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# Leaf photosynthetic light response of summer maize: comparison of models and analysis of parameters

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## Abstract

An experiment was performed in order to study the applicability of light-response models for summer maize (*Zea mays* L.) by using rectangular hyperbola model, nonrectangular hyperbola model, exponential model, binomial regression model, and modified rectangular hyperbola model (Ye model), respectively. Our results showed that the fitted effect of Ye model was best and photosynthetic parameters were closest to the observation. The photoinhibition coefficient was significantly negatively correlated with the light-saturation point ($I_s$), the light-saturation coefficient (γ), and maximum net photosynthetic rate at light-saturation point ($P_{Nmax}$), respectively. $P_{Nmax}$ and $I_s$, apparent quantum yield, and γ performed significantly positive relationship, respectively. When the soil volumetric water content varied from 13 to 21%, $P_{Nmax}$ had significant positive correlation with the soil water content and stomatal conductance. Under water and temperature stress, the net photosynthetic rate decreased and photoinhibition occurred, which could be well simulated by the Ye model. It seems that Ye model would have more applications, especially for the regions with strong solar radiation.

*Additional key words*: biophysical factors; model application; North China Plain; photosynthetic light-response curves.

## Introduction

The measurement and simulation of photosynthetic light-response curve is an important and useful tool for understanding the photosynthesis and ecology of plants, which is the basis for revealing the response of the photosynthetic process to environment (Li *et al*. 2019). The main physiological parameters, including maximum net photosynthetic rate ($P_{Nmax}$), apparent quantum yield (AQY), light-saturation point ($I_s$), light-compensation point ($I_c$), and dark respiration rate ($R_D$), can be obtained from the curve and thus determine the operation state of plant photosynthetic apparatus, photosynthetic capacity, and photosynthetic efficiency, as well as environmental changes influencing them (Ye and Yu 2008a, Xia *et al*. 2014). Plant photosynthetic rate varies with light intensity and light-response curve can be described by photosynthetic light-response models, including rectangular hyperbola (RH) model (Kirschbaum and Farquhar 1987), nonrectangular hyperbola (NRH) model (Prioul and Chartier 1977, Marshall and Biscoe 1980, Thornley 1998), exponential (Exp) model (Bassman and Zwier 1991, Prado and de Moraes 1997, Rascher *et al*. 2000), binomial regression (Binom) model (Jassby and Platt 1976, Zheng *et al*. 2012), *etc*. Light-response curves, which were fitted by RH, NRH, and Exp models, were all asymptotic curves with no extreme value under high PPFD. As a result, $I_s$ is invalid and $P_{Nmax}$ is overestimated. The deviation became obvious when photoinhibition occurred (Kyei-Boahen *et al*. 2003, Zheng *et al*. 2012). Although it seemed that photoinhibition can be well described by the Binom model, the fitted $I_c$ values were negative, which was out of the common sense (Ye and Yu 2007, Zheng *et al*. 2012, Ye *et al*. 2013). The modified rectangular hyperbola model (Ye 2007, Ye and Yu 2008b, Lobo *et al*. 2013, Fang *et al*. 2015), called the Ye model, can solve the above problems and show a better simulation results than other models (Ye 2007, Zheng *et al*. 2012, Lang *et al*. 2013, Xia *et al*. 2014).

Some photosynthetic parameters of photosynthetic light-response models were correlated with each other.

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*Abbreviations*: AQY – apparent quantum yield; $g_s$ – stomatal conductivity; $I_c$ – light-compensation point; $I_s$ – light-saturation point; $P_N$ – net photosynthetic rate; $P_{Nmax}$ – maximum net photosynthetic rate at light-saturation point; $R_D$ – dark respiration rate; SWC – relative soil water content; $T_a$ – temperature; rh – relative humidity; β – photoinhibition coefficient; γ – light-saturation coefficient.
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Gunasekera *et al*. (2013) simulated the photosynthetic light-response of rubber leaves using the Exp model. It was found that $I_s$ and $I_c$ had significant positive correlation with $P_{max}$. And AQY and $I_c$ were positively correlated with dark respiration ($R_D$). β and γ represent the bending degree of light-response curve at high light intensity. Ye and Kang (2012) analyzed Ye model and then pointed out that when the light-saturation coefficient (γ) was constant, the photoinhibition coefficient (β) was larger and the bending degree of light-response curve was greater, indicating that the photoinhibition happened more easily and the corresponding $I_s$ was smaller. On the other hand, when β was constant, lower γ and smaller AQY led to larger $P_{Nmax}$ and $I_s$.

Biophysical factors can affect plant growth and metabolism, especially photosynthesis. Many studies indicated that photosynthetic parameters varied due to biophysical factors. The observation in the field indicated that $P_{Nmax}$ and AQY obtained by the NRH model increased with increasing temperature ($T_a$), and then decreased significantly when $T_a$ was greater than 30°C (Berry and Björkman 1980, Greer and Weedon 2012). Zhao *et al*. (2016), based on the Binom model, simulated the effect of temperature on photosynthesis of different plants, including 11 woody plants, seven herbaceous plants, and three vines within 20–35°C. It was found that $P_{Nmax}$ of 9% woody plants, 57% herbaceous, and all vines increased with $T_a$ increasing and reached a maximum at 30°C. Based on the Ye model, $I_s$ and $I_c$ of *Quercus variabilis* Blume significantly increased with the increase of $T_a$; $P_{Nmax}$ and $I_s$ had significantly positive relationship with stomatal conductance ($g_s$) and relative humidity (rh), respectively (Ren *et al*. 2017). When soil water content (SWC) was within the optimal range, $P_{Nmax}$ simulated by the Ye model increased with the increase in SWC (Ge *et al*. 2012, Lang *et al*. 2013, Xia *et al*. 2014, Li *et al*. 2019).

