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


Key Laboratory of Water Cycle and Related Land Surface Processes, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 100101 Beijing, China*
College of Resources and Environment, University of Chinese Academy of Sciences, 100049 Beijing, China**
College of Forestry, Beijing Forestry University, 100083 Beijing, China***
State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest Agriculture and Forestry University, 712100 Yangling, Shanxi, China*
School of Life Sciences, University of Technology, Sydney, 2007 NSW, Australia**

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 (Iₕ), the light-saturation coefficient (γ), and maximum net photosynthetic rate at light-saturation point (Pₛₘₐₓ), respectively. Pₛₘₐₓ and Iₕ, apparent quantum yield, and γ performed significantly positive relationship, respectively. When the soil volumetric water content varied from 13 to 21%, Pₛₘₐₓ 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 (Pₛₘₐₓ), apparent quantum yield (AQY), light-saturation point (Iₕ), light-compensation point (Iₒ), and dark respiration rate (Rₒ), 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, Iₕ is invalid and Pₛₘₐₓ 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 Iₕ 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.
Gunasekera et al. (2013) simulated the photosynthetic light-response of rubber leaves using the Exp model. It was found that $I_c$ and $I_s$ had significant positive correlation with $P_{\text{max}}$. And AQY and $I_c$ were positively correlated with dark respiration ($R_D$). $\beta$ and $\gamma$ 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 ($\gamma$) was constant, the photoinhibition coefficient ($\beta$) was larger and the bending degree of light-response curve was greater, indicating that the photoinhibition happened more easily and the corresponding $I_c$ was smaller. On the other hand, when $\beta$ was constant, lower $\gamma$ and smaller AQY led to larger $P_{\text{max}}$ and $I_c$.

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 $P_{\text{max}}$ and AQY obtained by the NRH model increased with increasing temperature ($T_i$), and then decreased significantly when $T_i$ 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 $P_{\text{max}}$ of 9% woody plants, 57% herbaceous, and all vines increased with $T_i$ increasing and reached a maximum at 30°C. Based on the Ye model, $I_c$ and $I_s$ of Quercus variabilis Blume significantly increased with the increase of $T_i$; $P_{\text{max}}$ and $I_c$ 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, $P_{\text{max}}$ 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 ($T_i$), 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**

\[
P_N = \frac{\alpha \times I \times P_{\text{max}}}{P_{\text{max}} + \alpha \times I} - R_D \tag{1}
\]

where $I$ [μmol m$^{-2}$s$^{-1}$] is the photosynthetic photon flux density (PPFD), $P_N$ [μmol(CO$_2$) m$^{-2}$ s$^{-1}$] is the net photosynthetic rate, $P_{\text{max}}$ [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, $\alpha$ [μmol(CO$_2$) μmol$^{-1}$] is the apparent quantum yield (AQY).

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

\[
I_c = \frac{(R_D \times P_{\text{max}})}{[(P_{\text{max}} - R_D) \times \alpha]} \tag{2}
\]

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

\[
K = \frac{P_{\text{max}}}{\alpha} \tag{3}
\]

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

\[
P_{\text{max}} = P_{\text{max}} - R_D \tag{4}
\]
Nonrectangular hyperbola (NRH) model

\[ P_N = \frac{\alpha \times I + P_{\text{max}} - \frac{(\alpha \times I + P_{\text{max}})^2}{4 \times \alpha \times I \times P_{\text{max}}} - R_D}{20} \]  

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

When \( P_N = 0 \), \( I \) was expressed as follows:

\[ I_0 = \frac{R_D \times P_{\text{max}} - \theta \times R_D^2}{(P_{\text{max}} - R_D) \times \alpha} \]  

Ye model

\[ P_N = \alpha \times (1 - \beta \times I^s) \times (1 + \gamma \times I) \times I - R_D \]  

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

When \( P_N = 0 \), \( I \) was expressed as follows:

\[ I_0 = \frac{\alpha \times (1 - \beta \times I^s) \times (1 + \gamma \times I) \times I}{2 \times \alpha \times \beta} \]  

When \( dP_N/dI = 0 \), \( I \) was expressed as follows:

\[ I_\alpha = \frac{1 + (\beta + \gamma) / \beta}{\gamma} \]  

When \( I = I_\alpha \), \( P_{\text{Nmax}} \) was expressed as follows:

\[ P_{\text{Nmax}} = \frac{(\beta + \gamma - \beta \times \gamma)}{\gamma} \]  

Exponential (Exp) model

\[ P_N = P_{\text{max}} \times \left(1 - \frac{\alpha \times I}{e^{P_{\text{max}}}}\right) - R_D \]  

When \( P_N = 0 \), \( I \) was expressed as follows:

\[ I_0 = \frac{P_{\text{max}} \times \ln(1 - R_D/P_{\text{max}})}{\alpha} \]  

Binominal regression (Binom) model

\[ P_N = b \times I + a \times I - R_D \]  

where \( a \) and \( b \) are coefficients, other parameters are as described above.

