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HYDROACTIVE AND HYDROPASSIVE MOVEMENTS OF STOMATA RESPONDING TO VISIBLE AND INFRARED RADIATIONS

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KITANO M. and EGUCHI H. *Hydroactive and hydropassive movements of stomata responding to visible and infrared radiations.* BIOTRONICS **17**, 49–57, 1988. Movements of stomata responding to visible and infrared radiations were analyzed in an intact cucumber leaf by applying an improved heat balance method for evaluation of transpiration rate and leaf conductance. In step response to the visible radiation, photosynthetically active radiation (PAR) induced dynamics of water balance in the whole leaf through osmotic change in guard cells and mesophyll, and resulted in hydroactive stomatal oscillation with a natural period of about 30 min at the higher radiant intensities. In the infrared radiation, leaf-air vapor density difference ($W_L - W_A$) was rapidly raised by the thermal effect of the radiation, and subsequently rapid increase in the peristomatal transpiration caused hydropassive stomatal opening through hydraulic interaction between guard cells and adjacent epidermal cells. This hydropassive stomatal opening was more active at the more rapid changes in $W_L - W_A$; there was a linear relationship between degree of the hydropassive stomatal opening and changing rate of $W_L - W_A$. Thus, the visible radiation containing PAR brought about the hydroactive stomatal movement mainly through physiological processes, whereas the infrared radiation caused the hydropassive stomatal movement through physical processes in response to the thermal effect.

Key words: *Cucumis sativus* L.; cucumber leaf; hydroactive stomatal movement; hydropassive stomatal movement; visible radiation; infrared radiation; leaf heat balance method.

INTRODUCTION

In general, natural and artificial lights contain infrared radiation with visible radiation. The infrared radiation raises leaf temperature and subsequently increases water loss from leaf through rise in leaf-air vapor density difference (*5*). Stomatal movements have been studied in those lights composed of both visible and infrared radiations. For better understanding of stomatal movements, it is further necessary to examine respective effects of visible and infrared radiations on stomatal movements. In studies on stomatal movements, porometers and assimilation chambers have been widely employed for measurement of hydroactive stomatal movement (*2*, *6–8*, *13–16*). On the other hand, the hydropassive stomatal movement has been examined by microscopic inspection (*9*, *12*, *16*), for the reason that the hydropassive movement is too rapid and too transient to measure it reliably by porometers and assimilation chambers (*6*, *14*). In the previous paper (*10*), we have improved leaf heat balance method and analyzed hydroactive and hydropassive movements of stomata responding to dynamics of air condition and the tungsten light with both visible and infrared radiations.

The present paper deals with analyses of stomatal movements in respective visible and infrared radiations by applying the improved method of leaf heat balance.

MATERIAL AND METHODS

Plant material

Cucumber plants (*Cucumis sativus* L. var. Hort. Chojitsu-Ochiai) were potted in Vermiculite moistened with nutrient solution and grown at an air temperature of 23°C and a relative humidity of 70% under an artificial light of metal halide lamps at a photosynthetic photon flux density (PPFD) of 200 μmol m^{-2} s^{-1} with a photoperiod of 12 h (8:00–20:00). The intact 3rd leaf (about 20 cm long) of healthy plants at the 5 leaf stage was used as a specimen.

Experimental conditions

The leaf was fixed horizontally by supporting fine threads in an artificial light growth chamber, where air temperature and saturation deficit were controlled at 25°C and 15 g m^{-3} respectively. The direction of air current was parallel to the leaf surface, and the mean air velocity was about 0.7 m s^{-1} with a turbulence intensity of about 10%. After keeping the plant in the dark for 15 h, the leaf was irradiated with respective visible and infrared radiations from a tungsten lamp (1 kW): The tungsten light was divided into visible (V) and infrared (I) radiations by using an infrared absorbing filter (F_V, transmitting visible light; HG, Ohara Optical Glass Mfg. Co., Ltd.) and a visible light absorbing filter (F_I, transmitting infrared; RT2, Ohara Optical Glass Mfg. Co., Ltd.) as shown in Fig. 1 (The spectrum of the radiation transmitted through F_V filter distributed in a wave length region of 300 to 1000 nm, and it was called briefly "visible radiation" in this paper). Three radiant intensities in the respective radiations (V-a, b, c in the visible radiation and I-a, b, c in the infrared radiation) were set by adjusting the distance between the leaf and the light source; the visible radiations of V-a, b, c had intensities of 120, 30 and 7.5 W m^{-2} (200, 50 and 12.5 μmol m^{-2} s^{-1} in PPFD) respectively, and the infrared radiations of I-a, b, c had respective intensities of 540, 270 and 135 W m^{-2}. Step responses of stomatal movement to the respective V-a, b, c and I-a, b, c were examined. Furthermore, ramp response to the infrared radiation was examined by increasing the radiant intensity with different gradients of 140 and 35 W m^{-2} min^{-1} by adjusting the electric power applied to the lamp through a silicon controlled rectifier (SCR).

