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BRIEF COMMUNICATION

A new model for relationship between irradiance and the rate of photosynthesis in *Oryza sativa*

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Abstract

The calculated maximum net photosynthetic rate (P_N) at saturation irradiance (I_m) of 1 314.13 μmol m^{-2} s^{-1} was 25.49 μmol(CO_2) m^{-2} s^{-1}, and intrinsic quantum yield at zero irradiance was 0.103. The results fitted by nonrectangular hyperbolic model, rectangular hyperbolic method, binomial regression method, and the new model were compared. The maximum P_N values calculated by nonrectangular hyperbolic model and rectangular hyperbolic model were higher than the measured values, and the I_m calculated by nonrectangular hyperbolic model and rectangular hyperbolic model were less than measured values. Results fitted by new model showed that the response curve of P_N to I was nonlinear at low I for *Oryza sativa*, P_N increased nonlinearly with I below saturation value. Above this value, P_N decreased nonlinearly with I.

Additional keywords: apparent quantum yield; compensation irradiance; intrinsic quantum yield; saturation irradiance.

The irradiance (I) response curves of photosynthesis of different plant species have often been reported (Terashima and Saeki 1983, Vogelmann 1989, Ögren 1993, Kyei-boahen *et al.* 2003, Marschall and Proctor 2004, Liu *et al.* 2005, Chen and Xu 2006, Fu *et al.* 2006, Gao *et al.* 2006, Zhou *et al.* 2006). Accurate assessment of photosynthetic rate is of fundamental importance for understanding the photochemical yield of the process, and it is also fundamental to understanding the relationship between I and the net rate of photosynthesis (P_N) driven by photon energy. So many plant physiologists describe accurately the I-response curve of P_N as exponential (Steele 1962, Webb *et al.* 1974) or tangent (Jassby and Platt 1976) functions, or nonrectangular hyperbola (Prioul and Chartier 1977, Leverenz and Jarvis 1979, Farquhar *et al.* 1980, Marshall and Biscoe 1980, Ögren 1993, Marschall and Proctor 2004, Gao *et al.* 2006) or rectangular hyperbola (Baly 1935, Thornley 1998, Kyei-boahen *et al.* 2003, Liu *et al.* 2005) models, or binomial regression (Liu *et al.* 2005, Fu *et al.* 2006). The most extensively applied model is the nonrectangular hyperbola model and binomial regression method. Except for the binomial regression method, these models do not deal with photoinhibition of plants.

I made up a new model for the relationship between I and P_N. Then I modelled the I-response of leaf P_N of rice (*Oryza sativa* L. cv. Youming 86) and compared the fitted results using the nonrectangular hyperbolic model, rectangular hyperbolic model, binomial regression method, and the new model.

When environmental conditions (CO_2 concentration, temperature, humidity, and oxygen concentration) are given, the general form of leaf P_N response curve to I can be expressed as:

$$P(I) = \alpha \frac{1-\beta I}{1+\gamma I}(I - I_c) \quad (1)$$

where $P(I)$ is P_N, I_c is the compensation irradiance, and α, β, and γ are coefficients which are independent of I.

For $I = 0$, the rate of dark respiration (R_D) is:

$$R_D = -P(I = 0) = -\alpha I_c \quad (2)$$

R_D is only dependent on coefficient α and I_c.

The quantum yield of arbitrary I, $P'(I)$ is given by:

$$P'(I) = \alpha \frac{1 - 2\beta I - \beta\gamma I^2 + (\gamma+\beta) I_c}{(1+\gamma I)^2} \quad (3)$$

For $I = 0$, the quantum yield at this point which is defined as φ_0 (intrinsic quantum yield) is:

$$\varphi_0 = P'(I = 0) = \alpha[1 + (\gamma + \beta) I_c] \quad (4)$$

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For $I = I_c$, the quantum yield at this point which is defined as φ_c is obtained by:

$$\varphi_c = P'(I_c) = \alpha \frac{1 + (\gamma - \beta) I_c - \beta\gamma I_c^2}{(1 + \gamma I_c)^2} \quad (5)$$

If the Kok effect (Kok 1948) was ignored, $P'(I_c)$ would be the apparent quantum yield.

