A coupled model of photosynthesis-transpiration based on the stomatal behavior for maize (*Zea mays* L.) grown in the field

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Abstract

The study presents a theoretical basis of a stomatal behavior-based coupled model for estimating photosynthesis, *A*, and transpiration, *E*. Outputs of the model were tested against data observed in a maize (*Zea mays* L.) field. The model was developed by introducing the internal conductance, g_{ic}, to CO_2 assimilation, and the general equation of stomatal conductance, g_{sw}, to H_2O diffusion, into models of CO_2 and H_2O diffusion through the stomata of plant leaves. The coupled model is easier for practical use since the model only includes environmental variables, such as ambient CO_2 concentration, leaf temperature, humidity and photosynthetic photon flux received at the leaves within the canopy. Moreover, concept of g_{ic}, and factors controlling *A* and *E* were discussed, and applicability of the model was examined with the data collected in the maize field.

Introduction

In order to utilize water resources effectively, and to evaluate plant production and interaction between vegetation and environment quantitatively, material- and energy-exchange processes within soil–plant–atmosphere system through photosynthesis and transpiration have to be modelled. The processes of photosynthesis and transpiration occur through an identical path in stomata of plants leaves, since the same opening and closing movement of the stomata controls both processes. Therefore, it is very important to understand responses of stomata to environmental factors and to simulate the stomatal conductance. In these aspects, numerous researchers have contributed to the study (e.g., Jarvis, 1976; Kelliher et al., 1995; Rochette et al., 1991). In a series of our studies, the response characteristics of stomatal conductance

of maize to particular environmental factors were measured (Yu, 1999; Yu et al., 1996), and a combination model for estimating stomatal conductance over the long term was presented (Yu, 1999; Yu and Nakayama, 1997; Yu et al., 1998).

However, photosynthesis activity is actually acted on stomatal behavior, simultaneously, the stomatal behavior is subject to the feedback of photosynthesis activity (Ball et al., 1987; Jones, 1992; Leuning, 1990, 1995; Lloyd, 1991). Although transpiration and photosynthesis both occur through stomata, they show different behaviors (Kosugi, 1997; Yu, 1999). For example, the leaves may adjust stomatal conductance to maximize carbon assimilation for a given daily loss of water vapor (Cowan and Farquhar, 1977; Leuning, 1990). It is, therefore, important to comprehensively understand both of these processes. Moreover, if taking diffusion of H_2O and CO_2 as a combined physical and physiological phenomenon through the stomata of plant leaves, then, it may be expected to develop a

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coupled model of photosynthesis-transpiration based on the stomatal behavior.

A very useful empirical relationship between net assimilation rate of CO_2, A, and stomatal conductance, g_{sw}, was firstly proposed by Ball et al. (1987), and some modified versions were proposed by Lloyd (1991), Collatz et al. (1991) and Leuning (1990, 1995). On the other hand, a biochemical model for estimating the net assimilation rate was firstly presented by Farquhar et al. (1980), and thereafter this model was modified and applied by many researchers for C_3 plants (Caemmerer von and Farquhar, 1981; Harley et al., 1985, 1992; Leuning, 1995; McMurtrie et al., 1992) and C_4 plants (Boegh et al., 1999; Collatz et al., 1991, 1992). Furthermore, Leuning (1995) presented a combined stomatal–photosynthesis model for C_3 plants. Woodward et al. (1995) and Sellers et al. (1992, 1996) introduced a combined stomatal–photosynthesis model into the global climate models, and used the model to estimate global terrestrial primary productivity.

The models mentioned above provided very useful approaches for understanding the processes of photosynthesis and transpiration. However, too many parameters are needed to estimate photosynthesis, thus the models are inconvenient to use. To make this kind of model more practical and simpler, in this study, we attempt to provide a theoretical basis of a stomatal behavior-based coupled model for estimating photosynthesis and transpiration, and to test the model outputs against data collected from field-grown maize. The coupled model was obtained by introducing the internal conductance to CO_2 assimilation and the general equation of stomatal conductance model to H_2O diffusion proposed by Leuning (1995) into the models of CO_2 and H_2O diffusion through the stomata of plant leaves.

Model Formulations

Models of transpiration and net assimilation

The CO_2 and H_2O fluxes of the leaves are determined by several factors in atmosphere, plant, and soil. The CO_2 flux, or transpiration rate, E (mol H_2O m^{-2} s^{-1}), is basically described by

$$E = \frac{(W_i - W_a)}{1/g_{bw} + 1/g_{sw}} = g_{tw}(W_i - W_a), \qquad (1)$$

where W_i is mole fraction of water vapor in the stomata space (mol mol^{-1}), W_a is mole fraction of water vapor in the air (mol mol^{-1}), g_{bw} and g_{sw} are conductances of boundary layer and stomatal to H_2O (mol m^{-2} s^{-1}), respectively, g_{tw} is total conductance to H_2O (mol m^{-2} s^{-1}).

The CO_2 flux, or net assimilation, A (μmol m^{-2} s^{-1}), is generally described as

$$A = \frac{(C_a - C_i)}{1/g_{bc} + 1/g_{sc}} = g_{gc}(C_a - C_i), \qquad (2)$$

where C_a is ambient CO_2 concentration (μmol mol^{-1}), C_i is intercellular CO_2 concentration (μmol mol^{-1}), g_{bc} and g_{sc} are conductances of the boundary layer and stomata (mol m^{-2} s^{-1}) to CO_2, respectively, and g_{gc} is gas-phase conductance to CO_2 (mol m^{-2} s^{-1}). Equation (2) indicates that the control of the net assimilation rate is exerted by the supply of CO_2 through stomata and boundary layer, thus the equation is generally called a 'supply' function for the assimilation rate of plant leaves (Jones, 1992; Leuning, 1990, 1995).

However, the actual net assimilation rate is not only determined by the gas-phase diffusion, but also controlled by the biochemical and photochemical processes in leaf mesophyll, such as light reactions, dark reactions, or even the supply of phosphate. In simulation of the effects of bio- and photo-chemical processes, the biochemical model of Farquhar et al. (1980) and its modified versions have been widely used (see Introduction). These models indicate that the control of the net assimilation rate is exerted by the demand of CO_2 in the bio- and photo-chemical processes, thus they are generally called as 'demand' functions for the assimilation of plants (Leuning, 1990, 1995). To simplify the expression used to evaluate the regulation of bio- and photo-chemical processes on net assimilation rate, here we used another form of 'demand' function suggested by Jones (1992), i.e.

$$A = g_{ic}(C_i - \Gamma_*) \qquad (3)$$

In this equation, Γ_* is CO_2 compensation point without dark respiration (μmol mol^{-1}), and g_{ic} is defined as 'internal' conductance (mol m^{-2} s^{-1}).

The CO_2 compensation point without dark respiration, Γ_*, is dependent on the leaf temperature. An empirical second-order polynomial for C_3 plants (Brooks and Farquhar, 1985) was used in the study to describe dependence of the Γ_* on the leaf temperature,

$T_L(°C)$, namely

$$\Gamma_{*C3} = 42.7 + 1.68(T_L - 25) + 0.012(T_L - 25)^2$$
$$(4.1)$$

while for C_4 plants (Woodward and Smith, 1994), the Γ_* is

$$\Gamma_{*C4} = 0.1\Gamma_{*C3} \qquad (4.2)$$

Moreover, the net assimilation rate depending on both 'supply' and 'demand' functions can be written as

$$A = \frac{(C_a - \Gamma_*)}{1/g_{bc} + 1/g_{sc} + 1/g_{ic}} = g_{tc}(C_a - \Gamma_*), \quad (5)$$

where g_{tc} is total conductance to CO_2 assimilation (mol m^{-2} s^{-1}).