Evaluations of transpiration rate and leaf conductance

Transpiration rate (E) and leaf conductance (C_L) were analyzed in visible and

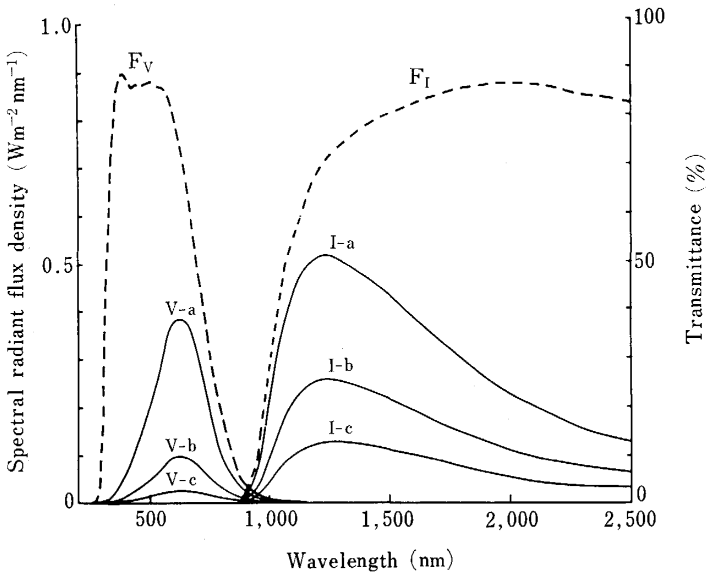

Fig. 1. Spectral transmittances (------) of an infrared absorbing filter (F_V, transmitting visible light) and a visible light absorbing filter (F_I, transmitting infrared), and spectral energy distributions (——) of visible radiations (V-a, b, c) transmitted through F_V filter and infrared radiations (I-a, b, c) transmitted through F_I filter from a tungsten lamp (1 kW): V-a, b, c are respective intensities of 120, 30 and 7.5 W m^{-2} (200, 50 and 12.5 μmol m^{-2} s^{-1} in PPFD), and I-a, b, c are 540, 270 and 135 W m^{-2}.

infrared radiations by applying an improved heat balance method reported in the previous paper (*10*). The heat balance method made it possible to evaluate E and C_L in on-line measurement under the condition where the whole leaf was directly exposed to the environment. E and C_L were given by

$$E=\frac{R_N-H-S_T}{\lambda}$$

$$=\Big\{R_I-(1-A_S)R_S-(1-A_L)R_L-2\varepsilon\sigma(273.15+T_L)^4$$

$$-2C_P\rho(T_L-T_A)/r_A-sm\frac{\Delta T_L}{\Delta t}\Big\}/\lambda \qquad (1)$$

$$C_L=\left(2\frac{W_L-W_A}{E}-r_A\mathrm{Le}^{2/3}\right)^{-1} \qquad (2)$$

where R_N is the net radiant flux density, H the sensible heat flux density, S_T the storage heat flux density, λ the latent heat for vaporization of water, R_I the total radiant flux density, R_S the short wave radiant flux density, R_L the long wave radiant flux density, A_S the short wave absorptivity of leaf, A_L the long wave absorptivity of leaf, ε the long wave emissivity of leaf, σ the Stefan-Boltzmann constant, T_L the leaf temperature, T_A the ambient air temperature, C_P the specific heat of air, ρ the density of air, r_A the leaf boundary layer resistance to heat transfer, s the specific heat of leaf, m the leaf weight per unit area, Δt the time interval, W_L

the water vapor density of intercellular space within leaf, W_A the water vapor density of ambient air and Le the Lewis number.

