the highest humidity condition),  $RH$  was adjusted from 80% (night) to 95% (fair midday), and  $ED_A$  was controlled at  $SED_A$  of 20  $\text{mg/m}^2/\text{s}$  under lower  $R_S$  condition, while  $ED_A$  increased to 50  $\text{mg/m}^2/\text{s}$  around the fair midday by the excessively high  $R_S$ .

$E_A$  varied diurnally with  $R_S$  and  $G_S$  even under the constant conditions of  $ED_A$ , but the level of  $E_A$  variation became higher in the higher  $ED_A$  chambers (Fig. 2). On the other hand,  $G_S$  appeared higher in the lower  $ED_A$  chambers. In particular,  $G_S$  under the lower  $R_S$  conditions (e.g. the early morning, cloudy midday and late afternoon) was remarkably high in the lowest  $ED_A$  chamber as

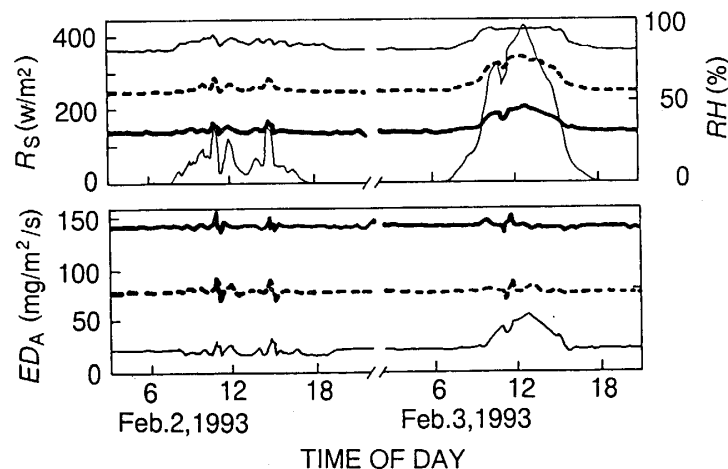


Fig. 1. Diurnal variations of short wave solar irradiance ( $R_S$ ), relative humidity ( $RH$ ) and evaporative demand ( $ED_A$ ) on a cloudy day (Feb. 2, 1993) and a fair day (Feb. 3, 1993) in three growth chambers lit with the natural light, where  $ED_A$  was controlled at around the respective desired values of 140 (—), 80 (---) and 20 (— · —)  $\text{mg/m}^2/\text{s}$  by adjusting  $RH$  according to variation in  $R_S$  at an air temperature of 23°C.

