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Kitano, Masaharu
Biotron Institute Kyushu University

Eguchi, Hiromi
Biotron Institute Kyushu University

Matsui, Tsuyoshi
Biotron Institute Kyushu University

https://hdl.handle.net/2324/8106

出版情報：BIOTRONICS. 12, pp.19-27, 1983-10. Biotron Institute, Kyushu University
バージョン：
権利関係：

BIOTRONICS **12**, 19–27, 1983

ANALYSIS OF HEAT BALANCE OF LEAF WITH REFERENCE TO STOMATAL RESPONSES TO ENVIRONMENTAL FACTORS

Masaharu KITANO, Hiromi EGUCHI and Tsuyoshi MATSUI

Biotron Institute, Kyushu University, Fukuoka 812, Japan

(Received April 2, 1983)

KITANO, M., EGUCHI H. and MATSUI T. *Analysis of heat balance of leaf with reference to stomatal responses to environmental factors.* BIOTRONICS **12**, 19–27, 1983. The heat balance of the intact cucumber leaf was examined by measuring leaf temperature and environmental factors, and transpiration rate and leaf conductance were calculated in course of time. When the leaf was radiated, leaf temperature, transpiration rate and leaf conductance rose rapidly and thereafter varied with the air conditions. Air temperature and saturation deficit affected the amplitudes of leaf conductance oscillation (period of 25–30 min); the amplitudes were larger at lower air temperatures and at higher saturation deficits. The saturation deficit influenced stomatal behaviour directly through change in vapour density difference (Δw) between inside of the leaf and the air, and stomatal response to air humidity was found in the physical process. However, the air temperature did not relate to Δw, as Δw was almost constant even when the air temperature was changed, for the reason that saturation vapour density inside of the leaf increased exponentially with temperature rise in the leaf. Thus, it seems that stomatal response to air temperature could not be caused directly through the physical process, but could be caused mainly through the physiological functions.

INTRODUCTION

In the plant-environment system, leaf temperature and heat balance of the leaf relate to each other through the heat transfer processes of radiation, sensible heat and latent heat (*3*, *8*, *21*). Therefore, stomatal opening is responsible for the leaf temperature through the latent heat transfer process of stomatal transpiration, which is affected by air temperature, air humidity, air velocity and radiation (*8*, *16*, *17*). So, the heat balance method may make it possible to analyze stomatal responses to environments in on-line measurements of the leaf temperature and the environmental factors (*2*, *10*, *12*).

Present paper deals with analysis of heat balance of the leaf for evaluation of stomatal responses to the environment.

MATERIAL AND METHODS

Cucumber plants (*Cucumis sativus* L. var. Hort. Chojitsu-Ochiai No. 2) were used in the experiments. The plants were potted in moistened Vermiculite and grown at air temperature of 25±1°C and relative humidity of 70±5% in a phytotron glass room. When the plant was 20 days old (5 leaves stage), the intact 3rd leaf of healthy growth was used as a specimen.

In a growth chamber, ambient air temperatures and humidities (saturation deficits) were controlled at 20, 25, 30 and 35±0.5°C, and at 5, 10, 15, 20 and 25±1.2 gm^{-3}, respectively. The direction of air current was parallel to the leaf surface, and the air velocity was 70±6 cm sec^{-1}. The carbon dioxide concentration in the air was kept at 330±10 ppm. The leaf was fixed horizontally and radiated vertically with tungsten light after keeping the plant in darkness for 15 hr. The total radiant flux density was 186±6 mW cm^{-2} in wavelength range of 0.35–60 μm, which consisted of short wave radiant flux density of 56 mW cm^{-2} in 0.35–3 μm (4 mW cm^{-2} in 0.4–0.7 μm) and long wave radiant flux density of 130 mW cm^{-2} in 3–60 μm. The thermocouple (copper-constantan) of 0.1 mm in diameter was inserted into the leaf. The voltage (0–2 mV) of the thermocouple was recorded as the temperature (0–50°C) in course of time with an accuracy of ±0.1°C. Mean of the temperatures measured at six points in a leaf was used as a representative temperature of the leaf.