The values for symbols on the right sides of Eqs. (1) and (2), such as environmental factors, leaf temperature, boundary layer resistance and leaf properties, were determined in the same manners as those reported in the previous paper (*10*). For exact analysis of leaf heat balance, the evaluation of r_A is most important. In this heat balance method, r_A was evaluated for the mixed (forced and free) convection by a parallel resistance model as

$$r_A = \frac{r_A' \cdot r_F}{r_A' + r_F}$$

where r_A' is the boundary layer resistance for forced convection and r_F is the boundary layer resistance for free convection.

For the rough surface cucumber leaf used, r_A' was evaluated experimentally to be 0.57 s cm^{-1} at a Reynolds number of 0.9×10^4 in the growth chamber, and r_F dependent on $T_L - T_A$ was evaluated theoretically by using Grashof number. The short wave absorptivity (A_S), which varied with spectral composition of radiation, was evaluated to be 0.64 for the visible radiation and 0.53 for the infrared radiation.

RESULTS AND DISCUSSION

Figure 2 shows the step responses of T_L, E and C_L to the respective visible radiations of V-a, b, c. In the previous paper, it has been examined that the present heat balance method is reliable for evaluation of E and C_L in visible radiation (*10*). Respective T_L, E and C_L appeared in different patterns at the different radiant intensities, and variations of T_L, E and C_L were more active at the higher radiant intensities. At the highest radiant intensity (V-a), T_L, E and C_L oscillated with a period of about 30 min, and the levels of E and C_L became higher. At the lowest radiant intensity (V-c), T_L, E and C_L were scarcely affected by the radiation.

It is well known that photosynthetically active radiation (PAR) causes osmotic change in guard cells and mesophyll which contain chlorophyll, and also known that the osmotic change brings dynamics of water balance in the whole leaf through the hydraulic feedback system, and in some cases this dynamics develops to the hydroactive stomatal oscillation with a natural period of about 30 min under high evaporative demand (*2*, *3*, *7*, *10*, *13*, *16–18*). From these facts, it could be suggested that the radiation of V-a (high PPFD) perturbed water balance in the whole leaf and induced the hydroactive stomatal oscillation. On the other hand, the radiation of V-c (low PPFD) scarcely affected the water balance.

Figure 3 shows the step responses of T_L, E and C_L to the respective infrared radiations of I-a, b, c. In the response to I-a, transpiration rate was also measured by weighing the plant and pot to examine accuracy of the heat balance method in the infrared radiation. E agreed well with the measured transpiration rate (E_M), even when $T_L - T_A$ was large and H was high in the infrared radiation. This indicates that the heat balance method is reliable for evaluations of E and C_L even in the infrared radiation. When the leaf was irradiated, T_L increased rapidly. E