Generally, although the Ye model has been applied widely in recent years, the characteristics of its photosynthetic parameters and the influences of biophysical factors had been rarely studied. Maize (*Zea mays* L.) is a $C_4$ plant growing in tropical and warm temperate regions with high photosynthesis efficiency. It has high light-saturation point, low light respiration rate, high photosynthetic efficiency, and high productivity. The objectives of this study were to compare photosynthetic light-response curves of different models, analyze their characteristics, and investigate the effect of biophysical factors on photosynthetic parameters so as to improve our understanding of maize photosynthesis characteristics.

## Materials and methods

**Study area**: The experiment was conducted in a summer field at the Yucheng Comprehensive Experiment Station (36°57'N, 116°36'E, 28 m a.s.l.) of the Chinese Academy of Sciences. It is located in the North China Plain, with a typical continental temperate monsoon climate. The soil texture is the alluvial deposit of the Yellow River. Mean annual temperature is 13.1°C, and annual solar radiation is 5,242 MJ $m^{-2}$. Mean annual precipitation is about 528 mm, and the summer (from June to August) value accounts for nearly 70% of the whole year. The typical cropping system in the local area is the biannual rotation with winter wheat and summer maize. In this study, maize (*Zea mays* L.) variety Dica 517 was sown on 10 June and harvested in early October, 2017.

**Leaf photosynthesis**: The measurements were conducted between 08:30–11:30 h every 3 d except for rainy weather. The light responses of photosynthesis of three fully developed and healthy summer maize leaves were selected to measure the photosynthetic light response using a portable infra-red gas analyzer, IRGA (*Li-6400XT*, *Li-Cor Inc.*, Lincoln, NE, USA). Before each measurement, the leaf was induced in the chamber by a given light at the intensity of 2,000 μmol(photon) $m^{-2}$ $s^{-1}$, which lasted for about 15 min. The formal observation would begin after the instrument stabilization. In the leaf chamber, the $CO_2$ concentration of sample chamber was stabilized at 400 μmol $mol^{-1}$ and the PPFD was controlled at 2,000; 1,800; 1,600; 1,400; 1,200; 900, 600, 400, 200, 150, 100, 50, 0 μmol $m^{-2}$ $s^{-1}$. The selected leaves were acclimated to each level of PPFD for 3 min before switching. Air temperature ($T_a$), relative humidity (rh), and stomatal conductance ($g_s$) were measured simultaneously by *Li-6400XT*. And the water content was measured by the convective oven-drying method. Soil water content was the ratio of the volumetric water content to average field capacity at the depth of 0–20 cm.

**Description of photosynthetic light-response model**: The light-response curves and photosynthetic parameters of summer maize leaves were fitted with rectangular hyperbola model, nonrectangular hyperbola model, exponential model, binomial regression model, and Ye model. The expressions and parameters of these models are described as follows:

**Rectangular hyperbola (RH) model**

$$P_N = \frac{\alpha \times I \times P_{max}}{P_{max} + \alpha \times I} - R_D \qquad (1)$$

where $I$ [μmol $m^{-2} \cdot s^{-1}$] is the photosynthetic photon flux density (PPFD), $P_N$ [μmol($CO_2$) $m^{-2}$ $s^{-1}$] is the net photosynthetic rate, $P_{max}$ [μmol($CO_2$) $m^{-2}$ $s^{-1}$] is the maximum photosynthetic rate, $R_D$ [μmol($CO_2$) $m^{-2}$ $s^{-1}$] is the dark respiration rate, α [μmol($CO_2$) $μmol^{-1}$] is the apparent quantum yield (AQY).

When $P_N = 0$, $I_c$ was expressed as follows:

$$I_c = (R_D \times P_{max})/[(P_{max} - R_D) \times \alpha] \qquad (2)$$

When $P_N = P_{max}/2$, semi-saturation point ($K$) was expressed as follows:

$$K = P_{max}/\alpha \qquad (3)$$

When $P_{max}$ and $R_D$ were known, $P_{Nmax}$ was expressed as follows:

$$P_{Nmax} = P_{max} - R_D \qquad (4)$$

**Nonrectangular hyperbola (NRH) model**

$$P_N = \frac{\alpha \times I + P_{max} - \sqrt{(\alpha \times I + P_{max})^2 - 4 \times \theta \times \alpha \times I \times P_{max}}}{2\theta} - R_D \quad (5)$$

where $I$, $P_N$, $P_{max}$, $R_D$, $\alpha$ are as described above, $\theta$ is the convexity. When $\theta = 0$, NRH model is converted into the rectangular hyperbola model. When $\theta = 1$, NRH model is converted into the Blackman curves.

When $P_N = 0$, $I_c$ was expressed as follows:

$$I_c = \frac{R_D \times P_{max} - \theta \times R_D^2}{(P_{max} - R_D) \times \alpha} \quad (6)$$

**Ye model**

$$P_N = \alpha \times (1 - \beta \times I)/(1 + \gamma \times I) \times I - R_D \quad (7)$$

where $\beta$ is the photoinhibition coefficient; $\gamma$ is the light-saturation coefficient. Other parameters are as described above.

