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STOMATAL RESPONSE TO WIND ON ABAXIAL AND ADAXIAL SURFACES OF CUCUMBER LEAF UNDER DIFFERENT HUMIDITY CONDITIONS

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YASUTAKE D., KITANO M., ARAKI T., NAGASUGA K., KAWANO T. and HAMAKOGA M. *Stomatal response to wind on abaxial and adaxial surfaces of cucumber leaf under different humidity conditions*. BIOTRONICS 30, 103–114, 2001. In order to elucidate stomatal response to wind, leaf gas exchange and stomatal conductance in an intact leaf of cucumber plants (*Cucumis sativus* L.) were measured under different conditions of air current and humidity. A leaf gas exchange cuvette was improved for individual measurements on the abaxial and adaxial leaf surfaces and for adjustment of the leaf boundary air current, where leaf boundary layer conductance can be adjusted at a desired value within a range from $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$ to $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$. Rates of leaf gas exchange and stomatal conductance were higher on the abaxial surface than on the adaxial surface. Stomatal response to wind was appeared more sensitive on the abaxial surface, while leaf gas exchange and stomatal conductance on the adaxial surface was scarcely affected by wind. Under the humid air condition, increase in leaf boundary layer conductance significantly enhanced stomatal conductance as well as rates of transpiration and photosynthesis on the abaxial surface. On the other hand, under the dry air condition, stomatal conductance was depressed by increase in leaf boundary layer conductance with little effect on transpiration and photosynthesis. These opposite changes in stomatal conductance found under the humid and dry air conditions were proved visually as change in stomatal aperture by the microscopic observation of the abaxial leaf surface. This stomatal response to wind found on the abaxial surface was not related to feedback stomatal response to transpirational water loss and intercellular CO_2 concentration in the leaf. The mechanism of stomatal response to wind was explained on the basis of water balance within the stomatal complex and on the antagonism relationship between turgors in guard and epidermal cells.

Key words: *Cucumis sativus* L.; stomatal response; gas exchange; wind; turgor; guard cells; epidermal cells

INTRODUCTION

Most of the studies on stomatal responses to environmental factors have been focused on the responses to light, humidity, CO₂ gas concentration, temperature of the ambient air and water conditions around roots, where the stomatal responses have been analyzed in relation to leaf gas exchange such as photosynthesis and transpiration, and the mechanism of the stomatal responses have been demonstrated on the basis of feedback or feedforward stomatal responses to transpirational water loss or intercellular CO₂ gas concentration of the leaf (e.g. 7, 12, 14, 15, 19).

Wind is one of the important environmental factors for plant growth (9) and can be estimated to affect leaf gas exchange through change in leaf boundary layer conductance. Effects of wind speed on leaf photosynthesis and root water absorption have been studied by using a wind tunnel for a whole plant (20, 21). As very few examples of studies on stomatal responses to wind, stomatal oscillation induced by rapid change in wind speed (13) and a simulation model for relationship between stomatal conductance and wind speed (1) have been reported. However, for quantitative analysis of the mechanism of direct response of stomata to wind, there are many difficulties which are complicated by heat (i.e., sensible and latent heat) and mass transport through the leaf boundary layer and by the heterogeneity between the abaxial and adaxial leaf surfaces. Furthermore, leaf gas exchange cuvettes generally used have not been applicable to analysis of stomatal response to wind, because the air current in these cuvettes is always highly stirred so as not to limit leaf gas exchange through the leaf boundary layer.

In the present study, stomatal conductance as well as rates of photosynthesis and transpiration was measured on the abaxial and adaxial surfaces of a cucumber leaf individually under different conditions of air current and humidity in the leaf boundary layer by using the special leaf cuvette established in the previous study (22), and the mechanism of stomatal response to wind was discussed.

MATERIALS AND METHODS

Plant materials

Cucumber plants (*Cucumis sativus* L. cv. Chojitsu-Ochiai) were potted in vermiculite with nutrient solution and were grown in a phytotron glass room at an air temperature of $25 \pm 1^\circ\text{C}$, a relative humidity of $70 \pm 5\%$ and a wind velocity of $25 \pm 5 \text{ cm s}^{-1}$. The intact third leaf of the plant at fifth leaf stage was used for the analysis of stomatal response to wind.

