

## Simulation of the Stomatal Conductance of Winter Wheat in Response to Light, Temperature and CO<sub>2</sub> Changes

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- **Background and Aims** The stomata are a key channel of the water cycle in ecosystems, and are constrained by both physiological and environmental elements. The aim of this study was to parameterize stomatal conductance by extending a previous empirical model and a revised Ball–Berry model.
- **Methods** Light and CO<sub>2</sub> responses of stomatal conductance and photosynthesis of winter wheat in the North China Plain were investigated under ambient and free-air CO<sub>2</sub> enrichment conditions. The photosynthetic photon flux density and CO<sub>2</sub> concentration ranged from 0 to 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and from 0 to 1400  $\mu\text{mol mol}^{-1}$ , respectively. The model was validated with data from a light, temperature and CO<sub>2</sub> response experiment.
- **Key Results** By using previously published hyperbolic equations of photosynthetic responses to light and CO<sub>2</sub>, the number of parameters in the model was reduced. These response curves were observed diurnally with large variations of temperature and vapour pressure deficit. The model interpreted stomatal response under wide variations in environmental factors.
- **Conclusions** Most of the model parameters, such as initial photon efficiency and maximum photosynthetic rate ( $P_{\text{max}}$ ), have physiological meanings. The model can be expanded to include influences of other physiological elements, such as leaf ageing and nutrient conditions, especially leaf nitrogen content.

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**Key words:** Stomatal conductance, light intensity, temperature, humidity, CO<sub>2</sub>, model.

### INTRODUCTION

Leaf stomata control plant CO<sub>2</sub> absorption through photosynthesis and water loss through transpiration. Their aperture regulates water use efficiency of crops and energy partitioning into sensible and latent heat. Therefore, parameterization of stomatal conductance is essential in the simulation of crop productivity and water-use efficiency in agricultural ecosystems. As stomatal aperture is a balance between CO<sub>2</sub> assimilation and water loss, its conductance is related to photosynthesis and transpiration (Cowan, 1965). Stomatal opening affects photosynthesis by regulating intercellular CO<sub>2</sub> concentration, and thereby the biochemical processes in chloroplasts (Yu *et al.*, 2001). The extent of stomatal opening is jointly determined by light intensity and water balance of the guard cells. Light intensity affects photosynthesis rate through light receptors which drive CO<sub>2</sub> fixation and lower intercellular CO<sub>2</sub> concentration, and the guard cells are conditioned jointly by the water balance of the bulk leaf tissue and the CO<sub>2</sub> concentration in the substomatal cavity.

In the simulation of stomatal conductance, the Jarvis model (Jarvis, 1976) has been applied widely to studies of evapotranspiration, land surface processes and the biogeochemical cycle (e.g. McMurtrie, 1992; Hanan and Prince, 1997; Cox *et al.*, 1998). The model is a typical empirical one, which is characterized by multiplying by a series of correction coefficients each of which represents a factor. It

does not include physiological feedbacks from changes in rates of photosynthesis and transpiration due to stomatal movements. A semi-empirical model, the Ball–Berry model (Ball *et al.*, 1987), has a solid experimental basis with a linear relationship between photosynthesis and stomatal conductance. But to take account of the feedback interaction between photosynthetic rate and stomatal conductance requires iteration of calculations. In this study, a hybrid stomatal model is proposed, based partly on those empirical and semi-empirical models, which gives a direct calculation of stomatal conductance from solar radiation, temperature, humidity, CO<sub>2</sub> concentration of air, and soil water potential, but has physiological relationships similar to the Ball–Berry model.

The objective of this study was to construct a Jarvis-type stomatal model with physiological relationships based on the Ball–Berry model, so as to enable the model to calculate the conductance directly from environmental variables, whilst maintaining a relevant physiological basis.

### MATERIALS AND METHODS

Experiments were conducted at the Yucheng Comprehensive Experiment Station (36°57'N, 116°36'E, 28 m a.s.l.), Chinese Academy of Sciences, which is located in the North China Plain. The light and CO<sub>2</sub> responses of photosynthesis, transpiration, and stomatal conductance of winter wheat were measured in the field. The light and CO<sub>2</sub> response curves were measured in a leaf chamber. Each

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measurement was made over a short period. Flag leaves were used for all measurements, which were conducted at the bearing stage (from 16 April to 6 May 2003). Every 2 h over the course of a day, light and CO<sub>2</sub> response curves were generated by varying light (400–700 nm) intensity between 0 and 2000 μmol m<sup>-2</sup> s<sup>-1</sup>, and CO<sub>2</sub> concentrations between 0 and 1400 μmol mol<sup>-1</sup>. Thus, environmental conditions varied greatly in light, temperature and CO<sub>2</sub> concentration.