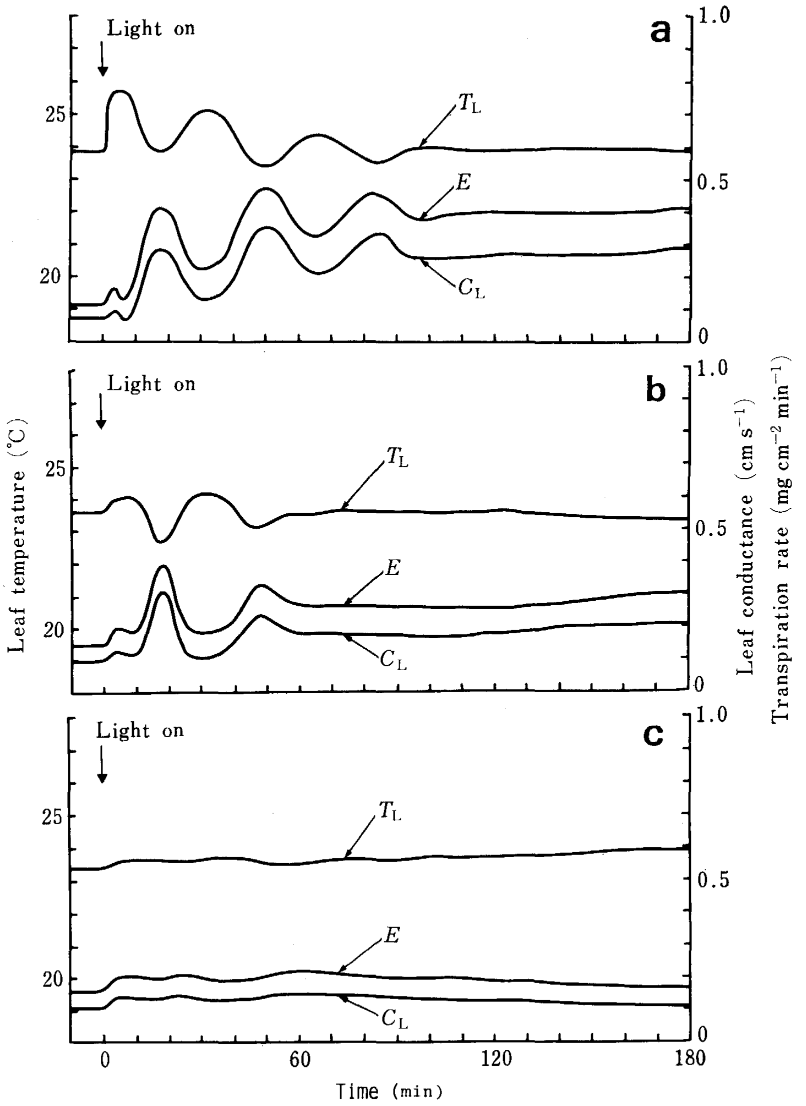

Fig. 2. Step responses of leaf temperature (T_L), transpiration rate (E) and leaf conductance (C_L) to the visible radiations of V-a (a; 120 W m^{-2}), V-b (b; 30 W m^{-2}) and V-c (c; 7.5 W m^{-2}) at an ambient air temperature of 25°C and a saturation deficit of 15 g m^{-3}.

and C_L rose temporarily just after the start of irradiation and thereafter dropped to the same levels as those in the dark, respectively. The temporary rises in E and C_L were more remarkable at the higher radiant intensities.

Rapid rise in evaporative demand perturbs the hydraulic interaction between guard and adjacent epidermal cells by inducing rapid increase in the peristomatal transpiration (*12*). It has been found that rapid turgor loss of the epidermal cells which have mechanical advantage to the guard cells, causes temporary stomatal opening through the hydropassive process (*1*, *4*, *9*, *11*, *13*, *16–18*). When the leaf was heated by the infrared radiation, leaf-air vapor density difference ($W_L - W_A$),