Measurement of leaf gas exchange

In the previous study (22), we established an open-type leaf gas exchange system, which made it possible to evaluate gas exchange parameters on the abaxial and adaxial leaf surfaces individually under different air currents of leaf

boundary layer. The system has two leaf cuvettes for the individual measurements on the respective abaxial and adaxial surfaces. Three modes of measurements (i.e., the abaxial measurement mode, the adaxial measurement mode and the both surfaces measurement mode) can be selected arbitrarily by switching a three-ways solenoid valve equipped on the air sampling path from each leaf cuvette. Furthermore, the leaf boundary layer conductance can be changed by varying the electric power applied to the microfan in each leaf cuvette. Boundary layer conductances on the abaxial and adaxial leaf surfaces (i.e., $G_{AV(L)}$ and $G_{AV(U)}$) were evaluated from evaporation rates measured by the system on the lower and upper surfaces of a wetted filter paper, respectively.

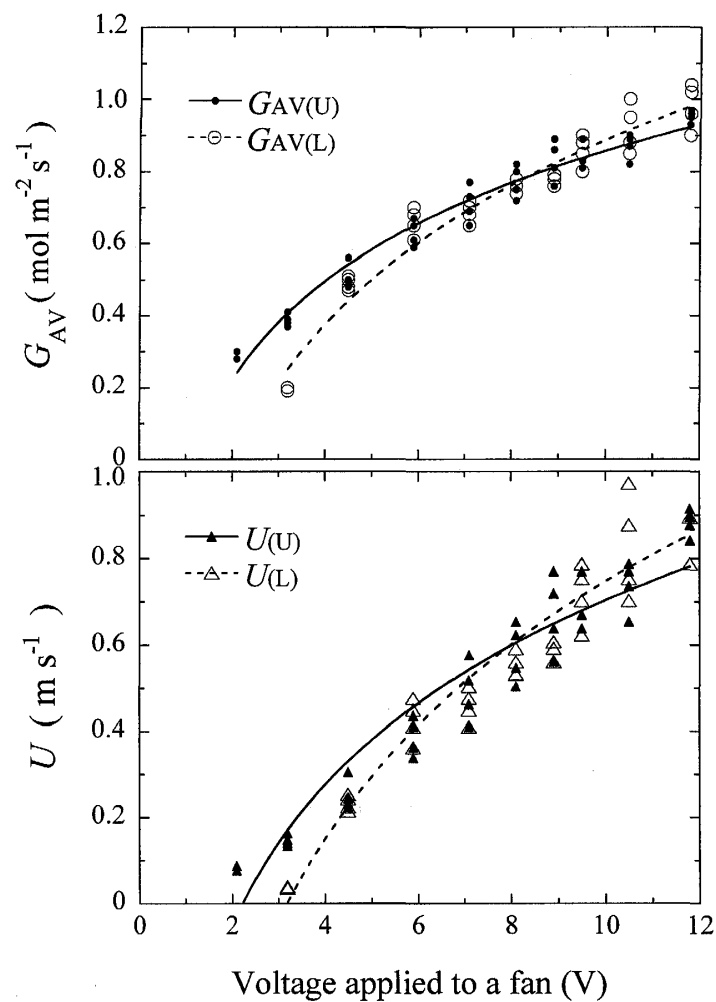


Fig. 1. Relationships of leaf boundary layer conductance (G_{AV}) and wind velocity (U) with voltage applied to the microfan in each abaxial and adaxial leaf cuvette: $G_{AV(L)}$ and $G_{AV(U)}$, leaf boundary layer conductances for vapor transfer on abaxial and adaxial leaf surfaces, respectively; $U(L)$ and $U(U)$, wind velocity in abaxial and adaxial leaf cuvettes, respectively, which were theoretically estimated from $G_{AV(L)}$ and $G_{AV(U)}$ based on the assumption of laminar forced convection in the leaf boundary layer.

Wind velocity in each cuvette was theoretically estimated from $G_{AV(L)}$ and $G_{AV(U)}$ based on the assumption of laminar forced convection in the leaf boundary layer (10). Figure 1 shows the relationships of leaf boundary layer conductance (G_{AV}) and estimated wind velocity (U) with voltage applied to the microfan in each cuvette. $G_{AV(L)}$ and $G_{AV(U)}$ were increased with increase in the applied voltage and distributed from the minimum of about $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$ to the maximum of about $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$. The dependence of G_{AV} on the applied voltage was somewhat different between both leaf cuvettes, and this difference can be attributed to different relationship between r.p.m of the microfan and the applied voltage in each cuvette. Wind velocity in each cuvette (i.e., $U_{(L)}$ and $U_{(U)}$) was estimated the range from the minimum of about 0.1 m s^{-1} to the maximum of about 0.8 m s^{-1} .