The infrared CO<sub>2</sub> analysis system LI-COR 6400 (LI-COR Inc., Lincoln, NE, USA) was used. The system was calibrated and found to give a stable performance. The wheat fields were routinely irrigated, according to soil water content, and were well fertilized. Irrigation water of about 70–100 mm was applied three times after the turning-green stage. The area of cultivation was more than 20 ha. For a detailed description of management and environmental conditions, see Yu *et al.* (2002).

### The model

There are five main environmental factors affecting stomatal conductance under natural conditions, i.e. solar radiation, air temperature, humidity, CO<sub>2</sub> concentration, and soil water potential. The actual stomatal conductance ( $g_s$ ) can be obtained from the maximum conductance ( $g_{\max}$ ) under suitable conditions modified by correction coefficients for all the above factors (Jarvis, 1976):

$$g_s = g_{\max} f(\text{PPFD}) f(T_a) f(C_a) f(\text{VPD}) f(\psi) \quad (1)$$

in which  $I$  is absorbed photosynthetic photon flux density (PPFD),  $T_a$  is air temperature,  $C_a$  is CO<sub>2</sub> concentration,  $D$  is vapour pressure deficit and  $\psi$  is soil water potential.

Ball *et al.* (1987) proposed a semi-empirical stomatal model in which the mathematical relationship between relative humidity at the leaf surface ( $h_s$ ), CO<sub>2</sub> concentration ( $C_s$ ) and photosynthetic rate ( $A_n$ ) was represented by the following equation under conditions of ample water supply:

$$g_s = a \frac{A_n h_s}{C_s} + g_0 \quad (1)$$

in which  $a$  is a constant,  $h_s$  is the relative humidity and  $C_s$  is the CO<sub>2</sub> concentration of air at the leaf surface,  $g_s$  is stomatal conductance, and  $g_0$  is a parameter. Since it is the vapour pressure deficit from stomatal pore to leaf surface ( $D_s$ ) which drives transpiration,  $D_s$  should replace  $h_s$  in the Ball–Berry model (Leuning, 1995). Here, the value of  $D$  in air is used instead of  $D_s$ , because  $D$  is a meteorological variable and can be easily obtained. Equation 2 is rewritten as

$$g_s = a \frac{A_n}{(C_s - \Gamma)(1 + D/D_0)} + g_0 \quad (2)$$

in which  $\Gamma$  is the CO<sub>2</sub> compensation point, and  $D_0$  is a parameter reflecting characteristics of response of stomata to atmospheric  $D$  (Pa), which determines the curvature of humidity response curve of stomatal conductance.

As stomatal conductance begins to increase immediately with increasing light, even below the light compensation point, Yu *et al.* (2001) proposed gross assimilation rate should be used instead of net assimilation and, correspondingly,  $C_s - \Gamma$  should be replaced by  $C_s$  in eqn (3):

$$g_s = a \frac{A_g}{C_s(1 + D/D_0)} \quad (4)$$

where  $A_g$  is the gross assimilation rate, and  $C_s$  is CO<sub>2</sub> concentration at leaf surface. In this expression, parameter  $g_0$  in eqn 3 is taken as 0, because  $A_g$  and  $g_s$  go to 0 in the dark.

$A_g$  is a function of environmental variables. A revision was adopted to take account of the limitation of photosynthesis by stomatal conductance:

$$A_g = \frac{A_m \alpha I \eta C_a}{A_m \alpha I + A_m \eta C_a + \alpha \eta C_a} \frac{g_s}{g_s + g_{\text{int}}} \quad (5)$$

in which  $A_m$  is the maximum catalytic capacity of Rubisco per unit leaf area,  $\alpha$  is initial photochemical efficiency, and  $\zeta$  is the initial slope of the CO<sub>2</sub> response curve [μmol m<sup>-2</sup> s<sup>-1</sup> (μmol mol<sup>-1</sup>)<sup>-1</sup>].  $g_{\text{int}}$  is a parameter. If  $g_{\text{int}} \rightarrow 0$ ,  $g_s/(g_s + g_{\text{int}}) = 1$ , and the equation shortens to the original light and CO<sub>2</sub> response curve.

$A_m$  is a function of temperature with a maximum given by (Collatz *et al.*, 1991):

$$A_m = A_0 \frac{Q_{10}^{(T_a - 25)/10}}{1 + \exp\{-a_1 + b_1(T_a + 273)\}/[R(T_a + 273)]} \quad (6)$$

in which  $a_1$ ,  $b_1$  are parameters,  $A_m = A_0$  at  $T_a = 25$  °C and  $R$  is the universal gas constant.

