

# An attempt to establish a synthetic model of photosynthesis-transpiration based on stomatal behavior for maize and soybean plants grown in field

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## Summary

A synthetic model of photosynthesis-transpiration was established based on a comprehensive consideration of models of CO<sub>2</sub> and H<sub>2</sub>O fluxes controlled by stomata of plant leaves. The synthetic model was developed by introducing the internal conductance to CO<sub>2</sub> assimilation,  $g_{ic}$ , and the general equation of stomatal conductance model to H<sub>2</sub>O diffusion,  $g_{sw} = g_0 + a_1 A_m f(D_s)/(C_s - \Gamma)$ , into models of CO<sub>2</sub> and H<sub>2</sub>O diffusion through the plant leaves stomata. In the above expression,  $g_0$  and  $a_1$  are coefficients,  $C_s$  ambient CO<sub>2</sub> concentration at leaf surface,  $\Gamma$  CO<sub>2</sub> compensation point, and  $f(D_s)$  the general function describing the response of stomatal conductance to humidity. Using the data observed in maize (*Zea mays* L.) and soybean (*Glycine max* Merr.) plants grown in the field, the parameters in the model were identified, and the applicability of the model was examined. The verification indicated that the developed model could be used to estimate net assimilation rate, transpiration rate, and water use efficiency with a high enough level of precision. The examination also showed that when  $f(D_s) = h_s$  or  $f(D_s) = (1 + D_s/D_0)^{-1}$  was employed, the estimation precision of the synthetic model was highest. In the study, the parameter  $g_{ic}$  was estimated by means of a linear function of  $Q_p$  because it was shown to be mostly correlated with photosynthetic photon flux,  $Q_p$ , among various environmental factors.

**Key words:** photosynthesis – stomatal conductance – synthetic model – transpiration – water use efficiency

**Abbreviations:**  $A_m$  net assimilation. –  $C_a$  ambient CO<sub>2</sub> concentration. –  $C_i$  intercellular CO<sub>2</sub> concentration. –  $C_s$  ambient CO<sub>2</sub> concentration at leaf surface. –  $D_s$  saturation deficit at leaf surface. –  $e$  water vapor pressure within canopy. –  $E_m$  transpiration rate. –  $e_w(T_L)$  saturated water vapor pressure at leaf temperature. –  $g_{bc}$ ,  $g_{bw}$  boundary layer conductance to CO<sub>2</sub> and H<sub>2</sub>O. –  $g_{gc}$  gas-phase conductance to CO<sub>2</sub>. –  $g_{ic}$  internal conductance to CO<sub>2</sub>. –  $g_{sc}$ ,  $g_{sw}$  stomatal conductance to CO<sub>2</sub> and H<sub>2</sub>O. –  $g_{tc}$  total conductance to assimilation. –  $g_{tw}$  total conductance to H<sub>2</sub>O. –  $h_s$  relative humidity at leaf surface. –  $Q_p$  photosynthetic photon flux density within canopy. –  $r_{bc}$ ,  $r_{bw}$  boundary layer resistance to

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CO<sub>2</sub> and H<sub>2</sub>O. –  $r_{ic}$  internal resistance to CO<sub>2</sub>. –  $r_{sc}$ ,  $r_{sw}$  stomatal resistance to CO<sub>2</sub> and H<sub>2</sub>O. –  $T_L$  leaf temperature. –  $W_a$ ,  $W_i$  mole fraction of water vapor in air and stomata space. – WUE<sub>m</sub> water use efficiency. –  $\Gamma$  CO<sub>2</sub> compensation point with dark respiration. –  $\Gamma^*$  CO<sub>2</sub> compensation point without dark respiration. –  $\psi_L$  leaf water potential

## Introduction

Material- and energy-exchange information within the soil-vegetation-atmosphere system, through processes of photosynthesis and transpiration, is an essential element for quantitatively evaluating plant production and interaction between vegetation and the environment. Photosynthesis and transpiration are coordinated processes since the same opening-closing movement of the stomata controls both. Therefore, it is important to clarify responses of stomata to environmental factors and to simulate the stomatal conductance. As a basis for of the sub-models of evapotranspiration and photosynthesis, the model of Jarvis (1976) and its modified versions, in which only environmental variables are employed, have been widely used for the scales from individual leaves to global climate. In a series of studies response characteristics of stomatal conductance of maize to certain environmental factors were made clear (Yu et al. 1996), and a combination model for estimating stomatal conductance over a long term was presented (Yu and Nakayama 1997, Yu et al. 1998).

Photosynthesis depends on stomatal behavior, simultaneously, stomatal behavior is subject to the feedback of photosynthesis activity. Therefore, it is critical to understand these two processes and to establish a synthetic model of transpiration-photosynthesis based on the stomatal behavior (Yu et al. 1999). A very useful empirical relationship between net assimilation rate of CO<sub>2</sub>,  $A_m$ , and stomatal conductance,  $g_{sw}$ , was first proposed by Ball et al. (1987), and its modified versions were proposed by Lloyd (1991), Collatz et al. (1991), and Leuning (1990, 1995). The empirical relationship between  $A_m$  and  $g_{sw}$  has been widely adopted by modelers at the scale of individual leaves (Leuning 1990, 1995, Tenhunen et al. 1990, Collatz et al. 1991, Harley et al. 1992), at the scale of canopy (Hatton et al. 1992), at the scale of landscape (McMurtrie et al. 1992), and in some global climate models (Sellers et al. 1992, 1996, Woodward and Smith 1994). A biochemical model for estimating net assimilation rate was first presented by Farquhar et al. (1980), and the model was thereafter modified and applied by many researchers to C<sub>3</sub> plants (von Caemmerer and Farquhar 1981, Brooks and Farquhar 1985, Harley et al. 1985, 1992, McMurtrie et al. 1992, Leuning 1995) and to C<sub>4</sub> plants (Collatz et al. 1991, 1992).

Despite the fact that the models mentioned above were very useful approaches for understanding both of the photosynthesis and the transpiration processes synthetically, they are too complicated to be used easily. To make the modeling

practical and simple, based on the data collected in maize field, Yu et al. (1999) proposed a synthetic model for estimating photosynthesis and transpiration from an angle different from the approach of Farquhar et al. (1980). The synthetic model was explored by introducing the internal conductance,  $g_{ic}$ , of CO<sub>2</sub> assimilation, and the general equation of stomatal conductance model of H<sub>2</sub>O diffusion proposed by Leuning (1995) into models of CO<sub>2</sub> and H<sub>2</sub>O diffusion through plant leaf stomata.

The objectives of this study were, first, to improve the model proposed by Yu (1999) using the data observed in maize (*Zea mays* L.) field, and to check its applicability to C<sub>3</sub> plant using the data measured in soybean (*Glycine max* Merr.) field; second, to identify the parameters in the synthetic model of photosynthesis-transpiration and examine the model for estimating net assimilation rate and transpiration rate of maize and soybean plants; and third, to establish a model for estimating water use efficiency based on this synthetic model.

## Model Formulations

### Models of transpiration and net assimilation

The CO<sub>2</sub> and H<sub>2</sub>O fluxes of the leaves are determined by several factors in atmosphere, plant, and soil. The H<sub>2</sub>O flux, or transpiration rate,  $E_m$  (mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>) is basically described as

$$E_m = \frac{W_i - W_a}{r_{bw} + r_{sw}} = \frac{g_{bw}g_{sw}(W_i - W_a)}{g_{bw} + g_{sw}} = g_{tw}(W_i - W_a) \quad (1)$$

where  $W_i$  is mole fraction of water vapor in the stomata space (mol mol<sup>-1</sup>),  $W_a$  is mole fraction of water vapor in the air,  $r_{bw}$  and  $g_{bw}$  are resistance (m<sup>2</sup> s mol<sup>-1</sup>) and conductance (mol m<sup>-2</sup> s<sup>-1</sup>) of boundary layer,  $r_{sw}$  and  $g_{sw}$  are resistance (m<sup>2</sup> s mol<sup>-1</sup>) and conductance (mol m<sup>-2</sup> s<sup>-1</sup>) of stomata, respectively, and  $g_{tw}$  is total conductance to H<sub>2</sub>O diffusion through the stomatal and boundary layer (mol m<sup>-2</sup> s<sup>-1</sup>).

The CO<sub>2</sub> flux, or net assimilation,  $A_m$  (μmol m<sup>-2</sup> s<sup>-1</sup>), is generally described as

$$A_m = \frac{C_a - C_i}{r_{bc} + r_{sc}} = \frac{g_{bc}g_{sc}(C_a - C_i)}{g_{bc} + g_{sc}} = g_{gc}(C_a - C_i) \quad (2)$$

where  $C_a$  is ambient CO<sub>2</sub> concentration (μmol mol<sup>-1</sup>),  $C_i$  is intercellular CO<sub>2</sub> concentration (μmol mol<sup>-1</sup>),  $r_{bc}$  and  $g_{bc}$  are resistance (m<sup>2</sup> s mol<sup>-1</sup>) and conductance to CO<sub>2</sub> (mol m<sup>-2</sup> s<sup>-1</sup>) of the boundary layer, respectively,  $r_{sc}$  is stomatal resistance (m<sup>2</sup> s mol<sup>-1</sup>),  $g_{sc}$  is stomatal conductance (mol m<sup>-2</sup> s<sup>-1</sup>), and

$g_{gc}$  is gas-phase conductance to  $\text{CO}_2$  diffusion through the stomatal and boundary layer ( $\text{mol m}^{-2} \text{s}^{-1}$ ).