Leaf gas exchange parameters such as photosynthetic rate (A), transpiration rate (E), stomatal conductance (G_S) and intercellular CO_2 concentration (C_i) on the abaxial and adaxial leaf surfaces were evaluated in steady state by the general method for the open-type system (2, 8, 11, 17, 18). The measurements were conducted under different conditions of air current and humidity at a constant air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$, where a high G_{AV} of $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$ and a low G_{AV} of $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$ were set under the respective high and low air currents in the humid air with a saturation vapor deficit of 15 hPa and in the dry air with a saturation vapor deficit of 30 hPa. Under the respective air conditions, photosynthetic photon flux density ($PPFD$) was changed stepwise at fifth levels (i.e., 1200, 800, 400, 200 and $0 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

Microscopic observation of stomatal aperture

For microscopic observation of leaf surfaces, the Suzuki's universal micro-printing method (SUMP method; Sigakonchu-fukyusha Co. Ltd., Japan) was applied, which is one of the replica methods. At first, stomatal frequency was investigated by using replicas of the both leaf surfaces. For visual observation of effect of air current on stomatal aperture, the replica of abaxial leaf surface was taken quickly just after removing the leaf cuvette, in which the leaf gas exchange became steady under the respective G_{AV} and humidity conditions at a $PPFD$ of $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$, an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$.

RESULTS AND DISCUSSION

Figure 2 shows relationships of A , E and G_S with $PPFD$ on abaxial and adaxial leaf surfaces at low G_{AV} ($0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high G_{AV} ($1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) under the humid air condition with a saturation vapor deficit of 15 hPa, an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$. A , E and G_S were higher on the abaxial surface than on the adaxial surface. The increase in G_{AV} from $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$ to $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$ enhanced G_S as well as A and E , and this effect of G_{AV} was remarkable on the abaxial surface as compared