It is assumed that  $g_s/(g_s + g_{\text{int}})$  is determined chiefly by leaf or soil water status for a particular plant. Therefore, eqn (5) can be converted into the following:

$$A_g = \frac{A_m \alpha I \eta C_a}{A_m \alpha I + A_m \eta C_a + \alpha \eta C_a} f(\psi) \quad (7)$$

The water-stress coefficient,  $f(\psi)$ , is simply characterized by a linear relationship from the water potential at wilting point ( $\psi_0$ ) to water potential at field capacity ( $\psi_m$ ), i.e. relative extractable water (Lagergren and Lindroth, 2002). Therefore, by combining eqns (4) and (7), stomatal conductance can be expressed as a function of environmental variables in the following form:

$$g_s = a \frac{A_m \alpha I \eta}{(A_m \alpha I + A_m \eta C_a + \alpha \eta C_a)} \frac{1}{(1 + D/D_0)} \frac{\psi - \psi_0}{(\psi_m - \psi_0)} \quad (8)$$

Stomata close in the dark, i.e.  $g_s$  is zero when  $I$  is zero, which is satisfied by eqn (8). Boundary conditions of stomatal response to light,  $D$  and water potential are also satisfied by eqn (8). The unit of  $a$  is the same as that of CO<sub>2</sub> concentration.

In conclusion, the stomatal conductance model (eqn 8) is based on both the relationship between stomatal conductance and gross photosynthesis (eqn 4; Yu *et al.*, 2002) and that between photosynthesis and  $I$  (eqn 7; Thornley, 1976). The parameters  $\alpha$  and  $A_m$  are related to biochemical

processes, which are influenced by environmental factors. The model consists of two parts: (1) the relationship between stomatal conductance and photosynthesis (eqn 4), where the influences of light, temperature and  $\text{CO}_2$  concentration on photosynthesis (eqns 6 and 7), and thereby on stomatal conductance, are integrated into one expression; and (2) the effects of evaporation demand ( $D$ ) and soil water potential on stomatal conductance are included in this expression (eqn 8).

## RESULTS

### *Relationship between stomatal conductance and photosynthetic rate in the model*

Figure 1 illustrates the responses of stomatal conductance, and net and gross photosynthetic rates to changes in light intensities. It is shown that both stomatal conductance and gross photosynthetic rate start from zero, which is a boundary condition of eqn (8). But net photosynthetic rate starts from a negative value representing dark respiration ( $-R_d$ ), the value of which depends on air temperature and other variables. Therefore, the revised version of the Ball–Berry stomatal model (eqn 4), expressing the relationship between  $g_s$  and  $A_g$  instead of net assimilation, will give a stronger relationship between stomatal conductance and photosynthesis.

To fit eqns (2) and (4) with experimental data, the parameters reflecting the physiological characters in the equations,  $D_0$  and  $\Gamma$ , should be given in advance. The  $\text{CO}_2$  concentration point is assumed to be about  $50 \mu\text{mol mol}^{-1}$ , and  $D_0$  is adjusted so that the relationship between stomatal conductance and stomatal conductance index (algebraic formula on the right of equations including environmental and physiological elements) achieves the highest coefficient of correlation, which is taken as the best fit obtained.

The relationship between stomatal conductance and stomatal conductance index in eqn (2) is significant ( $r^2 = 0.83$ ,  $P < 0.01$ ,  $n = 210$ ) for the simulation of original Ball–Berry model in Fig. 2A. Equation 4 gives a much better correlation in Fig. 2B ( $r^2 = 0.91$ ,  $P < 0.01$ ,  $n = 210$ ). There is a considerable improvement in the goodness-of-fit. The reason for this is that, since stomata respond to water loss, the relationship between rate of water loss and vapour pressure deficit is closer than that between water loss and leaf surface humidity (Sheriff, 1984; Aphalo and Jarvis, 1991).

### *The dependence of photosynthetic rate on light and $\text{CO}_2$*

Light response curves of photosynthesis were fitted to data collected from leaves under changing light intensities when other factors were kept stable for each measurement. Figure 3(A and B) shows two typical light response curves of photosynthesis of wheat in which the photosynthetic rate was observed under different atmospheric conditions of temperature, humidity and  $\text{CO}_2$  partial pressure. All light curves are similar in shape, but have different parameters due to differences in temperature and humidity.

