BRIEF COMMUNICATION

A mathematical model for describing light-response curves in *Nicotiana tabacum* L.

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Abstract

A modified exponential model was used to describe light-response curves of *Nicotiana tabacum* L. The accuracies of an exponential model, a nonrectangular hyperbola model, a rectangular hyperbola model, a modified rectangular hyperbola model and the modified exponential model were evaluated by Mean square error (MSE) and Mean absolute error (MAE). The tests MSE and MAE of the modified exponential model were the lowest among the five models. The light saturation point (LSP) obtained by the exponential model, the nonrectangular hyperbola model and the rectangular hyperbola model were much lower than the measured values, and the maximum net photosynthetic rates (P_{max}) calculated from these models, were greater than the measured values. P_{max} at LSP of 1,077 μmol m^{-2} s^{-1} calculated by the modified exponential model was 12.34 μmol(CO_2) m^{-2} s^{-1}, which was more accurate than the values obtained from the modified rectangular hyperbola model. The results show that the modified exponential model is superior to other models for describing light-response curves.

Additional key words: light-response curves; light saturation point; maximum net photosynthetic rate; modified exponential model; net photosynthetic rate; *Nicotiana tabacum* L.

In order to investigate the response of net photosynthetic rate (P_N) to light intensity, some mathematical models for describing light-response curves have been reported, such as the exponential model (Bassman and Zwier 1991), the tangent functions (Silva *et al.* 1998), the nonrectangular hyperbola model (Dias-Filho 2002) and the rectangular hyperbola model (Kubiske and Pregitzer 1996), and the extensively applied models are an exponential model, a nonrectangular hyperbola model and a rectangular hyperbola model. These models can conveniently estimate some parameters representing the photosynthetic characteristics of plants, for instance the maximum net photosynthetic rate ($P_{max,}$), the light saturation point (LSP) and the apparent quantum yield (AQY). However, their disadvantages are that the models do not actually produce LSP and P_{max} because the modelled photosynthesis strictly increases for light intensity above zero (Ye and Wang 2009). Thus LSP can not be calculated by these models directly (Steel 1962, Marshall and Biscoe 1980, Ye and Yu 2008) but linear combinations of the model values at low light intensity (Walker 1989, Qian *et al.* 2009), and the modelled LSP are much lower than the measured values (Ye 2007). Meanwhile P_{max} of these models are greater than the measured values (Steel 1962, Ye 2007, Ye and Wang 2009), for each of the light-response curves described by these models has an asymptote representing P_{max} at high light intensity (Moreno-Sotomayor *et al.* 2002, Peek *et al.* 2002, Kyei-Boahen *et al.* 2003). Therefore these models are not suitable for light saturation and photoinhibition of plants. In 2007, the modified rectangular hyperbola model was established to settle this problem successfully (Ye 2007). The modified rectangular hyperbola model includes the rectangular hyperbola model as a special case

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Abbreviations: AQY – apparent quantum yield; g_s – stomatal conductance; LCP – light compensation point; LSP – light saturation point; MAE – mean absolute error; MSE – mean square error; P_{max} – maximum net photosynthetic rate; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; R^2 – coefficients of determination; R_D – rate of dark respiration; θ – curvature of light-response curve.
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(Ye and Wang 2009). All the models described above are just used to fit the measured values, but not for testing yet. Fitting the data better does not mean predicting well in statistics, as overfitted models generally have poor predictive performance. Therefore the accuracy of a model needs to be confirmed by test.

In this study, a modified exponential model derived from a two-compartment model (Caumo *et al.* 1999) is established to describe light-response curves. In the model we assume that if environmental conditions (CO_2 concentration, temperature and relative humidity) are given, then P_N can be described by the modified exponential model as

$$P_N = \alpha\, e^{(-\beta PAR)} - \gamma\, e^{(-\xi PAR)} \quad (1)$$

where PAR is photosynthetically active radiation, and α, β, γ and ξ are coefficients. For β = 0, the exponential model is a special case of the modified exponential model. If PAR = 0, the rate of dark respiration (R_D) is

$$R_D = \alpha - \gamma \quad (2)$$

If P_N = 0, the light compensation point (LCP) is obtained as

$$LCP = \frac{\ln(\alpha) - \ln(\gamma)}{\beta - \zeta} \quad (3)$$

For any PAR ∈ [0, infinity], the derivative of Eq. 1 is

$$P_N{}' = -\alpha\beta\, e^{(-\beta PAR)} + \gamma\xi\, e^{(-\xi PAR)} \quad (4)$$