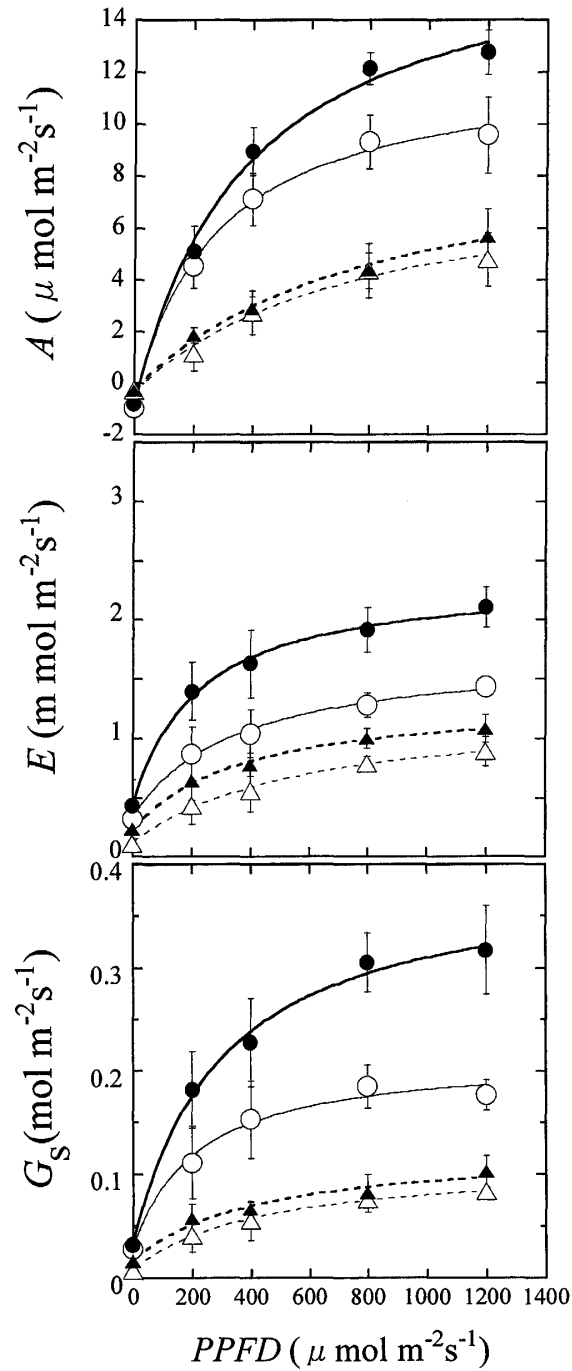


Fig. 2. Relationships of photosynthetic rate (A), transpiration rate (E) and stomatal conductance (G_s) with photosynthetic photon flux density ($PPFD$) on abaxial and adaxial leaf surfaces at low ($0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high ($1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) leaf boundary layer conductances under the humid air condition with a saturation vapor deficit of 15 hPa, an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$: \circ and \bullet , values for the abaxial surfaces at low and high leaf boundary layer conductances, respectively; \triangle and \blacktriangle , values for adaxial surfaces at low and high leaf boundary layer conductances, respectively. Means of four plants are shown with standard deviations.

with on the adaxial surface. These results suggest that increase in G_{AV} under the humid air condition can activate stomatal response to $PPFD$ and induces increase in stomatal aperture, in particular, on the abaxial surface.

Figure 3 shows relationships of A , E and G_S with $PPFD$ on abaxial and adaxial leaf surfaces at low G_{AV} ($0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high G_{AV} ($1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) under the dry air condition with a saturation vapor deficit of 30 hPa, an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$. Effect of increase in G_{AV} on A , E and G_S under the dry air condition was remarkably different from that under the humid air condition. Under the dry air condition, G_S on the abaxial surface was decreased by increase in G_{AV} , and resultantly A and E were not significantly increased in spite of increase in G_{AV} . These results suggest that increase in G_{AV} under the dry air condition can restrain stomatal response to $PPFD$ and decrease stomatal aperture.

Stomatal frequency measured by the replica method was $343.1 \pm 16.9 \text{ mm}^{-2}$ on the abaxial surface and $156.9 \pm 12.4 \text{ mm}^{-2}$ on the adaxial surface, and this larger stomatal frequency on the abaxial surface was considered to bring more active leaf gas exchange on the abaxial surface. Furthermore, response of G_S to change in G_{AV} appeared more sensitive on the abaxial surface, and this response of G_S appeared in opposite manners was found under the humid and dry air conditions as shown in Figs. 2 and 3. On the other hand, G_S on the adaxial leaf surface was low and was scarcely affected by change in G_{AV} , which can be attributed to results from the lower stomatal frequency and the thicker cuticular layer on the adaxial leaf surface. By applying the replica method on the abaxial leaf surface, response of G_S to change in G_{AV} (Figs. 2 and 3) was proved visually as change in stomatal aperture. Figure 4 shows micrographs of abaxial surface replicas of the intact third leaf of cucumber plant exposed to low G_{AV} (a; $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high G_{AV} (b; $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) in the humid air condition with a saturation vapor deficit of 15 hPa and exposed to high G_{AV} (c; $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) in the dry air condition with a saturation vapor deficit of 30 hPa at a $PPFD$ of $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$, an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$. Stomatal aperture under the humid air condition (a and b) was clearly increased by increase in G_{AV} , but under the dry air condition (c), increase in G_{AV} induced depression of stomatal aperture.

Stomatal response to change in air current of the leaf boundary layer can be conjectured to relate to changes in the intercellular CO_2 concentration and the transpirational water loss of the leaf. Figure 5 shows relationship between the leaf intercellular CO_2 concentration (C_i) and $PPFD$ at low G_{AV} ($0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high G_{AV} ($1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) in the humid air condition with a saturation vapor deficit of 15 hPa (a) and in the dry air condition with a saturation vapor deficit of 30 hPa (b) at an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$. C_i was evaluated by using gas exchange parameters measured for the abaxial leaf surface. C_i was dropped by lighting with the start of leaf photosynthesis. Furthermore, there was little effect of changes in G_{AV} and humidity, and the value of C_i was kept constant at about $250 \mu\text{mol mol}^{-1}$ under the different G_{AV} conditions. This fact suggests that stomatal