RESULTS AND DISCUSSION

Heat balance of a leaf

In the heat balance of a leaf, transpiration rate (E, g cm^{-2} min^{-1}) can be expressed as a function of latent heat (λ, J g^{-1}) for vapourization of water, net radiant flux density (R_n, mW cm^{-2}), storage heat flux density (ST, mW cm^{-2}), sensible heat flux density (SH, mW cm^{-2}) and the metabolic heat. In the leaf, R_n, ST and SH can be given by the following equations,

$$R_n = R_i - (1 - A_b) \cdot R_s - 2 \cdot \varepsilon \cdot \sigma \cdot (273.1 + T_l)^4 \tag{1}$$

$$ST = 10^3 \cdot s \cdot m \cdot \frac{dT_l}{dt} \tag{2}$$

$$SH = \frac{2 \times 10^3 \cdot C_p \cdot \rho \cdot (T_l - T_a)}{r_{ah}} \tag{3}$$

The metabolic heat in the leaf was remarkably small and neglected. Therefore, E can be calculated from

$$E = \frac{6 \times 10^{-2} \cdot (R_n - ST - SH)}{\lambda} \tag{4}$$

On the other hand, leaf conductance can be given by the following equation (*8*, *10*, *12*, *21*),

$$C_l = \left[\frac{1.2 \times 10^{-4} \cdot \{w(T_l) - \frac{RH}{100} \cdot w(T_a)\}}{E} - r_{ah} \cdot Le^{2/3} \right]^{-1} \tag{5}$$

The coefficient (A_b) of short wave absorption by the cucumber leaf was obtained in the following manners (*20*): Stomatal and cuticular transpirations were inhibited by applying abscisic acid (10^{-4} M) (*13*, *18*) and microcrystalline wax

(2×10^{-2} M) to the leaf. On the other hand, the black body plate was prepared with an aluminium plate of 0.4 mm in thickness, which was coated with camphor soot, as heat capacity (0.097 J cm^{-2} °C^{-1}) of the plate was almost the same as that of the leaf used. The respective temperatures of the leaf and of the black body plate were measured for a few seconds after radiation of the tungsten light under the air condition where the heat transferring between the leaf and the air was minimized (low velocity of air current and high humidity). Then, the respective storage heat flux densities of the leaf and of the black body plate were obtained from rising rates of those temperatures, and A_b was given by the ratio of the storage heat flux density of the leaf to that of the black body plate; A_b was 0.32 ± 0.02 in this experiment.

Boundary layer resistance (r_{ah}, sec cm^{-1}) can be given by a function (*9*, *11*) of resistance (r_f, sec cm^{-1}) to free convection and resistance (r'_{ah}, sec cm^{-1}) to forced convection as follows,

$$r_{ah}=\frac{r_f\cdot r'_{ah}}{r_f+r'_{ah}} \tag{6}$$

Respective resistances to free convection and to forced convection are

$$r_f=\frac{d}{\alpha\cdot D_h\cdot(Gr\cdot Pr)^{1/4}} \tag{7}$$

$$r'_{ah}=\beta\cdot\left(\frac{d}{U}\right)^{1/2} \tag{8}$$

As the proportional constant, α of 0.52 was used, which is almost the constant for the free convection on horizontal flat plate (*11*, *19*, *24*). The characteristics of the ambient air current is responsible for the proportional constant (β). In this

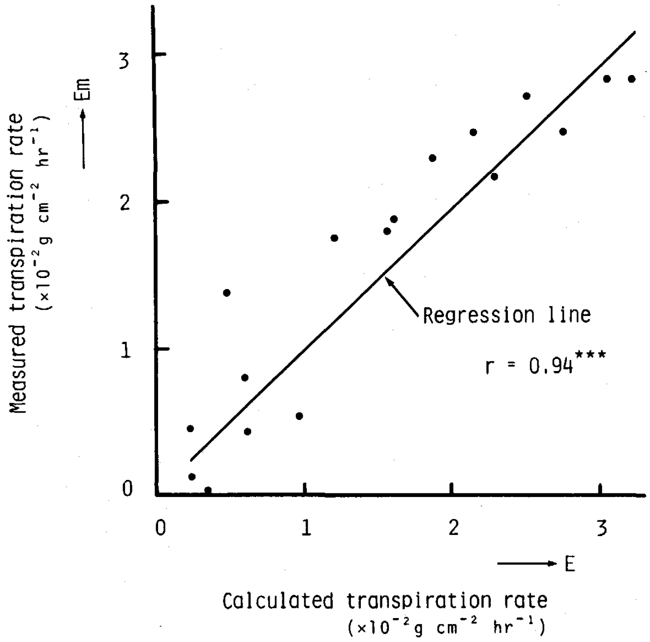

Fig. 1. Correlation between calculated and measured values of transpiration rate.

experiment, β was obtained in the following manners (*12*, *15*, *25*): The transpiration was inhibited in a leaf, and the equilibrium temperature of the radiated leaf was measured at each air velocity (U) of 44, 66, 78, 146 and 184 ± 6 cm sec^{-1} in the growth chamber. The sensible heat flux density (SH) was estimated equal to the net radiant flux density (R_n) when the leaf temperature reached to the equilibrium. Then, r_{ah} can be given by

$$r_{ah}=\frac{2\times10^3\cdot C_p\cdot\rho\cdot(T_l-T_a)}{R_n} \tag{9}$$

From Eqs. 6, 7, 8 and 9, β of 0.91 ± 0.10 $\text{sec}^{1/2}$ cm^{-1} was obtained in this experiment.