Stomatal behavior model

As a basis of the sub-models of evapotranspiration and photosynthesis, the stomatal conductance model of Jarvis (1976) and its modified versions have been widely used for the scale of individual leaves to some global climate models (Yu et al., 1998). An alternative approach to modeling stomatal conductance is to incorporate factors relating to leaf physiology and photosynthesis (or assimilation rates) into the model. Ball et al. (1987) first presented an empirical relationship, which incorporated the often-observed correlation between net assimilation rate, A, and stomatal conductance, g_{sw}, and included the effects of humidity and ambient CO_2 concentration on conductance, namely

$$g_{sw} = a_1 A h_s / C_s, \qquad (6)$$

where a_1 is a coefficient, h_s and C_s are relative humidity and ambient CO_2 concentration at the leaf surface, respectively. Ball et al. (1987) were able to collapse data from various leaf gas-exchange experiments onto a single line using Equation (6). Similarly, Leuning (1990) and Lloyd (1991) obtained good linear relationships when they plotted their data according to the model of Ball et al. (1987). This equation may be more useful if h_s is replaced by a more general humidity function $f(D_s)$, i.e.,

$$g_{sw} = g_0 + a_1 A f(D_s) / C_s, \qquad (7)$$

where, g_0 is residual stomatal conductance (as $A \to 0$ when $Q_p \to 0$) (Leuning, 1995). However, in its present form, Equation (7) is incapable of describing stomatal behavior at low CO_2 concentrations since conductance increases to a maximum value as C_s approaches the CO_2 compensation point, Γ, while $A \to 0$. Equation (7) predicts that $g_{sw} \to 0$ under these circumstances. To overcome this problem, Leuning (1995) accounted for these observations by replacing C_s with $C_s - \Gamma$, i.e.

$$g_{sw} = g_0 + a_1 A f(D_s) / (C_s - \Gamma) \qquad (8)$$

This modification ensures that g_{sw} remains large as $A \to 0$ while $C_s \to \Gamma$. Note that g_{sw} is not defined by this equation when $C_s = \Gamma$ (Leuning, 1995).

As for $f(D_s)$, general function describing response of stomatal conductance to humidity in Equation (8), numerous expression functions have been proposed (Ball et al. ,1987; Collatz et al., 1991; Leuning, 1995; Lloyd, 1991; Lohammer et al., 1980). Here we used the expression functions adopted by Ball et al. (1987),

$$f_1(D_s) = h_s \qquad (9.1)$$

and by Leuning (1995)

$$f_2(D_s) = (1 + D_s/D_0)^{-1} \qquad (9.2)$$

Stomatal behavior-based coupled model for estimating photosynthesis-transpiration

Equation (2) can be rewritten as

$$A = g_{gc}(C_a - C_i), \quad \text{where} \quad 1/g_{gc} = 1/g_{bc} + 1/g_{sc} \qquad (10)$$

Assuming $g_{sw} = 1.56 g_{sc}$ and $g_{bw} = 1.37 g_{bc}$, the intercellular CO_2 concentration, C_i, can be derived by combining Equation (8) with Equation (10),

$$C_i = C_a - \frac{1.56A}{g_0 + a_1 A f(D_s)/(C_a - \Gamma)} - 1.37A/g_{bw} \qquad (11)$$

The g_0 in Equation (8) can be assumed as a cuticular conductance to H_2O, and also $g_0 \ll g_{sw}$. Then, g_0 could generally be ignored when considering the diffusion of CO_2 through stomata. If assuming g_0 negligible, and combining Equation (11) with Equation (3) or combining Equation (8) with Equation (5), a stomatal behavior-based coupled model for estimating CO_2 assimilation rate is given as

$$A = \frac{(C_a - \Gamma_*) - 1.56(C_a - \Gamma)/[a_1 f(D_s)]}{1.37/g_{bw} + 1/g_{ic}} \qquad (12)$$

Table 1. Parameters and their values in the model for estimating the CO_2 compensation points, Γ

Parameters	Value (units) [Ref.]	Meaning
T_r	293.2 (K) [1]	Reference temperature
K_{cr}	203 (μmol mol^{-1}) [1]	Michaelis constant for CO_2 at T_r
K_{or}	256 (mmol mol^{-1}) [1]	Michaelis constant for O_2 at T_r
R_{dr}	0.32 (μmol s^{-1} m^{-2}) [1]	Day respiration at T_r
E_{Kc}	59 430 (J mol^{-1}) [2]	Activation energy for K_c
E_{Ko}	36 000 (J mol^{-1}) [2]	Activation energy for K_o
E_{Rd}	53 000 (J mol^{-1}) [2]	Activation energy for R_d
H_v	116 300 (J mol^{-1}) [2]	Activation energy for V_{cmax}
H_d	202 900 (J mol^{-1}) [2]	Deactivation energy for V_{cmax}
S_v	650 (J mol^{-1}) [2]	Entropy term

[1], from Leuning (1990 and 1995); [2], from Harley et al. (1992).

The CO_2 compensation point without dark respiration, Γ_*, can be calculated by Equation (4). The CO_2 compensation point with dark respiration, Γ, can be calculated by the following equation of Farquhar et al. (1980)

$$\Gamma = \frac{\Gamma_* + K_c R_d (1 + c_o/K_o) V_{cmax}}{1 - R_d/V_{cmax}}, \qquad (13.1)$$

where, c_o is intercellular oxygen concentration, supposed equal to 207.3 μmol mol^{-1} (Brooks and Farquhar, 1985). Dependences of K_c, K_o, and R_d on the leaf temperature could be described, respectively, by the following exponential functions

$$K_c = K_{cr} \exp[(E_{Kc}/RT_r)(1 - T_r/T_L)] \qquad (13.2)$$

$$K_o = K_{or} \exp[(E_{Ko}/RT_r)(1 - T_r/T_L)] \qquad (13.3)$$

$$R_d = R_{dr} \exp[(E_{Rd}/RT_r)(1 - T_r/T_L)], \qquad (13.4)$$

where R is the universal gas constant, E_{Kc}, E_{Ko} and E_{Rd} are the activation energy for K_c, K_o and R_d, respectively, and K_{cr}, K_{or}, and R_{dr} are the values of K_c, K_o, R_d at a reference temperature (293.3 °K), respectively. The temperature dependence of V_{cmax} was simulated according to Farquhar et al. (1980) and Harley et al. (1992):

$$V_{cmax} = \frac{V_{cmax0} \exp[(H_v/RT_r)(1 - T_r/T_L)]}{1 + \exp[(S_v T_L - H_d)/(RT_L)]}, \qquad (13.5)$$

where V_{cmax0} is the value of V_{cmax} at T_r, supposed equal to 28.9 μmol m^{-2} s^{-1} (Harley, 1986). H_v is the energy of activation, H_d is the energy of deactivation, and S_v is an entropy term. The values of these empirical constants in Equation (13) are obtained from Leuning (1995) and Harley et al. (1992), and shown in Table 1.

Moreover, by incorporating Equation (8) into Equation (1), a stomatal behavior-based coupled model for estimating the transpiration rate, E (mol H_2O m^{-2} s^{-1}), has the form of

$$E = \frac{(W_i - W_a}{1/g_{bw} + 1/[g_0 + a_1 A f(D_s)/(C_a - \Gamma)]} \qquad (14)$$

Materials and methods

Field experimental site

The investigation was conducted in the summer of 1998 in the experimental field of the Faculty of Horticulture, Chiba University, located in Matsudo (latitude 35°46'N and longitude 139°54'E), Japan. The soil in the experimental field was developed from volcanic ash, with a texture of sandy loam. The Maize (Zea mays L.) plants were grown in a 20 × 20 m plot, with planting density of 35 700 plants per hectare, row spacing of 0.7 m, and intrarow spacing of 0.4 m. Fertilization, disease and insect controls were carried out conventionally. The growing period was from the beginning of May to the end of August.