When \( P_N = 0 \), \( I \) was expressed as follows:

\[ I_0 = -\frac{a + \sqrt{a^2 - 4 \times b \times R_D}}{2b} \]  

When \( dP_N/dI = 0 \), \( I \) was expressed as follows:

\[ I_1 = -a/2b \]  

When \( I = I_1, P_{\text{Nmax}} \) was expressed as follows:

\[ P_{\text{Nmax}} = (-a^2/4b) - R_D \]  

Generally, the common method of calculating AQY is to use the slope of \( P_N-\text{PPFD} \) curves when PPFD was less than 200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). The measured values \( I_s \) 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. 1A). However, under wet conditions, photoinhibition phenomenon was not obvious and light-response curves of models were similar (Fig. 1B). As shown in the Fig. 1, \( P_N \) simulated by all models were close to the measured values when PPFD was less than 200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). 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 \( P_{\text{Nmax}}, \text{AQY}, \text{and } R_D \) of Ye model were closest to the measured values. The fitted \( P_{\text{Nmax}} \) 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 \( I_s \), the fitting effect of Ye model was second only to that of Exp model. \( I_s \) 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 \( P_{\text{Nmax}} \) and \( I_s \) obtained by Ye model were 35–55 \( \mu \text{mol(CO}_2\text{)} \text{m}^{-2} \text{s}^{-1} \) and 1,300–2,500 \( \mu \text{mol(photo)} \text{m}^{-2} \text{s}^{-1} \), respectively. The correspondent \( T \) and SWC varied from 29.9 to 36.5°C and from 13.3 to 20.8%, separately. \( P_{\text{Nmax}} \) and \( I_s \) were reduced under drought
and high temperature stress, and enlarged when stress was relieved after raining. The change trend of $P_{\text{Nmax}}$ and $I_a$ was very similar and consistent with the change trend of SWC and $g_c$. $R_0$ and $I_a$ 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 $R_0$ to $I_a$, the change trend of AQY was stable for 0.06–0.07 μmol(CO$_2$) μmol$^{-1}$. In addition, the change trend of $\beta$ and $\gamma$ 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). $P_{\text{Nmax}}$ and $I_a$ had significant positive correlation with $I_a$. $\beta$ was significantly negatively correlated with $I_a$, $\gamma$, and $P_{\text{Nmax}}$, respectively. These parameters can be obtained under high light intensity. $R_0$ was significantly positively correlated with $I_a$ and the ratio of $R_0$ to $I_a$ had significant positive correlation with AQY (Fig. 3). These parameters can be obtained under low light intensity. Besides, AQY and $\gamma$ 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, $P_{\text{Nmax}}$ had significant positive correlation with $T_a$, SWC, and $g_c$ ($P<0.05$). The significance of each factor to $P_{\text{Nmax}}$ was as follows: $g_c > \text{SWC} > T_a$. $I_a$ was positively correlated with $T_a$ ($P<0.05$) and the correlation with other factors was not significant. $\beta$ 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 $\theta$ 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 $P_{\text{Nmax}}$ was higher than the observed value (Ye and Kang 2012, Fang et al. 2015). As for Binom model, the fitting $L$ was negative, which was out of common sense (Ye and Yu 2007, Zheng et al. 2012). Ye and Yu (2007) replaced $P_{\text{Nmax}}$ with $\beta$ and $\gamma$ in the RH model and actually constituted a new model, called the Ye model (Lobo et al. 2014), which made the model highly advantageous in fitting the photoinhibition and light-saturation stages. $P_{\text{Nmax}}$ and $I_a$ simulated by Ye

![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.](image-url)

<table>
<thead>
<tr>
<th>Date</th>
<th>Method</th>
<th>$P_{\text{Nmax}}$ [μmol CO₂ m⁻² s⁻¹]</th>
<th>AQY [μmol CO₂ μmol⁻¹]</th>
<th>$R_D$ [μmol CO₂ m⁻² s⁻¹]</th>
<th>$I_c$ [μmol m⁻² s⁻¹]</th>
<th>$I_D$ [μmol m⁻² s⁻¹]</th>
<th>$K$ [μmol m⁻² s⁻¹]</th>
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<td>0.999</td>
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<tr>
<td></td>
<td>Binom</td>
<td>41.95</td>
<td>0.060</td>
<td>3.41</td>
<td>-55.62</td>
<td>1,506</td>
<td>-</td>
<td>1.000</td>
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<tr>
<td></td>
<td>Ye</td>
<td>45.60</td>
<td>0.063</td>
<td>3.67</td>
<td>59.29</td>
<td>1,729</td>
<td>-</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>Measurement</td>
<td>-</td>
<td>0.061</td>
<td>3.70</td>
<td>60.89</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
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<td>7/31</td>
<td>RH</td>
<td>87.20</td>
<td>0.089</td>
<td>5.54</td>
<td>66.42</td>
<td>-</td>
<td>1,045</td>
<td>0.998</td>
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<td>NRH</td>
<td>71.23</td>
<td>0.071</td>
<td>4.51</td>
<td>65.05</td>
<td>-</td>
<td>743</td>
<td>0.998</td>
</tr>
<tr>
<td></td>
<td>Exp</td>
<td>60.97</td>
<td>0.077</td>
<td>4.84</td>
<td>65.64</td>
<td>-</td>
<td>732</td>
<td>0.998</td>
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<tr>
<td></td>
<td>Binom</td>
<td>42.02</td>
<td>0.060</td>
<td>3.37</td>
<td>-54.91</td>
<td>1,507</td>
<td>-</td>
<td>0.997</td>
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<tr>
<td></td>
<td>Ye</td>
<td>54.79</td>
<td>0.073</td>
<td>4.54</td>
<td>64.45</td>
<td>2,329</td>
<td>-</td>
<td>0.999</td>
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<tr>
<td></td>
<td>Measurement</td>
<td>-</td>
<td>0.073</td>
<td>4.96</td>
<td>67.83</td>
<td>-</td>
<td>-</td>
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</table>

