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AN IMPACT COEFFICIENT OF EVAPORATIVE DEMAND ON PLANT WATER BALANCE

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KITANO M. and EGUCHI H. *An impact coefficient of evaporative demand on plant water balance.* BIOTRONICS **22**, 61–72, 1993. A coefficient was newly defined to evaluate the impact of evaporative demand on plant water balance, which we propose to call "impact coefficient (*Imp*) ". *Imp* varied from 0 to 1 with increase in ratio (G_S/G_{AV}) of tomatal conductance (G_S) to leaf boundary layer conductance (G_{AV}), and the impact of evaporative demand (ED_A) was evaluated by $Imp \times ED_A$. *Imp* became lower in small leaves plants and CAM plants which are adapted to sunny, hot and dry conditions in desert regions. Their lower *Imp*'s bringing smaller impacts of ED_A can be considered reasonably to contribute their adaptabilities to the desert conditions. Furthermore, ΔED_A and ΔImp triggered dynamics of plant water relations through the water balance, and midday stomatal depression on a fair day was attributed to larger ΔED_A and ΔImp but not to higher transpiration rate. Thus, environmental effects on plant water relations can be confirmed quantitatively in terms of the impact coefficient of evaporative demand.

Key words : Evaporative demand ; plant water balance ; impact coefficiect ; stomatal movement ; desert plants.

INTRODUCTION

Transpirational water loss from plants is induced by evaporative demand of the environment and is partially controlled by stomatal movement. In meteorological studies on transpiration (*4, 5, 16–19*), the sensitivity of transpiration to a change in stomatal conductance has been analyzed in the spatial scale from a leaf to a region by using a leaf-atmosphere decoupling coefficient (Ω), which has been introduced by Jarvis and McNaughton (*5*) to indicate the dependence of transpiration on change in stomatal conductance. Through processes of plant water balance, however, change in evaporative demand of environment affects plant water relations such as stomatal movement and leaf expansive growth (*13, 14, 15*). Therefore, quantitative analyses of the impact of evaporative demand on plant water balance are essential for better understanding of environmental effects on plant water relations.

By using physical environmental factors, we have evaluated evaporative demand as an evaporation rate from a wetted surface on the basis of heat balance (*10, 11*), and effects of step change in the evaporative demand on whole plant water balance, stomatal movement and leaf growth have been demonstrated to appear in different patterns under different conditions of environment (*13, 14*).

The present paper deals with a new definition of a numerical coefficient evaluating the impact of evaporative demand on plant water balance, and also deals with identification of the coefficient under various environmental conditions.

DEFINITION OF IMPACT COEFFICIENT OF EVAPORATIVE DEMAND

Evaporative demand (ED_A) per unit leaf area was defined on the basis of heat balance by using short wave irradiance, air temperature, air humidity and wind velocity as follows (*10, 11*)

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

with

$$G_E = G_{AH} + G_R = G_{AH} + 4\varepsilon_L \sigma T_E^3 / C_p \rho \tag{2}$$

where the symbols are explained in APPENDIX I.

Eq. (1) gives a theoretical expression of evaporation rate from a wetted surface, which can integrate dependences of evaporative demand on different environmental factors and leaf dimension (*12*). ED_A is independent of physiological stomatal function and can be evaluated from only physical environmental factors.

In a real leaf with stomatal function, leaf conductance (G_L) for vapor transfer from leaf to the environment can be expressed by using stomatal conductance (G_S) in addition to leaf boundary layer conductance (G_{AV}) as follows

$$G_L = G_S\ G_{AV}/(G_S + G_{AV}) \tag{3}$$

By substituting G_L for G_{AV} into Eq. (1), a theoretical expression of transpiration rate (E_{AT}) from unit area of a real leaf was given as

$$E_{AT} = \frac{2C_p \rho G_E\, SD + \Delta\{aR_S - 2\sigma\varepsilon_L(1-\varepsilon_A)T_A{}^4\}}{\{(2/n)\gamma(G_E/G_L) + \Delta\}\lambda} \tag{4}$$