The absolute value of slope between $I = 0$ and $I = I_c$, which is defined as φ_{c0} is given by:

$$\varphi_{c0} = | P(I = 0) / I_c | = \alpha \quad (6)$$

The saturation irradiance I_m is obtained by:

$$I_m = \frac{\sqrt{(\beta + \gamma)(1 + \gamma I_c)/\beta} - 1}{\gamma} \quad (7)$$

The maximum photosynthetic rate $P(I_m)$ is given by:

$$P(I_m) = \alpha \frac{1 - \beta I_m}{1 + \gamma I_m} (I_m - I_c) \quad (8)$$

Hence $P(I_m)$ is only dependent on coefficients α, β, and γ and on I_c.

Seeds of rice were sown on 1 May, 2004. Seedlings with 3 leaves were transplanted in 26.5 cm diameter plastic pots containing 16 kg rice soil and 5 g compound fertilizer which was taken as basic fertilizer (N 16 %, P 16 %, K 15 %) in a controlled environment. Water and nutrients were managed normally during the whole growth period. Leaf gas exchange was determined at 15 levels of photosynthetically active radiation, PAR (0, 25, 50, 100, 150, 200, 300, 400, 600, 800, 1 000, 1 200, 1 400, 1 600, 2 000 μmol m^{-2} s^{-1}) at 400±1 μmol(CO_2) m^{-2} s^{-1}, leaf temperature of 30±0.5 °C, and relative humidity of 75±1 %. Irradiance was increased gradually to increase the incident PAR to 2 000 μmol m^{-2} s^{-1}. Five minutes was allowed for reaching steady-state at each PAR prior to measurements. Three measurements were recorded automatically at 2-min intervals for each PAR per leaf. Relation of P_N to I was measured by a portable photosynthetic gas analysis system with a LED radiation source (*LI-COR 6400*, *LI-COR*, Lincoln, NE, USA).

In rice the P_N increased with I below the I_m (Fig. 1*A*). Above I_m, the P_N decreased as I increased, which means photoinhibition phenomenon. The intrinsic quantum yield of *O. sativa* was 0.103. Its apparent quantum yield would be 0.078, if the Kok effect were ignored. But practically, the Kok effect was not ignored because of $\varphi_0 > \varphi_{c0} > \varphi_c$. The respective values were: I_m 1 314.13 μmol m^{-2} s^{-1}, $P_N(I)$ 25.95 μmol(CO_2) m^{-2} s^{-1}, R_D –7.44 μmol(CO_2) m^{-2} s^{-1}, φ_0 0.103, φ_{c0} 0.090, φ_c 0.078.

The quantum yield decreased as I increased (Fig. 1*B*). It was equal to zero while the irradiance was saturating.