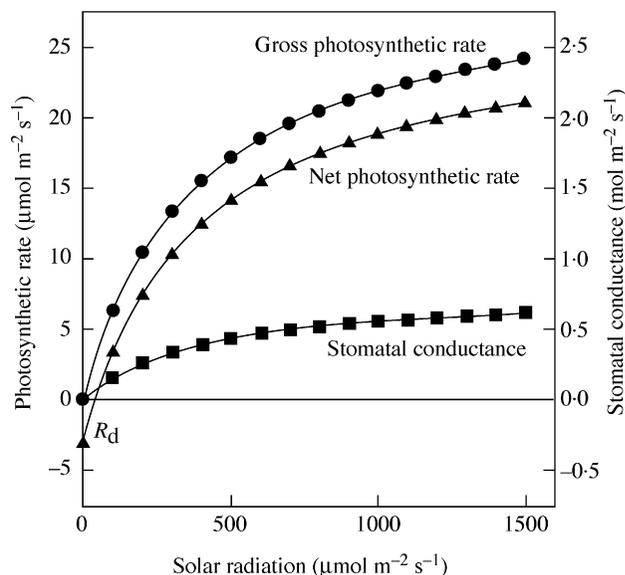


FIG. 1. Illustration of the relationship between stomatal conductance, net and gross photosynthetic rates and light intensity.

Temperature ranged from 25 to 30 °C over the period of observation, and relative humidity changed from 10 to 50 %.

Figure 3(C and D) shows the  $\text{CO}_2$  response of photosynthesis to  $\text{CO}_2$  concentration over the range 0–1400  $\mu\text{mol mol}^{-1}$ . The scatter of points is wider than that of the light response. When photosynthetic rates and light intensity in the field are fitted by a rectangular hyperbola (Fig. 3), a good relationship is obtained. The initial slope of the fitted curve ( $\alpha$ ) is about  $0.07 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$ . For common crops,  $\alpha$  is lower than its theoretical maximum (0.08), ranging from 0.04 to 0.07 under field conditions (Xu, 1984). The maximum photosynthetic rate is about  $30.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which is basically the photosynthetic rate at the saturation point of light (Fig. 3). The maximum photosynthetic rate under field conditions varied between 25.0 and  $35.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and stomatal conductance between 0.2 and  $0.4 \text{ mol m}^{-2} \text{s}^{-1}$ ; photosynthetic rate was higher and stomatal conductance lower under conditions of  $\text{CO}_2$  enrichment.

### *Model validation*

The data used in model validation are shown in the light and  $\text{CO}_2$  responses (Figs 4 and 5). The response curve of photosynthetic rate to light intensity is a typical Michaelis–Menten curve (Fig. 4). Stomatal conductance corresponds well to photosynthesis in a changing light environment.

Increased atmospheric  $\text{CO}_2$  concentration will raise the intercellular  $\text{CO}_2$ , and hence photosynthetic rate. Stomatal conductance decreases with increased  $\text{CO}_2$  concentration, whereas photosynthetic rate increases (Fig. 5).

As the experiment was conducted under ample water supply, the influence of water stress in eqn (8) is not included in the validation. The model was run with observational data of meteorological variables as inputs. After maximum carboxylation rate was obtained, the values

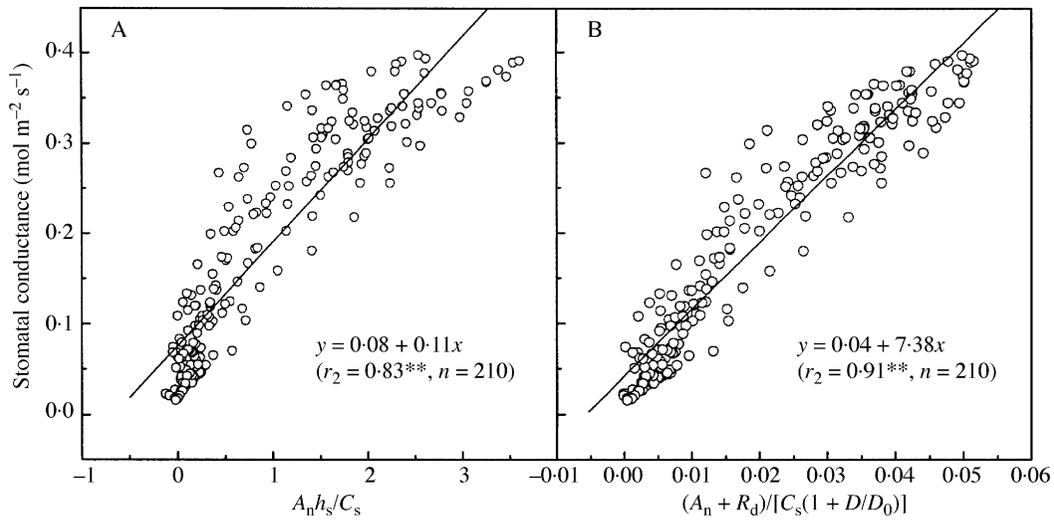


FIG. 2. Simulation of stomatal conductance using (A) the original Ball-Berry model, and (B) its revised form, eqn 4 (Yucheng, 16 and 18 April 2003; \*\* $P < 0.01$ ).