When $P_N = 0$, $I_c$ was expressed as follows:

$$I_c = \frac{\alpha - \gamma \times R_D - \sqrt{(\alpha - \gamma \times R_D)^2 - 4 \times \beta \times \alpha \times R_D}}{2 \times \alpha \times \beta} \quad (8)$$

When $dP_N/dI = 0$, $I_s$ was expressed as follows:

$$I_s = \frac{-1 + \sqrt{(\beta + \gamma)/\beta}}{\gamma} \quad (9)$$

When $I = I_s$, $P_{Nmax}$ was expressed as follows:

$$P_{Nmax} = \left(\frac{\sqrt{\beta + \gamma} - \sqrt{\beta}}{\gamma}\right)^2 - R_D \quad (10)$$

**Exponential (Exp) model**

$$P_N = P_{max} \times \left(1 - \frac{-\alpha \times I}{e^{P_{max}}}\right) - R_D \quad (11)$$

When $P_N = 0$, $I_c$ was expressed as follows:

$$I_c = \frac{-P_{max} \times \ln(1 - R_D/P_{max})}{\alpha} \quad (12)$$

**Binomial regression (Binom) model**

$$P_N = b \times I^2 + a \times I - R_D \quad (13)$$

where $a$ and $b$ are coefficients, other parameters are as described above.

When $P_N = 0$, $I_c$ was expressed as follows:

$$I_c = \frac{-a + \sqrt{a^2 - 4 \times b \times R_D}}{2b} \quad (14)$$

When $dP_N/dI = 0$, $I_s$ was expressed as follows:

$$I_s = -a/2b \quad (15)$$

When $I = I_s$, $P_{Nmax}$ was expressed as follows:

$$P_{Nmax} = (-a^2/4b) - R_D \quad (16)$$

Generally, the common method of calculating AQY is to use the slope of $P_N$-PPFD curves when PPFD was less than 200 μmol m$^{-2}$ s$^{-1}$. The measured values $I_c$ and $R_D$ are their intercept at the horizontal and vertical coordinates under low light intensity, respectively. The effects of biophysical factors on photosynthetic parameters were analyzed by simple and multiple linear regressions, respectively.

## Results

**Comparison and analysis of leaf photosynthetic light-response models**: Under dry conditions, photoinhibition phenomenon occurred and light-response curves of different models showed significant differences (Fig. 1*A*). However, under wet conditions, photoinhibition phenomenon was not obvious and light-response curves of models were similar (Fig. 1*B*). As shown in the Fig. 1, $P_N$ simulated by all models were close to the measured values when PPFD was less than 200 μmol m$^{-2}$ s$^{-1}$. With the increase in light intensity, the difference between simulated and measured values enlarged for RH, NRH, and Exp models. In addition, light-response curves that were fitted by RH, NRH, and Exp model were all asymptotic curves with no extreme value under high PPFD. Under photoinhibition conditions, only Ye model and Binom model had better fitting effect on the photosynthetic parameters. For the other three models, the fitted curves deviated from observation. All models had higher determination coefficients ($R^2$>0.98), and the fitting accuracy of Ye model was the highest ($R^2$≈1) (Table 1). It indicated that Ye model and Binom model were applied well because they could fit the curve well. In any cases, the simulated results of RH model were the worst among the above five models.

The fitted $P_{Nmax}$, AQY, and $R_D$ of Ye model were closest to the measured values. The fitted $P_{Nmax}$ of other models except for Binom model was higher than the measured values. The fitted AQY and $R_D$ of RH model and Exp model were higher than the measured values, respectively, while AQY and $R_D$ of NRH model and Binom model were lower than the measured values, respectively (Table 1). For $I_c$, the fitting effect of Ye model was second only to that of Exp model. $I_c$ obtained by Binom model was negative, which was out of common sense. RH model, Exp model, and NRH model got semi-saturation point ($K$) instead of $I_s$. Ye model and Binom model can fit $I_s$ well (Table 1). By the comparison and analysis of photosynthetic parameters, the simulation effect of Ye model was the best and RH model was the worst.

**The correlations of leaf photosynthetic parameters**: It was found that the photosynthetic parameters fitted by Ye model were not stable and varied with the change of the biophysical factors. The range of $P_{Nmax}$ and $I_s$ obtained by Ye model were 35–55 μmol($CO_2$) m$^{-2}$ s$^{-1}$ and 1,300–2,500 μmol(photon) m$^{-2}$ s$^{-1}$, respectively. The correspondent $T_a$ and SWC varied from 29.9 to 36.5°C and from 13.3 to 20.8%, separately. $P_{Nmax}$ and $I_s$ were reduced under drought

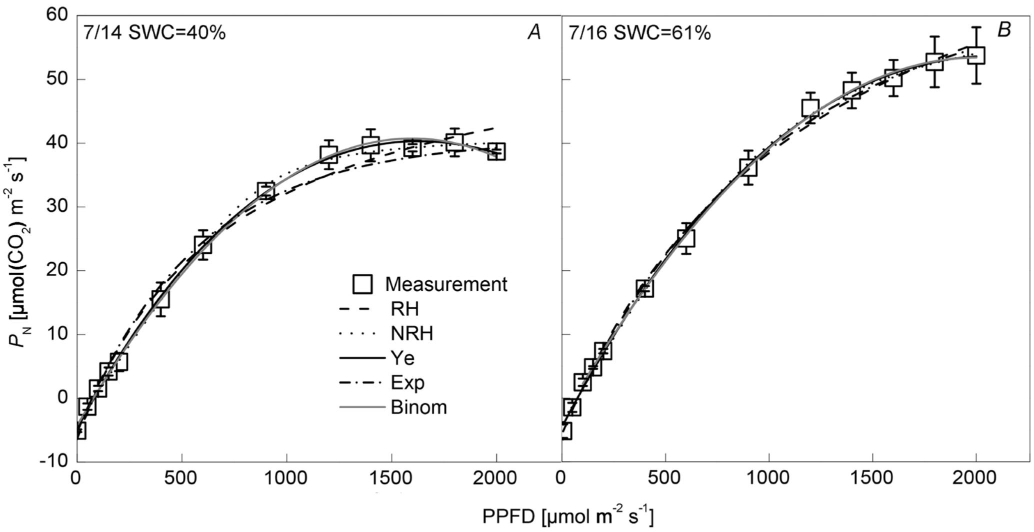


Fig.1. Comparison of photosynthetic light-response curves during the main growing season of summer maize under 40% soil water content (SWC) (*A*) and 61% SWC (*B*). Values are means ± SD. Binom – binomial regression model; Exp – exponential model; NRH – nonrectangular hyperbola model; RH – rectangular hyperbola model; Ye – modified rectangular hyperbolic model; $P_N$ – net photosynthetic rate; PPFD – photosynthetic photon flux density; SWC – relative soil water content.