Table 2. Post-emergence days, *D*, plant height, *H*, and leaf area index, *LAI*, and environmental conditions during the eight-day investigation period

Days	D (days)	H (m)	LAI	S_n MJ m^{-2} day^{-1}	R_n MJ m^{-2} day^{-1}	T_a (°C)	D_a (hPa)	Ψ_s −kPa	Ψ_L −kPa
Jul. 19	46	0.90	1.48	14.52	10.91	24.2	6.25	15.7	567
Jul. 26	53	1.22	1.86	14.83	11.49	27.5	7.40	5.9	507
Jul. 27	54	1.26	1.90	22.35	16.43	29.0	10.48	6.1	846
Aug. 3	61	1.51	2.01	15.15	11.09	30.3	12.24	30.7	605
Aug. 4	62	1.54	2.01	10.09	7.22	28.3	8.94	38.2	477
Aug. 6	64	1.59	1.99	10.74	7.66	27.3	7.90	51.3	375
Aug. 12	70	1.67	1.87	8.91	6.15	29.1	10.53	45.6	522
Aug. 16	73	1.66	1.77	9.89	7.23	26.8	7.98	14.6	606

Solar radiation (S_n), net radiation (R_n), air temperature (T_a), and saturation deficit (D_a) were the values determined at 2 m height above soil surface. Soil water potential (Ψ_s) was average value as determined at 0–40 m profile depths, while value of leaf water potential, Ψ_L, was the average value as determined at different heights within the canopy. The values of environmental variables were the daytime average values or cumulative values.

Measurement of net assimilation rate, transpiration rate and stomatal conductance

Net assimilation rate, transpiration rate, and stomatal conductance were measured every hour from 07:00 to 18:00 h of local time on the surfaces of the leaves of two designated plants by means of a portable photosynthesis system (LI-6200, Li-cor. Inc.). The measurements were at the center of the leaf surface at four different leaf positions, i.e., on the second, fourth, sixth, and eighth leaf from the top of the plants, sequentially for the first plant, followed by exactly the sequence for the second plant.

Observation of environmental variables

Solar radiation, R_s, and net radiation, R_n, were determined by means of a solarimeter (MR-21, EKO) and a radiometer (CN-21, EKO), respectively, at 2 m height above the soil surface. Air saturation deficit, D_a, and temperature, T_a, were determined by means of a ventilated psychrometer at 2 m height from the soil surface. Soil moisture content was measured using tensiometer (DIK-3100, Daiki Rika) inserted at depths of 0.1, 0.2, 0.3, 0.4, 0.6, 0.8 and 1.0 m in the maize field. Leaf temperature, saturation deficit and photosynthetic photon flux density within the canopy were also recorded by means of sensors attached to the portable photosynthesis system at the same time as the measurement of the stomatal conductance. The leaf temperature, T_L(°C), and the saturation deficit, D_e (hPa), within the canopy were the mean values at different leaf positions on the stem. The photosynthetic photon flux density, Q_p (μmol m^{-2} s^{-1}), within the

canopy was the average value of the downward flux received by the leaves at four different leaf positions of two plants. Simultaneously, leaf water potential, Ψ_L (MPa), of two nearby plants was measured using a pressure chamber (DIK-7000, Daiki Rika).

Data processing and model evaluation

Aiming at identifying the net assimilation rate, the transpiration rate, and the stomatal conductance within the canopy, we used averages of the values measured for several leaves within the canopy in the analysis. Another advantage in using these average values was the minimizing of the negative influence imposed by the time required for the response of the stomata to changes in the environmental variables. This is because the average values were assumed to represent the mean status of the measured items in the period of 15 to 20 min, during which stomatal conductance was measured on the two designated plants.

Values of the parameters in the model were calculated by the linear or non-linear least-squares method, and their applicabilities were evaluated with R^2, Sl and RMSE. Here R^2 is coefficient of determination of the regression formula for the model, Sl is slope of the linear regression curve established between the measured values and the values estimated by means of the model. RMSE is root mean square error for the values measured and estimated by means of the model.

Results

The observations

Post-emergence days, D, plant height, H, leaf area index, LAI, and environmental conditions during the 8-day investigation period are shown in Table 2. They are daytime average or cumulative values. Figure 1 shows the diurnal change of environmental factors, transpiration rate, stomatal conductance, and net assimilation rate for each observation day. The weather conditions were rainy or cloudy during the period of investigation. Thus there was little water stress from soil, and the solar radiation and the net radiation were less than that of common years. (Table 2).

On the other hand, net assimilation rate, A, transpiration rate, E, and stomatal conductance, g_{sw}, measured during daytime of the eight investigation days vary with the weather conditions, while the diurnal variations of A, E, and g_{sw} were mainly dependent on the trend of diurnal variation of Q_p. The average values of E, g_{sw}, and A, for all measurements were 4.45 ± 3.2 mmol m^{-2} s^{-1}, 0.439 ± 0.276 mol m^{-2} s^{-1}, and $14.611\pm8.512 \mu$mol m^{-2} s^{-1}, respectively, with the maxima of 15.1 mmol m^{-2} s^{-1}, 1.255 mol m^{-2} s^{-1}, and 34.26 μmol m^{-2} s^{-1}, respectively. Incidentally, the ambient CO$_2$ concentration within the canopy showed a little diurnal change similar to the diurnal change of A, and these values become the lowest at about noon. The average of ambient CO$_2$ concentration within the canopy during the investigation was $327.7\pm33.9 \mu$mol mol^{-1}, ranging from 259.5 to 411.4μmol mol^{-1}.

Estimation of photosynthesis and transpiration by the coupled models

There may exist difference between D_e within the canopy and D_s on leaf surface. However, D_s is difficult to measure directly. Using D_e not only can substitute D_s approximately but also can make the model easier to application. Therefore, in this study, we assumed the saturation deficit, D_e, within the canopy as the D_s in Equations (9.1) and (9.2). The constants of Equation (8) were determined by non-linear parameter estimation procedure, using the data of the eight investigation days observed in the field, Then the formula of stomatal conductance are

$$g_{sw} = 0.118 + 0.089 A h_s / (C_s - \Gamma) \quad (15.1)$$

and

$$g_{sw} = 0.109 + 10.132 A / [(1 - D_s/30)(C_s - \Gamma)] \quad (15.2)$$

The values of R^2 for the functions of Equations (15.1) and (15.2) were 0.530 and 0.516, significant at $P < 0.01$ levels. The g_0 obtained was about 0.1 mol m^{-2} s^{-1}, rather smaller than 0.12–0.16 mol m^{-2} s^{-1} of millet crop reported by Boegh et al. (1999) and much bigger than 0.01 mol m^{-2} s^{-1} of C$_3$ plant reported by Leuning (1990).

Moreover, to determine the internal conductance, g_{ic}, in the model of Equation (12) for estimating photosynthesis quantitatively, we made correlation analyses between g_{ic} and various environmental variables (Figure 2). From Figure 2, it was found that there are correlations between g_{ic} and various environmental variables, such as Q_p, D_s, T_L, and Ψ_L, but g_{ic} depends on Q_p (μmol m^{-2} s^{-1}) most strongly. The g_{ic} could be estimated by the following formula

$$g_{ic} = 0.000136 Q_p - 0.002479; \quad R^2 = 0.92; \quad n = 81 \quad (16)$$

This means that the irradiance is the most important input variable to decide g_{ic} since light determines the rate of RuBP regeneration, which will be discussed in detail in the section of discussion.

