EVALUATION OF LEAF BOUNDARY LAYER CONDUCTANCE OF A WHOLE PLANT BY APPLICATION OF ABSCISIC ACID INHIBITING TRANSPIRATION

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出版情報：BIOTRONICS. 24, pp.51-58, 1995-12. Biotron Institute, Kyushu University
バージョン：
権利関係：

BIOTRONICS **24**, 51–58, 1995

EVALUATION OF LEAF BOUNDARY LAYER CONDUCTANCE OF A WHOLE PLANT BY APPLICATION OF ABSCISIC ACID INHIBITING TRANSPIRATION

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(Received April 15, 1995; accepted May 20, 1995)

KITANO M., TATEISHI J. and EGUCHI H. *Evaluation of leaf boundary layer conductance of a whole plant by application of abscisic acid inhibiting transpiration.* BIOTRONICS **24**, 51–58, 1995. A method for evaluating leaf boundary layer conductance of an intact whole plant was newly proposed and applied to cucumber and lettuce plants in a growth cabinet. The method was based on difference between heat balance equations in the respective steady states before and after abscisic acid (ABA) was applied to the root media. After ABA treatment, remarkable decrease in transpiration and rise in leaf temperature were caused by stomatal depression, and leaf boundary layer conductance averaged over a whole plant was evaluated from the theoretical equation by measuring transpiration rate per plant, leaf temperature and air temperature before and after ABA treatment. The proposed method was suggested to be applicable to analysis of heat and mass transfer between a whole plant and the ambient air.

Key words: *Cucumis sativus* L.; *Lactuca sativa* L.; leaf boundary layer conductance; heat balance; abscisic acid; transpiration.

INTRODUCTION

For analysis of heat and mass transfer between leaf and air, it is necessary to evaluate leaf boundary layer conductance (G_A). Leaf boundary layer conductance or its reciprocal (resistance) has been evaluated by using a single real leaf (*3, 4, 8, 12, 13*) or a single model leaf (*1, 2, 5, 11, 14*). In studies on environmental physiology of a whole plant and for optimalizing the air current in environment control systems such as phytotron and growth cabinet, it is desired to evaluate G_A of an intact whole plant. However, the method for evaluating G_A by using an intact whole plant has not been established.

The present paper deals with a new method for evaluating leaf boundary layer conductance of an intact whole plant by applying abscisic acid (ABA) to inhibit transpiration.

MATERIALS AND METHOD

Evaluation of leaf boundary layer conductance

Leaf boundary layer conductance (G_A) averaged over a whole plant was evaluated on the basis of heat balance of the plant at different rates of transpiration. Heat balance of a whole plant in a steady state can be expressed as (See APPENDIX: List of symbols and Figure 1)

$$\Sigma A_i R_{si} + \Sigma A_{pi} R_{LIi} + \Sigma A_{oi} R_{LLi} - \Sigma A_{pi} R_{LOi} = \Sigma A_i \lambda E_i + \Sigma A_i SH_i \quad (1)$$

The left side of Eq. (1) represents net radiant flux, and the two terms in the right side represent latent heat flux and sensible heat flux, respectively. Sensible heat flux density (SH_i) can be expressed by using local boundary layer conductance (G_{Ai}) and local leaf temperature (T_{Li}) as $2C_P \rho G_{Ai}$ ($T_{Li} - T_A$), and then Eq. (1) can be written as

$$\Sigma A_i R_{si} + \Sigma A_{pi} R_{LIi} + \Sigma A_{oi} R_{LLi} - \Sigma A_{pi} R_{LOi} = \lambda \Sigma A_i E_i + 2C_p \rho \Sigma A_i G_{Ai} \ (T_{Li} - T_A) \quad (2)$$

By introducing leaf boundary layer conductance (G_A) and leaf temperature (T_L) averaged over a whole plant, Eq. (2) can be rewritten as

$$\Sigma A_i R_{si} + \Sigma A_{pi} R_{LIi} + \Sigma A_{oi} R_{LLi} - 2\varepsilon_L \sigma T_L^4 \Sigma A_{pi} = \lambda E + 2C_P \rho G_A (T_L - T_A) \Sigma A_i \quad (3)$$