To account for the interaction at the stomatal pores caused by transpiration, the correction described by Jarman (1974) and von Caemmerer and Farquhar (1981) was used, and Eq. (1) is converted to

$$E_m \left( 1 - \frac{W_i + W_a}{2} \right) = \frac{g_{bw} g_{sw} (W_i - W_a)}{g_{bw} + g_{sw}} \quad (3)$$

Then the total conductance to  $\text{H}_2\text{O}$ ,  $g_{tw}$ , can be calculated using

$$g_{tw} = \frac{g_{bw} g_{sw}}{g_{bw} + g_{sw}} = \frac{E_m [1 - (W_i + W_a)/2]}{W_i - W_a} \quad (4)$$

Also, Eq. (2) can be converted to,

$$A_m = \frac{g_{bc} g_{sc} (C_a - C_i)}{g_{bc} + g_{sc}} - \frac{C_a + C_i}{2} E_m \quad (5)$$

The intercellular  $\text{CO}_2$  concentration,  $C_i$ , is calculated using

$$C_i = \frac{(g_{gc} - E_m/2) C_a - A_m}{(g_{gc} - E_m/2)}, \text{ where } \frac{1}{g_{gc}} = \frac{1}{g_s} + \frac{1}{g_{bc}} \quad (6)$$

Eq. (2) and Eq. (5) indicate that the control of the net assimilation rate is exerted by the supply of  $\text{CO}_2$  diffusion through stomata and boundary layer, thus the equations are generally called 'supply' functions for the assimilation of plants (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. Here we used the form of 'demand functions' suggested by Jones (1992), i.e.

$$A_m = g_{ic} (C_i - \Gamma^*) = \frac{C_i - \Gamma^*}{r_{ic}} \quad (7)$$

to simplify the expression used to evaluate the regulation of net assimilation rate exerted by bio- and photo-chemical processes. In equation Eq. (7),  $\Gamma^*$  is the  $\text{CO}_2$  compensation point without dark respiration ( $\mu\text{mol mol}^{-1}$ ), and  $g_{ic}$  is defined as 'internal' conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ) and its reciprocal  $r_{ic}$  is defined as 'internal' resistance ( $\text{m}^2 \text{s mol}^{-1}$ ).

By ignoring the interaction (the connective effects) between water molecules leaving and entering the stomata, the net assimilation model can be written as

$$A_m = \frac{(C_a - \Gamma^*)}{r_{bc} + r_{sc} + r_{ic}} = g_{ic} (C_a - \Gamma^*) \quad (8)$$

where  $g_{ic}$  is total conductance to  $\text{CO}_2$  assimilation ( $\text{mol m}^{-2} \text{s}^{-1}$ ).

### Stomatal behavior model

As a basis of the sub-models of evapotranspiration and photosynthesis, the model of Jarvis (1976) and its modified versions have been widely used. Ball et al. (1987) first pre-

sented an empirical relationship, which incorporated the often-observed correlation between net assimilation rate,  $A_m$ , and stomatal conductance,  $g_{sw}$ , and included the effects of humidity and ambient  $\text{CO}_2$  concentration on conductance, namely

$$g_{sw} = a_1 A_m h_s / C_s \quad (9)$$

where  $a_1$  is a coefficient,  $h_s$  and  $C_s$  are relative humidity and ambient  $\text{CO}_2$  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 Eq. (9). Similarly, Leuning (1990) and Lloyd (1991) obtained good linear relationships when they plotted their data according to the model of Ball et al. (1987). The apparent simplicity of Eq. (9) has led to its adoption by modelers. The success of Ball et al. (1987), Leuning (1990), Lloyd (1991), and Collatz et al. (1991) in collapsing results of many experiments onto a single curve by using Eq. (9), further suggested that Eq. (9) might still be useful if  $h_s$  is replaced by a more general humidity function  $f(D_s)$  (Leuning 1995), i.e.

$$g_{sw} = g_0 + a_1 A_m f(D_s) / C_s \quad (10)$$

where,  $g_0$  is the residual stomatal conductance (as  $A_m \rightarrow 0$  when  $Q_p \rightarrow 0$ ,  $Q_p$  is photosynthetic photon flux density). However, in its present form, Eq. (10) is incapable of describing stomatal behavior at low  $\text{CO}_2$  concentration since conductance increases to the maximum value as  $C_s$  approaches to the  $\text{CO}_2$  compensation point with dark respiration,  $\Gamma$ , while  $A_m \rightarrow 0$ . Eq. (10) predicts that  $g_{sw} \rightarrow 0$  under these circumstances. Leuning (1990, 1995) accounted for these observations by replacing  $C_s$  with  $C_s - \Gamma$ , i.e.

$$g_{sw} = g_0 + a_1 A_m f(D_s) / (C_s - \Gamma) \quad (11)$$

This modification ensures that  $g_{sw}$  remains large as  $A_m \rightarrow 0$  while  $C_s \rightarrow \Gamma$ . Note that  $g_{sw}$  is not defined by this equation when  $C_s = \Gamma$ .

### Synthetic model of photosynthesis-transpiration

Eq. (2) can be rewritten as

$$A_m = (C_a - C_i) / r_{gc}, \text{ where } r_{gc} = r_{bc} + r_{sc} \quad (12)$$

Assuming  $g_{sw} = 1.56 g_{sc}$  and  $g_{bw} = 1.37 g_{bc}$ , the implication of Eq. (11) for the expected value of  $C_i$  can be seen by combining it with Eq. (12)

$$C_i = C_a - \frac{1.56 A_m}{g_0 + a_1 A_m f(D_s) / (C_a - \Gamma)} - 1.37 A_m r_{bw} \quad (13)$$

The  $g_0$  in Eqs. (11) and (13) is the residual stomatal conductance (as  $A_m \rightarrow 0$ , when  $Q_p \rightarrow 0$ ); it can be assumed as a cuticular conductance to  $\text{H}_2\text{O}$ , and also  $g_0 \ll g_{sw}$ . Therefore,  $g_0$  was ignored generally when considering the diffusion of  $\text{CO}_2$  through stomata. If assuming  $g_0$  negligible, and incorporating Eq. (13) into Eq. (7), or combining Eq. (11) with Eq. (8), the

synthetic model of photosynthesis-transpiration for estimating the CO<sub>2</sub> assimilation is given as

$$A_m = \frac{(C_a - \Gamma^*) - 1.56(C_a - \Gamma)/(a_1 f(D_s))}{1.37 r_{bw} + r_{ic}} \quad (14)$$

According to Yu et al. (1999), differences between the values of  $\Gamma^*$  and  $\Gamma$ , and between the values of  $(C_a - \Gamma^*)$  and  $(C_a - \Gamma)$  are not large in the field experimental conditions. In this sense, it might be judged that the estimation error of the photosynthesis arising from the difference between  $\Gamma^*$  and  $\Gamma$  should not be large. Thus, Eq. (14) can be simplified as

$$A_m = \frac{(C_a - \Gamma)[1 - 1.56/(a_1 f(D_s))]}{1.37 r_{bw} + r_{ic}} \quad (15)$$

Moreover, by incorporating Eq. (11) into Eq. (1), the synthetic model of photosynthesis-transpiration for estimating the transpiration rate,  $E_m$  (mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), has the form of

$$E_m = \frac{(W_i - W_a)}{r_{bw} + 1/[g_0 + a_1 A_m f(D_s)/(C_a - \Gamma)]} \quad (16)$$

By incorporating Eq. (15) into Eq. (16), the transpiration model of Eq. (16) becomes

$$E_m = \frac{(e_w(T_L) - e)P}{r_{bw} + 1/[g_0 + (a_1 f(D_s) - 1.56)/(1.37 r_{bw} + r_{ic})]} \quad (17)$$

where  $e_w(T_L)$  is saturated water vapor pressure at the leaf temperature (hPa),  $e$  is water vapor pressure of air within the canopy (hPa), and  $P$  is atmospheric pressure (1013 Pa).

## Materials and Methods

### Field experimental site

The investigation was conducted in the summers of 1998 and 1999 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 generated from volcanic ash, with a texture of sandy loam. The maize (*Zea mays* L.) plants were grown in a 20 m × 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. The soybean (*Glycine max* Merr.) plants were grown in a 10 m × 10 m plot, with planting density of 55,600 plants per hectare, row spacing of 0.6 m, and intrarow spacing of 0.3 m. Fertilization, disease, and insect controls were carried out conventionally for the two crop plants. The growing periods of the two crop plants were from the beginning of May to the end of August.

### Measurements in the field

At the field experimental site of maize and soybean plants, net assimilation rate, transpiration rate, and stomatal conductance were measured every hour from 7 to 18 h of local time on the surfaces of the leaves of two designated plants by means of portable photosynthesis system (LI-6200, LI-COR.). For maize plants, the site of measurement was at the center of the leaf surface at four different leaf positions, i.e., on the 2nd, 4th, 6th, and 8th leaf from the top of the plants. For soy-

bean plants, the middle pieces of the compound leaf at three leaf positions, upper, medium, and lower leaves from the top of the plant, were selected to measure the items mentioned above. The sampling protocol for these measurements involved first measuring these items of the leaf surfaces from the upper to the lower part of the 1st plant, and subsequently the same measurements as above were conducted for the 2nd plant by the same procedure.