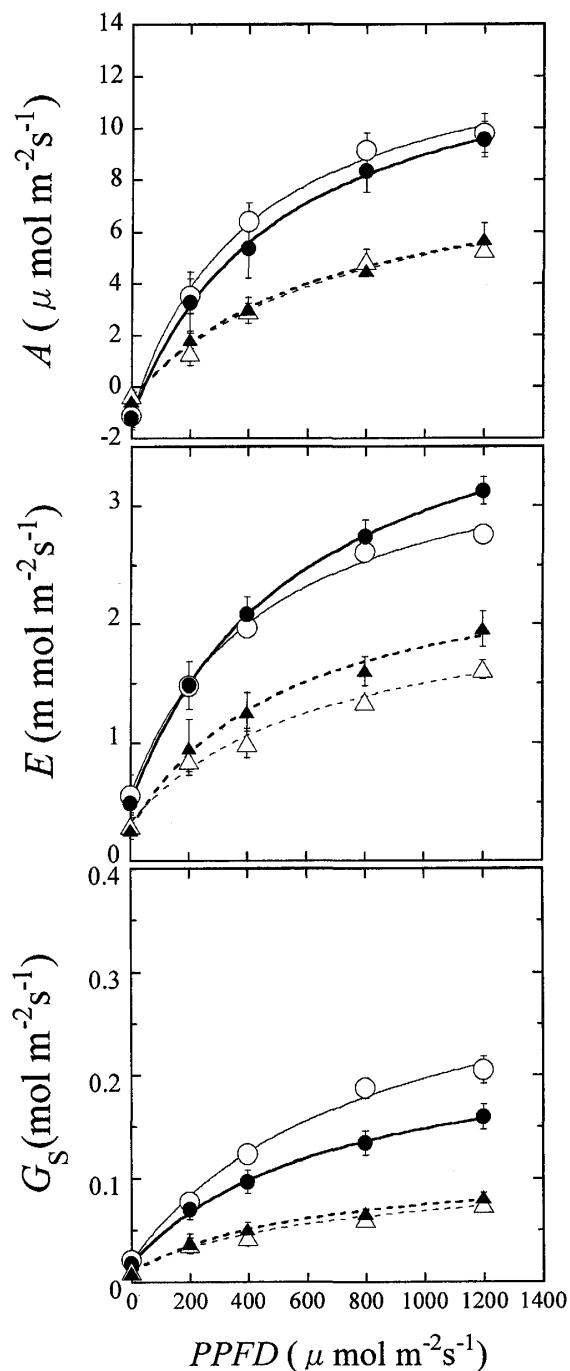


Fig. 3. Relationships of photosynthetic rate (A), transpiration rate (E) and stomatal conductance (G_s) with photosynthetic photon flux density ($PPFD$) on abaxial and adaxial leaf surfaces at low ($0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high ($1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) leaf boundary layer conductances under the dry air condition with a saturation vapor deficit of 30 hPa, an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$: \circ and \bullet , values for the abaxial surfaces at low and high leaf boundary layer conductances, respectively; \triangle and \blacktriangle , values for adaxial surfaces at low and high leaf boundary layer conductances, respectively. Means of four plants are shown with standard deviations.