By Eqs (1) and (4), E_{AT} was related to ED_A as follows

$$E_{AT} = Imp \times ED_A \tag{5}$$

where

$$Imp = \frac{C}{C + G_{AV}/G_S} = \frac{C}{C + 1/(G_S/G_{AV})} \tag{6}$$

and

$$C = 1 + n\Delta G_{AV}/(2\gamma G_E) = 1 + n\Delta G_{AV}/\{2\gamma(G_{AH} + G_R)\} \tag{7}$$

E_{AT} can be considered as a theoretical rate of transpirational water loss caused by ED_A. That is, E_{AT} quantitatively indicates the impact of ED_A on plant water balance. From Eq. (5), it can be suggested that dynamics of plant water balance is affected by changes in ED_A and *Imp* as follows

$$\Delta E_{AT} = Imp \times \Delta ED_A + ED_A \times \Delta Imp + \Delta ED_A \times \Delta Imp \qquad (8)$$

Thus, ED_A can be a measure of evaporative demand as a physical input to plant hydraulic system, and it's impact on plant water balance depends on *Imp*. Therefore, *Imp* can be a measure to evaluate the impact of ED_A on plant water balance, and we propose to call *Imp* *"impact coefficient"* of evaporative demand.

CHARACTERISTICS OF IMPACT COEFFICIENT

General characteristics

Eq. (6) indicates that *Imp* has no dimension and varies from 0 to 1 depending on G_S, G_{AV} and *C*. G_S varies with stomatal aperture which is affected by environmental factors through leaf water balance. G_{AV} is characterized by three different forms of leaf-to-air convection (*3, 9, 21, 22*). G_{AV} under forced convection mainly depends on wind velocity (*U*) and leaf characteristic dimension (*d*); G_{AV} becomes higher at higher *U* and at smaller *d*. On the other hand, G_{AV} under free convection becomes higher at larger temperature difference (T_L–T_A) between leaf and air. Futhermore, under the condition with lower *U*, larger *d* and larger T_L–T_A, mixed convection (forced convection+free convection) becomes the dominant form of the convection (*9*). Leaf boundary layer conductances for these three forms of convections are

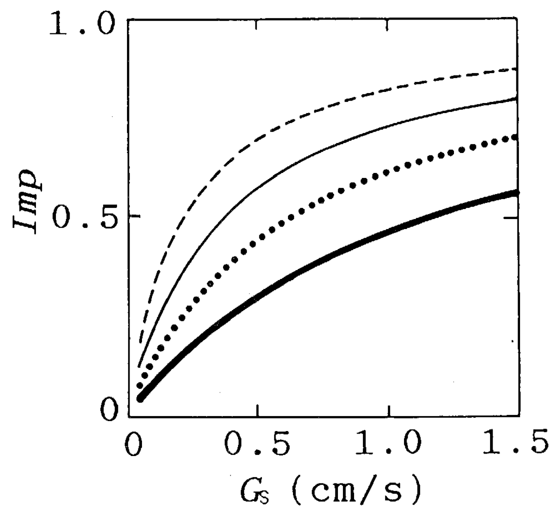

Fig. 1 Relationship between impact coefficient (*Imp*) of evaporative demand and stomatal conductance (G_S) at different leaf boundary layer conductances (G_{AV}) of 0.5 (---), 1.0 (——), 2.0 (· · ·) and 4.0 (**——**) cm/s under an equivalent temperature (T_E) of 25 ℃.