Leaf temperature, saturation deficit, and photosynthetic photon flux density within the canopy were also recorded by means of sensors attached to the photosynthesis system at the same time as the measurements above, such as net assimilation rate, etc. The leaf temperature,  $T_L$  (°C), and the saturation deficit,  $D_s$  (hPa), within the canopy were the mean values at different leaf positions on the stem. The photosynthetic photon flux density,  $Q_p$  (μmol m<sup>-2</sup> s<sup>-1</sup>), within the canopy was the average value of the downward flux received by several leaves. During the entire growing period of maize and soybean, solar radiation, net radiation, air saturation deficit, air temperature and soil moisture content were determined every day. Simultaneously, using a pressure chamber (DIK-7000, Daiki Rika), leaf water potential,  $\psi_L$  (MPa), of two nearby plants was measured. The weather conditions were rainy during the period of investigation in 1998 and 1999. Thus, little water stress from soil was exerted on either maize or soybean plants grown in the field.

### Data processing and model evaluation

To identify 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. 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 could represent the mean status of the measured items in the measurement period of 15 to 20 minutes, during which stomatal conductance and so on were measured on the two designated plants.

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

$$RMSE = \left[ \frac{1}{n-1} \sum (Y_{est} - Y_{mea})^2 \right]^{1/2} \quad (18)$$

where  $n$  is the number of the data,  $Y_{est}$  represents the estimated value,  $Y_{mea}$  is the measured value.

## Results

### Modeling stomatal conductance

The stomatal conductance,  $g_{sw}$ , measured during daytime of the period of investigation in 1998 and 1999 was different due to the weather conditions. In the stomatal conductance model represented by Eq. (11),  $f(D_s)$  is a general function describing response of stomatal conductance to humidity. So far, numer-

ous expressions have been proposed for this function. In this study, five of them were adopted

$$f_1(D_s) = h_s \quad (19.1)$$

$$f_2(D_s) = D_s^{-1} \quad (19.2)$$

$$f_3(D_s) = D_s^{-1/2} \quad (19.3)$$

$$f_4(D_s) = 1 - D_s/D_0 \quad (19.4)$$

$$f_5(D_s) = (1 + D_s/D_0)^{-1} \quad (19.5)$$

Eq. (19.1) was used by Ball et al. (1987), Eq. (19.2) and (19.3) by Lloyd (1991), Eq. (19.4) by Jarvis (1976), and Eq. (19.5) by Lohammer et al. (1980). Lloyd (1991) obtained the best result using Eq. (19.3), while his examination also showed that both Eq. (19.1) and (19.2) behaved excellently. Collatz et al. (1991) noted that  $f(D_s)$  might be described by Eq. (19.4) when  $D_s$  varies with air humidity at constant leaf temperature, other than the slope ( $1/D_0$ ) dependent on temperature. Moreover, after examining the conformability of Eqs. (19.1), (19.4), and (19.5), Leuning (1995) recommended Eq. (19.5).

In this study, the saturation deficit within the canopy was used to replace the  $D_s$  in Eq. (19.1) to Eq. (19.5). The values of the parameters  $g_0$  and  $a_1$  in Eq. (11) were calculated by the linear least square method based on the data collected in the maize and soybean fields. Leuning (1990) reported that the value of  $g_0$  was about  $0.01 \text{ mol m}^{-2} \text{ s}^{-1}$  and the values of  $D_0$  in Eq. (19.4) and Eq. (19.5) were 45 and 3.5 hPa, respectively, for  $C_3$  plant. Also, Yu et al. (1999) reported that the value of  $g_0$  was about  $0.11 \text{ mol m}^{-2} \text{ s}^{-1}$  and the values of  $D_0$  in Eq. (19.4) and Eq. (19.5) were 70 and 30 hPa, respectively, for maize. In the regression analysis, these values of  $D_0$  were used for soybean and maize, respectively. Results of the regression analysis are shown in Table 1. The  $R^2$  values of all the functions were significant at 0.01 levels, but the biggest  $R^2$  values were

obtained for the two species of plants using Eq. (19.1) and Eq. (19.5). The obtained  $g_0$  for maize was from 0.09 to  $0.19 \text{ mol m}^{-2} \text{ s}^{-1}$ , and the  $g_0$  for soybean was from 0.29 to  $0.40 \text{ mol m}^{-2} \text{ s}^{-1}$ . These values were rather bigger than those reported by Leuning (1990) and Yu et al. (1999).

When the data of the two years was combined into one set of data, corresponding to Eq. (19.1) and Eq. (19.5), the formulae of stomatal conductance for maize are

$$g_{sw} = 0.136 + 0.073 A_m h_s / (C_s - \Gamma); R^2 = 0.562, n = 143 \quad (20a)$$

and

$$g_{sw} = 0.127 + 8.222 A_m / [(1 + D_s/D_0)(C_s - \Gamma)]; R^2 = 0.540, n = 143 \quad (20b)$$

For soybean, they are

$$g_{sw} = 0.306 + 0.206 A_m h_s / (C_s - \Gamma); R^2 = 0.436, n = 73 \quad (21a)$$

and

$$g_{sw} = 0.336 + 82.78 A_m / [(1 + D_s/D_0)(C_s - \Gamma)]; R^2 = 0.436, n = 73 \quad (21b)$$

The  $R^2$  values for both species of plants varied from 0.44 to 0.65. The  $R^2$  values were not high, but these values were significant at 0.01 level.

## Modeling internal conductance

Employing Eq. (7), the internal resistance,  $r_{ic}$ , has a form of

$$r_{ic} = 1/g_{ic} = (C_i - \Gamma^*)/A_m \quad (22)$$

where  $\Gamma^*$  is  $\text{CO}_2$  compensation points ( $\mu\text{mol mol}^{-1}$ ) dependent on leaf temperature. An empirical second-order polynomial for  $C_3$  plants (Brooks and Farquhar 1985) was used in the

**Table 1.** Parameters of the regression formulas of  $f(D_s)$  in the models,  $g_{sw} = g_0 + a_1 A_m f(D_s) / (C_s - \Gamma)$ , for estimating stomatal conductance, and the coefficient of determination,  $R^2$ , for the regression formulas. The obtained values of  $D_0$  for  $f_4(D_s)$  and  $f_5(D_s)$  were 70 and 30 hPa for maize, and 45 and 3.5 hPa for soybean, respectively.

	$f(D_s)$	$g_0$	$a_1$	$R^2$
Maize (1998) Number of data, n = 74	$f_1(D_s) = h_s$	0.121	0.084	0.657
	$f_2(D_s) = D_s^{-1}$	0.142	77.20	0.446
	$f_3(D_s) = D_s^{-1/2}$	0.091	25.40	0.644
	$f_4(D_s) = 1 - D_s/D_0$	0.121	7.911	0.633
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.113	9.482	0.645
Maize (1999) Number of data, n = 69	$f_1(D_s) = h_s$	0.161	0.057	0.445
	$f_2(D_s) = D_s^{-1}$	0.195	58.95	0.277
	$f_3(D_s) = D_s^{-1/2}$	0.152	16.98	0.409
	$f_4(D_s) = 1 - D_s/D_0$	0.161	5.332	0.397
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.146	6.502	0.439
Soybean (1999) Number of data, n = 73	$f_1(D_s) = h_s$	0.306	0.206	0.436
	$f_2(D_s) = D_s^{-1}$	0.365	227.5	0.432
	$f_3(D_s) = D_s^{-1/2}$	0.290	61.08	0.435
	$f_4(D_s) = 1 - D_s/D_0$	0.396	21.87	0.396
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.336	82.78	0.436

study to describe dependence of the  $\Gamma^*$  on the leaf temperature,  $T_L$  (°C), namely

$$\Gamma_{c3} = 42.7 + 1.68(T_L - 25) + 0.012(T_L - 25)^2 \quad (23)$$

According to Woodward and Smith (1994),  $\Gamma^*$  relationship between  $C_4$  plants and  $C_3$  plants is

$$\Gamma_{c4} = 0.1\Gamma_{c3} \quad (24)$$

Additionally, to estimate the internal resistance,  $r_{ic}$ , in the models of Eq. (14) and (15), Yu et al. (1999) made correlation analysis between the internal conductance,  $g_{ic} = 1/r_{ic}$ , and various environmental variables. It was found that there are correlations between  $g_{ic}$  and  $Q_p$ ,  $D_s$ ,  $T_L$ , and  $\psi_L$ , but  $g_{ic}$  depends on  $Q_p$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) most strongly. On one hand, based on the data observed in 1998 and 1999 in maize field, the formulae obtained for estimating  $g_{ic}$  were, respectively,

$$g_{ic} = 1.39E-4 Q_p - 0.0036; R^2 = 0.935, n = 74 \text{ for } 1998 \quad (25a)$$

$$g_{ic} = 1.18E-4 Q_p - 0.0026; R^2 = 0.801, n = 69 \text{ for } 1999 \quad (25b)$$

On the other hand, by combining the data of the two years into one set of data,  $g_{ic}$  for maize could be estimated by formula

$$g_{ic} = 1.225E-4 Q_p - 0.0003; R^2 = 0.845, n = 143 \quad (25c)$$

For soybean, the formula is

$$g_{ic} = 0.636E-4 Q_p + 0.0124; R^2 = 0.795, n = 73 \quad (26)$$

### Estimation of photosynthesis by the synthetic models

When either Eq. (14) or Eq. (15) was used for estimating the photosynthesis, the parameters of  $\text{CO}_2$  compensation points without dark respiration,  $\Gamma^*$ , were calculated by Eq. (23) and Eq. (24), and  $\text{CO}_2$  compensation point with dark respiration,  $\Gamma$ , was calculated using the following equation of Farquhar et al. (1980)

$$\Gamma = \frac{\Gamma^* + K_c R_d (1 + c_o/K_o) / V_{cmax}}{1 - R_d / V_{cmax}} \quad (27)$$