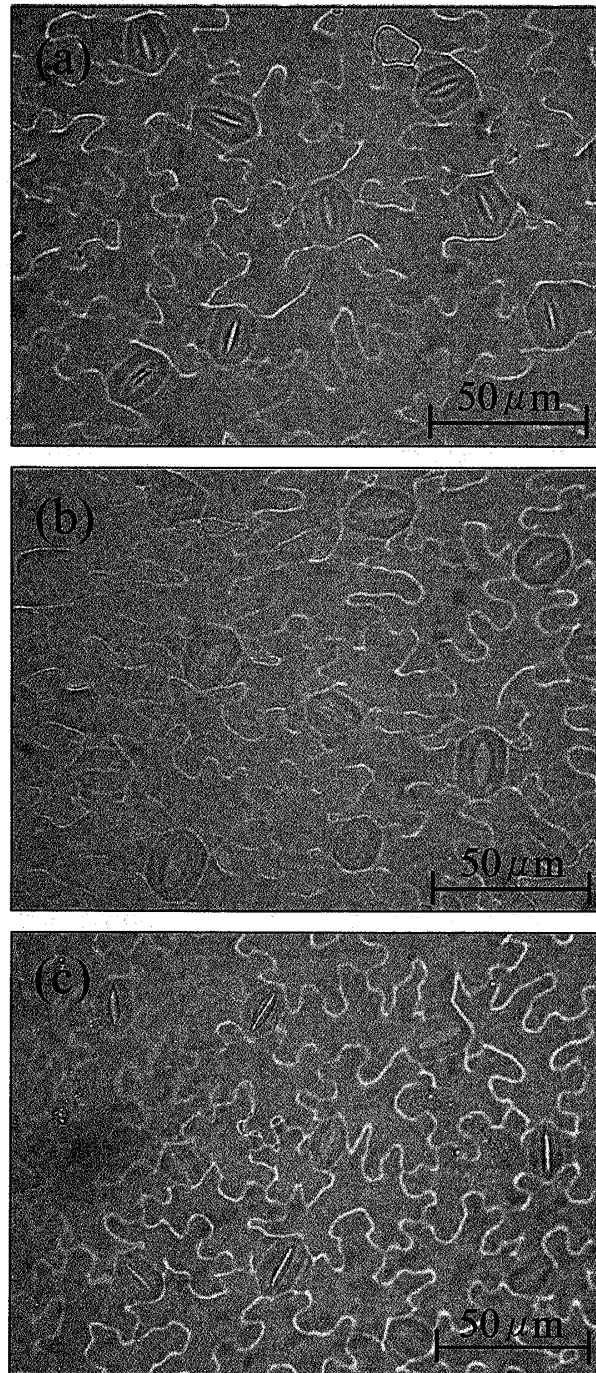


Fig. 4. Micrographs of abaxial surface replicas of the intact third leaf of cucumber plant exposed to low (a; $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high (b; $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) leaf boundary layer conductances in the humid air condition with a saturation vapor deficit of 15 hPa and exposed to high (c; $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) leaf boundary layer conductance in the dry air condition with a saturation vapor deficit of 30 hPa at a photosynthetic photon flux density (*PPFD*) of $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$, an air temperature of 25°C and an ambient CO_2 concentration of $350 \mu\text{mol mol}^{-1}$.

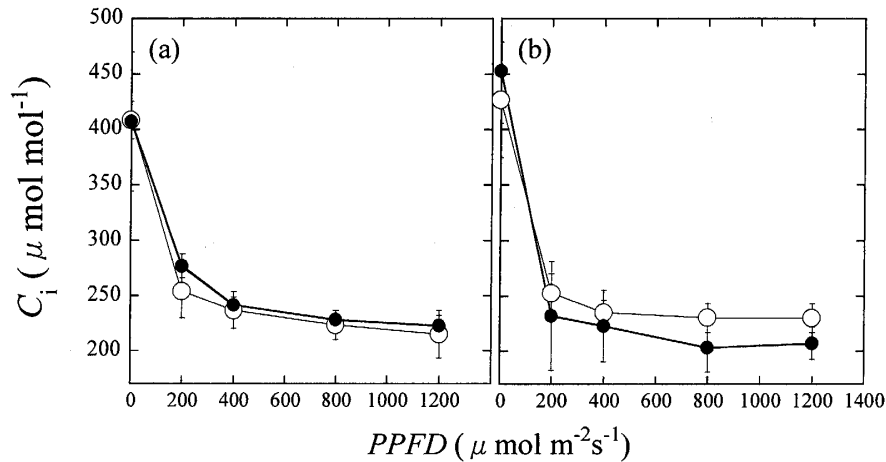


Fig. 5. Relationship between the leaf intercellular CO₂ concentration (C_i) and photosynthetic photon flux density (PPFD) at low ($0.3 \text{ mol m}^{-2} \text{ s}^{-1}$) and high ($1.0 \text{ mol m}^{-2} \text{ s}^{-1}$) leaf boundary layer conductances in the humid air condition with a saturation vapor deficit of 15 hPa (a) and in the dry air condition with a saturation vapor deficit of 30 hPa (b) at an air temperature of 25°C and an ambient CO₂ concentration of $350 \mu\text{mol mol}^{-1}$: ○ and ●, values evaluated by using gas exchange parameters for the abaxial surfaces at low and high leaf boundary layer conductances, respectively. Means of four plants are shown with standard deviations.

response to the change in air current of leaf boundary layer can not be attributed to the change in the leaf intercellular CO₂ concentration.