and high temperature stress, and enlarged when stress was relieved after raining. The change trend of $P_{Nmax}$ and $I_s$ was very similar and consistent with the change trend of SWC and $g_s$. $R_D$ and $I_c$ had same decreasing trend with time, ranging from 3–4 μmol($CO_2$) m$^{-2}$ s$^{-1}$ and 50–85 μmol(photon) m$^{-2}$ s$^{-1}$, respectively. AQY is an important indicator of light-utilization efficiency. Due to AQY for the ratio of $R_D$ to $I_c$, the change trend of AQY was stable for 0.06–0.07 μmol($CO_2$) μmol$^{-1}$. In addition, the change trend of β and γ was opposite during the whole observation period (Table 1, Fig. 2).

Some photosynthetic parameters fitted by the Ye model were associated with each other (Table 2). $P_{Nmax}$ had significant positive correlation with $I_s$. β was significantly negatively correlated with $I_s$, γ, and $P_{Nmax}$, respectively. These parameters can be obtained under high light intensity. $R_D$ was significantly positively correlated with $I_c$ and the ratio of $R_D$ to $I_c$ had significant positive correlation with AQY (Fig. 3). These parameters can be obtained under low light intensity. Besides, AQY and γ performed significantly the positive relationship, which indicated the close relationship between two groups of photosynthetic parameters (Table 2).

**The biophysical factors influencing leaf photosynthetic parameters**: Even with multiple linear regression analysis, only the single effect of each biophysical factor on photosynthesis parameters was found to be significant. Therefore, simple regression was used to replace multiple regression. As shown in Fig. 4, $P_{Nmax}$ had significant positive correlation with $T_a$, SWC, and $g_s$ ($P$<0.05). The significance of each factor to $P_{Nmax}$ was as follows: $g_s$ > SWC > $T_a$. $I_s$ was positively correlated with $T_a$ ($P$<0.05) and the correlation with other factors was not significant. β was negatively correlated with $T_a$ ($P$<0.05) and the correlation with other factors was not significant. All the relationships between other photosynthetic parameters and biophysical factors were not significant.

## Discussion

**Comparison of different light-response models**: Many studies showed that the Ye model had a greater simulation effect compared to other four light-response models (Ye 2007, Zheng *et al*. 2012, Lang *et al*. 2013, Ren *et al*. 2017), while the fitting capacity of RH model was the worst (Li *et al*. 2019). AQY obtained by RH model was often higher than the measured value (Gomes *et al*. 2006, Ye 2007, Xia *et al*. 2014). The same result was found in this study (Fig. 1). It may be explained that high AQY could make the fitting light-response curve in agreement with the observation values (Johnson *et al*. 1989). A convexity coefficient θ was added in the RH model and constituted a new model, NRH model, resulting in turning point of the curve being more obvious than that of RH model, which meant that the fitting curve was more stable with the increase in light intensity and AQY was closer to the measured value than before (Ye 2010, Calama *et al*. 2013). Although the fitting effect of Exp model was well under low light intensity, it was poor under high light intensity (Fang *et al*. 2015, Wan *et al*. 2018). Considering that RH model, NRH model, and Exp model were only an asymptote without extreme, they could not be used to simulate photoinhibition and the obtained $P_{Nmax}$ was higher than the observed value (Ye and Kang 2012, Fang *et al*. 2015). As for Binom model, the fitting $I_c$ was negative, which was out of common sense (Ye and Yu 2007, Zheng *et al*. 2012). Ye and Yu (2007) replaced $P_{Nmax}$ with β and γ in the RH model and actually constituted a new model, called the Ye model (Lobo *et al*. 2013), which made the model highly advantageous in fitting the photoinhibition and light-saturation stages. $P_{Nmax}$ and $l_s$ simulated by Ye

Table 1. Photosynthetic parameters of different photosynthetic light-response models. Binom – binomial regression model; Exp – exponential model; NRH – nonrectangular hyperbola model; RH – rectangular hyperbola model; Ye – modified rectangular hyperbolic model. $P_{Nmax}$ – the maximum net photosynthetic rate; $I_s$ – light-saturation point; $R_D$ – dark respiration rate; $I_c$ – light-compensation point; AQY – apparent quantum yield; $K$ – semi-saturation point; $R^2$ – determination coefficient.

