

BRIEF COMMUNICATION

A coupled model of stomatal conductance and photosynthesis for winter wheat

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Abstract

The model couples stomatal conductance (g_s) and net photosynthetic rate (P_N) describing not only part of the curve up to and including saturation irradiance (I_{\max}), but also the range above the saturation irradiance. Maximum stomatal conductance ($g_{s\max}$) and I_{\max} can be calculated by the coupled model. For winter wheat (*Triticum aestivum*) the fitted results showed that maximum P_N (P_{\max}) at 600 $\mu\text{mol mol}^{-1}$ was more than at 350 $\mu\text{mol mol}^{-1}$ under the same leaf temperature, which can not be explained by the stomatal closure at high CO_2 concentration because $g_{s\max}$ at 600 $\mu\text{mol mol}^{-1}$ was less than at 350 $\mu\text{mol mol}^{-1}$. The irradiance-response curves for winter wheat had similar tendency, e.g. at 25 °C and 350 $\mu\text{mol mol}^{-1}$ both P_N and g_s almost synchronously reached the maximum values at about 1 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. At 25 °C and 600 $\mu\text{mol mol}^{-1}$ the I_{\max} corresponding to P_{\max} and $g_{s\max}$ was 2 080 and 1 575 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively.

Additional key words: BWB model; irradiance; *Triticum*.

In the simulation of stomatal conductance (g_s), an empirical model for plant leaves by Ball *et al.* (1987), hereafter referred to as the BWB model, has been adopted widely in studies of ecological and physiological modelling. It has a solid experimental basis with a linear relationship between g_s and net photosynthetic rate, P_N (e.g. Ball *et al.* 1987, Di Marco *et al.* 1990, Collatz *et al.* 1991, Sellers *et al.* 1992, Loreto *et al.* 1992, Aphalo and Jarvis 1993, Leuning 1995, Kim and Lieth 2003, Tuzet *et al.* 2003, Yu *et al.* 2004, Messinger *et al.* 2006, Miyazawa *et al.* 2006, Bernacchi *et al.* 2007, Buckley 2008, Warren 2008). The apparent simplicity of BWB model has led to its adoption by modellers working at the scale of individual leaves (e.g. Leuning 1990, Tenhunen *et al.* 1990, Collatz *et al.* 1991, Harley *et al.* 1992, Kim and Lieth 2003, Yu *et al.* 2004, Messinger *et al.* 2006), at the scale of canopies (Hatton *et al.* 1992), at the landscape scale (McMurtrie *et al.* 1992), and in some

global climate models (Sellers *et al.* 1992). However, BWB model and its subsequently revised model can not predict the irradiance (I)-response curve of g_s of plant when relative humidity (h_s) and CO_2 concentration at leaf surface (C_s) are held constant. At the same time these models can not estimate maximal values ($g_{s\max}$ and maximal irradiance, I_{\max}).

The objective of this study was to formulate and test a coupled model for calculating $g_{s\max}$ and I_{\max} for winter wheat (*Triticum aestivum* L.) under different environmental conditions and analyze the synchronous question of I -response of P_N and g_s .

Experiments were conducted in the field 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 I -response curves in flag leaves of winter wheat were measured in a leaf chamber from 16 April to 6 May 2003. Every 2 h over

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the course of a day, the curves were generated by varying I (400–700 nm) between 0 and 2 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

The infrared CO_2 analysis system *LI-COR 6400* (*LI-COR*, Lincoln, NE, USA) was calibrated 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.

Ball *et al.* (1987) presented an empirical relationship which incorporates the often-observed correlation between g_s and P_N , and includes the effects of h_s and C_s on g_s , namely

$$g_s = k (P_N h_s) C_s^{-1} + g_0 \quad (1)$$

where g_0 is the residual conductance (limiting value of g_s at compensation I , I_c), k is a constant which represents the composite sensitivity of g_s to CO_2 concentration, relative humidity, and leaf temperature. This equation predicts that g_s increases with P_N and with h_s when C_s is held constant. The g_s will decrease with rising ambient CO_2 concentration, provided that P_N increases more slowly than C_s (Leuning 1995).