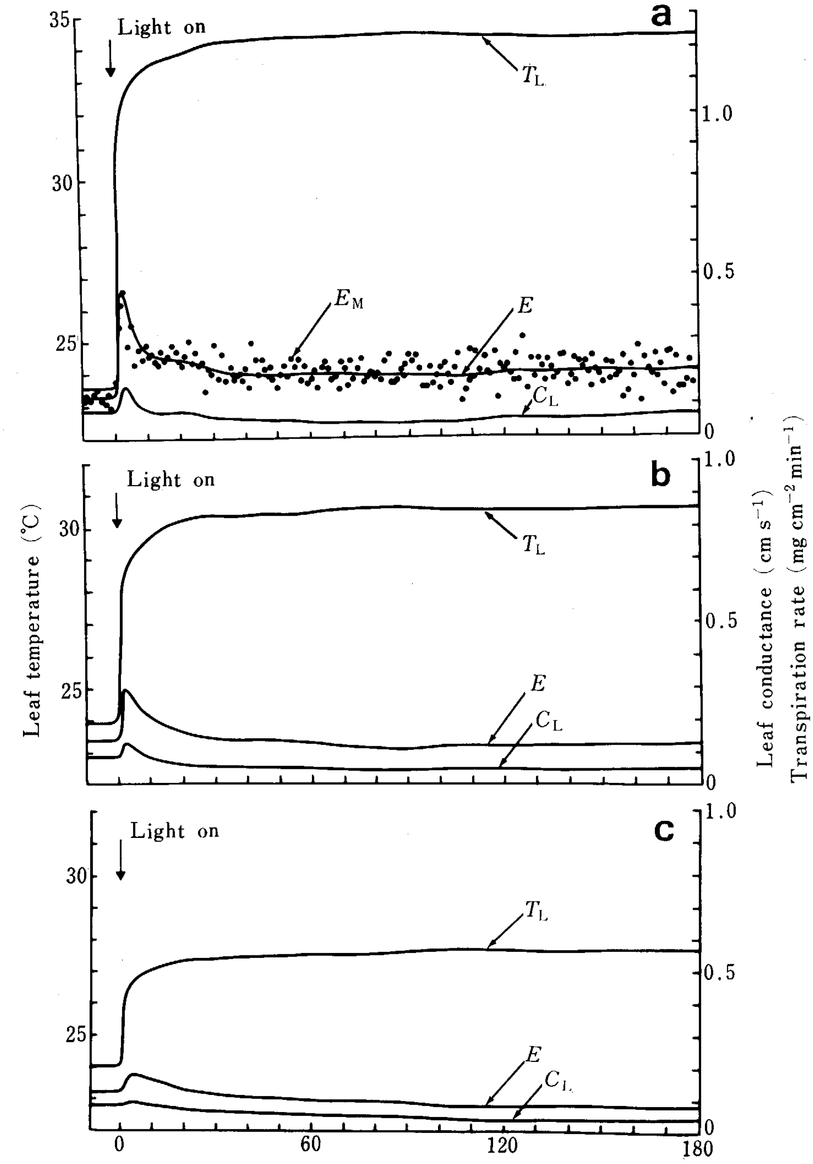

Fig. 3. Step responses of leaf temperature (T_L), transpiration rate (E) and leaf conductance (C_L) to the infrared radiations of I-a (a; 540 W m^{-2}), I-b (b; 270 W m^{-2}) and I-c (c; 135 W m^{-2}) at an ambient air temperature of 25°C and a saturation deficit of 15 g m^{-3}: E_M in (a) is transpiration rate measured by weighing the plant and pot.

which is responsible for the evaporative demand, rapidly increased together with rise in T_L. Thus, it was suggested that the temporary rises in E and C_L just after the start of infrared irradiation can be caused by the hydropassive stomatal opening through the thermal effect of the infrared radiation. This thermal effect of radiation was found slightly also in the visible radiation (Fig. 2). Furthermore, stomatal closure subsequent to the hydropassive opening in the infrared radiation was considered to be induced by turgor loss in the stomatal complex, which was caused by the excessive transpiration during the stomatal opening under high $W_L - W_A$. From the more active hydropassive openings at the higher infrared intensities, it could be supposed that activity of the hydropassive stomatal movement depends on changing rate of evaporative demand through turgor unbalance between guard cells and adjacent epidermal cells.

In order to examine the relationship between changing rate of the evaporative demand and activity of hydropassive stomatal movement, ramp responses to the infrared radiation were also analyzed. Figure 4 shows step responses (a) and ramp responses (b and c) of T_L, E and C_L to the infrared radiation. In the step response (a), the leaf was irradiated by I-a, and in the ramp responses of (b) and (c), the infrared radiant intensities increased with the respective gradients of 140 and 35 W m^{-2} min^{-1} to the same intensity of I-a. The hydropassive stomatal opening in the ramp responses were sluggish in comparison with that in the step response to I-a. In the ramp response (c) with the lower gradient of radiant intensity, the hydropassive stomatal opening was scarcely found. This indicates that the hydropassive stomatal movement occurs more actively when the leaf was exposed to the more rapid change in evaporative demand through thermal effect on leaf temperature.

Figure 5 shows distributions of dE/dt and dC_L/dt on $d(W_L - W_A)/dt$ during the hydropassive stomatal opening in step and ramp responses to the infrared radiation. At $d(W_L - W_A)/dt$ larger than 1 g m^{-3} min^{-1}, the linear relationships were found, and both dE/dt and dC_L/dt increased in proportion to $d(W_L - W_A)/dt$. Thus, activity of the hydropassive stomatal movement depended on changing rate of evaporative demand. Cowan (*2*) and Cooke *et al.* (*1*) have reported a linear relationship between respective changes in epidermal turgor and stomatal aperture.

