Development of a Model for Estimating Stomatal Conductance of Maize Leaves

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Abstract

Based on a study of the characteristics of the stomatal response to environmental factors, a new environmental variable model for estimating stomatal conductance over a long time period was developed. This model was based on multiplying the potential stomatal conductance by the relative degree of stomatal opening during daytime. The estimated precision of this model was quite high.

Key words: Environmental variable model, Maize, Stomatal conductance.

1 Introduction

Developing a model for estimating stomatal conductance is very important because stomatal conductance is often used to explain fluxes of CO₂ and water vapor between plant and atmosphere. Jarvis (1976) took each environmental factor which influences stomatal conductance as an independent response function, and proposed an environmental variable model that combined these response functions (now called Jarvis' model). At present, this model is widely used and has become the prototype of most models.

The authors optimized Jarvis' model by using measurements made at a maize field in 1992–1994. As a result, in the case of a short time period of one year, a relatively high estimated precision was obtained with the two-variable model, but in a long time period of three years, the coefficient of determination of the model was only 0.45, even if the model was constructed with four variables (Yu *et al.*, 1996c). The variability of stomatal conductance and the characteristics of stomatal response to environmental variables over long-period scales have been examined (Yu *et al.*, 1996a,b). Here, we attempt to develop a new environmental variable model based on the previous studies.

2 Combination Model

Under natural conditions, the opening and closing of stomata are mainly influenced by environmental factors such as sunlight, temperature, saturation deficit, water stress, CO₂ concentration, etc. (Jarvis, 1976). When the photosynthetic photon flux density

(Q_p), leaf temperature (T_L), saturation deficit (D_e), leaf water potential (Ψ_L), etc. are used as the parameters of the environmental factors, Jarvis' model can be represented by

$$G_{st} = \text{opt} \left\{ \prod_I^N G(X_I) \right\} \quad (1)$$

where $X = (X_1, \dots, X_I, \dots, X_N) \in (Q_p, D_e, \Psi_L, T_L, \dots)$ are environmental variables, $N=1, 2, \dots$ are the number of variables in the models, and $I=1, 2, \dots, N$ are the variable numbers. 'opt' means the optimization of the model. $G(X_I) \in \{G_i(Q_p), g_j(D_e), g_q(\Psi_L), g_k(T_L), \dots\}$ are the functions of each environmental variable influencing stomatal conductance.

For a long period scale, the stomatal conductance (G_{st}) is influenced by both the relative degree of the stomatal opening (RDO) and the potential conductance (G_{Max}) during daytime (Yu *et al.*, 1996b). The RDO depends on the relative variation of environmental variables, and G_{Max} is determined by the mean of the environmental variables during daytime. Therefore, the combination model for estimating the stomatal conductance can be represented by

$$G_{st} = G_{Max} RDO \quad (2.1)$$

$$G_{Max} = \text{opt} \left\{ \prod_I^N G(X_{m,I}) \right\} \quad (2.2)$$

$$N=1, 2, 3, \dots; I=1, 2, \dots, N$$

$$RDO = \text{opt} \left\{ \prod_I^N R(X_{R,I}) \right\} \quad (2.3)$$

$$N=1, 2, 3, 4, I=1, 2, \dots, N$$

where $X_{m,i}=(X_{m,1}, \dots, X_{m,i}, \dots, X_{m,N})$ are the daytime means of each environmental variable, and $G(X_{m,i})$ are the response functions of G_{Max} to $X_{m,i}$. $X_{R,i}=(X_{R,1}, \dots, X_{R,i}, \dots, X_{R,N})$ are the relative variations of each environmental variable and $R(X_{R,i})$ are the response functions of RDO to $X_{R,i}$.

3 Material and Methods

3.1 Experimental conditions

The experiment was conducted at a maize (*Zea mays* L.) field at the Faculty of Horticulture, Chiba University during the summers of 1992-1994. The area of the field was about 20 m × 20 m and the soil was volcanic ash. The planting density varied from 31300 to 35700 plants per hectare depending on the year. The row spacing was 70-80 cm and the intrarow spacing was 40 cm. The growth period was from about the first ten days of June to the end of August. 1992 was an average year, 1993 was a rainy year with a cool summer, and 1994 was a megathermal and drought year (cf. Yu *et al.*, 1996a).

3.2 Collection of data

Stomatal resistance was measured every hour from 5:30 to 18:30 on two specified plants with a porometer (LI-1600, Li-Cor) under natural conditions in the field. The measured positions were at the center on the adaxial and abaxial surfaces of each leaf at three positions, separately, i.e. at the upper (from the top of stem the 2nd, 3rd), middle (the 5, 6th) and lower part (the 8, 9th) on the stem. The stomatal conductance (G_{st} , cm s⁻¹) to both sides was calculated by

$$G_{st}=1/r_{std}+1/r_{sib} \quad (3)$$

where r_{std} and r_{sib} are the stomatal resistances (s cm⁻¹) on the adaxial and abaxial surfaces, separately.