Although the BWB model and its subsequently revised models can describe the relationship between g_s and P_N which summarized the results of many observations of the stomatal behaviour of well-watered plants, these models do not describe the I -response curves of g_s even if they are coupled with rectangular or non-rectangular hyperbolae (Thornley 1976), or other photosynthesis model (Prado and Moraes 1997). Additionally, $g_{s\text{max}}$ and I_{max} can not be estimated directly by these models. Providing BWB model coupled with a photosynthesis model (Ye 2007), these questions can be resolved simultaneously.

Most of the existing models and equations can not describe the process of the leaf P_N response to I when I is above I_{max} . Rectangular and non-rectangular hyperbolae (Thornley 1976) have been used widely to describe the irradiance-response curves of P_N (*e.g.* Thornley 1976, Evans *et al.* 1993; Kyei-Boahen *et al.* 2003, Yu *et al.* 2004, Messinger *et al.* 2006). However, the maximum net photosynthetic rate (P_{max}) calculated by these hyperbolae is much higher than the measured data (*e.g.* Kyei-Boahen *et al.* 2003, Yu *et al.* 2004, Messinger *et al.* 2006). Ye (2007) proposed a new photosynthesis model which can accurately describe the irradiance-response curve of photosynthesis, including irradiance below compensation (I_c) and above I_{max} (Ye 2007). Through mathematical transformation, the new photosynthesis model (Ye 2007) can be also expressed as:

$$P_N = \alpha (1 - \beta I) (1 + \gamma I)^{-1} - R_D \quad (2)$$

where I is irradiance, R_D is dark respiration, α is the initial slope of irradiance-response curve of photosynthesis when irradiance approaches zero, β and γ are coefficients which are independent of I .

Substituting for P_N into Eq. 1 yields

$$g_s = \alpha k \frac{h_s}{C_s} \left(\frac{1 - \beta I}{1 + \gamma I} I - R_D \right) + g_0 \quad (3)$$

When other factors are held constant, Eq. 3 can be rewritten as

$$g_s = \alpha_0 (1 - \beta I) (1 + \gamma I)^{-1} + g_{s0} \quad (4)$$

where $\alpha_0 = \alpha k h_s C_s^{-1}$ and $g_{s0} = g_0 - \alpha_0 R_D$

The I_{max} can be obtained by Eq. 5:

$$I_{\text{max}} = \frac{\sqrt{(\beta + \gamma)/\beta} - 1}{\gamma} \quad (5)$$

The $g_{s\text{max}}$ can be calculated by Eq. 6:

$$g_{s\text{max}} = \alpha_0 \left(\frac{\sqrt{\beta + \gamma} - \sqrt{\beta}}{\gamma} \right)^2 + g_{s0} \quad (6)$$

I -response curves of P_N were fitted to data collected from leaves under changing I when other factors were held constant for each measurement. The response of P_N to I was curvilinear and differed markedly for each leaf C_s .

An objective non-linear parameter estimation procedure was used to fit Ye model to observed values of P_{max} for winter wheat leaves. Values were calculated for I_{max} , P_{max} , R_D , and r^2 (Fig. 1A,B). Good agreement was obtained between model calculations and observations of P_N for winter wheat. In winter wheat P_N increased with I below I_{max} . Above I_{max} , P_N decreased with I (Fig. 1A). The response of P_N to I was curvilinear and differed markedly for each leaf C_s .

An objective non-linear parameter estimation procedure was used to fit Eq. 4 to observed values of g_s for winter wheat leaves. Values were calculated for I_{max} , $g_{s\text{max}}$, and r^2 . Good agreement was obtained between model calculations and observations of g_s for winter wheat. In winter wheat g_s increased with I below I_{max} , then g_s decreased with I above I_{max} (Fig. 1C).