If PAR = 0, the slope of the light-response curve at this point which is defined as AQY (Landhäusser and Lieffers 2001) is

$$AQY = P_N{}'\,(PAR = 0) = -\alpha\beta + \gamma\xi \quad (5)$$

If αβ > 0, γξ > 0 and β − ξ ≠ 0, the light saturation point (LSP) is given by

$$LSP = \frac{\ln(\alpha\beta) - \ln(\gamma\zeta)}{\beta - \zeta} \quad (6)$$

The maximum net photosynthetic rate (P_{max}) is calculated by

$$P_{max} = P_N\,(LSP) = \alpha\, e^{(-\beta LSP)} - \gamma\, e^{(-\xi LSP)} \quad (7)$$

In order to test the accuracy of the models described above, tobacco (*Nicotiana tabacum* L.) seeds were germinated in pots containing 2.0 kg of sand soil and 0.05 kg of powder of rapeseed after extracting rapeseed oil in a greenhouse at China West Normal University (30°49'N, 106°3'E) on November 5th, 2008. The seedlings were maintained at 24.7 ± 0.4°C, relative humidity of 55 ± 2%, and PAR of 800 ± 20 µmol m^{-2} s^{-1} by incandescent lamp (from 7:00 to 19:00 h). Water and fertilizer of these seedlings were controlled in the same conditions. Seedlings with seven leaves were transplanted in pots (0.36 m in diameter) filled with 18 kg of sand soil and fertilizer mixture including 0.2 kg of powder of rapeseed and 0.005 kg of carbamide on April 3rd, 2009. Then they were exposed to natural conditions, with daily mean temperature of 22°C and average diurnal PAR approx. 1,300 µmol m^{-2} s^{-1}.

When the plants with twelve leaves were about 0.50 m high and still at the vegetative stage, P_N of the tenth leaf was measured by a portable photosynthetic gas analysis system with a LED radiation source (*LI-6400*, *LI-COR Inc*., Lincoln, NE, USA). The leaf was illuminated at the PAR of 600 µmol m^{-2} s^{-1} for a steady-state condition about 10 min prior to measurement. P_N was determined at thirteen levels of PAR (0, 20, 50, 80, 100, 200, 400, 600, 800, 1,000; 1,200; 1,500; and 1,800 µmol m^{-2} s^{-1}) at 382 ± 2 µmol(CO_2) m^{-2} s^{-1}, relative humidity of 61 ± 3% and temperature of 25.3 ± 0.6°C in the chamber. The stomatal conductance (g_s) of leaves was 0.13 ± 0.03. PAR was decreased gradually from 1,800 to 0 µmol m^{-2} s^{-1}. Three measurements were recorded automatically at 180-s intervals for each PAR per leaf, and three tobacco plants were measured during the first week of May 2009.

The measured data were divided into two groups. One group included ten levels of PAR below 1,200 µmol m^{-2} s^{-1}, and the other group contained the remaining data. The first group of data was used to fit with the exponential model, the nonrectangular hyperbola model, the rectangular hyperbola model, the modified rectangular hyperbola model and the modified exponential one. The P_N values obtained from the best fit of each model were called fitted values. Parameter estimation was completed using the nonlinear regression module of *SPSS V15.0* (*SPSS Inc*., Chicago. IL, USA), and the equations of the five models could be obtained from the results. Coefficients of determination (R^2) were taken as measures for the quality of the fit. Then the other group of data was used to test the precision of the models. At PAR values of 1,200; 1,500; and 1,800 µmol m^{-2} s^{-1}, P_N could be obtained from the model equations by *Microsoft Excel 2003*. The calculated P_N values were called predicted values. The following errors were defined to evaluate the precision of the fitted and test results computed by these models.

