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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_{smax}) 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 μmol mol^{-1} was more than at 350 μmol mol^{-1} under the same leaf temperature, which can not be explained by the stomatal closure at high CO_2 concentration because g_{smax} at 600 μmol mol^{-1} was less than at 350 μmol mol^{-1}. The irradiance-response curves for winter wheat had similar tendency, *e.g.* at 25 °C and 350 μmol mol^{-1} both P_N and g_s almost synchronously reached the maximum values at about 1 600 μmol m^{-2} s^{-1}. At 25 °C and 600 μmol mol^{-1} the I_{max} corresponding to P_{max} and g_{smax} was 2 080 and 1 575 μmol m^{-2} 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_{smax} and maximal irradiance, I_{max}).

The objective of this study was to formulate and test a coupled model for calculating g_{smax} 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 µmol m^{-2} 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

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

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_{smax} 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 hyperbolas 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:

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

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

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

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

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

where $\alpha_0 = \alpha\, k\, h_s\, C_s^{-1}$ and $g_{s0} = g_0 - \alpha_0\, R_D$ (4)

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

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

The g_{smax} can be calculated by Eq.6:

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

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. 1*A,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. 1*A*). 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_{smax}, 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. 1*C*).

At 25 °C, 350 and 600 µmol 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 µmol m^{-2} s^{-1}. Moreover, at 25 °C and 350 µmol mol^{-1} both g_s and P_N almost synchronously reached the maximum value as I_{max} was at about 1 600 µmol m^{-2} s^{-1} (Fig. 1*A,C*). At 25 °C and 600 µmol mol^{-1}, the I_{max} corresponding to P_{max} and g_{smax} were 2 080 and 1 575 µmol m^{-2} s^{-1}, respectively. Both g_s and P_N did not synchronize completely (Fig. 1*B,D*).

The g_{smax} 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

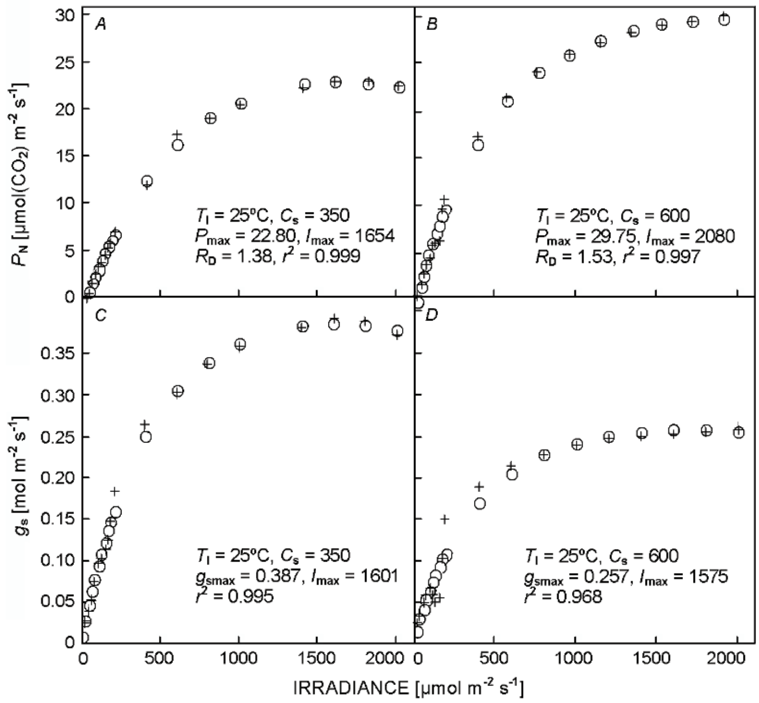

Fig. 1. Irradiance-response curves of (*A, B*) net photosynthetic rate (P_N) and (*C, D*) stomatal conductance (g_s) of winter wheat at 25 °C, 350 and 600 µmol mol^{-1}. + represents measured points, ○ fitted points. T_l − leaf temperature; C_s − CO_2 concentration at the leaf surface; g_{smax} – maximum 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_{smax} and I_{max} can be calculated directly by the coupled model. P_{max} at 25 °C and 600 µmol mol^{-1} was higher than at 25 °C and 350 µmol mol^{-1}, which can not be explained reasonably by g_s limitation at high CO_2 concentration because g_{smax} at 600 µmol mol^{-1} was more than 350 µmol 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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