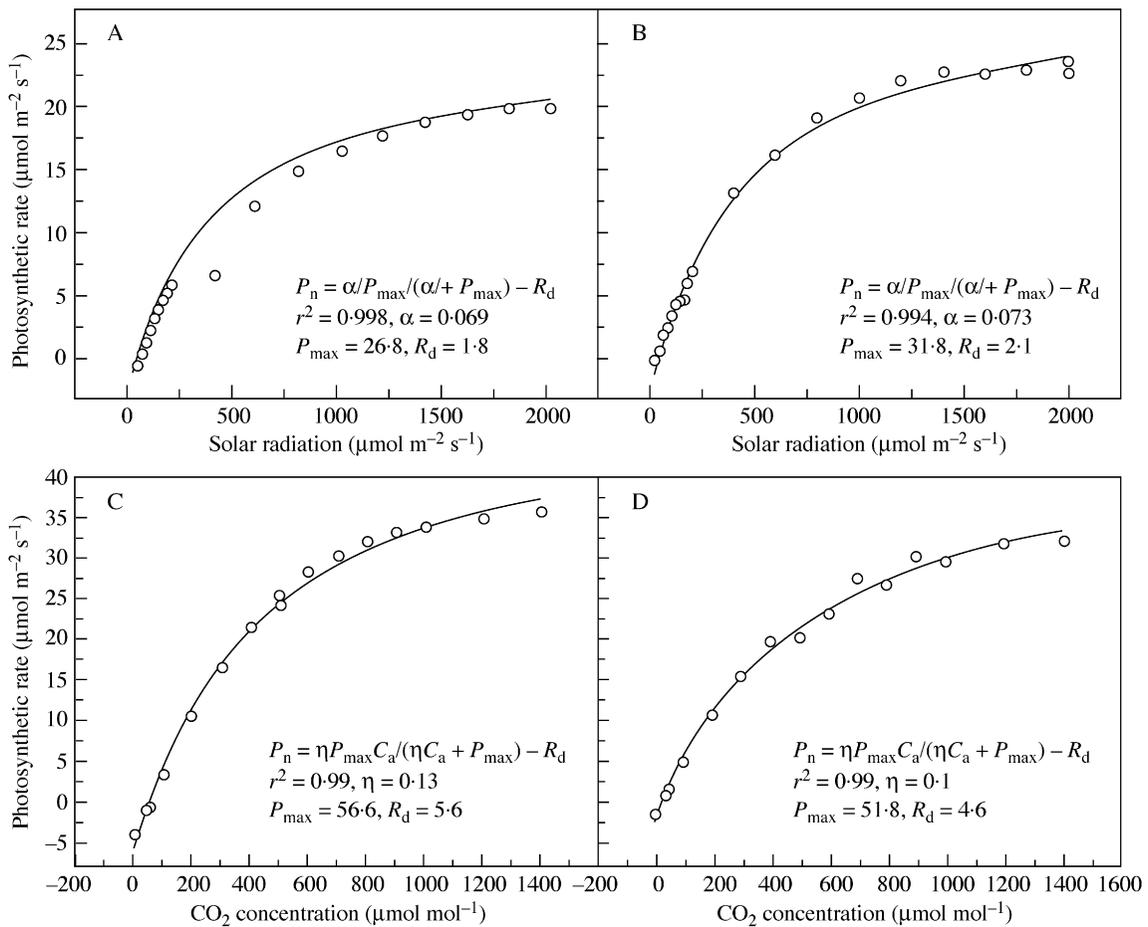


FIG. 3. Fitted responses of photosynthesis to changes in light intensities and CO<sub>2</sub> concentrations (Yucheng, 16 and 21 April and 2 and 6 May 2003). (A and B) Typical light response curves. (C and D) Typical CO<sub>2</sub> response curves over the range 0–1400 μmol mol<sup>-1</sup>.