1. Mean square error (MSE) was the average of squared forecast errors.

$$MSE = \frac{1}{n}\sum_{t=1}^{n}(y_t - \hat{y}_t)^2 \quad (8)$$

2. Mean absolute error (MAE) was the sum of the absolute values of the errors divided by the number of errors.

$$MAE = \frac{1}{n}\sum_{t=1}^{n}\left|y_t - \hat{y}_t\right| \quad (9)$$

y_t and $\hat{y}_t$ in the equations above represented the measured value and the fitted or predicted value,

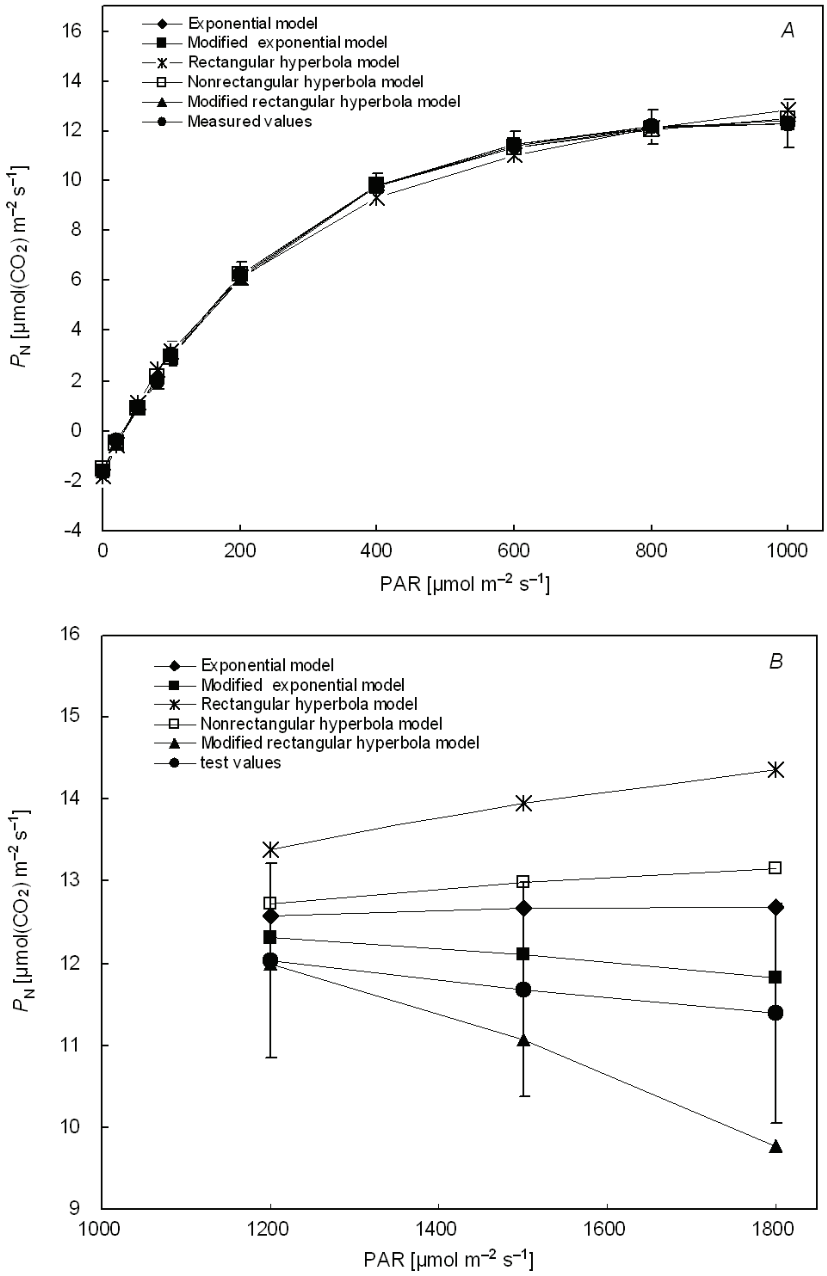

Fig. 1. Comparison of the measured values and fitted values (*A*), the predicted values and measured values (*B*). Error bars, meaning ± 1 SE, represent variability of measurements on individual leaves (9 measurements per leaf for tobacco). PAR – photosynthetically active radiation, P_N – photosynthetic rate.

respectively (Zhang and Fang 2006). Then the measured, fitted, and predicted values of the models were plotted in order to show errors between the measured values and calculated values. Moreover some parameters, such as LSP, P_{max} and R_D, were compared with the measured values.