The photosynthetic photon flux density (Q_p , μ mol m⁻² s⁻¹), leaf temperature (T_L , °C) and saturation deficit (D_e , hPa) were also measured by sensors attached to the porometer at the time the stomatal resistance was measured. The measurement of water potential (ψ_L , MPa) used a pressure chamber at two plants near the plants used for measuring stomatal resistance.

3.3 Adaptation and evaluation of the model

To analyze the characteristics of the mean stomatal response in the crop community, the mean

values of G_{st} at various leaf positions and the environmental factors in the community were used. For adapting the model, the parameters were calculated by the linear or non-linear minimum squares method and the adaptation of the model was evaluated by the coefficient of determination (R^2) and the estimated error of mode (Se).

4 Results and Discussion

4.1 Model for estimating G_{Max}

It was found that G_{Max} was influenced by the daytime mean water potential ($\psi_{L,m}$), saturation deficit ($D_{e,m}$) and leaf temperature ($T_{L,m}$) based on the results of an analysis of response characteristics of G_{Max} to environmental variables (Yu *et al.*, 1996b). Therefore, the model of equation (2.2) for estimating G_{Max} can be determined by

$$G_{\text{Max}}=\text{opt}\{G_j(D_{e,m})G_q(\psi_{L,m})G_k(T_{L,m})\} \quad (4)$$

where a lot of expressions of $G_j(D_{e,m})$, $G_q(\psi_{L,m})$, $G_k(T_{L,m})$ are included in the model. To simplify, we used the following functions:

$$G_j(D_{e,m})$$

$$G_1(D_m)=b_1-b_2D_{e,m}; \quad R^2=0.349$$

$$G_2(D_m)=1/(b_1+b_2D_{e,m}); \quad R^2=0.408$$

$$G_3(D_m)=1/(1-b_1D_{e,m}^{b_2}); \quad R^2=0.328$$

$$G_q(\psi_{L,m})$$

$$G_1(\psi_m)=c_1+c_2\psi_{L,m}; \quad R^2=0.761$$

$$G_2(\psi_m)=G_M-c_1\exp(-c_2\psi_{L,m}); \quad R^2=0.224$$

$$G_3(\psi_m)=G_M/(1+c_1(-\psi_{L,m})^{c_2}); \quad R^2=0.815$$

$$G_k(T_{L,m})$$

$$G_1(T_m)=d+d_1T_{L,m}+d_2T_{L,m}^2; \quad R^2=0.514$$

$$G_2(T_m)=G_M\left[\frac{T_{L,m}-T_l}{T_o-T_l}\right]\left[\frac{T_h-T_{L,m}}{T_h-T_o}\right]^\alpha; \quad R^2=0.574$$

$$\alpha=(T_h-T_l)/(T_o-T_l)$$

where G_M is the maximum (cm s⁻¹) of G_{Max} , and b_1 and b_2 , c_1 and c_2 , d and d_1 , d_2 are constants for each function. T_l , T_o and T_h are the lower limit, upper limit and optimal leaf temperature (°C) for opening of the stomata.

By comparing R^2 of the regression formula of these functions, we found that the strongest factor influencing G_{Max} was the leaf water potential. After optimizing the three-variable model of equation (4), the following optimal model is obtained.

$$G_{\text{Max}} = \frac{d_0 + d_1 T_{L,m} + d_2 T_{L,m}^2}{(b_1 + b_2 D_{e,m})(1 + c_1 (-\psi_{L,m})^{c_2})} \quad (5)$$

where $b_1=0.702$, $b_2=0.073$, $c_1=8.269$, $c_2=4.033$, $d_0=3.763$, $d_1=0.515$ and $d_2=0.0144$ are the constants. The estimated precision of this model was quite high (Fig. 1).

Fig. 1 Relationship between the measured value and the estimated value of G_{Max} by the model based equation (5).

4.2 Model for estimating RDO

If the difference of the response curves in the two processes of stomatal opening and closing is ignored, the response functions of RDO to four variables are expressed by the formulas ①-④.

$$R(Q_p) = A_1 + A_2 Q_p / Q_{p,\text{Max}}; \quad R^2 = 0.757 \quad ①$$

$$R(D_e) = B_1 \exp(B_2 D_e / D_{e,\text{Max}}); \quad R^2 = 0.414 \quad ②$$

$$R(\psi_L) = C_1 \exp(C_2 \psi_L / \psi_{L,\text{Min}}); \quad R^2 = 0.389 \quad ③$$

$$R(T_L) = D_1 \exp(D_2 T_L / T_{L,\text{Max}}); \quad R^2 = 0.519 \quad ④$$

where $Q_p / Q_{p,\text{Max}}$, $D_e / D_{e,\text{Max}}$, $T_L / T_{L,\text{Max}}$, $\psi_L / \psi_{L,\text{Min}}$ are the relative variations of the environmental variables with 151 samples.