Figure 1 shows correlation between calculated and measured transpiration rates. The measured transpiration rate was obtained by weighing the plant and pot where the soil surface was sealed with polyethylene film to prevent the evaporation. There was high correlation ($r=0.94$, $p<0.001$) between calculated and

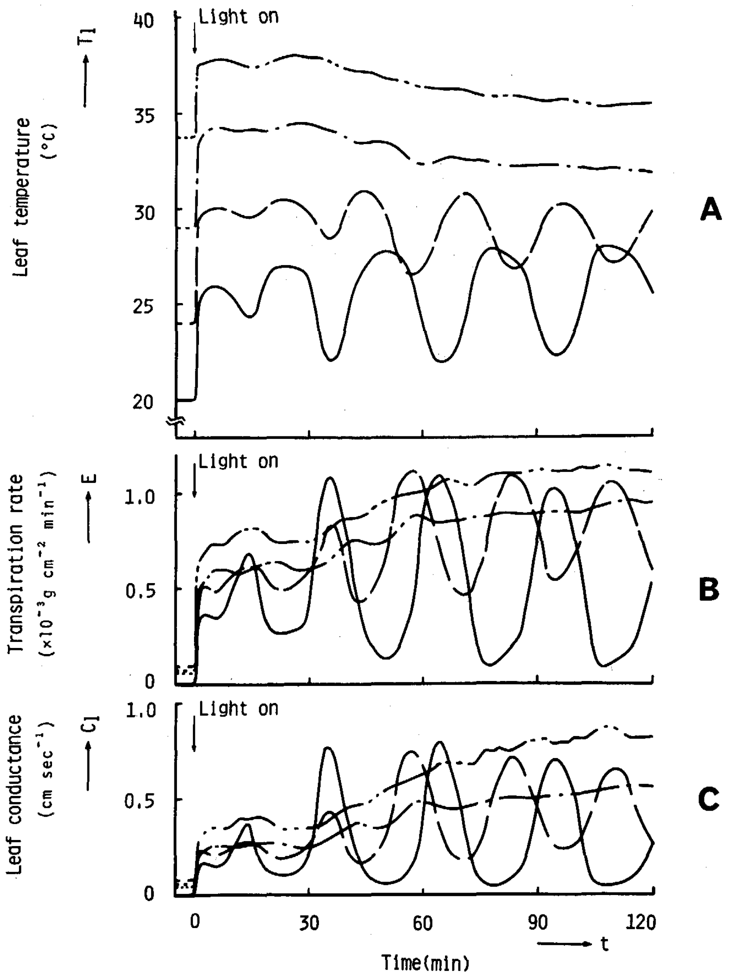

Fig. 2. Patterns of leaf temperature (A), transpiration rate (B) and leaf conductance (C) in course of time at respective air temperatures of 20 (——), 25 (— —), 30 (— · —) and 35°C (— · · —) at a constant saturation deficit of 15 g m^{-3}.

measured transpiration rates. Thus, it could be estimated that transpiration rate and leaf conductance calculated from heat balance of the leaf can be used for evaluation of stomatal responses to the environmental factors.

Stomatal responses to the environment

Figure 2 shows the patterns of T_l, E and C_l in course of time at different air temperatures and a constant saturation deficit of 15 g m^{-3}. When the leaf was radiated, T_l, E and C_l rose rapidly and thereafter appeared in variations at the respective air temperatures. The elevations of T_l, E and C_l declined at lower air temperatures. At air temperatures of 20 and 25°C, T_l, E and C_l oscillated with the period of 25–30 min, synchronizing with each other. The amplitudes were larger at air temperature of 20°C as compared with those at 25°C. At air temperatures of 30 and 35°C, however, the oscillations did not occur.

In general, it is known that the evaporative demand affects the water balance of the leaf through stomata (*1*, *4–7*, *10*, *14*, *22*, *23*, *26*). The stomatal response to evaporative demand has been explained in the physical process by Farquhar and Cowan (1974) as "environmental gain ($G=\partial E/\partial C_l$)": they reported that C_l oscillation occurs more sensitively at higher evaporative demands where G is higher (*6*).