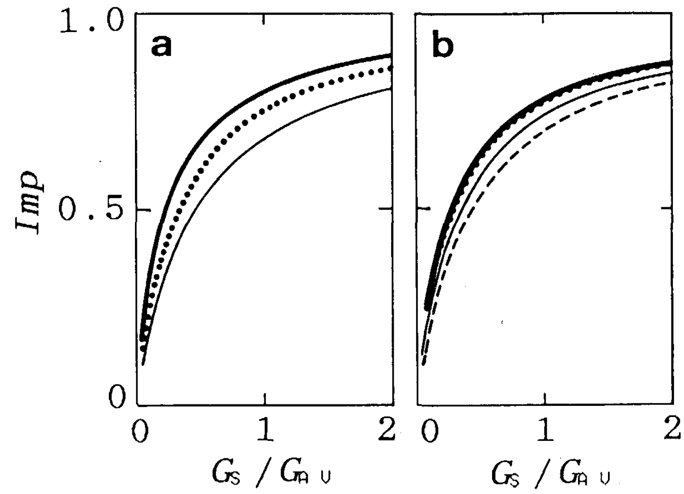

Fig. 2 Relationship between impact coefficient (*Imp*) of evaporative demand and ratio (G_S/G_{AV}) of stomatal conductance (G_S) to leaf boundary layer conductance (G_{AV}) : (a), the relationship under different equivalent temperatures (T_E) of 15 (——), 25 (· · ·) and 35 (▬▬) ℃ at G_{AV} of 1.0 cm/s ; (b), the relationship under different G_{AV}'s of 0.5 (– – –), 1.0 (——), 2.0 (· · ·) and 4.0 (▬▬) cm/s at T_E of 25 ℃.

expressed in APPENDIX II. A physical parameter C depends on n, Δ, γ, G_{AV}, G_{AH} and G_R $(=4\varepsilon_L \sigma T_E{}^3/C_p\,\rho)$ as expressed by Eq. (7). C is also influenced by the equivalent temperature (T_E), because the slope (Δ) of saturation vapor density curve and the radiative transfer conductance (G_R) largely depend on T_E ; T_E was evaluated as $(T_L+T_A)/2$ by using T_L estimated in APPENDIX II.

Figure 1 shows distribution of *Imp* on G_R under different conditions of G_{AV} at T_E of 25℃. *Imp* increased with G_S, and its increase rate became higher at lower G_S and at lower G_{AV}. Furthermore, *Imp* became lower at the higher G_{AV}. Figure 2 shows distribution of *Imp* on G_S/G_{AV} under different conditions of T_E and G_{AV}. *Imp* increased with increase in G_S/G_{AV}, and its increase rate became higher at lower G_S/G_{AV}. Furthermore, the increase pattern of *Imp* with G_S/G_{AV} was scarcely affected by T_E and G_{AV}. Thus, *Imp* varies from 0 to 1 mainly depending on G_S/G_{AV} which is determined by stomatal function in a leaf and physical processes of convection in the leaf boundary layer.

Characteristics in desert plants

It has been well known that plants with small leaves and plants with CAM (crassulacean acid metabolism) are adaptable to sunny, hot and dry conditions of desert regions (*3, 21, 22*). For the small leaves plants, there has been a well established rule that their small dimension (*d*) brings high G_{AV} and G_{AH} which prevent highly irradiated leaves from excessive temperature rise by the strong convective coupling between leaves and atmosphere (*3, 20–22*). However, this high G_{AV} of small leaves can be estimated to impose high evaporative demand through the storong convective coupling, which is