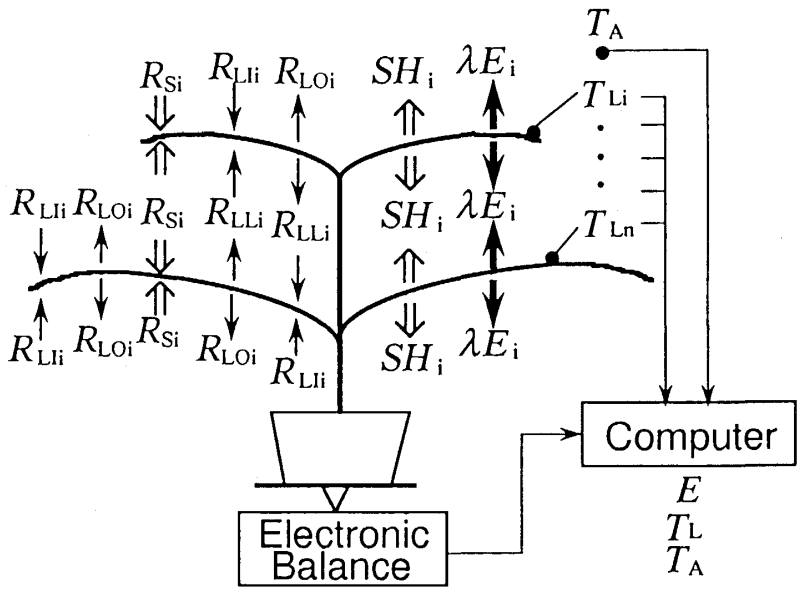

Fig. 1. Schematic diagram of heat fluxes in a whole plant and on-line system for measuring transpiration rate per plant and temperatures of leaves and air. E, transpiration rate per plant; R_{si}, short wave radiant flux density absorbed; R_{LIi}, long wave radiant flux density absorbed; R_{LLi}, long wave radiant flux density exchanged between overlapped leaves; R_{LOi}, long wave radiant flux density radiated from leaf; SH_i, sensible heat flux density; λE_i, latent heat flux density; T_A, ambient air temperature; T_L, leaf temperature averaged over a whole plant; T_{Li}, local leaf temperature; subscript i, the i-th part of leaf.

where E is the transpiration rate per plant ($=\Sigma A_i E_i$).

It is impossible to solve Eq. (3) for G_A, because of difficulties in determinations of absorbed short wave radiant flux ($\Sigma A_i R_{si}$) and absorbed long wave radiant fluxes ($\Sigma A_{pi} R_{LLi}$ and $\Sigma A_{oi} R_{LLi}$). These indeterminable radiant fluxes could be eliminated by comparing heat balance equations obtained on the same shoot with different transpiration rates under a constant light condition. Transpiration rate can be manipulated by changing environmental factors such as humidity and CO_2 gas concentration, but more drastic change in transpiration rate is caused by applying antitranspirants such as ABA (*6, 7, 10*). ABA induces turgor loss in only guard cells and causes stomatal closure while keeping turgidity of the external form of the plant. Therefore, transpiration rate is remarkably depressed by ABA without any changes in optical and aerodynamic properties of the plant.

Under constant light and wind condition, which is estimated to keep $\Sigma A_i R_{Si}$ and G_A constant, the heat balance at different two rates of transpiration before and after ABA treatment can be written as

$$\Sigma A_i R_{si} + \Sigma A_{pi} R_{LIUi} + \Sigma A_{oi} R_{LLUi} - 2\varepsilon_L \sigma T_{LU}^4 \Sigma A_{pi} = \lambda E_U + 2C_P \rho G_A (T_{LU} - T_{AU}) \Sigma A_i \tag{4}$$

$$\Sigma A_i R_{si} + \Sigma A_{pi} R_{LITi} + \Sigma A_{oi} R_{LLTi} - 2\varepsilon_L \sigma T_{LT}^4 \Sigma A_{pi} = \lambda E_T + 2C_p \rho G_A (T_{LT} - T_{AT}) \Sigma A_i \tag{5}$$

where the subscripts of $_U$ and $_T$ affixed to the terms such as E, T_L and T_A represent the respective steady states before and after ABA treatment. After ABA treatment, transpiration rate is depressed, and consequently leaf temperature rises (i. e. $E_T < E_U$ and $T_{LT} > T_{LU}$). The absorbed short wave radiant flux ($\Sigma A_i R_{si}$) is eliminated by subtracting Eq. (4) from Eq. (5) as