When the model of Equation (12) for estimating photosynthesis and the model of Equation (14) for transpiration are used, the CO$_2$ compensation points without dark respiration, Γ_*, can be obtained by Equation (4), and the CO$_2$ compensation with dark respiration, Γ, can be calculated by Equation (13).

In the experimental conditions, the values of Γ_* and Γ which were calculated using Equations (4) and (13) were 5.9 ± 0.6 μmol mol^{-1} and 9.9 ± 1.2 μmol mol^{-1}, respectively. Also, the values of $(C_a-\Gamma_*)$ and $(C_a-\Gamma)$ in Equation (12) were 321.9 ± 34.3 μmol mol^{-1} and 318.0 ± 34.7 μmol mol^{-1}, respectively. In this sense, it might be judged that the estimation error of the photosynthesis arising from the difference between Γ_* and Γ should not be large. Thus, Equation (12) can be simplified as

$$A = \frac{(C_a - \Gamma_*)[1 - 1.56/(a_1 f(D_s))]}{1.37/g_{bw} + 1/g_{ic}} \quad (17)$$

For model validation, using the data set collected in the field, we estimated the net assimilation rate using Equations (12) and (17) with different $f(D_s)$ of Equations (9.1) and (9.2), where g_{ic} is the measured value.
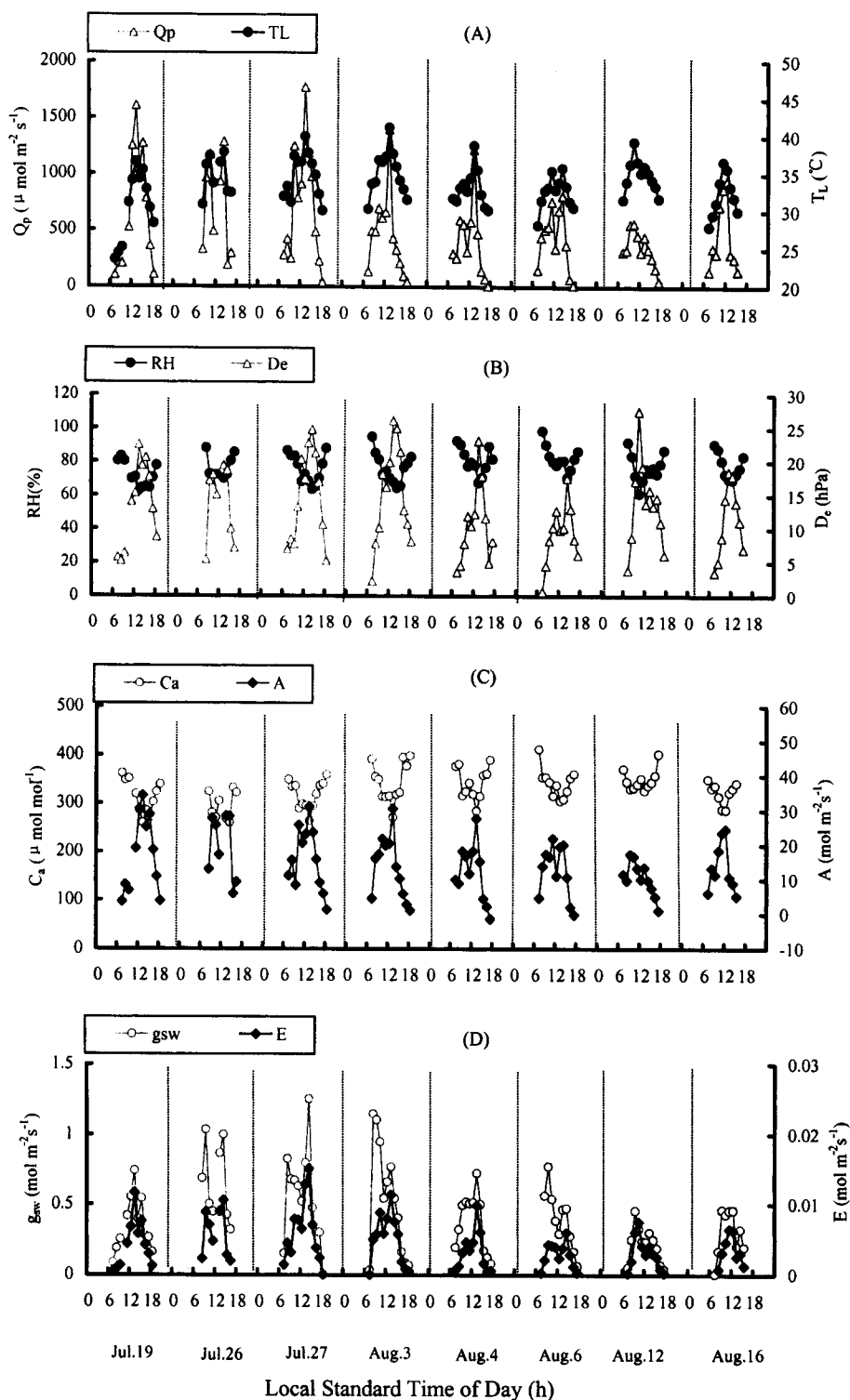
Figure 1. Comparison of diurnal changes of environmental variables and net assimilation rate, *A*, transpiration rate, *E*, stomatal conductance, g_{sw}, during the eight-day investigation period. Photosynthetic photon flux, Q_p, leaf temperature, T_L, relative humidity, RH, saturation deficit, D_e, ambient CO_2 concentration, C_a, were the values determined within the canopy.
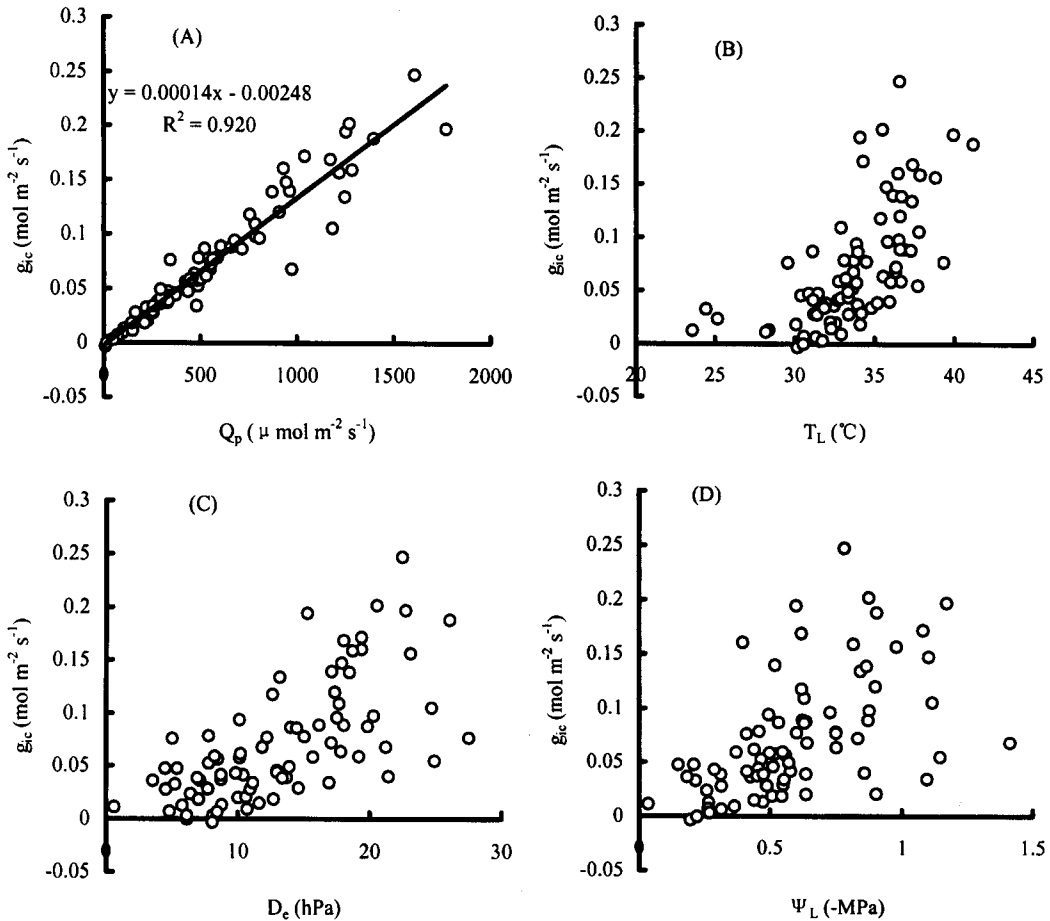
Figure 2. Relationships between internal conductance, g_{ic}, and photosynthetic photon flux, Q_p, leaf temperature, T_L, saturation deficit, D_e, and leaf water potential, Ψ_L.