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

$$K_c = K_{cr} \exp\left[\frac{E_{Kc}}{RT_r}(1 - T_r/T_L)\right] \quad (28a)$$

$$K_o = K_{or} \exp\left[\frac{E_{Ko}}{RT_r}(1 - T_r/T_L)\right] \quad (28b)$$

$$R_d = R_{dr} \exp\left[\frac{E_{Rd}}{RT_r}(1 - T_r/T_L)\right] \quad (28c)$$

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 ( $293.3^\circ\text{K}$ ), respectively. The temperature dependence of

$V_{cmax}$  was simulated according to Farquhar et al. (1980) and Harley et al. (1992)

$$V_{cmax} = \frac{V_{cmax0} \exp\left[\frac{H_d}{RT_r}(1 - T_r/T_L)\right]}{1 + \exp\left[\frac{S_v T_L - H_d}{RT_L}\right]} \quad (28d)$$

where  $H_v$  is the energy of activation,  $H_d$  is the energy of deactivation,  $S_v$  is an entropy term, and  $V_{cmax0}$  is the value of  $V_{cmax}$  at  $T_r$ , supposed equal to  $28.9 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Harley 1986). The values of these empirical constants in Eq. (28) are obtained from Leuning (1995) and Harley et al. (1992), and shown in Table 2.

Using the data observed in the field, the net assimilation rate was estimated by means of Eq. (14) and Eq. (15), while Eqs. (19.1) to Eq. (19.5) were employed for functions of  $f(D_s)$ . As indicated in Table 3, the estimation precision for the net assimilation rate varied with adoption of different functions; such as  $f_1(D_s)$  and  $f_5(D_s)$ , where the  $g_{ic}$  is measured value and  $g_{bw} = 1.6 \text{ mol m}^{-2} \text{s}^{-1}$ . Obviously, the results were satisfactory. In Figure 1A and B, as a representative example, the net assimilation rates estimated by means of the models were plotted against the measured ones.

In the experimental conditions of soybean and maize, there was no significant difference between the values of  $\Gamma^*$  and  $\Gamma$  when calculated with Eqs. (23), (24) and (27), respectively. This implies that when Eq. (14) and Eq. (15) were used to estimate photosynthesis, the differences between the values of  $\Gamma^*$  and  $\Gamma$  could not significantly increase the estimation precision between Eq. (14) and Eq. (15) (Table 3). Thus, it is plausible to expect that good estimation can be made by employing the simplified form of Eq. (15).

In addition, the net assimilation rates were estimated by combining the  $g_{ic}$  model represented by Eq. (25) and Eq. (26) and the different functions of  $f(D_s)$  into Eq. (14), or its simplified form of Eq. (15). Table 4 lists the estimation precision of Eq. (15) when the functions of  $f_1(D_s)$  and  $f_5(D_s)$  were used. Comparison of Table 4 and Table 3 indicates that using  $g_{ic}$ ,

**Table 2.** Parameters and their values in the model for estimating the  $\text{CO}_2$  compensation points,  $\Gamma$ .

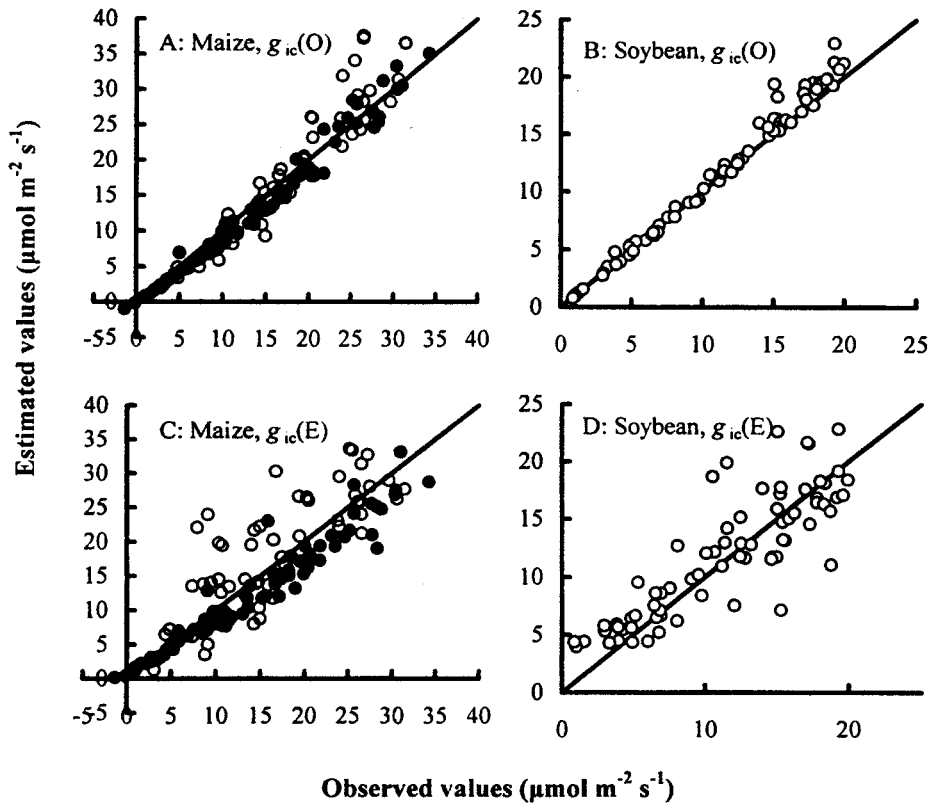
Parameters	Value (units) [ref.]	Meaning
$T_r$	293.2 (K) [1]	Reference temperature
$K_{cr}$	203 ( $\mu\text{mol mol}^{-1}$ ) [1]	Michaelis constant for $\text{CO}_2$ at $T_r$
$K_{or}$	256 ( $\text{mmol mol}^{-1}$ ) [1]	Michaelis constant for $\text{O}_2$ at $T_r$
$R_{dr}$	0.32 ( $\mu\text{mol s}^{-1} \text{m}^{-2}$ ) [1]	Day respiration at $T_r$
$E_{Kc}$	59430 ( $\text{J mol}^{-1}$ ) [2]	Activation energy for $K_c$
$E_{Ko}$	36000 ( $\text{J mol}^{-1}$ ) [2]	Activation energy for $K_o$
$E_{Rd}$	53000 ( $\text{J mol}^{-1}$ ) [2]	Activation energy for $R_d$
$H_v$	116300 ( $\text{J mol}^{-1}$ ) [2]	Activation energy for $V_{cmax}$
$H_d$	202900 ( $\text{J mol}^{-1}$ ) [2]	Deactivation energy for $V_{cmax}$
$S_v$	650 ( $\text{J mol}^{-1}$ ) [2]	Entropy term

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

**Table 3.** Estimation precision of the net assimilation rate models, Eq. (14) and Eq. (15), with the different functions,  $f_1(D_s)$  and  $f_5(D_s)$ . The internal conductance,  $g_{ic}$ , using the measured values and the boundary layer conductance  $g_{bw}$  taken to  $1.6 \text{ mol m}^{-2} \text{ s}^{-1}$ . The numbers of data are the same as those in Table 1.

	$f(D_s)$	Eq. (14)			Eq. (15)		
		$R^2$	$SI$	RMSE	$R^2$	$SI$	RMSE
Maize (1998)	$f_1(D_s) = h_s$	0.972	0.972	1.592	0.972	0.965	1.612
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.968	0.976	1.670	0.968	0.969	1.692
Maize (1999)	$f_1(D_s) = h_s$	0.915	1.062	3.201	0.914	1.051	3.131
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.899	1.087	3.657	0.897	1.078	3.585
Soybean (1999)	$f_1(D_s) = h_s$	0.984	1.056	1.064	0.984	1.053	1.054
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.983	1.038	0.931	0.983	1.034	0.913

$R^2$  is the coefficient of determination,  $SI$  is the slope (b) of the equation,  $A_m' = b A_m$ , established between the measured values ( $A_m$ ) and the values estimated by means of the model ( $A_m'$ ). RMSE is root mean square error ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ).



**Figure 1.** Comparison of net assimilation rates,  $A_m$ , measured and estimated by means of the simplified models, Eq. (15), for maize (A and C) and soybean (B and D). For the functions of  $f(D_s)$ ,  $f_1(D_s) = h_s$  was used, while for the internal conductance,  $g_{ic}$ , the values measured (A and B) and estimated (C and D) by means of Eqs. (25) and Eq. (26) were used for maize and soybean, respectively. The boundary layer conductance,  $g_{bw}$ , taken to  $1.6 \text{ mol m}^{-2} \text{ s}^{-1}$ . The solid line represents a line of 1: 1, the symbol ● is the data of 1998 and ○ is the data of 1999 for maize (A and C).

which was estimated by Eq. (25) and Eq. (26), largely lowered the estimation precision of the net assimilation rate model, as compared to using the measured  $g_{ic}$ . Evidently, estimation of the  $g_{ic}$  could significantly affect the estimation precision of net assimilation rate by the model. Nevertheless, the estimation precision of net assimilation rate by Eq. (14) or its simplified

form as Eq. (15) was still acceptable, even if using the  $g_{ic}$  estimated by means of Eq. (25) and (26). As an example, Figures 1C and D demonstrate a comparison of the net assimilation rate measured and estimated by means of the models. It can be said that the models performed well in estimating the net assimilation rate with acceptable precision.