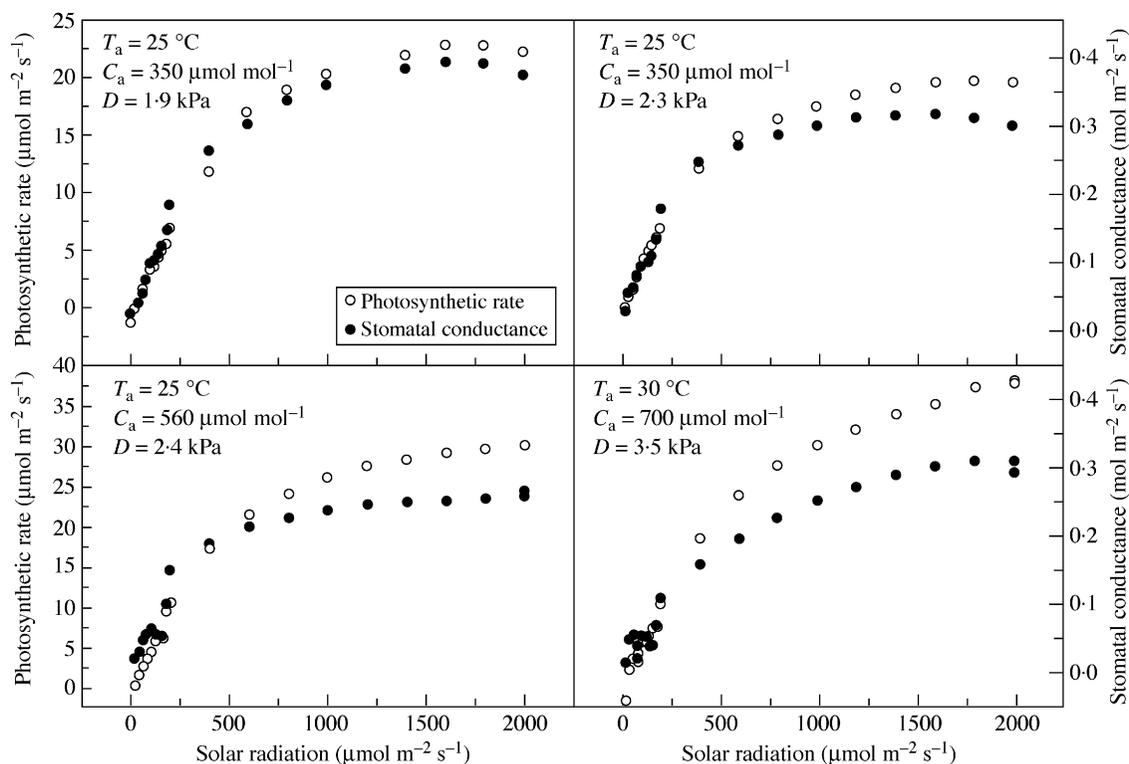


FIG. 4. Measured responses of photosynthesis and stomatal conductance to changes in light intensities (Yucheng, 16, 20 and 21 April 2003).

of other parameters were adjusted according to previous studies (Collatz *et al.*, 1991; Leuning, 1995; Yu *et al.*, 2002), so that there is a very high coefficient of correlation between stomatal conductance and the index of stomatal conductance, i.e.

$$\frac{A_m \alpha \eta}{A_m \alpha + A_m \eta C_a + \alpha \eta C_a} \frac{1}{1 + D/D_0}$$

Then, the measured stomatal conductance was compared with the index. The parameters used were as follows:  $A_m = 60.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $Q_{10} = 2.4$ ,  $a_1 = 220.0 \text{ kJ mol}^{-1}$ ,  $b_1 = 703.0 \text{ J mol}^{-1} \text{ K}^{-1}$ ,  $D_0 = 3.5 \text{ kPa}$ ,  $\alpha = 0.06$ ,  $\eta = 0.03$ . The constant  $R$  is  $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ .

Figures 6 and 7 are comparisons between measured stomatal conductance and the stomatal conductance index under changing light intensities and  $\text{CO}_2$  concentrations, respectively. Figure 6 shows that stomatal conductance agrees well with the index calculated from light, temperature,  $D$  and  $\text{CO}_2$  concentration (Fig. 6). There is a good linear relationship between stomatal conductance and the index with a slope of 1.067, and the intercept on the y-axis of simulated values is  $-0.01$ , which is very close to 0. That means that the model predicts stomatal conductance quite well. Agreement between measured stomatal conductance and predicted index under changing  $\text{CO}_2$  concentration is also good, with the intercept also near to zero. However, the spread of points is slightly greater than that of the light response (Fig. 7).