Because when measuring the rate of photosynthesis of leaf with the portable photosynthesis system, the wind speed in leaf chamber is set as a constant, so boundary layer conductance, g_{bw}, is also set as a constant. Here we adopted this constant, i.e., $g_{bw}=2.0$ mol m^{-2} s^{-1}. The estimation precision of the net assimilation rate models is shown in Table 3.

Furthermore, net assimilation rates were estimated by combining the g_{ic} model of Equation (16) with Equations (12) and (17), respectively, adopting Equations (9.1) and (9.2) for $f(D_s)$. The results showed that the estimation precision of net assimilation rate in the case of using estimated g_{ic} by the model of Equation (16) was rather lower than that in the case of using the measured g_{ic}. However, the R^2 values of these models were >0.92, the RMSE were <0.28μmol m^{-2} s^{-1}. Figure 3 compares the values of net assimilation rate measured and estimated by means of the models. Fig-

ure 3A, B are the cases of using Equation (12), and Figure 3C, D are the cases of using Equation (17). While Figure 3A, C are the cases of using the function of $f_1(D_s)=h_s$, Figure 3B, D are those of using $f_2(D_s)=1/(1+D_s/D_0)$.

From Table 3 and Figure 3, it could be seen that these models had adequate precision, and they could be well used for estimating the net assimilation rate, even if employing a simplified form of Equation (17). Thus, we recommend employing their simplified form as Equation (17) because it avoids the calculation of the CO_2 compensation, Γ, and makes the model simpler for C4 pants.

On the other hand, using Equations (9.1) and (9.2), we estimated the transpiration rate by means of the transpiration model as Equation (14). The result of analysis indicates that the values of R^2 are >0.83 and the RMSE are <0.2 mmol m^{-2} s^{-1}. Figure 4A, B
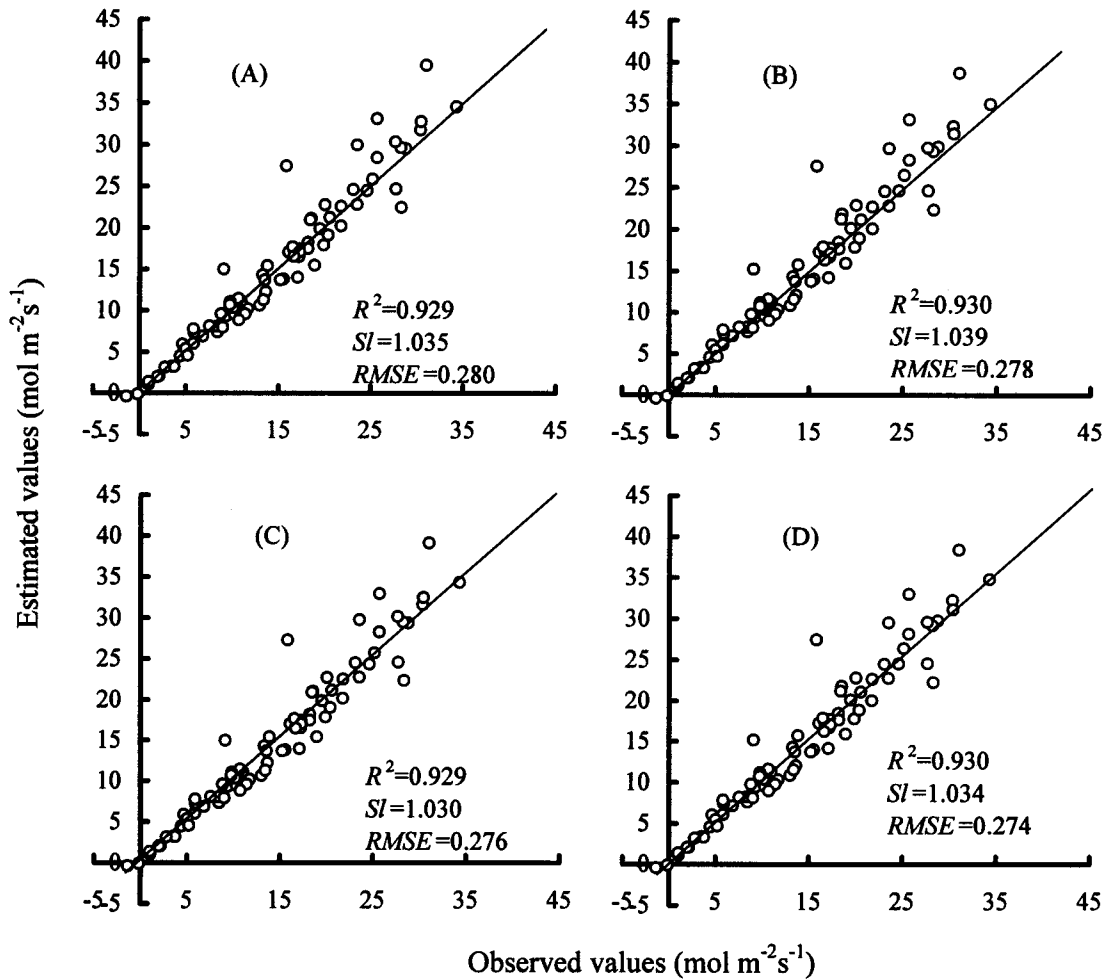
Fig. 3 Comparison of net assimilation rates measured and estimated by means of the net assimilation models, Eq. (12) (A, B) and Eq. (17) (C, D). For the function of $f(D_s)$, $f_1(D_s)=h_s$ (A, C) and $f_2(D_s)=1/(1+D_s/D_0)$ (B, D) were used, while for internal conductance, g_{ic}, estimated values by Eq. (16) were used. The solid line represents a line of 1:1.