| Date | Method | $P_{Nmax}$ [μmol($CO_2$) $m^{-2}$ $s^{-1}$] | AQY [μmol($CO_2$) $μmol^{-1}$] | $R_D$ [μmol($CO_2$) $m^{-2}$ $s^{-1}$] | $I_c$ [μmol $m^{-2}$ $s^{-1}$] | $I_s$ [μmol $m^{-2}$ $s^{-1}$] | $K$ [μmol $m^{-2}$ $s^{-1}$] | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| 7/14 | RH | 60.05 | 0.092 | 6.40 | 77.05 | - | 723 | 0.986 |
| | NRH | 41.59 | 0.050 | 4.00 | 80.07 | - | 475 | 0.998 |
| | Exp | 43.33 | 0.078 | 5.91 | 80.92 | - | 612 | 0.993 |
| | Binom | 35.45 | 0.056 | 4.27 | –73.80 | 1,409 | - | 0.998 |
| | Ye | 39.80 | 0.062 | 4.80 | 80.37 | 1,605 | - | 0.999 |
| | Measurement | 40.20 | 0.054 | 4.41 | 81.49 | 1,630 | - | - |
| 7/16 | RH | 94.76 | 0.079 | 5.66 | 76.21 | - | 1,275 | 0.997 |
| | NRH | 63.64 | 0.056 | 4.09 | 73.55 | - | 695 | 0.999 |
| | Exp | 63.86 | 0.071 | 5.20 | 76.64 | - | 838 | 0.998 |
| | Binom | 81.32 | 0.058 | 4.15 | –70.14 | 2,924 | - | 0.999 |
| | Ye | 54.76 | 0.062 | 4.52 | 74.46 | 2,131 | - | 0.999 |
| | Measurement | - | 0.064 | 4.90 | 76.31 | - | - | - |
| 7/19 | RH | 93.49 | 0.081 | 6.19 | 82.04 | - | 1,212 | 0.996 |
| | NRH | 63.27 | 0.057 | 4.58 | 80.90 | - | 693 | 0.997 |
| | Exp | 62.12 | 0.071 | 5.66 | 82.77 | - | 831 | 0.997 |
| | Binom | 38.46 | 0.059 | 4.55 | –75.67 | 1,467 | - | 0.998 |
| | Ye | 52.37 | 0.062 | 4.93 | 81.10 | 2,043 | - | 0.998 |
| | Measurement | - | 0.071 | 5.82 | 82.21 | - | - | - |
| 7/22 | RH | 74.30 | 0.082 | 4.32 | 55.92 | - | 961 | 0.994 |
| | NRH | 45.71 | 0.056 | 2.88 | 51.78 | - | 471 | 0.997 |
| | Exp | 49.41 | 0.075 | 4.04 | 56.35 | - | 615 | 0.995 |
| | Binom | 47.28 | 0.064 | 3.40 | –52.50 | 1,592 | - | 0.998 |
| | Ye | 39.96 | 0.061 | 3.18 | 53.13 | 1,315 | - | 0.998 |
| | Measurement | 40.80 | 0.059 | 3.24 | 54.64 | 1,370 | - | - |
| 7/25 | RH | 85.16 | 0.078 | 4.50 | 61.03 | - | 1,156 | 0.998 |
| | NRH | 57.21 | 0.059 | 3.44 | 58.82 | - | 611 | 0.999 |
| | Exp | 56.40 | 0.071 | 4.17 | 61.10 | - | 720 | 0.999 |
| | Binom | 41.95 | 0.060 | 3.41 | –55.62 | 1,506 | - | 1.000 |
| | Ye | 45.60 | 0.063 | 3.67 | 59.29 | 1,729 | - | 1.000 |
| | Measurement | - | 0.061 | 3.70 | 60.89 | - | - | - |
| 7/31 | RH | 87.20 | 0.089 | 5.54 | 66.42 | - | 1,045 | 0.998 |
| | NRH | 71.23 | 0.071 | 4.51 | 65.05 | - | 743 | 0.998 |
| | Exp | 60.97 | 0.077 | 4.84 | 65.64 | - | 732 | 0.998 |
| | Binom | 42.02 | 0.060 | 3.37 | –54.91 | 1,507 | - | 0.997 |
| | Ye | 54.79 | 0.073 | 4.54 | 64.45 | 2,329 | - | 0.999 |
| | Measurement | - | 0.073 | 4.96 | 67.83 | - | - | - |

model were very close to the measured value (Ye and Yu 2007, Wan *et al*. 2018).

Some photosynthetic light-response models were associated with each other and can be transformed under certain conditions. For example, when θ was 0, NRH model was changed into RH model (Thornley 1976) and thus RH model can be seen as a special case of NRH model. When β was 0 and γ was the ratio of AQY to $P_{Nmax}$, Ye model was changed into RH model (Ye and Kang 2012) and thus RH model was also regarded as a special case of Ye model. Both NRH model and Ye model were the improved versions of RH model. The former focused on improving the fitting curve under low light intensity so as to make AQY closer to the measured value. The latter emphasizes the importance on improving the fitting effect under high light intensity in order to make $P_{Nmax}$ closer to the measured value and obtain $I_s$ that cannot be gained from most of other models. NRH model is more suitable for areas with