R^2 values of the five models were greater than 0.9964, and their fitted MSE and MAE were less than test, implying their good fit to the measured values (Table 1), and the fitted values of all tested models were very close to the measured values actually (Fig. 1*A*). However the predicted P_N values (Fig. 1*B*) estimated by the non-rectangular hyperbola model, the rectangular hyperbola model and the exponential model were higher than the measured values and increased continuously with PAR, indicating that their LSP could not be obtained directly by the fitted equations of these models and P_{max} would exceed the measured values. The predicted values calculated by modified rectangular hyperbola model and the modified exponential model decreased after the extreme value, suggesting that LSP and P_{max} could be obtained from the fitted equations.

Table 1. Comparison of the accuracy and photosynthetic parameters of five models. AQY – apparent quantum yield; LCP – light compensation point; LSP – light saturation point; MAE – mean absolute error; MSE – mean square error; P_{max} – maximum net photosynthetic rate; R_D – rate of dark respiration; R^2 – coefficients of determination; θ – curvature of light-response curve.

Parameters	Measured values	Modified exponential model	Modified rectangular hyperbola model	Nonrectangular hyperbola model	Rectangular hyperbola model	Exponential model
R^2	-	0.9997	0.9996	0.9995	0.9964	0.9996
Fitted MSE	-	0.009	0.0106	0.0134	0.0963	0.0116
Fitted MAE	-	0.0735	0.0714	0.1079	0.2665	0.0806
Test MSE	-	0.1496	1.0057	1.7741	5.2607	0.9828
Test MAE	-	0.3796	0.7611	1.2568	2.1952	0.9413
LCP [μmol m^{-2} s^{-1}]	20~35	30.56	30.29	31.29	29.46	30.64
LSP [μmol m^{-2} s^{-1}]	≈1000	1077	942	430	512	401
P_{max} [μmol(CO_2) m^{-2} s^{-1}]	≈12.30	12.34	12.30	15.46	18.61	14.33
R_D [μmol(CO_2) m^{-2} s^{-1}]	1.62	1.58	1.62	1.51	1.86	1.63
AQY	-	0.055	0.057	0.05	0.07	0.056
θ	-	-	-	0.05	-	-

Photosynthetic parameters computed by these models were contrasted with the measured values (Table 1). In this experiment, LCP, R_D, and AQY obtained by these models showed little difference comparing with the measured values. The LSP of the exponential model, the nonrectangular hyperbola model and the rectangular hyperbola model were far below the measured values, and their P_{max} were higher in contrast with the measured values. P_{max} and LSP of the modified exponential model and the modified rectangular hyperbola model were close to the measured values. The P_N given by the modified rectangular hyperbola model was 12.28 μmol(CO_2) m^{-2} s^{-1} at 1,000 μmol m^{-2} s^{-1} below the measured value 12.30 μmol(CO_2) m^{-2} s^{-1}, illustrating that the P_N of this model decreased gradually beyond 942 μmol m^{-2} s^{-1}. The errors between the predicted and measured values of the modified rectangular hyperbola model were obvious, especially at PAR above 1,200 μmol m^{-2} s^{-1}, but the predicted values of the modified exponential model were much close to the measured values (Fig. 1*B*). Moreover the test MSE and MAE of the modified exponential model were smaller than the MSE and MAE of the modified rectangular hyperbola model. Thus LSP and P_{max} calculated by the modified exponential model were more accurate than those calculated by the modified rectangular hyperbola model.

In conclusion, the photosynthetic parameters of tobacco obtained by the modified exponential model are: P_{max} 12.34 μmol(CO_2) m^{-2} s^{-1}, LSP 1,077 μmol m^{-2} s^{-1}, LCP 30.56 μmol m^{-2} s^{-1}, R_D 1.62 μmol(CO_2) m^{-2} s^{-1}, and AQY 0.055, respectively. The light-response curve of tobacco was best described by the modified exponential model, especially when light intensity is beyond light saturation point. This model may be widely applicable to light-response curves of other plant species.

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