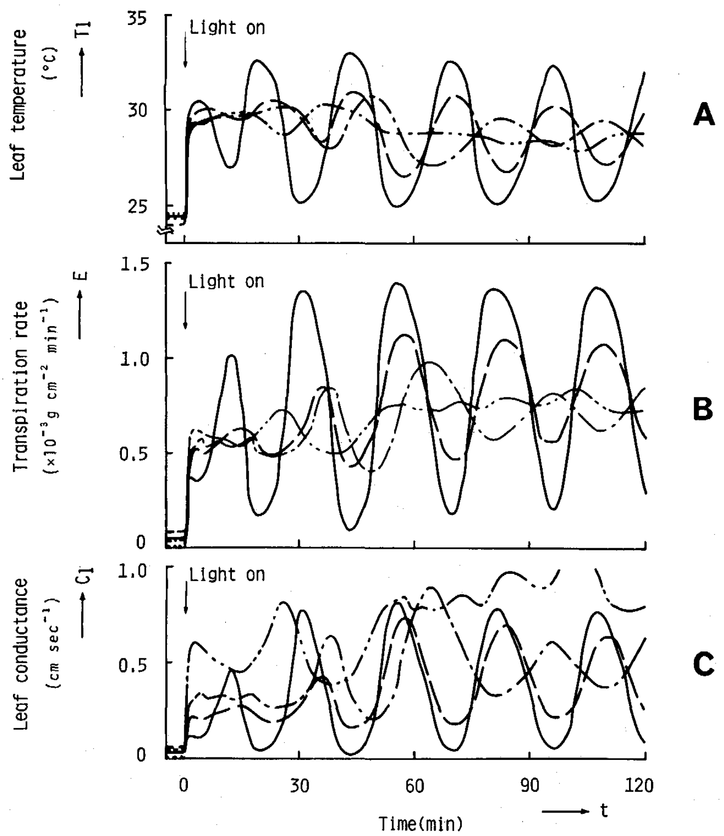

Fig. 3. Patterns of leaf temperature (A), transpiration rate (B) and leaf conductance (C) in course of time at respective saturation deficits of 20 (——), 15 (— —), 10 (– – –) and 5 g m^{-3} (– · – ·) at a constant air temperature of 25°C.

In this experiment, the degree of evaporative demand in plant-environment system was represented by vapour density difference (Δw, g m^{-3}) between inside of the leaf and the air. The temperature differences (ΔT) between the air and the radiated leaf were smaller at higher air temperatures, but changes in Δw did not relate necessarily to the air temperatures, as Δw was almost constant even when air temperature was changed, for the reason that saturation vapour density, w (T_l) inside of the leaf increased exponentially with temperature rise in the leaf; when air temperatures were 20, 25, 30 and 35°C, Δw were about 21, 21, 20 and 20 g m^{-3}, respectively. Thus, the air temperature influenced the amplitude of C_l oscillations, but did not relate to evaporative demand. From these facts, it could be conceivable that stomatal response to air temperature could not be caused only through the physical process.

Figure 3 shows the patterns of T_l, E and C_l in course of time at different saturation deficits and a constant air temperature of 25°C. At saturation deficits of 10, 15 and 20 g m^{-3}, T_l, E and C_l oscillated with the period of 25–27 min, synchronizing with each other. The amplitudes were larger at higher saturation deficits. At the lowest saturation deficit of 5 g m^{-3}, however, the oscillations were not clear, and C_l oscillation occurred more sensitively at higher saturation deficits. The saturation deficit related to Δw; when saturation deficits were 5, 10, 15 and 20 g m^{-3}, Δw were about 11, 16, 21 and 26 g m^{-3}, respectively. Thus, evaporative demand increased in proportion to rise in the saturation deficit. This fact indicates that air humidity influences stomatal behaviour mainly through the physical process.