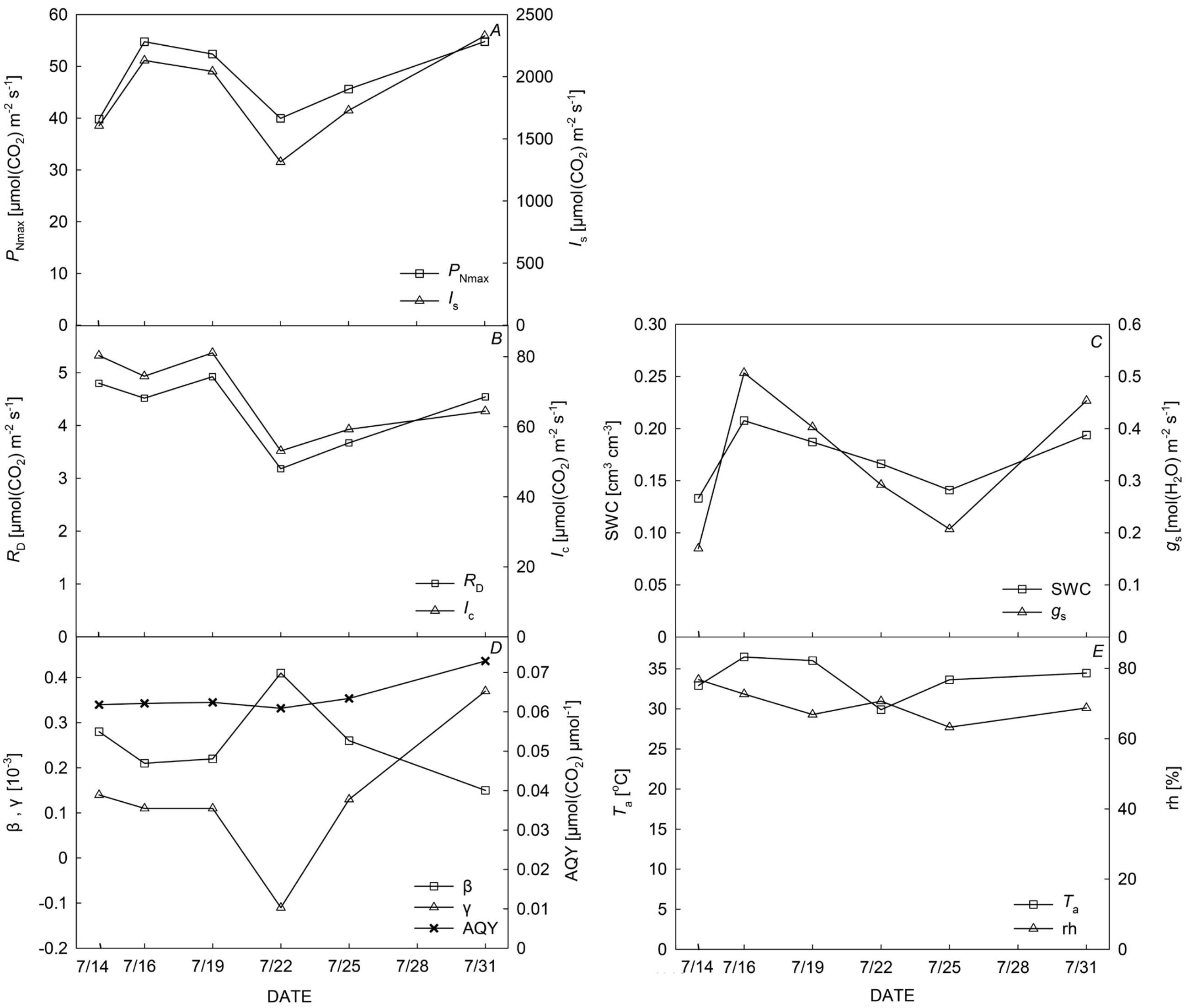


Fig. 2. Diurnal dynamics of photosynthetic parameters obtained by Ye model and biophysical factors during the main growing season of summer maize. AQY – apparent quantum yield; $g_s$ – stomatal conductivity; $I_c$ – light-compensation point; $I_s$ – light-saturation point; $P_{Nmax}$ – maximum net photosynthetic rate at light-saturation point; $R_D$ – dark respiration rate; SWC – relative soil water content; $T_a$ – temperature; rh – relative humidity; β – photoinhibition coefficient; γ – light-saturation coefficient.

Table 2. Correlation coefficients of leaf photosynthetic parameters obtained by Ye model. * and ** indicate significant correlation of photosynthetic parameters at $P<0.05$ and $P<0.01$, respectively. AQY – apparent quantum yield; $I_c$ – light-compensation point; $I_s$ – light-saturation point; $P_{Nmax}$ – maximum net photosynthetic rate at light-saturation point; $R_D$ – dark respiration rate; β – photoinhibition coefficient; γ – light-saturation coefficient.

| Parameters | $P_{Nmax}$ | AQY | β | γ | $R_D$ | $I_s$ |
|---|---|---|---|---|---|---|
| AQY | 0.540 | | | | | |
| β | –0.846* | –0.676 | | | | |
| γ | 0.606 | 0.859* | –0.901* | | | |
| $R_D$ | 0.502 | 0.226 | –0.725 | 0.597 | | |
| $I_s$ | 0.951** | 0.679 | –0.961** | 0.810 | 0.656 | |
| $I_c$ | 0.285 | –0.155 | –0.472 | 0.280 | 0.927** | 0.394 |

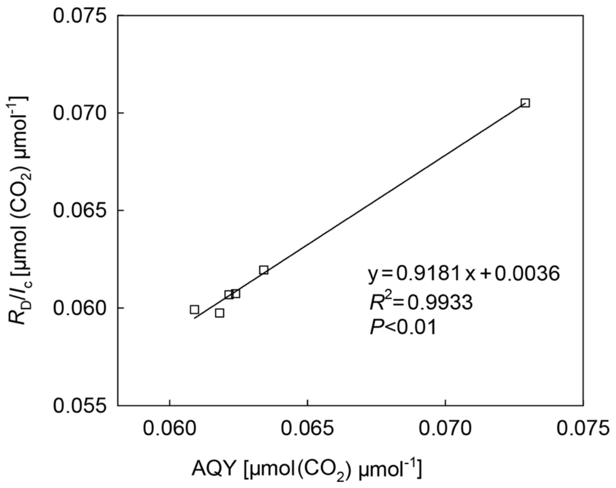


Fig. 3. Correlations of the ratio of dark respiration rate to light-compensation point ($R_D/I_c$) and apparent quantum yield (AQY) during the main growing season of summer maize (the parameters obtained by Ye model).

low light intensity such as Sichuan, and Ye model can be used in the regions with strong solar radiation such as Tibetan Plateau. Currently, NRH model was used more widely than other models in recent years. It is believed, with more and more applications, Ye model can become more popular in the near future.