Table 3. Estimation precision for the net assimilation rate, A, when using Equations (12) and (17) and using the different functions for $f(D_s)$ in $g_{sw}=a_1 A f(D_s)/(C_s-\Gamma)$. For the internal conductance, g_{ic}, measured values were used

$f(D_s)$	Equation (12)			Equation (17)		
	R^2	Sl	RMSE	R^2	Sl	RMSE
$f_1(D_s)=h_s$	0.963	1.042	0.214	0.963	1.037	0.220
$f_2(D_s)=(1+D_s/D_0)^{-1}$	0.959	1.047	0.226	0.959	1.042	0.231

R^2 is the coefficient of determination, Sl is the slope (b) of the equation, $A'=bA$, established between the measured values (A) and the values estimated by means of the model (A'). RMSE is root mean square error (μmol m^{-2} s^{-1}).
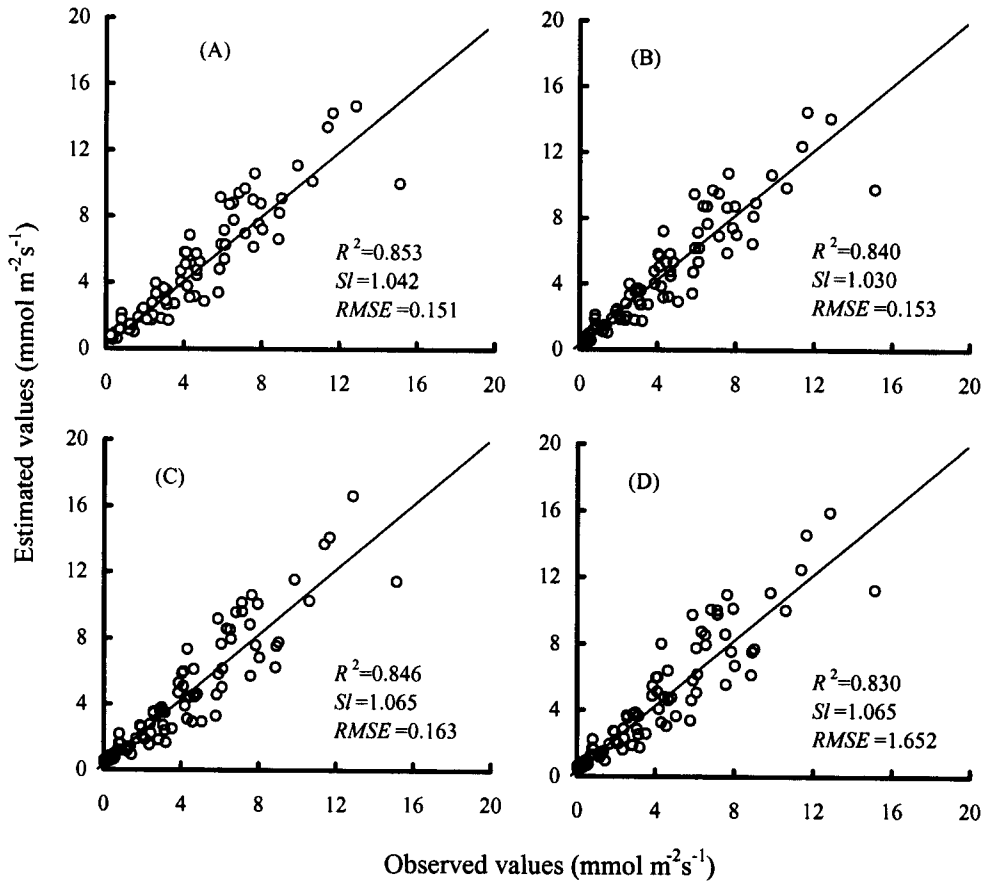
Figure 4. Comparison of transpiration rates measured and estimated by means of the transpiration rate model, Equation (14) (A, B) and Equation (18) (C, D). For the functions of $f(D_s)$, $f_1(D_s)=h_s$ (A, C) and $f_2(D_s)=1/(1+D_s/D_0)$ (B, D) were used, while for the net assimilation, A, and internal conductance, g_{ic}, were used the estimated values by Equations (17) and (16), respectively. The solid line represents a line of 1:1.

show a comparison of the measured values and the estimated values of transpiration rate obtained by means of the models. From Figure 4, it can be found that the estimated values of the transpiration rate obtained by means of the models agreed approximately with the measured values, and these models performed well in estimating the transpiration rate. Moreover, by substituting Equation (17) into Equation (14), Equation (14) can be simplified as

$$E = \frac{(e_w(T_L) - e)/P}{1/g_{bw}+1/[g_0+(a_1 f(D_s)-1.56)/1.37/g_{bw}+1/g_{ic})]} \tag{18}$$

where $e_w(T_L)$ is saturated water vapor pressure at leaf temperature (hPa), e is water vapor pressure of air within the canopy (hPa), P is atmospheric pressure (1013 hPa). Figure 4C, D show that the model per-

formed well in estimating the transpiration rate even if a simplified form as Equation (18) is employed.

With regard to the bigger scattering of the values measured and estimated by means of the models, we think that it should be ascribed to the error of transpiration data obtained in leaf chambers, because energy balance of the leaves is usually changed when they are put in the chamber. Anyway, the estimation precision of the models is still acceptable.

Factors controlling net assimilation rate and transpiration

According to Equations (2), (3) and (5), net assimilation rate is mainly determined by the ambient CO_2 concentration of leaves, C_a, intercellular CO_2 concentration, C_i, CO_2 compensation point, Γ_*, boundary layer conductance, g_{bc}, stomatal conductance, g_{sc}, and internal conductance, g_{ic}. Among these factors, g_{ic},

g_{sc}, C_i, and Γ_* are main physiological factors of plant. Γ_* is mainly determined by leaf temperature, while C_i, which is calculated by Equation (11), is influenced by C_a and A.

In the process of photosynthesis, CO_2 assimilation of leaves is controlled by both the biochemical processes and the diffusion of CO_2 through stomata to intercellular spaces. Jones (1985, 1992) presented a method for evaluating the relative limitation resulting from stomata and mesophyll in controlling A. In principle, the ratio of the conductances of different components or the concentration drops across them is a measure of their relative control of A (Jones, 1985). On this basis, the relative control of stomatal and internal processes for assimilation of CO_2 can be defined as

$$R_{cs} = (1/g_{sw})/(1/g_{bc} + 1/g_{sw} + 1/g_{ic}) \qquad (19)$$

and

$$R_{ci} = (1/g_{ic})/(1/g_{bc} + 1/g_{sw} + 1/g_{ic}) \qquad (20)$$

Actually, R_{cs} and R_{ci} have counter correlation because of the relatively small value of r_{bc}. Figure 5 shows the diurnal change of the relative control of stomatal- and internal-processes for CO_2 assimilation, and the relationships between A and the relative contributions. The average of R_{cs} was 0.191 ± 0.084 with the maximum of 0.405. The average of R_{ci} was 0.772 ± 0.099 with the maximum of 0.940. This implies that the internal conductance that depends on the activities of bio- and photo-chemical processes strongly limited the net assimilation rate during the experiment. The diurnal change of R_{cs} showed that the value was small in the morning and evening, but large at noon. The diurnal change of R_{ci} showed an opposite trend to that of R_{cs}. Thus, the net assimilation rate was positively correlated with the R_{cs} (Figure 5B), but negatively with the R_{ci} (Figure 5C). Based on the above analyses, it can be easily found that A became larger with the strengthening of the activities of bio- and photochemical processes which were induced by increasing Q_p at daytime.

On the other hand, using Equation (1), transpiration rate is determined by vapor pressure deficit, boundary layer conductance, and stomatal conductance. Equation (18) shows that the transpiration rate is a function depending on g_{ic}, $f(D_s)$, $e_w(T_L)$, and e. In this study, g_{bw} was given as 2.0 mol m^{-2} s^{-1}, and g_{ic}, which can be estimated with Equation (16), is a function of Q_p. Figure 6 shows the relationships

between transpiration rate and stomatal conductance and between transpiration rate and vapor pressure deficit, VPD. If H_2O flux occurs from wetted leaf surface, then $g_{sw}=0$, and the H_2O flux, E_{pb}, at this time depends only on g_{bw}. The dotted line in Figure 6B shows the values of E_{pb} calculated using Equation (1) when assuming $g_{bw}=2.0$ mol m^{-2} s^{-1} and $g_{sw}=0$ mol m^{-2} s^{-1}. Also, if stomata open to its maximum degree, the H_2O flux, E_{pmax}, is assumed depending on the maximum stomatal conductance g_{swmax}. Assuming $g_{bw}=2.0$ mol m^{-2} s^{-1} and $g_{sw}=g_{swmax}=1.225$ mol m^{-2} s^{-1}, the maximum H_2O flux, E_{pmax}, was calculated with Equation (1) and shown in Figure 6B by the dotted line. Figure 6 shows that the actual flux is rather smaller than E_{pmax} and E_{pb}. Thus, it can be said that, among the factors controlling transpiration rate, stomatal conductance plays a significant role.