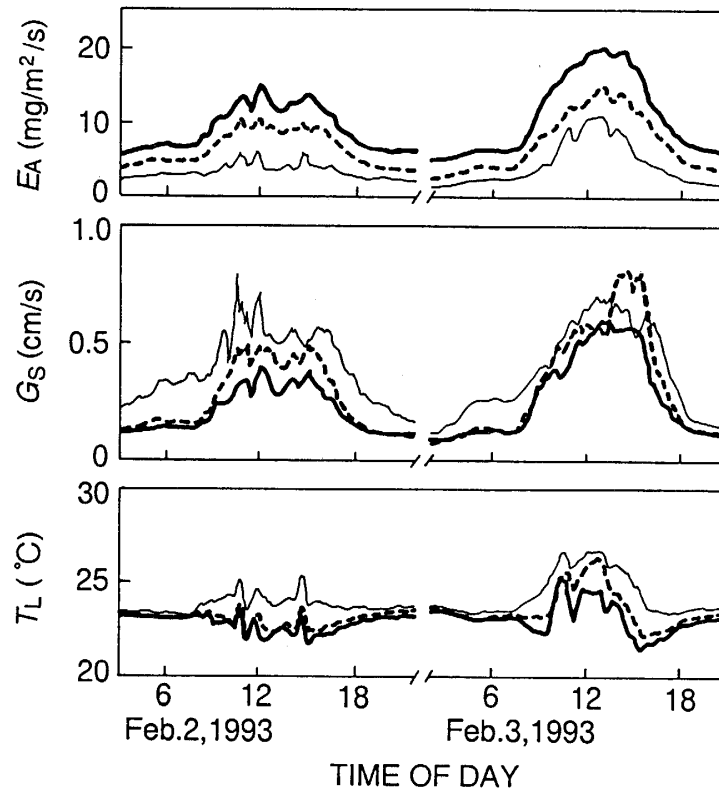


Fig. 2. Diurnal variations of transpiration rate ( $E_A$ ), stomatal conductance ( $G_s$ ) and leaf temperature ( $T_L$ ) on a cloudy day (Feb. 2, 1993) and a fair day (Feb. 3, 1993) in three growth chambers lit with the natural light, where  $ED_A$  was controlled at around the respective desired values of 140 (—), 80 (---) and 20 (— · —)  $\text{mg}/\text{m}^2/\text{s}$  at an air temperature of 23°C as shown in Fig. 1.

compared with that in the higher  $ED_A$  chambers.  $T_L$  appeared higher in the lower  $ED_A$  chambers because of the lower evaporative cooling brought with the lower  $E_A$ . The mean values of  $E_A$ ,  $G_s$  and  $T_L$  during the 10 days cultivations under the respective  $ED_A$  conditions were calculated by separating the daytime (6:00–18:00) and nighttime (18:00–6:00) values (Table 1). The mean  $E_A$  under the lowest  $ED_A$  (20  $\text{mg}/\text{m}^2/\text{s}$ ) was 60 to 70% lower than that under the highest  $ED_A$  (140  $\text{mg}/\text{m}^2/\text{s}$ ), whereas the mean  $G_s$  became 56 to 79% higher under the lowest  $ED_A$  as compared with the highest  $ED_A$ . Difference found in the mean  $T_L$  was not more than 1.3°C.

Growth indices ( $DW(L)$ ,  $DW(S)$ ,  $DW(L+S)$ ,  $LA$ ,  $DW(L)/LA$  and  $SL$ ) and  $WUE$  after the 10 days cultivations under the different  $ED_A$  conditions were listed in Table 2. The larger dry weights were obtained under the lower  $ED_A$  conditions, and the dry weights were about 40% larger in the lowest  $ED_A$  than in the highest  $ED_A$ . Furthermore,  $LA$  was much more increased in the lower  $ED_A$  conditions, and  $LA$  under the lowest  $ED_A$  became 63% larger than that in the highest  $ED_A$ . This larger increase in  $LA$  resulted in the lower dry weight per unit leaf area ( $DW(L)/LA$ ), and  $DW(L)/LA$  under the lowest  $ED_A$  became 87%

Table 1. Transpiration rate per unit leaf area ( $E_A$ ), stomatal conductance ( $G_s$ ) and leaf temperature ( $T_L$ ) in the daytime (D) from 6:00 to 18:00 and in the nighttime (N) from 18:00 to 6:00 under the different conditions of evaporative demand ( $ED_A$ ) of 140, 80 and 20 mg/m<sup>2</sup>/s at an air temperature of 23°C. The values of  $E_A$ ,  $G_s$  and  $T_L$  are the mean values for 10 successive days, and each value in the parenthesis is the relative percentage compared with the value under  $ED_A$  of 140 mg/m<sup>2</sup>/s.

$ED_A$ (mg/m <sup>2</sup> /s)	$E_A$ (mg/m <sup>2</sup> /s)		$G_s$ (cm/s)		$T_L$ (°C)	
	D	N	D	N	D	N
140 (100)	14.20 (100)	7.72 (100)	0.35 (100)	0.13 (100)	23.2	23.4
80 (57)	10.00 (70)	4.56 (59)	0.42 (121)	0.14 (109)	23.6	23.4
20 (14)	5.72 (40)	2.34 (30)	0.55 (156)	0.23 (179)	24.5	23.8

Table 2. Dry weights ( $DW$ ) of leaves (L) and stems (S), leaf area ( $LA$ ), dry weight per unit leaf area ( $DW(L)/LA$ ), shoot length ( $SL$ ) and water use efficiency ( $WUE$ ) after the 10 days cultivations under different conditions of evaporative demand ( $ED_A$ ) of 140, 80 and 20 mg/m<sup>2</sup>/s at an air temperature of 23°C. Each value in the parenthesis is the relative percentage compared with the value under  $ED_A$  of 140 mg/m<sup>2</sup>/s.