At 25 °C, 350 and 600 $\mu\text{mol mol}^{-1}$, the fitted results and the measured data simultaneously showed that both the g_s and P_N versus I were similar (Fig. 1). They had the same response tendency for I of 0–2 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Moreover, at 25 °C and 350 $\mu\text{mol mol}^{-1}$ both g_s and P_N almost synchronously reached the maximum value as I_{max} was at about 1 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1A,C). At 25 °C and 600 $\mu\text{mol mol}^{-1}$, the I_{max} corresponding to P_{max} and $g_{s\text{max}}$ were 2 080 and 1 575 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Both g_s and P_N did not synchronize completely (Fig. 1B,D).

The $g_{s\text{max}}$ and I_{max} can not be estimated by BWB model and its revised models that can not describe the I -response curves of g_s for winter wheat because g_s in these models do not involve I . Even if these models are coupled with non-rectangular or rectangular hyperbola (Thornley 1976), these questions could not be resolved

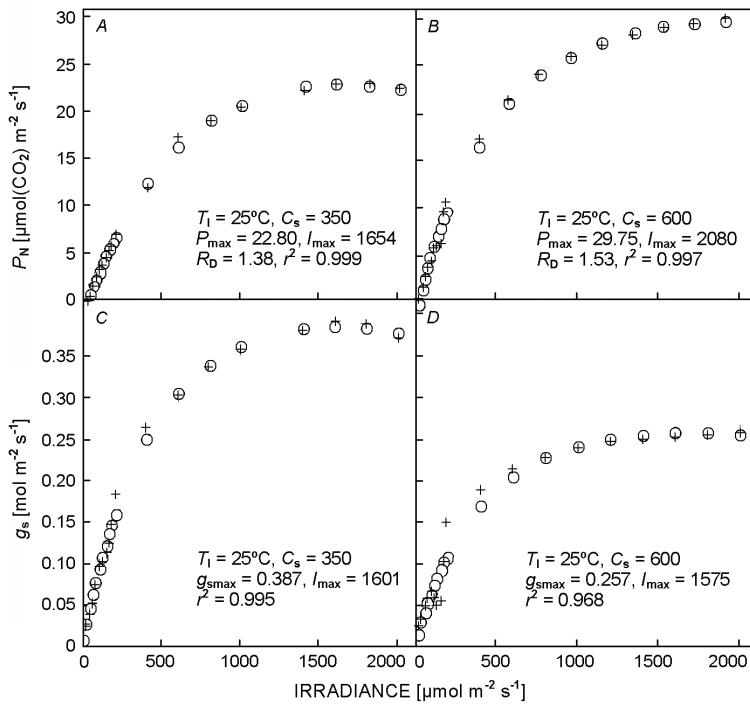


Fig. 1. Irradiance-response curves of (A, B) net photosynthetic rate (P_N) and (C, D) stomatal conductance (g_s) of winter wheat at 25 °C, 350 and 600 $\mu\text{mol mol}^{-1}$. + represents measured points, o fitted points. T_l – leaf temperature; C_s – CO_2 concentration at the leaf surface; $g_{s\text{max}}$ – maximum g_s ; P_{max} – maximum net photosynthetic rate; I_{max} – saturation irradiance; I_c – compensation irradiance; R_D – dark respiration rate.

still because the two hyperbolas are asymptotes without extreme values. A model that couples BWB model or its subsequently improved models with a new model of I -response curve of photosynthesis (Ye 2007) can describe well the relationship between g_s and I . The coupled model describes not only part of the curve up to and including I_{max} , but the range above it. The $g_{s\text{max}}$ and I_{max}

can be calculated directly by the coupled model. P_{max} at 25 °C and 600 $\mu\text{mol mol}^{-1}$ was higher than at 25 °C and 350 $\mu\text{mol mol}^{-1}$, which can not be explained reasonably by g_s limitation at high CO_2 concentration because $g_{s\text{max}}$ at 600 $\mu\text{mol mol}^{-1}$ was more than 350 $\mu\text{mol mol}^{-1}$. Maybe there is other mechanism that affects photosynthetic process of winter wheat because g_s decreases with C_s .

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