Discussion

Concept of internal conductance

To strictly distinguish the concept of internal conductance used in this study, several concepts of conductances from bulk atmosphere to site of carboxylation are described in Figure 7. Among these conductances, the boundary layer conductance, g_{bc}, and the stomatal conductance, g_{sc}, are gas-phase conductances. The carboxylation conductance, g_{xc}, represents the efficiency of carboxylation in the chloroplast, associated with 'enzyme' component that depends on the activities of biochemical and photochemical processes. It was assumed that the mesophyll conductance, g_{mc}, represented the efficiency of CO_2 liquid-phase transport. Thus it was sometimes termed as the transport conductance (Jones and Slatyer, 1972) or the liquid-phase conductance (Farquhar and Sharkey, 1982). Jones (1992) termed the total of carboxylation conductance, g_{xc}, and mesophyll conductance, g_{mc}, as the liquid-phase (or mesophyll) conductance, g_m, and described it as follow

$$1/g_m = (C_i - \Gamma)/A \qquad (21)$$

The major component of g_m is probably a carboxylation conductance, thus it is appropriate to term it as a reciprocal of 'carboxylation efficiency' (Jones, 1992).

Using Equation (3), g_{ic} can be expressed by a form of

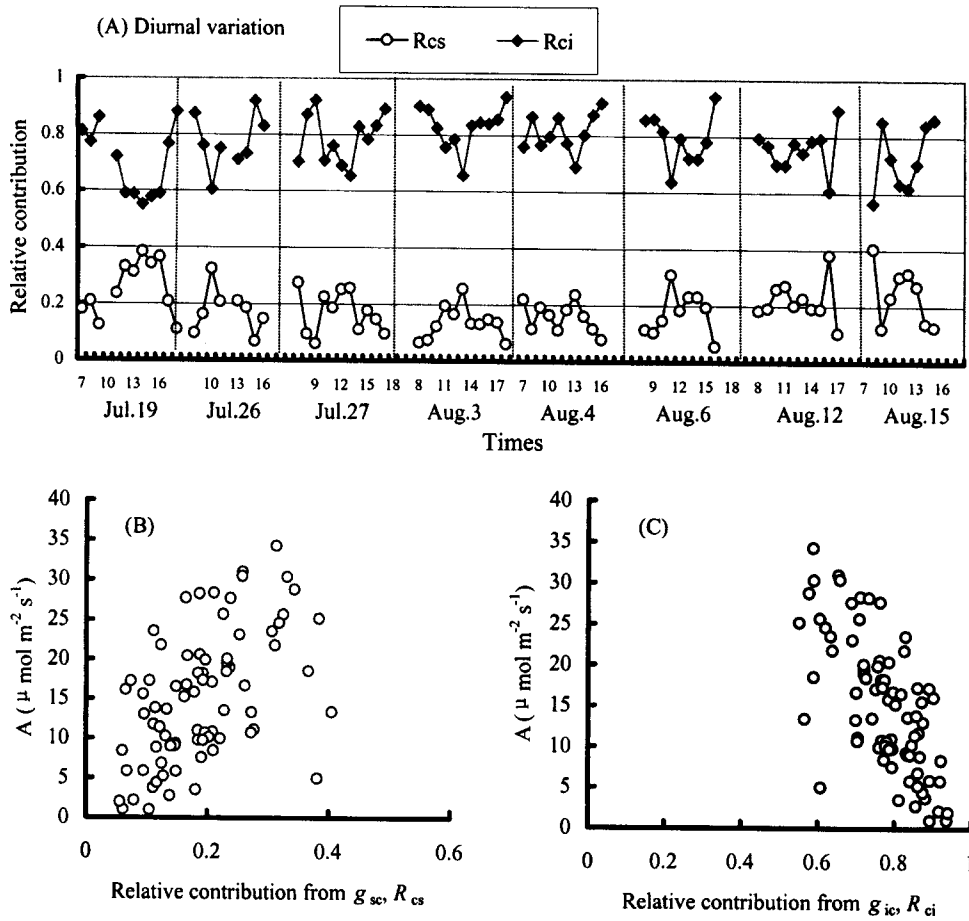$$1/g_{ic} = (C_i - \Gamma_*)/A \qquad (22)$$

Figure 5. Comparison of diurnal changes of relative contributions of stomatal and internal processes to the control of net assimilation rate, *A*, during the 8-day investigation period (A), while (B) and (C) shows the relationships between the *A* and relative contributions of the stomatal processes, R_{cs}, and between the *A* and relative contributions of the internal processes, R_{ci}, respectively.
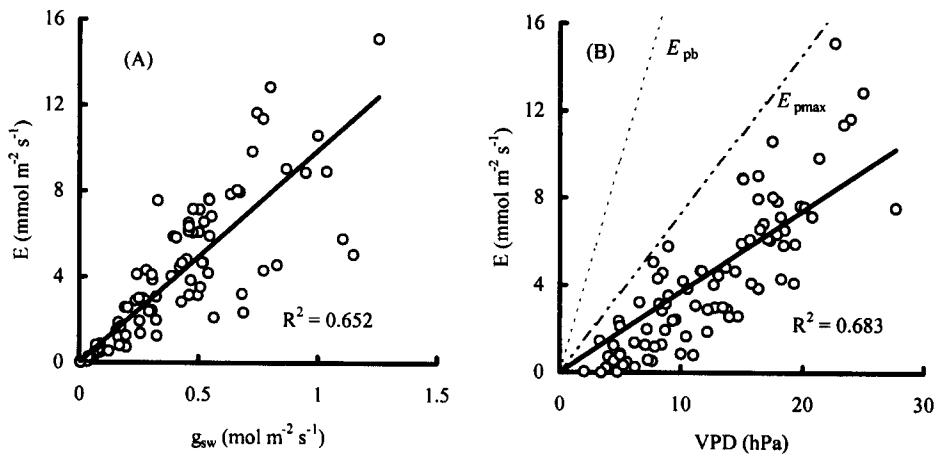

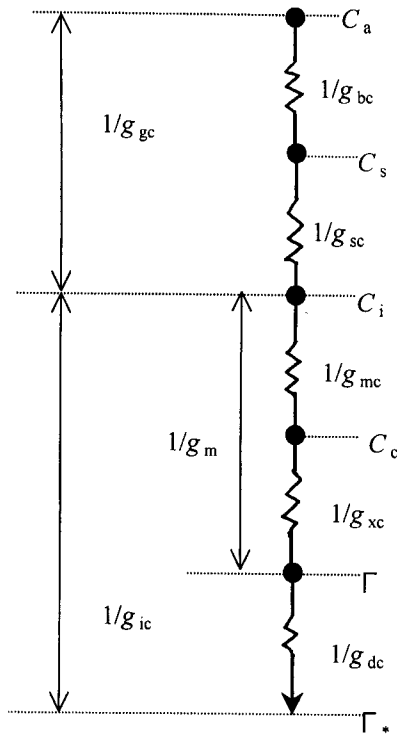*Figure 6.* Transpiration rate, *E*, as functions of stomatal conductances, g_{sw}, and of vapor pressure deficit, VPD.