**Table 4.** Estimation precision of the net assimilation rate model, Eq. (15), with the different functions,  $f_1(D_s)$  and  $f_5(D_s)$ . The internal conductance,  $g_{ic}$ , using the values estimated by means of Eqs. (25) and (26) for maize and soybean, respectively. The boundary layer conductance  $g_{bw}$  taken to  $1.6 \text{ mol m}^{-2} \text{ s}^{-1}$ . All symbols are the same as those in Table 3 and the numbers of data are the same as those in Table 1.

	$f(D_s)$	$R^2$	SI	RMSE
Maize (1998)	$f_1(D_s) = h_s$	0.930	0.880	2.889
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.929	0.885	2.841
Maize (1999)	$f_1(D_s) = h_s$	0.751	1.066	4.932
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.731	1.091	5.256
Soybean (1999)	$f_1(D_s) = h_s$	0.689	1.001	2.986
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.701	0.983	2.845

### Estimation of transpiration by the synthetic models

Using different function of  $f(D_s)$ , we estimated the transpiration rate by means of transpiration model of Eq. (16) or Eq. (17). Table 5 shows the estimation precision of the models for the transpiration rate using  $f_1(D_s)$  and  $f_5(D_s)$ . In Eq. (16), the net assimilation rate,  $A_m$ , is the measured values, and in Eq. (17), the  $g_{ic}$  is the values estimated by the model of Eqs. (25) and (26). Figure 2, as an example, shows a comparison of values of transpiration rate measured and estimated by means of the models as Eq. (16) (Figs. 2A and B) and Eq. (17) (Figs. 2C and D) with  $f_1(D_s) = h_s$ . From Table 5 and Figure 2, it can be seen that the transpiration rate estimated by means of the models agreed approximately with the measurements. This indicates that these models performed well in estimating the transpiration rate. However, for the maize and soybean in 1999, the estimation precision of the models was lower. Also, the estimated precision in Figures 2C and D was lower than that in Figures 2A and B. This was attributed to the relative lower estimation precision of  $g_{ic}$ .

**Table 5.** Estimated precision of transpiration rate models, Eq. (16) and Eq. (17), with the different functions  $f_1(D_s)$  and  $f_5(D_s)$ . For Eq. (16), the net assimilation rate using the measured values, and for Eq. (17), the internal conductance,  $g_{ic}$ , using the values estimated by means of Eqs. (25) and (26) for maize and soybean, respectively. The boundary layer conductance  $g_{bw}$  taken to  $1.6 \text{ mol m}^{-2} \text{ s}^{-1}$ . All symbols are the same as those in Table 3, the RMSE is in  $\text{mmol cm}^{-2} \text{ s}^{-1}$ , and the numbers of data are the same as those in Table 1.

	$f(D_s)$	Eq. (16)			Eq. (17)		
		$R^2$	SI	RMSE	$R^2$	SI	RMSE
Maize (1998)	$f_1(D_s) = h_s$	0.894	0.959	0.966	0.865	0.884	1.163
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.882	0.946	1.017	0.843	0.869	1.242
Maize (1999)	$f_1(D_s) = h_s$	0.771	0.997	1.878	0.631	1.008	2.482
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.742	0.994	1.961	0.563	1.012	2.676
Soybean (1999)	$f_1(D_s) = h_s$	0.661	1.069	3.202	0.551	1.087	3.948
	$f_5(D_s) = (1 + D_s/D_0)^{-1}$	0.544	1.012	3.076	0.391	1.010	3.624

### Modeling water use efficiency by the synthetic models

The water use efficiency,  $WUE_m$ , is defined as the ratio of  $A_m$  to  $E_m$ , i.e.  $A_m/E_m$  in  $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ . By combining Eq. (1) with Eq. (2), a simple model of  $WUE_m$ , which is based on leaf gas exchange, was obtained as

$$WUE_m = \frac{(C_a - C_i)}{(e_w(T_L) - e_a)/P} \frac{(r_{bw} + r_{sw})}{(r_{bc} + r_{sc})} = \frac{r_{tw}}{r_{gc}} \frac{(C_a - C_i)}{(e_w(T_L) - e_a)/P} \quad (29)$$

where  $r_{gc} = r_{bc} + r_{sc}$  and  $r_{tw} = r_{bw} + r_{sw}$ . The  $\text{CO}_2$  resistances ( $r_{bc} + r_{sc}$ )  $\approx 1.56(r_{bw} + r_{sw})$ , Eq. (29) can be simplified as

$$WUE_m = \frac{C_a(1 - C_i/C_a)}{1.56(e_w(T_L) - e_a)/P} \quad (30)$$

where the ratio of  $C_i/C_a$  is usually assumed as a constant dependent on species. The value of  $C_i/C_a$  is lower for  $C_4$  plant than for  $C_3$  plant, approximately 0.3 for  $C_4$  plant and near 0.7 for  $C_3$  plant (Jones 1992). Besides, if Eq. (1) is combined with Eq. (8), the  $WUE_m$  model is given as

$$WUE_m = \frac{(C_a - \Gamma^*)}{(e_w(T_L) - e_a)/P} \frac{(r_{bw} + r_{sw})}{(r_{bc} + r_{sc} + r_{ic})} = \frac{r_{tw}}{r_{ic}} \frac{(C_a - \Gamma^*)}{(e_w(T_L) - e_a)/P} \quad (31)$$

assuming  $r_{ic} = r_{bc} + r_{sc} + r_{ic}$  and  $\Gamma^*$  as a constant. Given that dry matter yield is often of concern in agronomic studies, it is more popular to express equations in terms of mass fluxes of  $\text{CO}_2$  ( $WUE$ ,  $\text{mg CO}_2/\text{g H}_2\text{O}$ ),

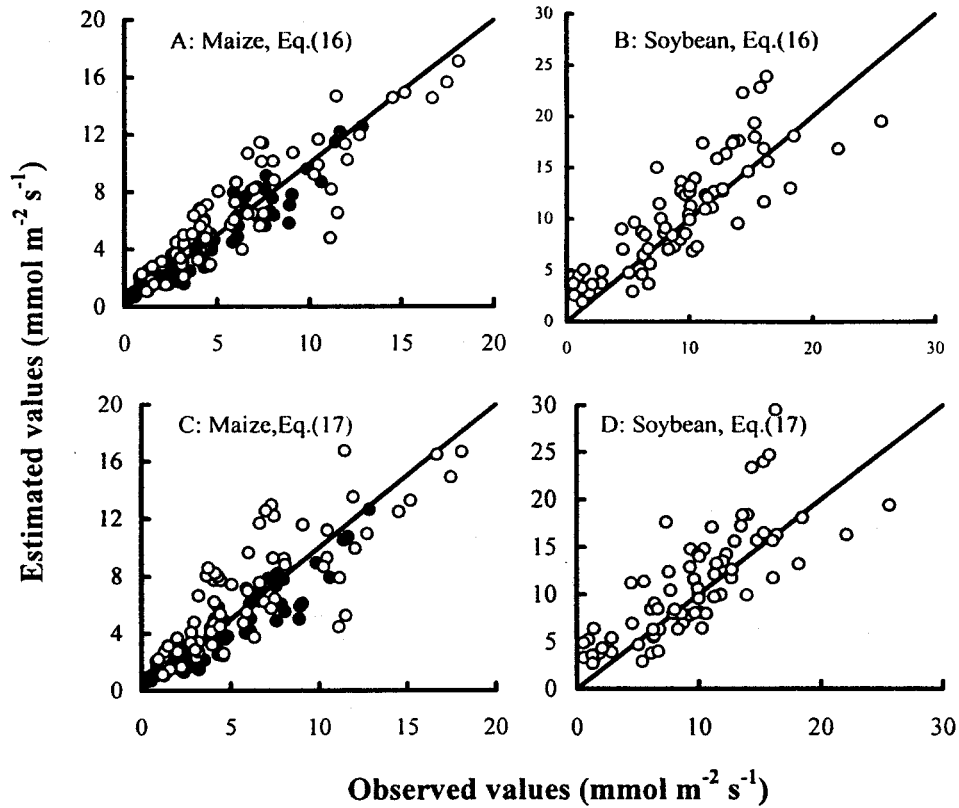
$$WUE = \frac{M_c \times 10^{-3} A_m}{M_w E_m} = \frac{44}{18000} \frac{A_m}{E_m} \quad (32)$$

According to Eq. (30) and Eq. (31), the relation between  $C_i/C_a$  and  $r_{tw}/r_{ic}$  can be described as

$$r_{tw}/r_{ic} = \frac{C_a}{1.56(C_a - \Gamma^*)} \left(1 - \frac{C_i}{C_a}\right) \quad (33)$$

In the case of  $\Gamma^* \ll C_a$ , a linear relationship exists between  $C_i/C_a$  and  $r_{tw}/r_{ic}$ .





**Figure 2.** Comparison of transpiration rate,  $E_m$ , measured and estimated by means of the models, Eq. (16) (A, B) and Eq. (17) (C, D), for maize (A and C) and soybean (B and D). For the functions of  $f(D_s)$ ,  $f_1(D_s) = h_s$  was used, while for net assimilation rates,  $A_m$ , in Eq. (16) used the observed values (A, B), the interal conductance,  $g_{ic}$ , in Eq. (17) used the values estimated (C and D) by means of Eq. (25) and Eq. (26) for maize and soybean, respectively. The boundary layer conductance,  $g_{bw}$ , taken to  $1.6 \text{ mol m}^{-2} \text{ s}^{-1}$ . The solid line represents a line of 1:1, the symbol ● is the data of 1998 and ○ is the data of 1999 for maize (A and C).