When the two processes of stomatal opening and closing were separated, the opening curve ($R_o(D_e)$ and $R_o(T_L)$) and closing curve ($R_c(D_e)$ and $R_c(T_L)$) are expressed by formulas ⑤ and ⑦, ⑥ and ⑧.

$$R_o(D_e) = B_{o1} + B_{o2} D_e / D_{e,\text{Max}}; \quad R^2 = 0.704 \quad ⑤$$

$$R_c(D_e) = B_{c1} \exp(B_{c2} D_e / D_{e,\text{Max}}); \quad R^2 = 0.517 \quad ⑥$$

$$R_o(T_L) = D_{o1} + D_{o2} T_L / T_{L,\text{Max}}; \quad R^2 = 0.688 \quad ⑦$$

$$R_c(T_L) = D_{c1} \exp(D_{c2} T_L / T_{L,\text{Max}}); \quad R^2 = 0.719 \quad ⑧$$

According to R^2 , the confidence limit of the above formulas exceeded 99%, in which R^2 of formula ① was the highest. For D_e and T_L , when the two processes of stomatal opening and closing were distinguished, the significances of the regression formulas were higher.

By the above-mentioned reasoning, if the difference between the two curves for opening and closing of stomata was neglected, $R(X_{R,i})$ of the multi-variable model (2.3) of RDO are expressed by formulas ①-④. $R(X_{R,i})$ for the opening process of stomata are expressed by formulas ①, ③, ⑤, ⑦ and $R(X_{R,i})$ for the closing process are expressed by formulas ①, ③, ⑥, ⑧. R^2 of these assembled RDO models with from 1 to 4 variables is shown in Table 1.

Table 1 Coefficients of determination (R^2) of the regression formulas to the multi-variable model of RDO .

Models	R_1^2	R_2^2	R_o^2	R_c^2
$R(Q_p)$	0.757	0.757		
$R(Q_p, D_e)$	0.754	0.773	0.771	0.785
$R(Q_p, T_L)$	0.753	0.783	0.751	0.783
$R(Q_p, D_e, T_L)$	0.744	0.767	0.732	0.787
$R(Q_p, D_e, \psi_L, T_L)$	0.743	0.768	0.732	0.789

Where R_1^2 and R_2^2 are the coefficients of determination of curves without distinguishing stomatal opening and closing and separating them into two processes. R_o^2 and R_c^2 are the coefficients of determination for the curves of stomatal opening and closing.

According to Table 1, the R^2 for RDO models without distinguishing the two processes of the opening and closing, could not be improved by increasing the number of the input variables. It appears that the RDO model is sufficiently expressed by

$$RDO = R(Q_p) = A_1 + A_2 Q_p / Q_{p,\text{Max}} \quad (6)$$

where $A_1=0.089$ and $A_2=0.773$ are the constants.

However, when the two processes of opening and closing were distinguished, the R^2 of the two-variable models (either $R(Q_p, D_e)$ or $R(Q_p, T_L)$) for estimating RDO showed a rather higher precision than that of the one-variable model $R(Q_p)$ (Table 1). The regression formulas of $R(Q_p, D_e)$ and $R(Q_p, T_L)$ can be written into the following formulas:

$$R_o(Q_p, D_e) = (0.108 + 0.115 Q_p / Q_{p, \text{Max}}) (-0.005 + 4.498 D_e / D_{e, \text{Max}}) \quad (7.1)$$

$$R_c(Q_p, D_e) = (0.018 + 0.128 Q_p / Q_{p, \text{Max}}) (5.292 \exp(0.109 D_e / D_{e, \text{Max}})) \quad (7.2)$$

$$R_o(Q_p, T_L) = (0.033 + 0.139 Q_p / Q_{p, \text{Max}}) (0.001 + 5.384 T_L / T_{L, \text{Max}}) \quad (8.1)$$

$$R_c(Q_p, T_L) = (0.031 + 0.207 Q_p / Q_{p, \text{Max}}) (2.144 \exp(0.531 T_L / T_{L, \text{Max}})) \quad (8.2)$$

Fig. 2. Comparison of the measured value and the estimated value of stomatal conductance (G_{st}) from the model based equations (9), (10) and (11).

4.3 Model for estimating G_{st}

If formula (5) is combined with formulas (6), (7), (8), the combination model of equation (2) for estimating G_{st} is constructed

$$G_{st} = G_{\text{Max}} R(Q_p) \quad (9)$$

$$G_{st} = G_{\text{Max}} R(Q_p, D_e) \quad (10)$$

$$G_{st} = G_{\text{Max}} R(Q_p, T_L) \quad (11)$$

The estimated precision of these models is shown in Fig. 2. Although the estimated precision of G_{st} obtained with equations (10) and (11) are rather higher than that obtained with equation (9), from the point of view of simplicity, we think that equation (9) is better. In other words, a model for estimating stomatal conductance can be represented by

$$G_{st} = \frac{(A_1 + A_2 Q_p / Q_{p, \text{Max}})(d_0 + d_1 T_{L, m} + d_2 T_{L, m}^2)}{(b_1 + b_2 D_{e, m})(1 + c_1 (-\psi_{L, m})^2)} \quad (12)$$

where Q_p and $Q_{p, \text{Max}}$ are the instantaneous and the maximum values of the photosynthetic photon flux density during daytime, and $T_{L, m}$, $D_{e, m}$, $\psi_{L, m}$ are the daytime means of leaf temperature, saturation deficit and leaf water potential. The experimental coefficients in the equation are the same as those in formulas (5) and (6).

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