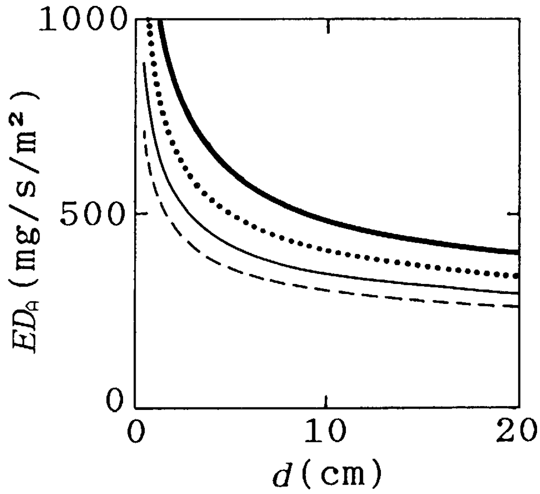

Fig. 3 Relationship between evaporative demand (ED_A) and leaf characteristic dimension (d) at different wind velocities (U) of 25 (- - -), 50 (——), 100 (· · ·) and 200 (━━) cm/s under a desert condition simulated with a high solar irradiance of 800 W/m^2, a high air temperature of 40 ℃ and a high saturation deficit of 40 g/m^3.

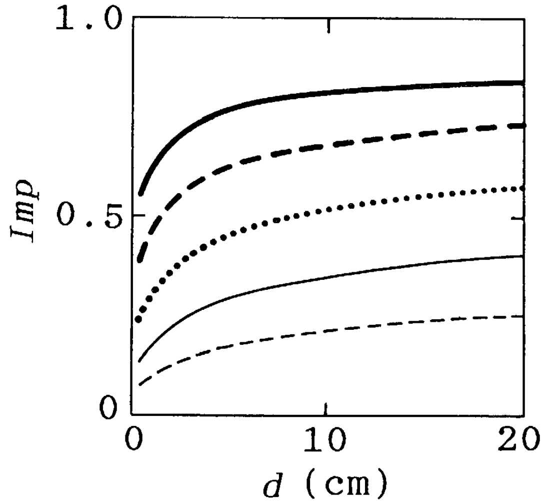

Fig. 4 Relationship between impact factor (Imp) of evaporative demand and leaf characteristic dimension (d) at different stomatal conductances (G_S) of 0.1 (- - -), 0.2 (——), 0.4 (· · ·), 0.8 (━ ━ ━) and 1.6 (━━) cm/s under a desert condition simulated with a high solar irradiance of 800 W/m^2, a high air temperature of 40 ℃ and a high saturation deficit of 40 g/m^3 at a wind velocity of 100 cm/s.

unfavorable for adaptation to desert conditions.

Figure 3 shows distribution of ED_A on d at different U's under a desert condition simulated with T_A of 40 ℃, SD of 40 g/m^3 and R_S of 800 W/m^2. For very small leaves with d smaller than 5 cm, ED_A remarkably increased with decrease in d under all conditions of U. Figure 4 shows distribution of *Imp* on d at different G_S's under the simulated desert condition. In contrast with ED_A, *Imp* of leaves smaller than 5 cm remarkably decreased with decrease in d. This decrease of *Imp* in smaller leaves can be estimated to compensate the unfavorably increased ED_A. Furthermore, the lower *Imp* at lower G_S can indicate that CAM plants have lower *Imp* under high irradiance, because their stomata primarily close during the daytime. Thus, small leaves plants and CAM plants adaptable to desert conditions have the lower *Imp* under the high ED_A condition.

DYNAMICS OF WATER RELATIONS AND IMPACT COEFFICIENT

Oscillations in plant water relations such as transpiration, root water uptake, stomatal movement and leaf expansive growth have been observed to be triggered by changes in environmental factors such as irradiance, humidity and wind velocity (e.g. *1, 2, 6–8, 13, 14, 15*) : Changes in environmental factors imposed ΔE_{AT} on plant water balance, and transient unbalance between transpirational water loss and root water uptake resulted in oscillations in plant water relations. From those observations, it can be suggested that larger ΔE_{AT} brings larger amplitude in the oscillations. That is, the instability of plant water relations can be estimated to depend on ΔE_{AT} which is brought by not only ΔED_A but ΔImp as indicated by Eq. (8).