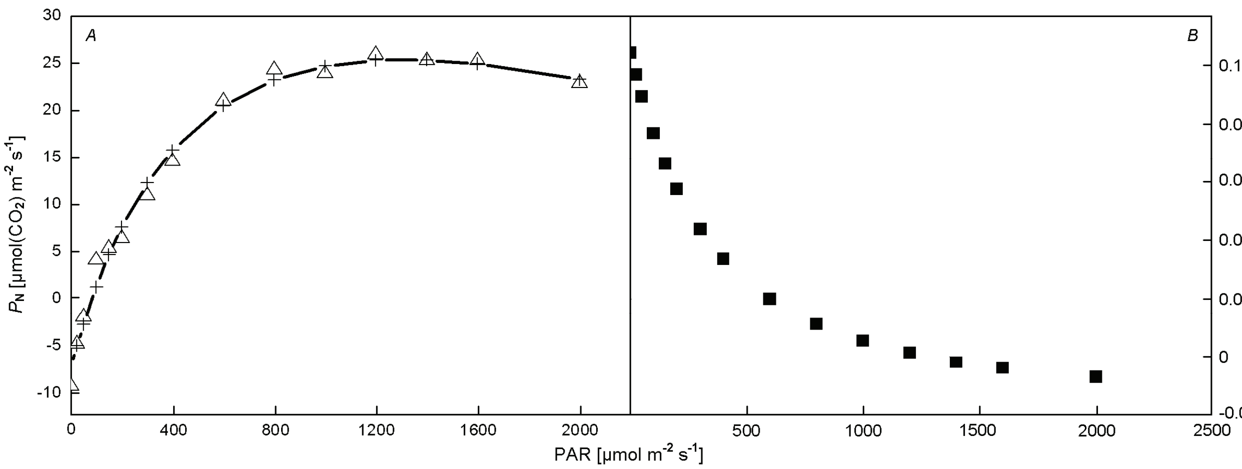

Fig. 1. Irradiance (PAR) responses of net photosynthetic rate, P_N (*A*) and quantum yield (*B*) of *Oryza sativa*. In *A*, Δ represent measured points, + fitted points.

Then the quantum yield was negative as I increased above the saturation value. Hence P_N decreased as I increased.

The fitted results show that the response of leaf P_N to any I can be dealt with by the new model, even at low irradiance and at photoinhibition (Fig. 1*A*). It is useful to study photoinhibition and photosynthetic behaviour at low I. No hypotheses were given, the saturation irradiance, maximum P_N, R_D, intrinsic quantum yield, I_c, φ_c, and φ_{c0} were calculated directly by the new model using measured values for *O. sativa*. Table 1 shows that the maximum P_N calculated by nonrectangular hyperbolic model and rectangular hyperbolic model was much higher than the measured data, and the I_m calculated by nonrectangular hyperbolic model and rectangular hyperbolic model were far less than the measured data. R_D calculated by binomial regression was less than the measured data, and I_c was higher than the measured data.

The maximum P_N calculated by the new model at I_m of 1 314.13 μmol m^{-2} s^{-1} was 25.49 μmol(CO_2) m^{-2} s^{-1} for rice. I_c of rice was 83.11 μmol(CO_2) m^{-2} s^{-1}, and the calculated intrinsic quantum yield φ_0 at zero I was 0.103.

Table 1. Results fitted by four models of irradiance-response curve of photosynthesis and measured data. Units: R_D and I_m [μmol m^{-2} s^{-1}], $P(I_m)$ [μmol(CO_2) m^{-2} s^{-1}].

Photosynthesis parameters	Nonrectangular hyperbolic model	Rectangular hyperbolic model	Binomial regression	New model	Measured data
Maximum net photosynthetic rate, $P(I_m)$	35.05	40.06	24.78	25.49	≈26.00
Apparent quantum yield (AQY)	0.090	0.155	—	—	—
Quantum yield at I_c (φ_c)	0.068	0.094	0.043	0.078	
Compensation irradiance (I_c)	89.03	72.86	108.64	83.11	≈85.00
Saturation irradiance (I_m)	543.18	743.32	1198.00	1314.13	≈1 300.00
Rate of dark respiration (R_D)	–7.14	–8.81	–3.54	–7.44	–9.00
Convexity (θ)	0.728	—	—	—	—
Intrinsic quantum yield (φ_0)	0.090	0.155	0.047	0.103	—
Absolute values of slope between $I = 0$ and $I = I_c$ (φ_{c0})	0.090	0.155	0.033	0.090	—

The fitted results were close to the measured values (Table 1). Because of $\varphi_0 > \varphi_{c0} > \varphi_c$, the relationship between I and P_N was nonlinear in the vicinity of I_c for rice, and the new model can describe the I-response curve of leaf P_N of rice at low I. But nonrectangular hyperbolic model and rectangular hyperbolic model can not describe the I-response curve of leaf P_N of rice below the I_c because of $\varphi_0 = \varphi_{c0} =$ apparent quantum yield. It means that the relationship between I and P_N of rice is linear when I is below the I_c.

The presented fitted results indicate that from zero I up to the photoinhibition, the I-response curve of leaf P_N for rice is best described by the new model. For most purposes, the new model suffers from disadvantage, compared to the others, of difficulty in either mathematical analysis or numerical computation.

In conclusion, the fitted results of *O. sativa* showed that the new model of leaf P_N response to I can be used especially at photoinhibition or low PAR.

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