**Correlations of photosynthetic parameters obtained by Ye model**: There were close relationships among some photosynthetic parameters. Gunasekera *et al.* (2013), based on Exp model, found that $I_s$ had significant positive correlation with $P_{Nmax}$ and $I_c$ was positively correlated with $R_D$. The result was the same in this study (Table 2). $P_{Nmax}$ represents the maximum photosynthetic capacity of leaves, thus determining photosynthetic rate at high light intensity (Li *et al.* 2019). $I_s$ is the light intensity when photosynthetic rate reaches its maximum. Great $P_{Nmax}$ means that the plant has strong photosynthetic capacity and photoinhibition can hardly occur, resulting in a large $I_s$. Conversely, low $I_s$ implies that $P_{Nmax}$ was easy to obtain and photoinhibition would occur easily. $R_D$ means the rate of photosynthetic products that plants consumed in the darkness. $I_c$ is the critical light intensity when $P_N$ is equal to 0. When PPFD is less than $I_c$, negative $P_N$ means that no net $CO_2$ is absorbed by plants. Great $R_D$ implies rapid consumption of photosynthates by plants. More light flux intensity is absorbed by plant to balance the respiration, leading to a large $I_c$. In this study, β had significant negative correlation with $I_s$, γ, and $P_{Nmax}$ (Table 2). These parameters exhibited the photosynthetic characteristics under strong light. Other parameters, including AQY, $R_D$, and $I_c$, revealed the photosynthetic characteristics under weak light intensity. However, obvious correlation between AQY and γ in this study revealed the association of two parameters groups which could not be distinguished completely.

β and γ represent the bending degree of light-response curve at high light intensity. When γ was constant, larger β and greater AQY implied smaller $I_s$, which indicated that photoinhibition was more easy to happen (Ye and Kang 2012). The same result was found in this study and $I_s$ had significant negative correlation with β (Table 2). According to Ye *et al.* (2013), both β and γ were the function of $g_i/g_k$, where $g_i$ and $g_k$ mean degeneration of energy level of photosynthetic pigment molecules in the ground state i and the excited state k, respectively. It was obvious that β declined, while γ enlarged with the increase in $g_i/g_k$. That was the reason why β was negatively correlated to γ at a significant level (Fig. 2, Table 2).

**Factors influencing light-response parameters of Ye model**: Many studies on traditional light-response models showed that photosynthetic parameters were related with bio-environmental factors significantly. When temperature was below or beyond the optimum, $P_{Nmax}$ augmented or declined with the increase in temperature, respectively (Berry and Björkman 1980, Battaglia *et al.* 1996, Yamori *et al.* 2005, Hikosaka *et al.* 2006, Greer and Weedon 2012, Tong *et al.* 2014, Zhao and Li 2016). In the summer, when temperature was beyond 25°C, $P_{Nmax}$ and $I_c$ of white spruce were reduced with the increase in temperature (Man and Lieffers 1997). Photoinhibition occurred under high temperature. It may be attributed to too much energy, absorbed by the photosynthetic pigment, which cannot be released in time (Zhou *et al.* 2007), resulting in the occurrence of photoinhibition. During the growing season, the enzyme activity of leaves was higher and $P_N$ in the leaves was increasing, leading to $P_{Nmax}$ and $I_s$ increasing when temperature was close to the optimum temperature of the enzyme. When the ambient temperature was lesser or higher than that of the optimum, the enzyme activities, such as those of Rubisco carboxylase, PPDK carboxylase, and PEPC carboxylase were suppressed, resulting in the decline of ATP supply capacity, carbon assimilation, and photosynthetic rate in the leaves was low (Slayter and Morrow 1977, Mackey *et al.* 2013, Perdomo *et al.* 2017). However, in the study on Ye model, $P_{Nmax}$ and $I_s$ enlarged and β declined when $T_a$ increased from 29 to 36°C (Table 3, Fig. 4). Our results were different from those in other studies and could not be interpreted by current plant physiology and biochemistry mechanisms. It may be false results because the range of observed temperature was too narrow to overcome the disturbance from other biophysical factors, *e.g.*, soil moisture.

Soil drought would suppress photosynthesis in plants to some extent, thus affecting $P_{Nmax}$. It was found that $P_{Nmax}$ significantly decreased with the decrease of soil water content (Xu *et al.* 2013, Li *et al.* 2019). In this study, SWC ranged between 39–61% of the field capacity. $P_{Nmax}$ showed the significant positive correlation with SWC (Fig. 4), which was consistent with the result of northern meadow (Ge *et al.* 2012). $P_{Nmax}$ was relatively high under the optimal soil water content and decreased when soil moisture was below or beyond the optimal range (Lang *et al.* 2013, Xu *et al.* 2013, Xia *et al.* 2014, Li *et al.* 2019). The decrease of $P_N$ under water deficit may be due to the low leaf water potential, which is caused by the high transpiration rate, the accelerated decomposition of chlorophyll, the decrease of leaf stomatal conductance, and the obstruction of $CO_2$