Under diurnal variations of solar irradiance, stomatal depression around fair midday has been observed even under well watered conditions (*11, 21, 23–25*). However, physical and physiological conditions which induce midday stomatal depression (MSD) have remained to be known well. Therefore, we examined diurnal variations of transpiration, stomatal movement and the impact of ED_A on well watered cucumber plants (*Cucumis sativus* L. cv Chojitsu–Ochiai) on a fair day under different conditions of ED_A in three natural light growth chambers: In each growth chamber, ED_A was controlled around the respective desired values (SED_A) of 140, 80 and 20 mg/m^2/s by manipulating relative humidity (RH) according to variation in solar irradiance (R_S). Transpiration rate per leaf area (E_A) was measured by weighing the plant and pot. G_S was evaluated from E_A and leaf temperature measured by fine thermocouples, and then *Imp* was evaluated from Eq. (6).

Figure 5 shows diurnal variations of R_S, RH, ED_A, E_A, G_S and *Imp*. In two growth chambers with higher SED_A conditions (i.e. lower humidity conditions), RH's were manipulated in the respective ranges from 30% (night) to 45% (midday) and from 55% (night) to 75% (midday), and each ED_A was kept constant at 140 mg/m^2/s and 80 mg/m^2/s. In the growth chamber with the lowest SED_A of 20 mg/m^2/s (i.e. the highest humidity condition), RH was manipulated in the range from 80% (night) to 95% (midday), and ED_A was kept lower than 50 mg/m^2/s: ED_A was controlled at SED_A of 20 mg/m^2/s under lower R_S condition but increased to 50 mg/m^2/s at fair midday by the