From Eq. (30) and Eq. (31), it can be understood that  $C_i/C_a$  and  $r_{tw}/r_{tc}$  are critical physiological parameters in determining WUE. Once either  $C_i/C_a$  or  $r_{tw}/r_{tc}$  is determined, Eq. (30) and Eq. (31) will become more effective for estimating WUE by leaf-air vapor pressure in different climates. However, the ratios of  $C_i/C_a$  and  $r_{tw}/r_{tc}$  not only were different between the two species of plants, but also varied largely with WUE of each of the species. Although the ratios of  $r_{tw}/r_{tc}$  of the two species of plants were proportional to WUE, with almost the same linear relation, the values varied widely. For maize, the measured ratio of  $r_{tw}/r_{tc}$  ranged from  $-0.047$  to  $0.432$ , and the average value was  $0.176 \pm 0.091$ . For soybean, the ratio ranged from  $0.002$  to  $0.213$ , with an average value of  $0.090 \pm 0.042$ . Moreover, between the  $C_i/C_a$  and the WUE of the two species of plants, there existed a significant negative relationship. The measured ratio of  $C_i/C_a$  ranged from  $0.863$  to  $0.969$ , with an average value of  $0.862 \pm 0.0524$  for soybean, and for maize ranged from  $0.359$  to  $1.0$ , with an average value of  $0.720 \pm 0.134$ . This suggests difficulty in using Eq. (30) to determine WUE in this study.

If Eq. (14) is combined with (16), the  $WUE_m$  model has a form of

$$WUE_m = \frac{(C_a - \Gamma^*) - 1.56(C_a - \Gamma)[a_1 f(D_s)]}{(e_w(T_L) - e_a)/P} K_r \quad (34)$$

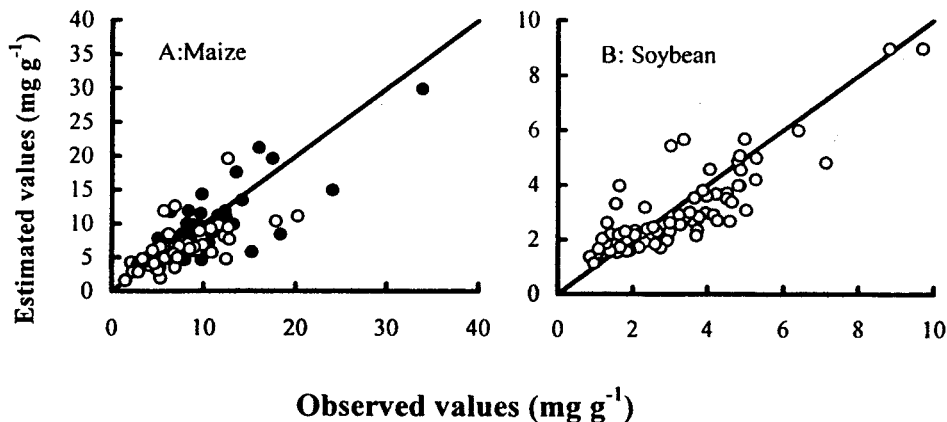
where  $K_r$ , a term related to the  $r_{bw}$ ,  $r_{ic}$  and  $f(D_s)$ , is described as

$$K_r = \left[ \frac{r_{bw}}{1.37r_{bw} + r_{ic}} + \frac{1}{g_0(1.37r_{bw} + r_{ic}) + a_1 f(D_s) - 1.56} \right] \quad (35)$$

In addition, by combining Eq. (15) with Eq. (16), a simplified model of  $WUE_m$  can be achieved,

$$WUE_m = \frac{(C_a - \Gamma^*)(1 - 1.56[a_1 f(D_s)])}{(e_w(T_L) - e_a)/P} K_r \quad (36)$$

By combining the internal conductance,  $g_{ic}$ , models represented by Eq. (25) and Eq. (26), and the different expression functions of  $f(D_s)$  into the WUE models, the WUE could be estimated. Using the data observed in this experiment, we estimated the WUE values of soybean and maize by Eq. (34) and Eq. (36). In the estimation,  $f_1(D_s)$  and  $f_5(D_s)$  were used for the function of  $f(D_s)$ , and  $1.6 \text{ mol m}^{-2} \text{ s}^{-1}$  for  $g_{bw}$ . A comparison of Eqs. (34) and (36) in the precision of estimating WUE indicated that Eq. (36) was better than Eq. (34), although the dif-



**Figure 3.** Comparison of the values of water use efficiency, WUE, measured and estimated by means of Eq. (36) for maize (A) and soybean (B). The internal conductance,  $g_{ic}$ , used the estimated value by means of the models as Eq. (25) and Eq. (26) for maize and soybean, respectively. The functions of  $f(D_s)$ ,  $f_1(D_s) = h_s$  were used, and the boundary layer conductance,  $g_{bw}$ , was taken to be  $1.6 \text{ mol m}^{-2} \text{ s}^{-1}$ . The solid line represents a line of 1:1, the symbol ● is the data of 1998 and ○ is the data of 1999 for maize (A).

ference was almost negligible. Therefore, the simplified model represented by Eq. (36) was suitable for estimating the WUE. In addition, the difference of estimation precision in using  $f_1(D_s)$  and  $f_3(D_s)$  was also negligible.

Figures 3 A and B demonstrate a comparison of WUE measured and estimated by means of Eq. (36) using  $f_1(D_s)$ , and the values of  $g_{ic}$  estimated by means of Eqs. (25) and (26) for maize and soybean, respectively. The  $R^2$  value was 0.69 for soybean and 0.61 for maize. The RMSE was less than  $1.04 \text{ mg g}^{-1}$  for soybean and less than  $3.58 \text{ mg g}^{-1}$  for maize.

## Discussion

A very useful graphical device for investigating the mechanism of the relationships between  $A_m$  and conductances, as well as  $\text{CO}_2$  concentration drops within air-to-leaf, was introduced by Jones (1992). Figure 4 shows the relationships between  $A_m$  and  $g_{sc}$ ,  $g_{ic}$  as well as total conductance,  $g_{tc}$ , and that between  $A_m$  and  $\text{CO}_2$  concentration drops for air-to-leaf,  $C_a - C_i$ ,  $C_i - \Gamma^*$  as well as  $C_a - \Gamma^*$  for maize and soybean, respectively. Figure 5 shows the relationships between  $A_m$  and  $C_i$ ,  $C_i/C_a$  as well as  $g_{sc}$ , and that between  $g_{ic}$  and  $C_i$ ,  $C_i/C_a$  as well as  $g_{sc}$  for maize and soybean, respectively. From Figure 4 and Figure 5, some interesting results can be seen by comparing the observation in soybean field with that made in maize field.

The values of  $A_m$  of the two species were positively proportional to  $g_{sc}$  (Fig. 4A). As shown in Table 6, the  $R^2$  values of a linear regression formula were 0.107 and 0.467 for soybean and maize, respectively. However, when a rectangular hyperbola was employed, the  $R^2$  value of regression formula was 0.158 for soybean. For soybean, the rectangular hyperbola was better than the linear formula, the converse of maize. The slope,  $\partial A_m / \partial g_{sc}$ , of the linear regression formula for maize

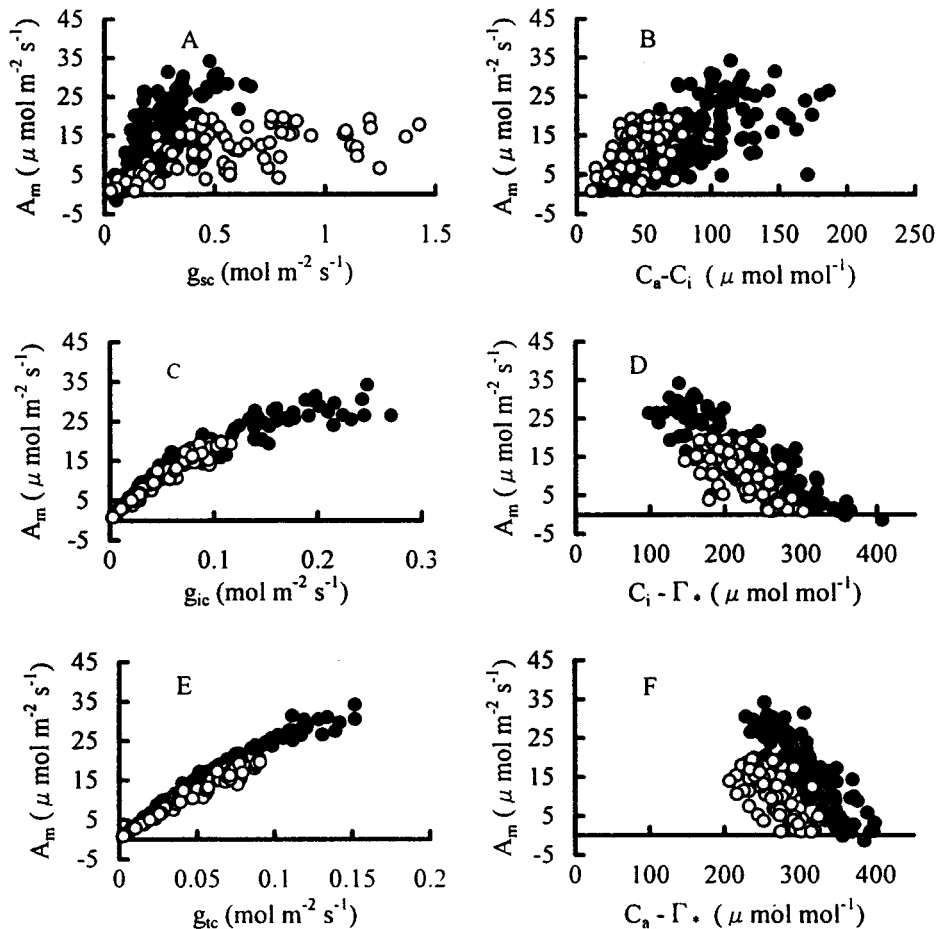
was approximately 3.37 times that of soybean. Regarding the relationship between the  $A_m$  and the  $g_{ic}$  (Fig. 4C), the best expression function was a linear function for soybean and a rectangular hyperbola function for maize (Table 6). The slope,  $\partial A_m / \partial g_{ic}$ , for maize was approximately 0.81 times as much as that for soybean. Moreover, the relationship between  $A_m$  and  $g_{tc}$  (Fig. 4E) was shown as the same as that between  $A_m$  and  $g_{ic}$ . Therefore, the best expression function was a linear function for the two species of plants (Table 6).