This effect of Δw on stomatal behaviour was similar to that of G. In this experiment, C_l and E were examined in change in Δw under radiation. Within

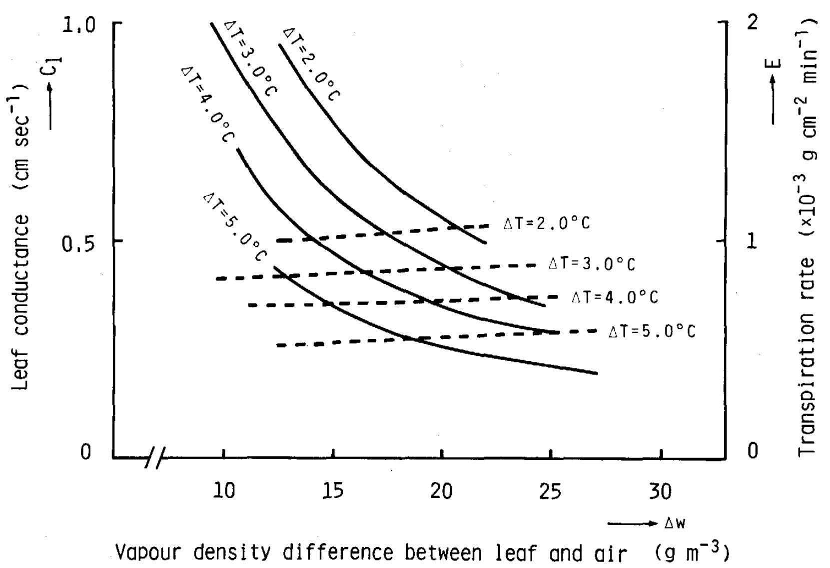

Fig. 4. Patterns of distributions of leaf conductance (——) and transpiration rate (-----) on vapour density difference between the leaf and the air at the time of 3–120 min after radiation at an air temperature of 25°C; ΔT is temperature difference (T_l-T_a) between the leaf and the air.

about 3 min after radiation, C_l and E increased with rise in T_l as found in Figs. 2 and 3. Rise in T_l made Δw increase exponentially, and this event resulted in $dC_l/d\,(\Delta w)>0$ and $dE/d\,(\Delta w)>0$. From this fact, it could be estimated that when the evaporative demand (Δw) rapidly increases for a few minutes after radiation, the stomatal movement occurs in the hydropassive process. On the other hand, at the time of 3–120 min after radiation, patterns of C_l and E appeared different from those within about 3 min after radiation. Figure 4 shows the distributions of C_l and E on Δw at respective ΔT where T_a is 25°C. In this time course, the pattern of C_l decreased with increase in Δw, but E was scarcely affected by Δw; $dC_l/d\,(\Delta w)\leqq 0$ and $dE/d\,(\Delta w)\doteqdot 0$. That is, C_l varied with Δw, out of relation to E. Similar patterns were observed at the other air temperatures.

Thus, the evaporative demand related directly to effect of air humidity on stomatal behaviour, but did not relate necessarily to effect of air temperature. So, it seems that stomatal response to air temperature could be caused mainly through physiological functions complicated with many factors.

APPENDIX: LIST OF SYMBOLS

A_b	coefficient of short wave absorption by leaf.
C_l (cm sec^{-1})	leaf conductance.
C_p (J g^{-1} °C^{-1})	specific heat of air.
d (cm)	characteristic length of leaf.
D_h (cm^2 sec^{-1})	thermal diffusivity of air.
E (g cm^{-2} min^{-1})	transpiration rate.
G (g m^{-3})	environmental gain.
Gr	Grashof number.
Le	Lewis number.
m (g cm^{-2})	leaf weight per unit area.
Pr	Prandtl number.
r_{ah} (sec cm^{-1})	boundary layer resistance of leaf to heat transfer.
r'_{ah} (sec cm^{-1})	resistance to forced convection.
r_f (sec cm^{-1})	resistance to free convection.
RH (%)	relative humidity.
R_i (mW cm^{-2})	total radiant flux density.
R_n (mW cm^{-2})	net radiant flux density.
R_s (mW cm^{-2})	short wave radiant flux density.
s (J g^{-1} °C^{-1})	specific heat of leaf.
SH (mW cm^{-2})	sensible heat flux density.
ST (mW cm^{-2})	storage heat flux density.
t (sec)	time.
T_a (°C)	air temperature.
T_l (°C)	leaf temperature.
ΔT (°C)	T_l-T_a.
U (cm sec^{-1})	air velocity.
w (T_a) (g m^{-3})	saturation vapour density at air temperature of T_a.
w (T_l) (g m^{-3})	saturation vapour density at leaf temperature of T_l.
Δw (g m^{-3})	$w\,(T_l)-\frac{RH}{100}\cdot w\,(T_a)$.

α	proportional constant in Eq. 7.
β (sec$^{1/2}$ cm^{-1})	proportional constant in Eq. 8.
ε	emissivity of leaf.
λ (J g^{-1})	latent heat for vapourization of water.
ρ (g cm^{-3})	density of air.
σ (mW cm^{-2} K^{-4})	Stefan-Boltzmann constant.

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