$$\begin{aligned} &\Sigma A_{pi}(R_{LITi} - R_{LIUi}) + \Sigma A_{oi}(R_{LLTi} - R_{LLUi}) - 8\varepsilon_L \sigma T_{LM}^3 (T_{LT} - T_{LU}) \Sigma A_{pi} \\ &\quad = \lambda (E_T - E_U) + 2C_P \rho G_A \{(T_{LT} - T_{AT}) - (T_{LU} - T_{AU})\} \Sigma A_i \end{aligned} \tag{6}$$

where T_{LM} is the mean of T_{LU} and T_{LT}. The difference in the absorbed long wave radiant flux ($\Sigma A_{Pi}(R_{LITi} - R_{LIUi})$) can be approximated as

$$\Sigma A_{Pi}(R_{LITi} - R_{LIUi}) = 8\varepsilon_A \varepsilon_L \sigma T_{AM}^3 (T_{AT} - T_{AU}) \Sigma A_{Pi} \tag{7}$$

where T_{AM} is the mean of T_{AU} and T_{AT}. Furthermore, the differnce ($\Sigma A_{oi}(R_{LLTi} - R_{LLUi})$) in long wave radiant flux exchanged among the overlapped leaves was considered to be negligible as compared with the other terms, because temperature differences among the overlapped leaves were estimated to be scarcely affected by ABA treatment.

Therefore, G_A can be expressed by rearranging Eq. (6) as

$$G_A = \frac{8\varepsilon_A \varepsilon_L \sigma T_{AM}^3 (T_{AT} - T_{AU}) \Sigma A_{Pi} - 8\varepsilon_L \sigma T_{LM}^3 (T_{LT} - T_{LU}) \Sigma A_{pi} - \lambda (E_T - E_U)}{2C_P \rho \{(T_{LT} - T_{AT}) - (T_{LU} - T_{AU})\} \Sigma A_i} \tag{8}$$

From Eq. (8), G_A can be evaluated by measuring transpiration rate per plant, leaf temperature and air temperature in the respective steady states before and after ABA treatment. Transpiration rate per plant was measured by the weighing method with an electronic balance (Fig. 1). Leaf temperature averaged over a whole plant was evaluated from the mean voltage of five T-thermocouples (0.1 mm in diameter) inserted into leaves (*4, 6*), and the ambient air temperature was also measured with the thermocouple. Signals from the electronic balance and the thermocouples were transmitted to a computer on-line at intervals of 4 s through interfaces and smoothed by moving average for 1 min. These values were averaged over 10 minutes in the respective steady states before and after ABA treatment. Area of each leaf was measured by leaf area meter and summed up as the total leaf area (ΣA_i). Plane area of the whole plant (ΣA_{Pi}) was evaluated from the plane image of the plant.

ABA treatment

ABA is fed into the guard cells by applying ABA solution to root media or by spraying the solution directly to leaves. The direct spray to leaves, however, keeps the leaves wet with the solution, and there is the possibility to change optical and aerodynamic properties of the leaves. On the other hand, ABA applied to the root media is transported to guard cells through transpiration stream in the plant and induces stomatal depression without any changes in optical and aerodynamic properties of the plant. Therefore, 10^{-4} M ABA solution (*6*) was applied to the root media of the material plant for about two hours.

Plant materials and environmental condition

A cucumber plant (*Cucumis sativus* L. cv. Chojitsu-Ochiai) of three-leaf stage and a lettuce plant (*Lactuca sativa* L. cv. Okayama) of 12-leaf stage potted in vermiculite were used for evaluating G_A from Eq. (8). In a reach-in type growth cabinet system (*9*), G_A of each plant was evaluated at different three positions within the growth compartment ($1.5W \times 1.0D \times 1.0H\ m^3$), where the controlled air was supplied through the perforated side wall and flowed laterally into the return air chamber. In each G_A evaluation, the plant was irradiated with a constant light of a halogen lamp (300W) under an air temperature of 25 ± 0.3℃ and a relative humidity of 60 ± 5%RH. Air current characteristics (mean velocity and intensity of turbulence) at each position were measured by a hot wire anemometer. Changes in $\Sigma A_i R_{Si}$ and G_A before and after ABA treatment were estimated to be negligible, and distributions of G_A and air current characteristics in the growth cabinet were examined.