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 $\theta$ was 0, NRH model was changed into RH model (Thornley 1976) 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 $P_{\text{Nmax}}$ closer to the measured value. The former focused on improving the AQY value and obtain $I_c$ 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; $P_{\text{max}}$ – maximum net photosynthetic rate at light-saturation point; $R_D$ – dark respiration rate; SWC – relative soil water content; $T_a$ – temperature; rh – relative humidity; $\beta$ – photoinhibition coefficient; $\gamma$ – 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; $P_{\text{max}}$ – maximum net photosynthetic rate at light-saturation point; $R_D$ – dark respiration rate; $\beta$ – photoinhibition coefficient; $\gamma$ – light-saturation coefficient.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>$P_{\text{max}}$</th>
<th>AQY</th>
<th>$\beta$</th>
<th>$\gamma$</th>
<th>$R_D$</th>
<th>$I_s$</th>
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</thead>
<tbody>
<tr>
<td>AQY</td>
<td>0.540</td>
<td></td>
<td>-0.846*</td>
<td>-0.676</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta$</td>
<td>0.606</td>
<td>0.859*</td>
<td>-0.901*</td>
<td>0.502</td>
<td>0.226</td>
<td>0.927**</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>0.951**</td>
<td>0.679</td>
<td>-0.961**</td>
<td>0.810</td>
<td>0.656</td>
<td>0.394</td>
</tr>
</tbody>
</table>
The result was the same in this study (Table 2). According to Ye et al. (2013), both \( \beta \) and \( \gamma \) were the function of \( g_i/g_s \), where \( g_i \) and \( g_s \) mean degeneration of energy level of photosynthetic pigment molecules in the ground state \( i \) and the excited state \( k \), respectively. It was obvious that \( \beta \) declined, while \( \gamma \) enlarged with the increase in \( g_i/g_s \). That was the reason why \( \beta \) was negatively correlated to \( \gamma \) 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, \( P_{\text{Nmax}} \) 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, \( P_{\text{Nmax}} \) 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 \( P_s \) in the leaves was increasing, leading to \( P_{\text{Nmax}} \) and \( I_c \) 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, \( P_{\text{Nmax}} \) and \( I_c \) enlarged and \( \beta \) declined when \( T_i \) 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 \( P_{\text{Nmax}} \). It was found that \( P_{\text{Nmax}} \) 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. \( P_{\text{Nmax}} \) showed the significant positive correlation with SWC (Fig. 4), which was consistent with the result of northern meadow (Ge et al. 2012). \( P_{\text{Nmax}} \) 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 \( P_s \) 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 \( \text{CO}_2 \).
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; $P_{\text{max}}$ – maximum net photosynthetic rate at light-saturation point; $R_d$ – dark respiration rate; SWC – relative soil water content; $T_a$ – temperature; rh – relative humidity; $\beta$ – photoinhibition coefficient; $\gamma$ – 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., \( T_a \), \( r_h \), and \( SWC \)) can be attributed to \( g_s \) (Zhang et al. 2012, Tong et al. 2014). In this study, \( P_{\text{max}} \) 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 \( \text{H}_2\text{O} \), \( \text{CO}_2 \), and \( \text{O}_2 \), 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 photosynthesis by the Ye model indicated that Ye model was suitable in the regions with strong solar radiation. During the observation period, \( P_{\text{max}} \) and AQY obtained by Ye model ranged from 35 to 55 \( \mu \text{mol} \text{(CO}_2 \text{)} \text{ m}^{-2} \text{ s}^{-1} \) and from 0.06 to 0.07 \( \mu \text{mol} \text{(CO}_2 \text{)} \text{ mol}^{-1} \), respectively. \( P_{\text{max}} \) was small under drought and high temperature stress. Significant positive correlations were found between \( P_{\text{max}} \) with \( I_o \), \( R_0 \) with \( I_o \), and AQY with \( \gamma \). \( \beta \) was negatively correlated with \( I_o \), \( \gamma \), and \( P_{\text{max}} \).

When SWC varied from 39 to 61%, \( P_{\text{max}} \) 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.

**References**


Ye Z.P., Yu Q.: [Comparison of new and several classical models of photosynthesis in response to irradiance.] – J. Plant Ecol. 32: 1356-1361, 2008a. [In Chinese]

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