Under the humid air condition, the increase in air current enhanced leaf transpirational water loss and yet increased stomatal aperture contrary to the feedback response of stomata to leaf transpirational water loss (Figs. 2 and 4-b). Furthermore, decrease in air humidity under the high air current induced remarkable depression in G_s by 50% but no effect was found under the low air current (Figs. 2 and 3). Consequently, in the dry air condition, the depressed stomatal aperture was found under the high air current, although leaf transpirational water loss was little affected by the change in air current (Figs. 3 and 4-c). From these facts, it is suggested that stomatal response to the change in air current of leaf boundary layer can not be attributed to the feedback response of stomata to leaf transpirational water loss.

It has been well known that stomatal aperture conclusively depends on antagonism relationship between turgors (i.e., positive hydrostatic pressure) in guard cells and their neighbouring epidermal cells (e.g., subsidiary cells) (e.g., 12, 14). This dependence on turgors in guard and epidermal cells has been expressed by linear models for stomatal aperture and stomatal conductance. For example, stomatal conductance can be expressed by (3, 4, 5)

$$G_s = a_g P_g - a_e P_e + G_{s0} \quad [1]$$

where P_g is the turgor in guard cells, P_e is the turgor in epidermal cells adjacent to the guard cells, a_g and a_e are positive coefficients termed as the influence

coefficients for P_g and P_e , respectively, and G_{S0} is the stomatal conductance at $P_g = P_e = 0$. Therefore, response of G_S to change in G_{AV} can be expressed as

$$\frac{\partial G_S}{\partial G_{AV}} = a_g \frac{\partial P_g}{\partial G_{AV}} - a_e \frac{\partial P_e}{\partial G_{AV}} \quad [2]$$

Under the humid air condition, increase in G_{AV} induced increase in G_S (Fig. 2), that is $\partial G_S / \partial G_{AV} > 0$. This response of G_S can be triggered by the following relationship:

$$\left| \frac{\partial P_g}{\partial G_{AV}} \right| < \frac{a_e}{a_g} \left| \frac{\partial P_e}{\partial G_{AV}} \right| \quad [3]$$

On the other hand, under the dry air condition increase in G_{AV} depressed G_S (Fig. 3), that is $\partial G_S / \partial G_{AV} < 0$. This response of G_S can be triggered by the following relationship:

$$\left| \frac{\partial P_g}{\partial G_{AV}} \right| > \frac{a_e}{a_g} \left| \frac{\partial P_e}{\partial G_{AV}} \right| \quad [4]$$

In the antagonism relationship of Eq. [1], the mechanical advantage of the epidermal cells (i.e., $a_g < a_e$) has been observed in *Tradescantia virginiana* (6), and the antagonism ratio (i.e., a_e/a_g) has been estimated mathematically to be approximately 1.5 (3). This suggests that turgor change in the epidermal cells can produce larger change in stomatal aperture. Therefore, the relationship of Eq. [3] is expected to be a possible case, and small turgor loss in the epidermal cells under the high air current can drive stomata to open. Changes in P_g and P_e depend on balance between water loss and water supply in guard and epidermal cells, and relative distribution of evaporative water loss and water supply within the stomatal complex (i.e., guard, epidermal and mesophyll cells surrounding substomatal cavity) can be considered to affect $\partial P_g / \partial G_{AV}$ and $\partial P_e / \partial G_{AV}$. Under the dry air condition, rate of transpiration was 1.5 to 2.0 times higher than rate under the humid air condition (Figs. 2 and 3). This higher transpiration rate may direct the water flow to mesophyll cells surrounding the substomatal cavity which is dominant sites of transpirational water loss (16). This event may cause the unbalance between evaporative water loss and water supply in guard cells distant from xylems. Therefore, under the higher transpiration rate in the dry air conditions, significant turgor loss in the guard cells and the relationship of Eq. [4] also can be considered to be a possible case.

In this study, stomatal response to wind in the leaf boundary layer was proved numerically and visually. The mechanism of the stomatal response to wind observed under different conditions of leaf boundary layer conductance and humidity was explained on the basis of water balance within the stomatal complex and on the antagonism relationship between turgors in guard and epidermal cells.

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