Figure 7. Several concepts of conductance (or resistance) from the atmosphere to the site of carboxylation. C_a, C_s, C_i and C_c are CO_2 concentrations at the ambient, at the leaf surface, at intercellular space and at the site of carboxylation, respectively. Γ and Γ_* are CO_2 compensation points for the cases with and without the dark respiration, respectively. g_{bc}, g_{sc}, g_{ic}, g_{mc}, g_{xc}, g_{dc} are boundary layer-, stomatal-, internal-, mesophyll-, carboxylation- and dark respiration conductance, respectively, and g_{gc} is gas-phase conductance, g_m is liquid-phase (or mesophyll) conductance.

The definition of the internal conductance, g_{ic}, in Equation (22), involves an important extension of the transport conductance in Equation (21) to biochemical processes. When subtracting Equation (21) from Equation (22), we have

$$1/g_{ic} - 1/g_m = 1/g_{dc} = (\Gamma - \Gamma_*)/A \qquad (23)$$

The term g_{dc} is referred to as dark respiration conductance.

According to the above analyses, the internal conductance, g_{ic}, is determined by three factors: physical diffusion of CO_2 in liquid-phase from intercellular space to site of carboxylation, efficiency of carboxylation, and dark respiration rate. According to Farquhar et al. (1980), Collatz et al. (1991) and Leuning (1990, 1995), the efficiency of carboxylation can actually be described using the dependence of photosynthesis on light (through RuBP regeneration) and on intercellular concentration (through Rubisco activity), i.e., the

photosynthesis rate of leaf is determined by the minimum of assimilation limited by Rubisco activity or RuBP regeneration. In the experimental conditions, the g_{ic} was linearly related to Q_p (Figure 2A), which implies that the irradiance-limited efficiency of carboxylation is the most important factor in determining g_{ic}. Of course, this is true in the case of maize, a C4 plant, in this study. Whether this phenomenon is a general result for all plants or not still need a great deal of experiment data to verify, especially the variability under water and nutrient stresses. To investigate these aspects, further work need to be carried out.

Likewise, if taking practical computation of net assimilation rate using the photosynthesis model into consideration, we think that there are some favorable points when replacing g_m and Γ with g_{ic} and Γ_*. Firstly, Γ_* can be derived from several literatures more safely than Γ. Secondly, the estimation formula of Γ_* is rather simpler than that of Γ (see Equations (4) and (13)), which can avoid the difficulty in determining the physiological parameters. Thirdly, in the case that dark respiration rate is unknown, it is relieved to use Γ_* for the replacement of Γ since the value of Γ_* is smaller than Γ for many C3 plants, or even can be simply assumed as $\Gamma_*=0$ for C4 plants (Jones, 1992).

Applicability of the models

The principal objective of the paper was to present a theoretical basis for a new modeling approach for estimating photosynthesis and transpiration. The main contribution of this paper is using the results of other researchers, summing them up, and deriving two simplified practical equations based on stomatal behavior, Equations (12) and (14), for estimating photosynthesis and transpiration, and to verify it using the data observed in maize field. These models or their modified version of Equations (17) and (18) can be used well for estimating net assimilation rate and transpiration rate with adequate precision. We recommend employing their simplified forms of Equations (17) and (18) because they can avoid complicated determination of physiological parameters. Likewise, the model only includes environmental variables, such as ambient CO_2 concentration, leaf temperature, humidity, and PAR received at the leaves within canopy.

Here the boundary layer conductance, g_{bw}, used the default value of photosynthesis system, $g_{bw}=2.0$ mol m^{-2} s^{-1} for model test. Actually, it can be estimated by wind speed and leaf width (Jones, 1992; Yu, 1999). The model presented as a single layer model

for two-sided leaf within the maize canopy without environmental stresses, does not attempt to consider the stratum of the canopy.

Conclusions

Based on the consideration for the models of CO_2 and H_2O diffusion controlled through stomata of plant leaves, a stomatal behavior-based coupled model for estimating photosynthesis and transpiration was developed. The parameters in the model were identified using the data observed in maize field, and the applicability of the coupled models was examined. The coupled model was obtained by introducing the internal conductance for CO_2 assimilation and the general equation of stomatal conductance model into the models of CO_2 and H_2O diffusion through the stomata of plant leaves. Also, the internal conductance was indicated as having the closest correlation with the photosynthetic photon flux as compared with other environmental factors, and it can be estimated by a linear function of photosynthetic photon flux.

To a large extent, it can be said that the coupled model is easier for practical use since the model only includes environmental variables, such as ambient CO_2 concentration, leaf temperature, humidity, and PAR received at the leaves within the canopy. Besides, by discussing the concept of internal conductance and the factors controlling net assimilation rate and transpiration, the physiological mechanism of the model was clarified.

List of main symbols

Assimilation, transpiration, conductance and resistance

A	net assimilation rate of CO_2 (μmol m^{-2} s^{-1})
E	transpiration rate (mol m^{-2} s^{-1})
E_{pb}	transpiration rate determined only by g_{bw} (mol m^{-2} s^{-1})
E_{pmax}	maximum transpiration rate depending on the maximum stomatal conductance g_{swmax} (mol m^{-2} s^{-1})
g_{bw}, g_{bc}	boundary layer conductance to H_2O and to CO_2 (mol m^{-2} s^{-1})
g_{dc}	dark respiration conductance to CO_2 (mol m^{-2} s^{-1})
g_{gc}	gas-phase conductance (mol m^{-2} s^{-1})
g_{ic}	internal conductance (mol m^{-2} s^{-1})
g_m	liquid-phase (or mesophyll) conductance (mol m^{-2} s^{-1})
g_{mc}	mesophyll conductance (mol m^{-2} s^{-1})
g_{sw}, g_{sc}	stomatal conductance to H_2O and to CO_2 (mol m^{-2} s^{-1})
g_{xc}	carboxylation conductance (mol m^{-2} s^{-1})
g_{tw}, g_{tc}	total conductance to fluxes of H_2O and CO_2 for leaves (mol m^{-2} s^{-1})

Environmental variables and physiological parameters

C_a	ambient CO_2 concentration (μmol mol^{-1})
C_c	CO_2 concentration at the site of carboxylation (μmol mol^{-1})
C_s	CO_2 concentration at the leaf surface (μmol mol^{-1})
C_i	intercellular CO_2 concentration (μmol mol^{-1})
D_a	saturation deficit at 2 m height above soil surface (hPa)
D_e	saturation deficit within the canopy (hPa)
D_s	saturation deficit at leaf temperature (hPa)
e	water vapor pressure of air within the canopy (hPa)
$e_w(T_L)$	saturated water vapor pressure at leaf temperature (hPa)
RH	relative humidity within the canopy (%)
Q_p	photosynthetic photon flux within the canopy (μmol m^{-2} s^{-1})
R_{cs}	relative contribution of stomatal processes for CO_2 assimilation
R_{ci}	relative contribution of internal processes for CO_2 assimilation
R_n	net radiation at 2 m height above soil surface (MJ m^{-2}d^{-1})
S_n	solar radiation at 2 m height above soil surface (MJ m^{-2}d^{-1})
T_a	air temperature at 2 m height above soil surface (°C)
T_s	air temperature within the canopy (°C)
T_L	leaf temperature within the canopy (°C)
VPD	leaf-to-air vapor pressure difference (hPa)
W_a	mole fraction of water vapor in the air (mol mol^{-1})
W_i	mole fraction of water vapor in the stomata (mol mol^{-1})
Γ	CO_2 compensation point with dark respiration (μmol mol^{-1})
Γ_*	CO_2 compensation point without dark respiration (μmol mol^{-1})
Ψ_s	soil water potential, within 0–40 m profile depths (kPa)

Ψ_L leaf water potential averaged within the canopy (kPa)

Statistical terminology

R^2 coefficient of determination of regression formula of the model

RMSE   root mean square error for the values measured and estimated by model

Sl   slope (*b*) of the linear regression curve between the values measured and estimated by model

n   number of data (sample size)

Acknowledgements

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