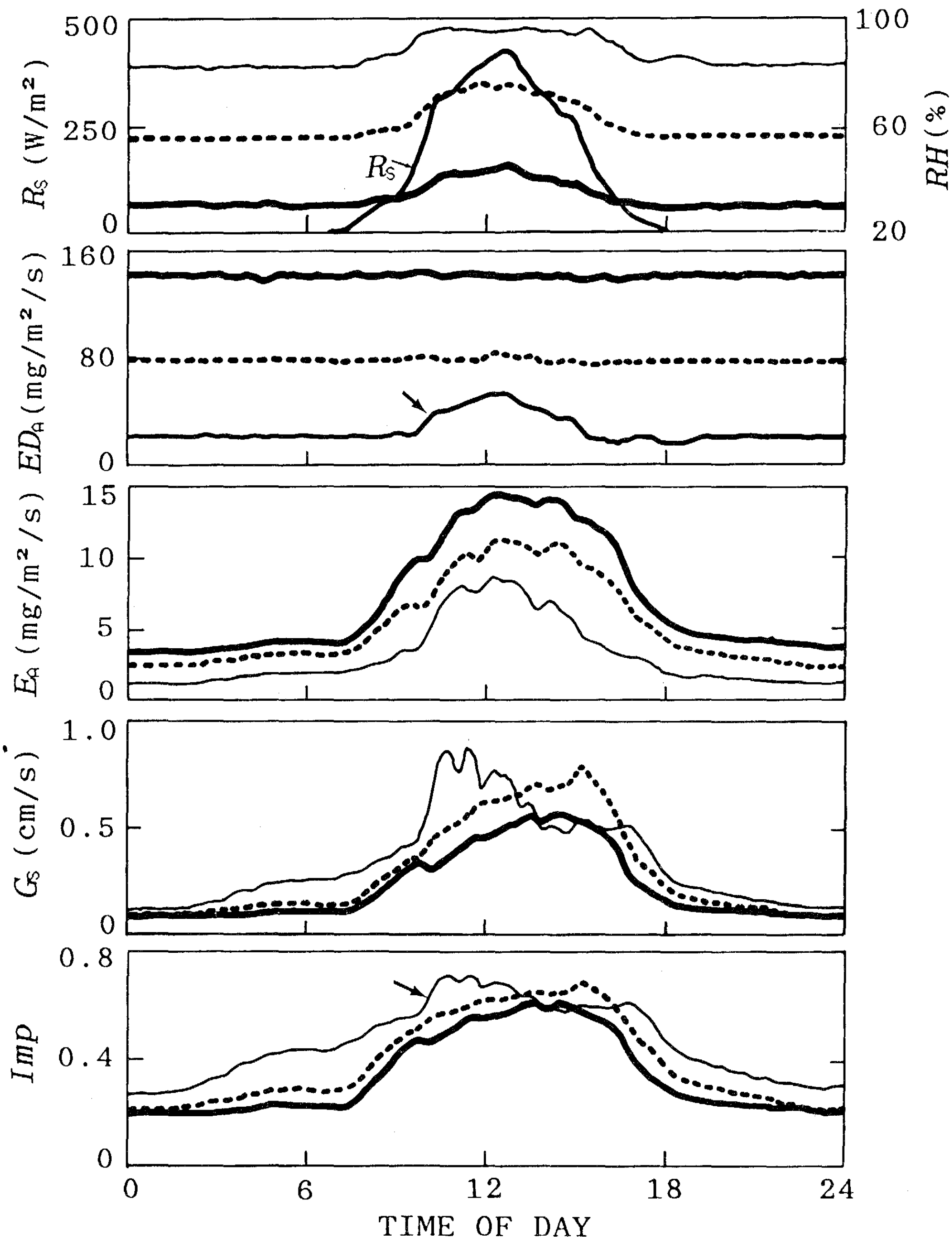

Fig. 5 Diurnal variations of solar irradiance (R_S), relative humidity (RH), evaporative demand (ED_A), impact factor (*Imp*), transpiration rate (E_A) and stomatal conductance on a fair day in three natural light growth chambers, where the respective desired values (SED_A) of ED_A were set at 140 (——), 80 (---) and 20 (——) mg/m²/s at an air temperature of 25 ℃: Arrows in ED_A and *Imp* indicate increments of ED_A and *Imp* which triggered midday stomatal depression under the lowest SED_A of 20 mg/m²/s.

excessive R_S. Only under the lowest SED_A of 20 mg/s/m^2, MSD (i.e. depression in G_S around midday) occurred from about 11:00, although E_A was kept remarkably lower as compared with those found in the higher SED_A chambers. Under the lowest SED_A, larger increments of *Imp* and ED_A (i.e. positive ΔImp and ΔED_A) were found between 10:00 and 11 : 00 as arrowed in Fig. 5. As indicated by Eq. (8), these larger ΔImp and ΔED_A can be estimated to impose larger impact (i.e. larger ΔE_{AT}) on plant water balance and to trigger the transient water deficit and MSD. On the other hand, under the higher ED_A, ΔImp and ΔED_A between 10:00 and 11:00 were remarkably smaller, and MSD was not induced, although the higher water loss (E_A) was caused. Thus, larger ΔImp and ΔED_A can be estimated to induce transient water deficit and stomatal depression even under higher humidity conditions and lower transpiration rates.

CONCLUSION

ED_A of Eq. (1) was used as a quantitative measure of evaporative demand, which can integrate respective influences of four environmental factors (R_S, T_A, *SD* and *U*) and leaf dimension (*d*) on evaporative demand. The impact of ED_A on plant water balance was newly quantified by introducing a coefficient, which was named as "impact coefficient (*Imp*)". *Imp* varied from 0 to 1 with increase in G_S/G_{AV}. That is, the degree of impact of evaporative demand became larger with increase in G_S and with decrease in G_{AV}. This characteristic brought the lower *Imp* to desert plants such as samall leaves plants and CAM plants, and the adaptability of these plants to the desert condition was attributed to this lower *Imp*. Furthermore, dynamic responses of plant water relations to environmental factors were understood in terms of *Imp* as well as ED_A. In particular, the occurence of midday stomatal depression on a fair day was attributed to the larger ΔED_A and ΔImp but not to the higher transpiration rate. Thus, newly introduced *Imp* of ED_A contributed to quantitative and comprehensive understand of environmental effects on plant water relations.