## DISCUSSION

Plant transpiration is a physical process in which part of the net radiation energy is converted into latent heat, under physiological control by changes in stomatal aperture (Jarvis and McNaughton, 1986). In the Penman–Monteith evapotranspiration model based on energy balance, canopy resistance to water vapour diffusion is the sole factor reflecting physiological regulation (Thom, 1975). Therefore, determination of resistance, the reciprocal of conductance, is a key topic in the simulation of evapotranspiration. In this study, a stomatal model is proposed as a function of solar radiation,  $\text{CO}_2$  concentration and temperature, as well as  $D$  and soil water content. The mechanism of stomatal closure remains to be explored under conditions of changing climate, which is essential for the evaluation of primary production and water consumption. If it is not necessary to calculate photosynthesis, as in some hydrological models (Hatton, 1992; Gottschalck *et al.*, 2001), the stomatal model can be directly applied to calculate evapotranspiration.

In addition to many relationships between stomatal conductance and atmospheric humidity or  $D_s$ , Monteith (1995), based on many experimental results, proposed that stomata respond to humidity in such a way that stomatal conductance decreases linearly with an increase in the rate of transpiration. This linear relationship between stomatal conductance and transpiration is identical to the non-linear relationship between conductance and  $D_s$  (Leuning, 1995). Dewar (1995) has given thorough interpretations of stomatal

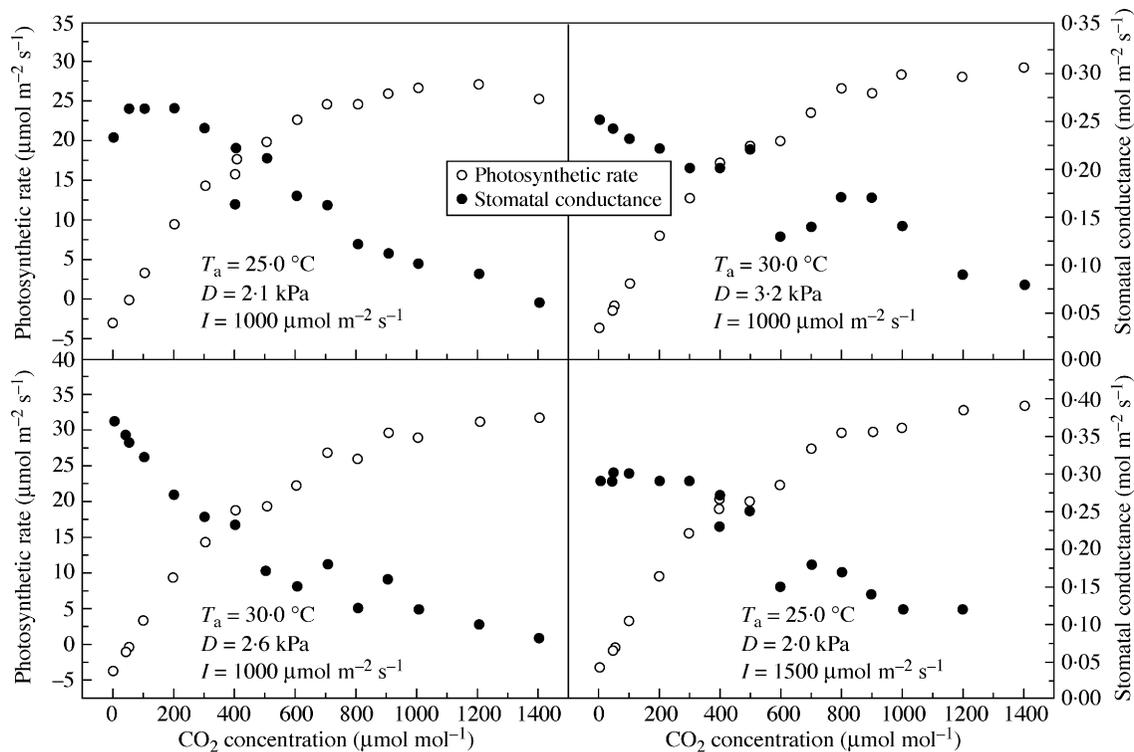


FIG. 5. Measured responses of photosynthesis and stomatal conductance to changes in  $\text{CO}_2$  concentrations (Yucheng, 24 April and 6 May 2003).

conductance in relation to environmental factors, photosynthesis and transpiration in these stomatal models.