RESULTS AND DISCUSSION

For reliability of the G_A evaluation by Eq. (8), it is essential to confirm that ABA treatment brings about noticeable change in heat balance of the whole plant through stomatal depression. Table 1 shows effects of ABA treatment on stomatal conductance and terms constituting Eq. (8) in each whole plant of cucumber and lettuce under a wind velocity of 64 cm s^{-1} in the growth cabinet. In cucumber plant after ABA treatment, stomatal conductance was drastically

Table 1. Effects of ABA treatment on stomatal conductance, transpiration rate per plant, leaf temperature and terms constituting Eq. (8) in cucumber and lettuce plants under a wind velocity of 64 cm s^{-1} in a growth cabinet. The steady state before ABA treatment is expressed as untreatment. $8\varepsilon_A\varepsilon_L T^3_{AM}(T_{AT}-T_{AU})\Sigma A_{Pi}$, change in long wave radiant flux absorbed by the plant; $8\varepsilon_L\sigma T^3_{LM}(T_{LT}-T_{LU})\Sigma A_{Pi}$, change in long wave radiant flux radiated from the plant; $\lambda(E_T-E_U)$, change in latent heat flux; $2C_P\rho\{(T_{LT}-T_{AT})-(T_{LU}-T_{AU})\}\Sigma A_i$, denominator of Eq. (8). Symbols are explained in APPENDIX.

	Cucumber		Lettuce	
	Untreated	ABA treated	Untreated	ABA treated
Stomatal conductance (cm s^{-1})	0.29	0.03	0.10	0.04
Transpiration rate (mg s^{-1})	2.271	0.453	1.518	0.618
Leaf temperature (℃)	28.3	32.9	30.8	32.3
Air temperature (℃)	24.8	24.8	24.9	24.8
$8\varepsilon_A\varepsilon_L\sigma T^3_{AM}(T_{AT}-T_{AU})\,\Sigma A_{pi}$ (W)	0.00		−0.02	
$8\varepsilon_L\sigma T^3_{LM}(T_{LT}-T_{LU})\,\Sigma A_{pi}$ (W)	1.58		0.46	
$\lambda\,(E_T-E_U)$ (W)	−4.41		−2.18	
$2C_P\rho\{(T_{LT}-T_{AT})-(T_{LU}-T_{AU})\}\Sigma A_i$ (J cm^{-1})	3.03		1.67	
Bounday layer conductance (G_A; cm s^{-1})	0.93		1.02	

depressed by 90%, which brought 80% decrease in transpiration rate and 4.6℃ rise in leaf temperature. In lettuce plant, ABA treatment caused 60% decreases in stomatal conductance and transpiration rate, which resulted in 1.5℃ rise in leaf temperature. These larger changes in transpiration rate and leaf temperature csused by ABA treatment resulted in larger contribution of changes in latent heat flux and leaf-air temperature difference to the G_A evaluation by Eq. (8). On the other hand, changes in long wave radiant fluxes, which involved uncertainty with the approximations, showed smaller contribution to the G_A evaluation as compared with change in latent heat flux. Furthermore, larger change in leaf-air temperature difference in the denominator of Eq. (8) can be considered to reduce influence of errors brought with terms in the numerator. Larger rise in leaf temperature has been reported to increase G_A by buoyancy effect under lower wind velocities (*5*), and G_A evaluated by Eq. (8) can be considered to involve the buoyancy effect. However, 4.6℃ rise observed in this experiment under a wind velocity of 64 cm s^{-1} was estimated to bring only 5% increase in G_A after ABA treatment (*5*). Thus, ABA was applied with higher reliability to the G_A evaluation through remarkable changes in transpiration rate and leaf-air temperature difference.