APPENDIX I : List of symbols

a	short wave absorption coefficient of a leaf ($a \simeq 0.5$ for solar irradiance).
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	characteristic dimension of a leaf or an evaporating surface evaluated on the chord basis.
E_A	transpiration rate per unit leaf area.

E_{AT}	theoretical transpiration rate given by Eq. (4) on the basis of leaf heat balance, which can be a quantitative measure of impact of ED_A on plant water balance.
ΔE_{AT}	change in E_{AT}
ED_A	evaporative demand per unit leaf area.
ΔED_A	change in ED_A
g	acceleration of gravity.
G_{AH}	leaf boundary layer conductance for heat transfer.
G_{AV}	leaf boundary layer conductance for vapor transfer.
G_E	parallel conductance of G_{AH} and G_R.
G_{FO}	leaf boundary layer conductance for forced convection.
G_{FR}	leaf boundary layer conductance for free convection.
G_R	radiative transfer conductance $(4\varepsilon_L \sigma T_E^3/C_p \rho)$.
G_S	stomatal conductance.
Imp	impact factor of evaporative demand on plant water balance defined by Eq. (6).
ΔImp	change in Imp.
Le	Lewis number ($\simeq 0.89$ for water vapor).
MSD	midday stomatal depression.
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.
SD	saturation deficit of ambient air.
SED_A	desired value of evaporative demand.
T_A	temperature of ambient air.
T_L	temperature of a leaf or an evaporating surface.
T_E	equivalent temperature evaluated by $(T_L+T_A)/2$.
U	wind velocity of ambient air.
β	coefficient of thermal expansion of air.
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.

κ thermal diffusivity of air.

λ latent heat for vaporization of water.

ν coefficient of kinematic viscosity of air.

ρ density of air.

σ Stefan–Boltzmann constant (5.67×10^{-8} W/m^2/K^4).

APPENDIX II

Leaf boundary conductances (G_{AH} and G_{AV})

G_{AH} and G_{AV} for respective transfers of heat and water vapor were expressed for forced convection (a), free convection (b) and mixed convection (c) as follows (*11, 21*)

(a) Forced convection

$$G_{AH} = G_{FO} = \frac{0.66\kappa^{0.67}}{d^{0.5}\nu^{0.17}}U^{0.5} \tag{A1}$$

$$G_{AV} = G_{FO}/\mathrm{Le}^{0.67} \tag{A2}$$

where Le is the Lewis number ($\simeq$0.89)

(b) Free convection

$$G_{AH} = G_{FR} = \frac{b\beta^{0.25}g^{0.25}\kappa}{d^{0.25}\nu^{0.5}}|T_L-T_A|^{0.25} \tag{A3}$$

$$G_{AV} = G_{FR}/\mathrm{Le}^{0.75} \tag{A4}$$

(c) Mixed convection

$$G_{AH} = G_{FO} + G_{FR} \tag{A5}$$

$$G_{AV} = G_{FO}/\mathrm{Le}^{0.67} + G_{FR}/\mathrm{Le}^{0.75} \tag{A6}$$

Temperature (T_L) of an evaporating surface

For evaluating T_E, Δ, G_R, G_{AH} and G_{AV}, temperature (T_L) of an evaporating wetted surface is required to be determined. T_L was estimated from environmental factors on the basis of heat balance as follows (*10, 11*)

$$T_L = T_A + \frac{(2/n)\gamma(G_E/G_{AV})}{(2/n)\gamma(G_E/G_{AV})+\Delta}\times\left\{\frac{aR_S-2\sigma\varepsilon_L(1-\varepsilon_A)T_A{}^4}{2C_p\rho G_E}-\frac{SD}{(2/n)\gamma(G_E/G_{AV})}\right\} \tag{A7}$$

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