Parameters in empirical models do not have a clear physiological significance which changes with the specific plot or variety (Calvet, 2000), and the complexity of the determination of their values increases sharply with the number of parameters included. Application of the Jarvis model (eqn 1) usually includes some of the five environmental variables, i.e. light intensity, temperature, humidity,  $\text{CO}_2$  concentration and soil water. Semi-empirical models are based on physiological characteristics of the plant, although they are not theoretical expressions. Parameters used in semi-empirical models with some physiological basis may extend the generality of the model. For example,  $P_{\max}$ ,  $\alpha$  and  $\eta$  have physiological significance, which makes their values meaningful. Some parameters in the model may include the influence of other factors. For example, maximum photosynthetic rate is a function of leaf nitrogen content. As photosynthetic parameters are applied, the relationship between stomatal conductance and photosynthetic rate is included, and plant nutrition can be included in the parameter  $P_{\max}$ .

There are many parameters in empirical stomatal models. The semi-empirical model can reduce the number of parameters by means of theoretical analysis. For example, stomatal conductance and gross photosynthetic rate increase from zero, and this boundary condition suggests a constant ratio of the two quantities and the intercept,  $g_0$ , goes to zero (eqn 4). The introduction of a light and  $\text{CO}_2$  response equation (Thornley, 1976) also reduces the number of

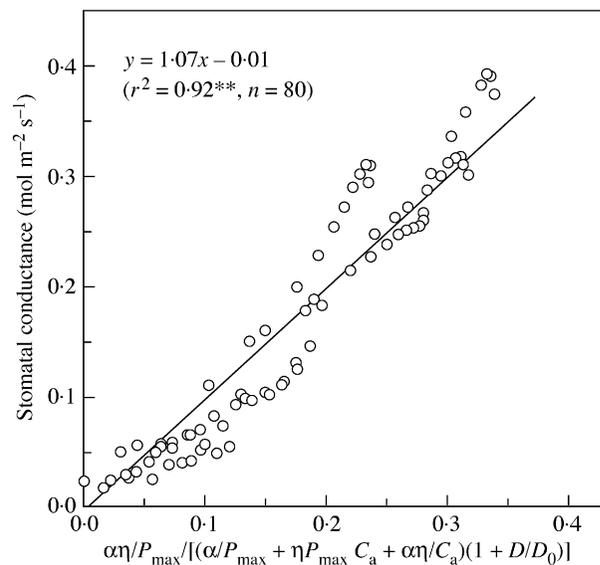


FIG. 6. Measured stomatal conductance vs. calculated stomatal conductance index under changing light intensities (data from Fig. 4).

parameters required when the effects of light and  $\text{CO}_2$  are considered separately. Cannell and Thornley (1998) proposed that temperature and  $\text{CO}_2$  were two important factors affecting  $P_n$  in the form of non-rectangular hyperbolas. In this study, the simple rectangular hyperbola was used as the light response curve.

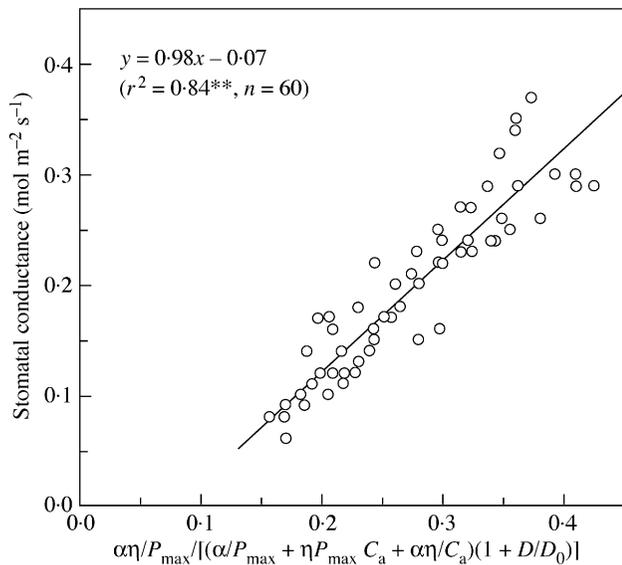


FIG. 7. Measured stomatal conductance vs. calculated stomatal conductance index under changing CO<sub>2</sub> concentrations (data from Fig. 5).

The model was validated by measurement of data under controlled conditions of light and CO<sub>2</sub> over a wide range, designed to verify its universality. The stomatal conductance model was validated by data over a wide range of temperatures, including diurnal variation, as well as light intensities and CO<sub>2</sub> concentration.

The climate in the North China Plain is characterized by high solar radiation and low humidity. The light response curve is no longer a hyperbola when the observation time is extended, as photosynthetic rate decreases with the increase in light intensity beyond a certain limit (Yu *et al.*, 2002). In this study, the data were confined to a period from early morning to 1100 h each day. There was a significant decrease in photosynthetic rate with increasing light intensity after that hour due to photoinhibition, similar to the phenomenon reviewed by Leverenz (1994).

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