Figure 2 shows air current characteristics and G_A values of cucumber and lettuce plants at different three positions (A, B and C) at a height of 50 cm in the growth cabinet. The position B was the center of the growth cabinet, and the windward position A and the leeward position C were 50 cm apart from the center position B. Wind velocity and intensity of turbulence were highest at the windward position A, where G_A became about 1.5 times higher than those at the positions B and C on the leeward of A. Even in the reach-in type growth

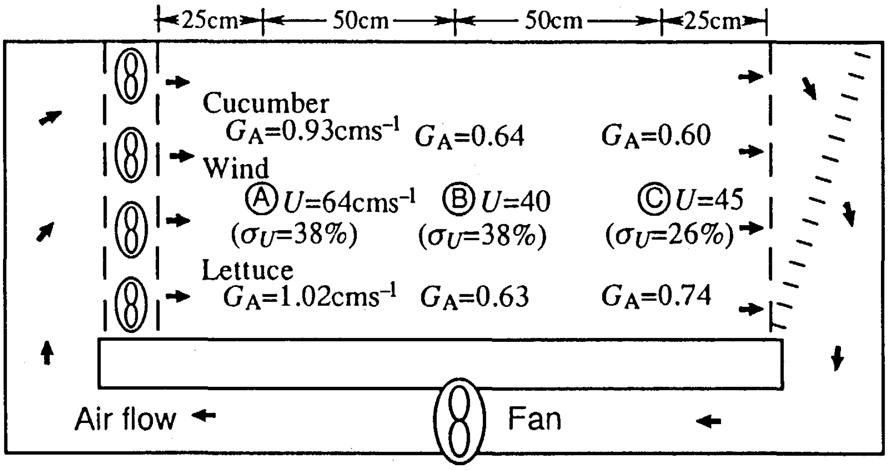

Fig. 2. Air current characteristics and leaf boundary layer conductances of cucumber and lettuce plants at different three positions (A, B and C) at a height of 50 cm in a growth cabinet ($1.5\mathrm{W}\times1.0\mathrm{D}\times1.0\mathrm{H}\ \mathrm{m}^3$). G_A, leaf boundary layer conductance; U, mean wind velocity; σ_U, intensity of turbulence.

cabinet, there found remarkable difference in G_A among plant locations, and this G_A distribution was considered to be brought by distributions of wind characteristics in the growth cabinet. Thus, on the basis of difference between heat balance equations before and after ABA treatment, leaf boundary layer conductance averaged over an intact whole plant was evaluated. From the results, it is suggested that the proposed method is applicable to analysis of heat and mass transfer between a whole plant and the ambient air.

APPENDIX : List of symbols

ABA : abscisic acid.
A_i : area of the i-th part of leaf.
A_{oi} : area of the i-th part of leaf overlapped with other leaves
A_{pi} : plane area of the i-th part of leaf.
$C_P\rho$: volumetric heat capacity of air.
E_i : transpiration rate per unit area of the i-th part of leaf.
E : transpiration rate per plant.
E_U : transpiration rate per plant before ABA treatment.
E_T : transpiration rate per plant after ABA treatment.
G_{Ai} : local boundary layer conductance of the i-th part of leaf.
G_A : leaf boundary layer conductance averaged over a whole plant.
R_{Si} : short wave radiant flux density absorbed on the i-th part of leaf.
R_{LIi} : long wave radiant flux density absorbed on plane area of the i-th part of leaf.
R_{LLi} : long wave radiant flux density exchanged on the i-th part of leaf overlapped with other leaves.
R_{LOi} : long wave radiant flux density radiated from plane area of the i-th

part of leaf.

SH_i : sensible heat flux density of the i-th part of leaf.

T_A : ambient air temperature

T_{AU} : ambient air temperature before ABA treatment.

T_{AT} : ambient air temperature after ABA treatment.

T_{AM} : $(T_{AU}+T_{AT})/2$

T_{Li} : leaf temperature of the i-th part of leaf.

T_{LU} : leaf temperature averaged over a whole plant before ABA treatment.

T_{LT} : leaf temperature averaged over a whole plant after ABA treatment.

T_{LM} : $(T_{LU}-T_{LT})/2$

T : subscript for the steady state after ABA treatment. (treated wuth ABA)

U : subscript for the steady state before ABA treatment. (untreated with ABA)

U : mean wind velocity.

ε_A : emissivity of plant environment.

ε_L : emissivity of leaf.

λ : latent heat of vaporization of water.

ρ : density of air.

σ : Stefan-Boltzmann constant.

σ_U : intensity of turbulence of wind.

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