The relationships between the  $A_m$  of two species of plants and  $\text{CO}_2$  concentration drop from air to intercellular space,  $C_a - C_i$ , were shown a positive correlation (Fig. 4B). Unfortunately, the  $R^2$  values for the linear regression formula only reached 0.179 for soybean and 0.397 for maize (Table 6). The slope,  $\partial A_m / \partial (C_a - C_i)$ , for soybean was 0.241, about 1.44 times as much as that for maize. The relationship between the  $A_m$  and the  $C_i - \Gamma^*$  was generally in a negative linear correlation for the two species of plants. Moreover, the relationship between the  $A_m$  and the total  $\text{CO}_2$  concentration drop,  $C_a - \Gamma^*$ , was found to be similar to that between the  $A_m$  and the  $C_i - \Gamma^*$  (Fig. 4F and Table 6).

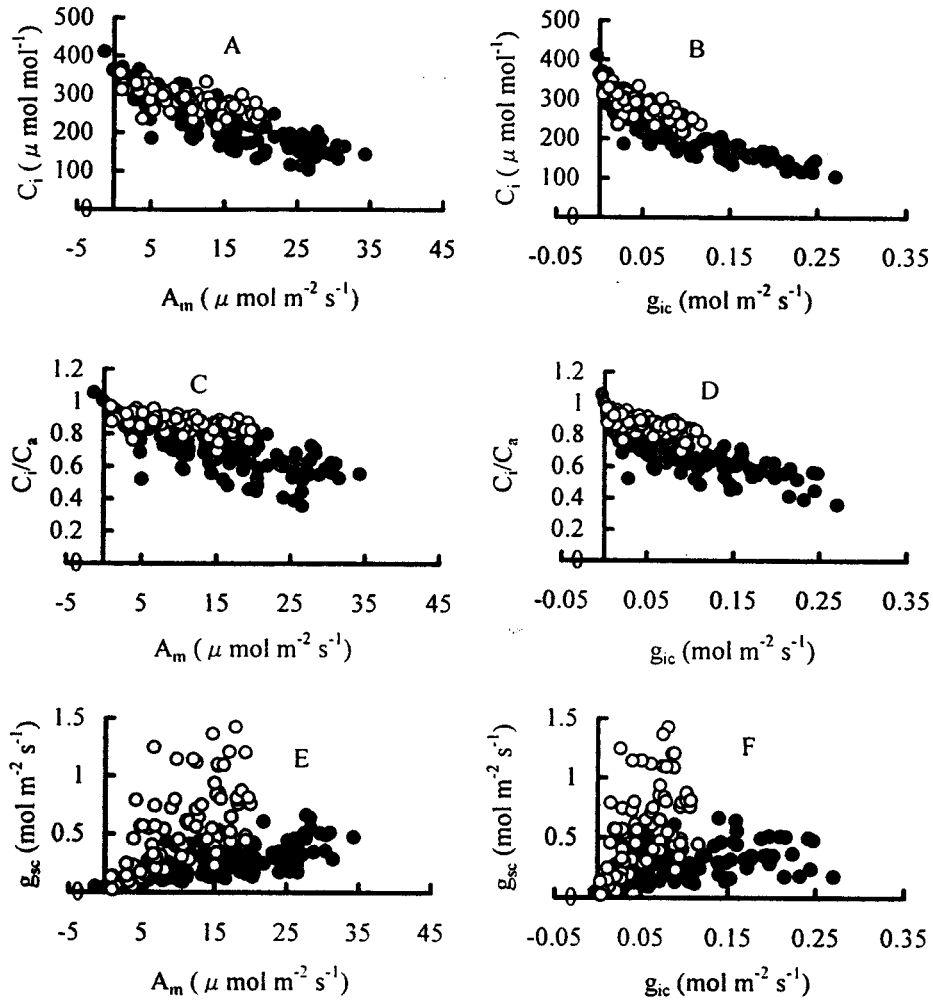
Figure 5 demonstrates the negative correlations between  $A_m$  and  $C_i$  as well as  $C_i/C_a$  (Fig. 5A, C), and between  $g_{ic}$  and  $C_i$  as well as  $C_i/C_a$  (Figs. 5B, D). According to the investigations of Jones (1992), if the values of  $r_{bc}$  and  $g_{ic}$  are constants, the slopes of the linear relationships between  $A_m$  and  $C_i - \Gamma^*$  are equal to  $-1/r_{sc} = -g_{sc}$ . These relationships represent photosynthetic 'supply' functions, indicating a drop in mole fraction across the gas-phase and showing how  $C_i$  would fall below  $C_a$  while  $A_m$  increases. Therefore, the increase of  $A_m$  with  $g_{ic}$ , which was determined by the activities of bio- and photochemical processes, led to uptake of more  $\text{CO}_2$  by leaves from the atmosphere for photosynthesis, and in turn, better assimilation of  $\text{CO}_2$  at the stomatal space. As a result,  $C_i$  and  $C_i/C_a$  decreased, and both  $C_i - \Gamma^*$  and  $C_a - \Gamma^*$  also became

**Table 6.** Comparing soybean with maize for the relationships between net assimilation rate,  $A_m$ , and conductances ( $g_{sc}$ ,  $g_{ic}$  and  $g_{tc}$ ), as well as  $CO_2$  concentration drops for air-to-leaf ( $C_a - C_i$ ,  $C_i - \Gamma^*$ , and  $C_a - \Gamma^*$ ).

	Conductance		Concentration drops for air-to-leaf	
	Regression formula	$R^2$	Regression formula	$R^2$
Soybean	$A_m = 16.532g_{sc}$	0.107	$A_m = 0.2409(C_a - C_i)$	0.179
	$A_m = 23.70g_{sc}/(0.8199 + g_{sc})$	0.158		
	$A_m = 195.78g_{ic}$	0.929	$A_m = -0.1166(C_i - \Gamma^*) + 36.705$	0.500
	$A_m = 54.347g_{ic}/(0.2011 + g_{ic})$	0.625		
	$A_m = 229.47g_{ic}$	0.958	$A_m = -0.1332(C_a - \Gamma^*) + 46.245$	0.390
	$A_m = 71.943g_{ic}/(0.2446 + g_{ic})$	0.568		
Maize	$A_m = 55.774g_{sc}$	0.467	$A_m = 0.168(C_a - C_i)$	0.397
	$A_m = 37.594g_{sc}/(0.421 + g_{sc})$	0.021		
	$A_m = 158.05g_{ic}$	0.741	$A_m = -0.1092(C_i - \Gamma^*) + 39.571$	0.692
	$A_m = 46.083g_{ic}/(0.1429 + g_{ic})$	0.855		
	$A_m = 255.00g_{ic}$	0.929	$A_m = -0.1978(C_a - \Gamma^*) + 76.736$	0.697
	$A_m = 80.00g_{ic}/(0.224 + g_{ic})$	0.837		



**Figure 4.** Net assimilation rate,  $A_m$ , as functions of stomatal conductance,  $g_{sc}$ , internal conductance,  $g_{ic}$ , and total conductance,  $g_{tc}$ , and as functions of  $CO_2$  concentration drops,  $C_a - C_i$ ,  $C_i - \Gamma^*$ , and  $C_a - \Gamma^*$ , for air-to-leaf. The symbol ● is maize and ○ is soybean.



**Figure 5.** Relationships between intercellular  $CO_2$  concentration,  $C_i$ , and net assimilation rate,  $A_m$ , as well as internal conductance,  $g_{ic}$ , between the ratio of intercellular  $CO_2$  concentration to ambient  $CO_2$  concentration,  $C_i/C_a$ , and  $A_m$  as well as  $g_{ic}$ , and between stomatal conductance,  $g_{sc}$ , and  $A_m$  as well as  $g_{ic}$ . The symbol ● is maize and ○ is soybean.

smaller. Due to this change, negative correlations occurred between  $A_m$  and  $C_i - \Gamma^*$  as well as  $C_a - \Gamma^*$  (Fig. 4D and Fig. 4F), between  $A_m$  and  $C_i$  as well as  $C_i/C_a$  (Figs. 5A, C), and between  $g_{ic}$  and  $C_i$  as well as  $C_i/C_a$  (Figs. 5B, D).