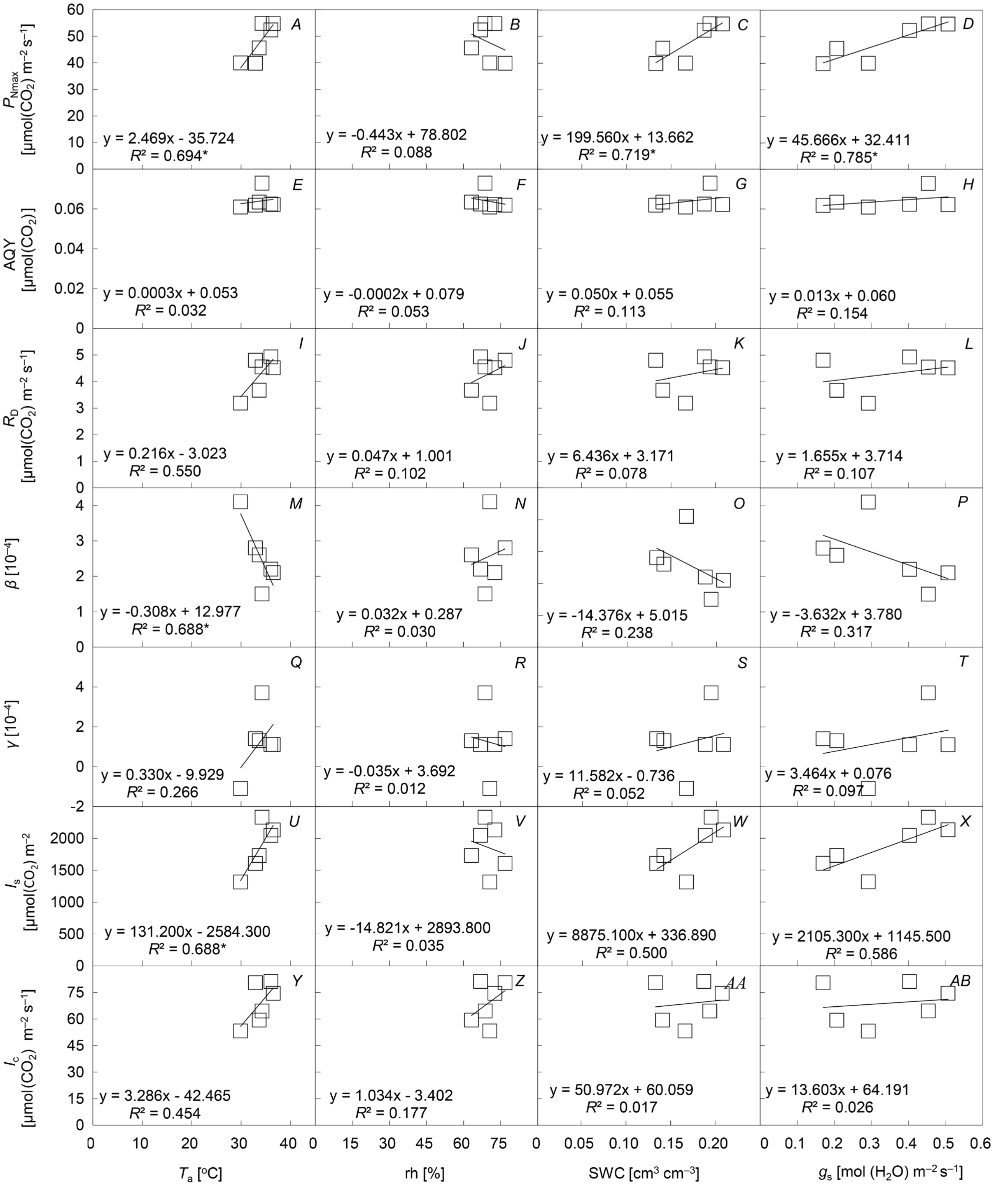


Fig. 4. The relationships between biophysical factors and photosynthetic parameters obtained by Ye model during the growing seasons of summer maize. * indicates significant correlation at $P$<0.05. AQY – apparent quantum yield; $g_s$ – stomatal conductivity; $I_c$ – light-compensation point; $I_s$ – light-saturation point; $P_{Nmax}$ – maximum net photosynthetic rate at light-saturation point; $R_D$ – dark respiration rate; SWC – relative soil water content; $T_a$ – temperature; rh – relative humidity; β – photoinhibition coefficient; γ – light-saturation coefficient.

supply in chloroplast.

Considering the strong correlation between $g_s$ and $P_N$, the effect of biophysical factors on $P_N$ (*i.e.*, $T_a$, rh, and SWC) can be attributed to $g_s$ (Zhang *et al*. 2012, Tong *et al*. 2014). In this study, $P_{Nmax}$ had a significant positive correlation with $g_s$ (Fig. 4), which was similar to the study of wheat by Tong *et al*. (2014) and the study of trees by Ren *et al*. (2017). When leaf water content was below the minimum, stomata would be closed and photosynthetic rate declined rapidly. As the breath path of plant leaves, stomata control the leaf-air exchange of $H_2O$, $CO_2$, and $O_2$, therefore affecting photosynthesis significantly.

**Conclusions**: Among five models, the simulation biases of the Ye model were the least on the fitting light-response curve and parameters of maize but those of RH model were the largest. The satisfied simulation of photoinhibition by the Ye model indicated that Ye model was suitable in the regions with strong solar radiation.

During the observation period, $P_{Nmax}$ and AQY obtained by Ye model ranged from 35 to 55 μmol($CO_2$) $m^{-2}$ $s^{-1}$ and from 0.06 to 0.07 μmol($CO_2$) $μmol^{-1}$, respectively. $P_{Nmax}$ was small under drought and high temperature stress. Significant positive correlations were found between $P_{Nmax}$ with $I_s$, $R_D$ with $I_c$, and AQY with γ. β was negatively correlated with $I_s$, γ, and $P_{Nmax}$.

When SWC varied from 39 to 61%, $P_{Nmax}$ had significant positive correlation with SWC and $g_s$. The influence of SWC on photosynthesis may be attributed to the effect of $g_s$. Since it is hard to analyze temperature influence in a small temperature change, it is necessary to investigate the temperature effects on photosynthetic parameters in a wide temperature range, and further explore the comprehensive effects of multi-factors on photosynthesis parameters.

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