PHOTOSYNTHETICA 46 (4): 637-640, 2008

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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Received 14 December 2007, *accepted* 4 August 2008.

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Acknowledgements: We thank Prof. Govindjee for his great help and encouragement. We also thank Prof. John Evans and Dr. Xinguang Zhu for their valuable suggestions and help during the preparation of this paper. The authors are also grateful to anonymous referees for comments and helpful suggestions. The authors would like to thank editors for editing the paper and correcting the language. This work is supported by the Science and Technology Department of Jiangxi Province, and the National High Technology Research and Development Program of China (grant No. O6F60080AH).

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

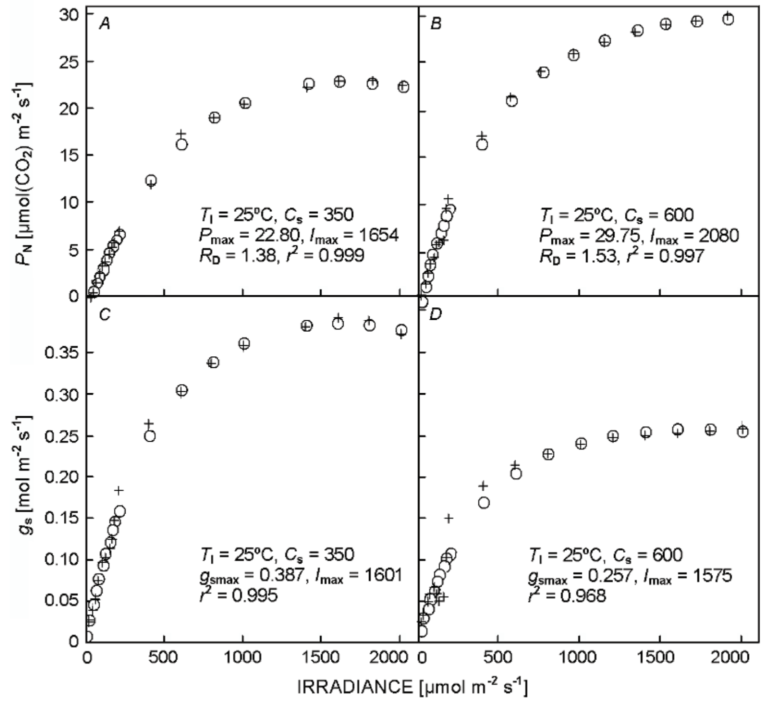

Fig. 1. Irradiance-response curves of (*A, B*) net photosynthetic rate (P_N) and (*C, D*) stomatal conductance (g_s) of winter wheat at 25 °C, 350 and 600 μmol mol^{-1}. + represents measured points, ○ fitted points. T_l − leaf temperature; C_s − CO$_2$ concentration at the leaf surface; g_{smax} – maximum 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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