$ED_A$ (mg/m <sup>2</sup> /s)	$DW(L)$ (g)	$DW(S)$ (g)	$DW(L+S)$ (g)	$LA$ (m <sup>2</sup> )	$DW(L)/LA$ (g/m <sup>2</sup> )	$SL$ (cm)	$WUE$ (mg/g)
140	2.66 (100)	0.86 (100)	3.52 (100)	0.856 (100)	3.11 (100)	47.7 (100)	1.87 (100)
80	3.34 (125)	1.04 (121)	4.38 (124)	1.114 (130)	3.00 (96)	53.4 (112)	2.88 (154)
20	3.79 (142)	1.21 (141)	5.00 (142)	1.391 (163)	2.73 (87)	55.0 (115)	5.03 (269)

of that under the highest  $ED_A$ . A slight difference was also found in  $SL$ , and  $SL$  under the lowest  $ED_A$  was 15% larger than that in the highest  $ED_A$ .  $WUE$  under the lowest  $ED_A$  became more than 2.5 times higher than that under the highest  $ED_A$ .

Effects of the low  $ED_A$  condition (high humidity) on the growth indices were further studied under the different conditions of daytime (D)/nighttime (N)  $ED_A$ , where the seedlings were grown for 10 days under the respective D/N  $ED_A$  conditions of 140/140, 140/20 and 20/140 mg/m<sup>2</sup>/s (Table 3).  $DW$ 's and  $LA$  under D/N  $ED_A$  conditions of 140/20 and 20/140 mg/m<sup>2</sup>/s became larger than those under 140/140  $ED_A$  condition, and those increases in  $DW$ 's and  $LA$  appeared more clearly under D/N  $ED_A$  of 20/140 mg/m<sup>2</sup>/s as compared with under D/N  $ED_A$  of 140/20 mg/m<sup>2</sup>/s. That is, the daytime low  $ED_A$  brought larger effects than the nighttime low  $ED_A$ .

Transpiration extremely increased with evaporative demand from the environment, but a proportional relationship was not found between them

Table 3. Dry weights (*DW*) of leaves (L) and stems (S), leaf area (*LA*), dry weight per unit leaf area (*DW(L)/LA*) and shoot length (*SL*) after the 10 days cultivations under different daytime/nighttime conditions of evaporative demand (*ED<sub>A</sub>*) of 140/140, 140/20 and 20/140 mg/m<sup>2</sup>/s at an air temperature of 23°C. Each value in the parenthesis is the relative percentage compared with the value under daytime/nighttime *ED<sub>A</sub>* of 140/140 mg/m<sup>2</sup>/s. D, daytime from 6:00 to 18:00; N, nighttime from 18:00 to 6:00.

<i>ED<sub>A</sub></i> (mg/m <sup>2</sup> /s)		<i>DW</i> (L)	<i>DW</i> (S)	<i>DW</i> (L+S)	<i>LA</i>	<i>DW</i> (L)/ <i>LA</i>	<i>SL</i>
D	N	(g)	(g)	(g)	(m <sup>2</sup> )	(g/m <sup>2</sup> )	(cm)
140	140	3.16 (100)	1.14 (100)	4.30 (100)	1.059 (100)	2.98 (100)	49.0 (100)
140	20	3.47 (110)	1.34 (118)	4.81 (112)	1.389 (131)	2.50 (84)	57.6 (118)
20	140	4.64 (147)	1.77 (155)	6.41 (149)	1.803 (170)	2.57 (86)	62.5 (128)

because of stomatal response to the evaporative demand (i.e.  $G_s$  increase under the lower  $ED_A$  conditions). Stomatal aperture and leaf expansion were remarkably enhanced under the lower evaporative demand which brought about higher turgor in guard cells and epidermal cells by depressing water loss from these cells. Effect of evaporative demand on dry matter production can be considered to be brought through change in photosynthetic productivity regulated by stomatal movement and through change in turgor-driven leaf expansion: The effect of the daytime low  $ED_A$  relates to both of those changes, whereas the effect of the nighttime low  $ED_A$  can be attributed to only the latter change. The larger stomatal conductance and the larger leaf area brought under the lower evaporative demand contribute to the higher dry matter production by photosynthesis, and this higher dry matter production with the depressed water loss resulted in the higher water use efficiency. These effects of evaporative demand suggest that the control of evaporative demand can be a reliable measure for manipulating transpiration and resultantly for optimizing plant water relations and growth.

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