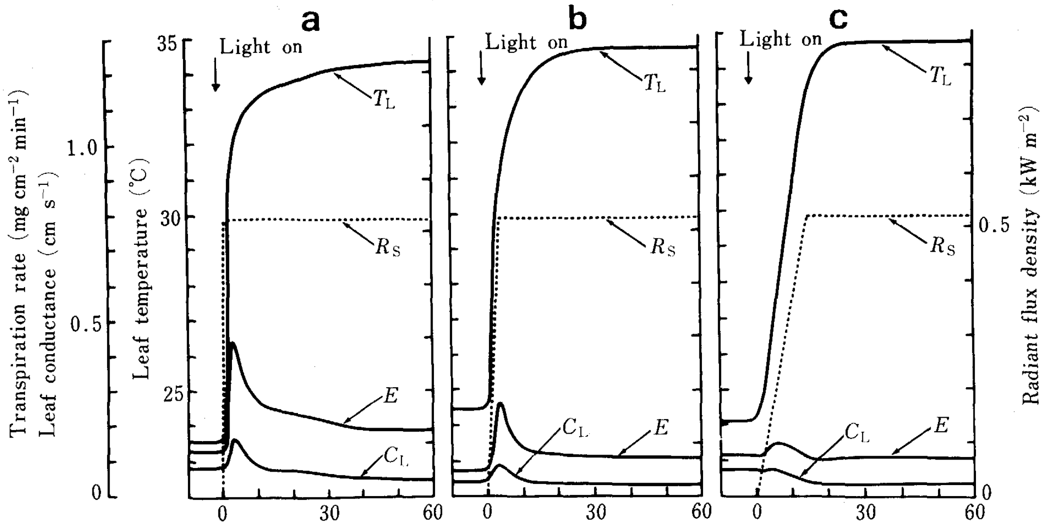

Fig. 4. Step responses (a) and ramp responses (b and c) of leaf temperature (T_L), transpiration rate (E) and leaf conductance (C_L) to the infrared radiation at an ambient air temperature of 25°C and a saturation deficit of 15 g m^{-3}: Gradients of radiant intensity (R_S) in ramp responses of (b) and (c) are 140 W m^{-2} min^{-1} and 35 W m^{-2} min^{-1}, respectively.

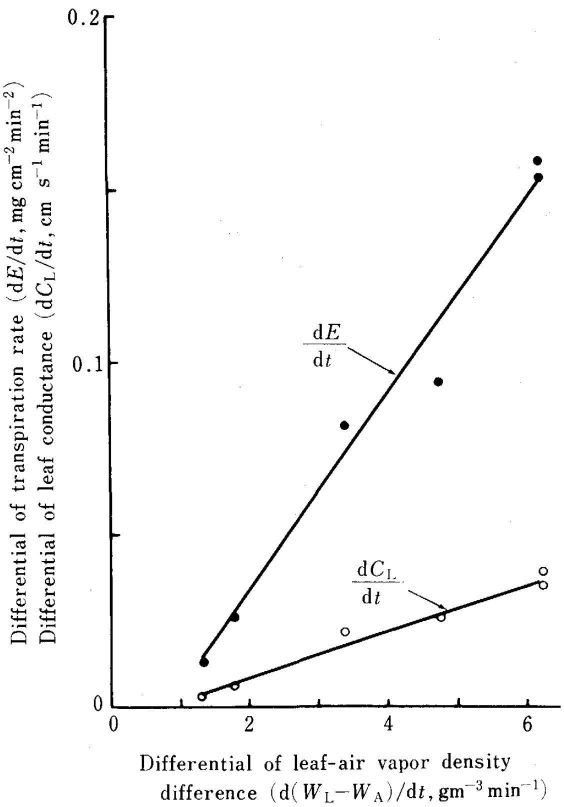

Fig. 5. Distributions of respective differentials of transpiration rate (E) and leaf conductance (C_L) on differential of leaf-air vapor density difference ($W_L - W_A$) during hydropassive stomatal opening in step and ramp responses to the infrared radiation.

From the linear relationship between $d(W_L - W_A)/dt$ and dC_L/dt, it can be conceivable that there are linear relationships among respective changes in evaporative demand, water loss, epidermal turgor and stomatal aperture. Furthermore, dE/dt and dC_L/dt became 0 at a remarkably low $d(W_L - W_A)/dt$ of about 1 g m^{-3} min^{-1}. This indicates that the hydraulic interaction between guard cells and adjacent epidermal cells is affected by the minor change in evaporative demand, as hydraulic capacitances of these cells are small (*3*, *4*, *17*, *18*).

Thus, the visible radiation containing PAR brought about the hydroactive stomatal movement mainly through physiological processes. On the other hand, the infrared radiation caused the hydropassive stomatal movement through physical processes in response to the thermal effect.

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