In addition, to supply  $CO_2$  to the photosynthesis while  $A_m$  and  $g_{ic}$  increase, the leaf stomata usually opens wide, leading to the reduction of  $r_{sc}$ . As depicted in Figure 5E and Figure 5F, the  $g_{sc}$  of soybean increased exponentially with  $A_m$  and with  $g_{ic}$ , respectively ( $R^2 = 0.451$  and  $R^2 = 0.352$ ), but the  $g_{sc}$  of maize was related linearly with  $A_m$  and  $g_{ic}$ , respectively ( $R^2 = 0.519$  and  $R^2 = 0.293$ ). It is worth noting that the  $\partial g_{sc}/\partial A_m$  and the  $\partial g_{sc}/\partial g_{ic}$  for soybean are much bigger than those for maize. This implies that the difference of  $g_{sc}$  between the two species of plants becomes larger with increases of  $A_m$  and  $g_{ic}$  (Figs. 5E and F). Moreover, the slope,  $\partial A_m/\partial g_{sc}$ , of a linear regression formula for maize was about 3.37 times as much

as that for soybean (Fig. 4A), and the slope,  $\partial A_m/\partial (C_a - C_i)$ , of a linear regression formula for soybean was about 1.44 times as much as that of maize (Fig. 4B). The slopes,  $\partial A_m/\partial g_{sc}$  and  $\partial A_m/\partial (C_a - C_i)$ , are defined as the contribution to  $A_m$  of unit change of  $g_{sc}$  and  $C_a - C_i$ , respectively, and conversely, the slope,  $\partial g_{sc}/\partial A_m$ , represents the requirement of  $g_{sc}$  by the unit change of  $A_m$ . Based on the above considerations, it is easily understood that in order to reach the same level of  $A_m$ , soybean had to open its stomata more widely in order to maintain a smaller  $r_{sc}$ , as compared to maize. This is because  $C_3$  plants are different from  $C_4$  plants in the pathway of photosynthesis. More efficient utilization of  $CO_2$  usually causes a higher photosynthesis rate in maize plants, even though  $CO_2$  concentration is low. In contrast, to obtain the same photosynthesis rate as maize plants, the soybean plants always need relatively higher level of  $C_i$ . In this study,  $C_i$  of maize

plants decreased to about  $233.0 \pm 63.7 \mu\text{mol mol}^{-1}$ , but  $C_i$  of soybean plants was reduced to about  $280.7 \pm 30.6 \mu\text{mol mol}^{-1}$ , about 1.21 times as much as that of maize (Figs. 5A, B).

The principal objective of this study was to present a theoretical basis for a new modeling approach to estimating photosynthesis, transpiration, and WUE, and to verify it using the data observed in maize and soybean field. The model was presented as a single layer model within maize and soybean canopy without soil water stresses. It didn't involve the energy balance of plant leaves and the effects of environmental stresses in estimating photosynthesis, transpiration, and WUE. We admit that using only the data of maize and soybean grown in a specific environmental condition is rather inadequate for a general examination of the proposed modeling approach. Therefore, more species of plants in various environmental conditions must be used to evaluate and improve the model, especially for the universality of the empirical parameters. Also, energy balance of plant leaves should be emphasized in the future improvement of the model.

## Conclusions

In the synthetic consideration for the models of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  diffusion controlled through stomata of plant leaf, a stomatal behavior-based, synthetic model for estimating photosynthesis and transpiration was established. The parameters of the model were identified using the data collected in maize and soybean field, and the critical appraisal of the synthetic models was made. In addition, based on the synthetic model, the model for estimating WUE was proposed.

This synthetic model was developed by introducing the internal conductance,  $g_{ic}$ , for  $\text{CO}_2$  assimilation and the general equation of stomatal conductance model,  $g_{sw} = g_0 + a_1 A_m f(D_s) / (C_s - \Gamma)$ , into the models of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  diffusion through the stomata of plant leaf. The estimation precision of the synthetic model was the highest when selecting  $f(D_s) = h_s$  or  $f(D_s) = (1 + D_s/D_0)^{-1}$ , as a function describing the response of stomatal conductance to humidity in the models. Also,  $g_{ic}$  was indicated as having the closest correlation with the photosynthetic photon flux as compared with the other environmental factors. In view of the fact that the model avoids the difficulty of determining the physiological parameters, and only employs environmental variables such as ambient  $\text{CO}_2$  concentration, leaf temperature, humidity, and PAR received at the leaves within the canopy, it can therefore be said that the synthetic model is easier for practical use.

Finally, through discussing some physiological factors controlling  $A_m$ , it is made clear that the requirement of unit change of  $A_m$  to  $g_{sc}$  differs between the two species of plants. To obtain the same level of  $A_m$  as that of maize, soybean, which needs a higher level of  $C_i$  than maize, has to open its stomata more widely in order to maintain a smaller  $r_{sc}$  since different pathways of the photosynthesis in  $C_3$  and  $C_4$  plants exist.

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## References

- Ball JT, Woodrow IE, Berry JA (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggins I (ed) *Progress in Photosynthesis Research*. Martinus Nijhoff Publishers, Dordrecht, pp 221–224
- Brooks A, Farquhar GD (1985) Effect of temperature on the  $\text{CO}_2/\text{O}_2$  specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta* 165: 397–406
- Collatz GJ, Ball JT, Grivet TC, Berry JA (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric For Meteorol* 54: 107–136
- Collatz GJ, Ribas-Carbo M, Berry JA (1992) Coupled photosynthesis-stomatal conductance model for leaves of  $C_4$  plants. *Aust J Plant Physiol* 19: 519–538
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic  $\text{CO}_2$  assimilation in leaves of  $C_3$  species. *Planta* 149: 78–90
- Harley PC, Weber JA, Gates DM (1985) Interactive effects of light, leaf temperature,  $\text{CO}_2$  and  $\text{O}_2$  on photosynthesis in soybean. *Planta* 165: 249–263
- Harley PC, Thomas RB, Reynolds JF, Strain BR (1992) Modelling photosynthesis of cotton grown in elevated  $\text{CO}_2$ . *Plant Cell Environ* 15: 271–282
- Hatton TJ, Walker J, Dawes WR, Dunin FX (1992) Simulation of hydro-ecological responses to elevated  $\text{CO}_2$  at the catchment scale. *Aust J Bot* 40: 679–696
- Jarman PD (1974) The diffusion of carbon dioxide and water vapor through stomata. *J Exp Bot* 25: 927–936
- Jarvis PJ (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil Trans R Soc Lond Ser B* 273: 593–610
- Jones HG (1992) *Plants and Microclimate*, 2nd ed. Cambridge University Press, New York, pp 163–214
- Leuning R (1990) Modeling stomatal behavior and photosynthesis of *Eucalyptus grandis*. *Aust J Plant Physiol* 17: 159–175
- Leuning R (1995) A critical appraisal of a combined stomatal-photosynthesis model for  $C_3$  plants. *Plant Cell Environ* 18: 339–355
- Lloyd J (1991) Modelling stomatal responses to environment in *Macadamia integrifolia*. *Aust J Plant Physiol* 18: 649–660
- Lohammer T, Larsson S, Linder S, Falk SO (1980) FAST-simulation models of gaseous exchange in Scots Pine. *Ecol Bull (Stockholm)* 32: 505–523
- McMurtrie RE, Leuning R, Thompson WA, Wheeler AM (1992) A model of canopy photosynthesis and water use incorporating a mechanistic formulation of leaf  $\text{CO}_2$  exchange. *Forest Eco Manag* 52: 261–278

- Sellers PJ, Berry JA, Collatz GJ, Field CB, Hall FG (1992) Canopy reflectance, photosynthesis and transpiration. III. A reanalysis using improved leaf model and a new canopy integration scheme. *Remote Sensing Environ* 42: 187–216
- Sellers PJ, Randall DA, Gollatz GJ, Berry A, Field CB, Dazlich DA, Zhang C, Collelo GD, Bounoua L (1996) A revised land surface parameterization (SiB2) for atmospheric GCMs. Part I: Model formulation. *J Climate* 9: 676–705
- Tenhunen JD, Sala Serra A, Harley PC, Dougherty RL, Reynolds JF (1990) Factors influencing carbon fixation and water use by Mediterranean sclerophyll shrubs during summer drought. *Oecologia* 82: 381–393
- von Caemmerer S, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376–387
- Woodward FI, Smith TM (1994) Global photosynthesis and stomatal conductance: Modelling the controls by soil and climate. *Adv Bot Res* 23: 1–41
- Yu G-R (1999) A study on modeling stomatal conductance of maize (*Zea mays* L.) leaves. *Tech Bull Fac Hort Chiba Univ* 53: 145–239 (in Japanese with English summary)
- Yu G-R, Nakayama K, Lu H-Q (1996) Responses of stomatal conductance in field-grown maize leaves to certain environmental factors over a long term. *J Agric Meteorol* 52(4): 311–320
- Yu G-R, Nakayama K (1997) Development of model for estimating stomatal conductance of maize leaves. *J Agric Meteorol* 52: 505–508
- Yu G-R, Nakayama K, Matsuoka N, Kon H (1998) A combination model for estimating stomatal conductance of maize (*Zea mays* L.) leaves over a long term. *Agric For Meteorol* 92: 9–28
- Yu G-R, Nakayama K, Zhuang J (1999) Study on synthesis of photosynthesis and transpiration models. In: *Society of Agricultural Meteorology of Japan (ed) Summary of Annual General Meeting*, pp 310–312 (in Japanese)