Response Mechanisms of Winter Wheat Photosynthetic Characteristics to CO2 Concentration and Soil Water Content: Postprint

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Abstract

Photosynthesis is a crucial indicator for assessing plant responses to environmental conditions. Quantifying photosynthetic characteristics through light-response curve fitting can reveal the self-regulation and adaptation mechanisms of plants under different growth environments from a physiological perspective. This study measured the light-response curves of flag leaves at the grain-filling stage of winter wheat under four different treatment conditions using a Li-6400 portable photosynthesis system. The light-response data were fitted using the Rectangular Hyperbola Model (RHM), Non-Rectangular Hyperbola Model (NRHM), Modified Rectangular Hyperbola Model (RHMM), Exponential Model (EM), and Modified Exponential Model (MEM) to analyze the effects of different CO2 concentrations and soil water contents on the photosynthetic characteristics of winter wheat. The results demonstrated that the Modified Rectangular Hyperbola Model exhibited the best fitting performance, with fitted values for both the light-response curves and photosynthetic parameters of winter wheat under various treatments being closest to the measured values. With increasing CO2 concentration, the apparent quantum efficiency ( ), light saturation point (LSP), and maximum net photosynthetic rate (Pnmax) of winter wheat under all water treatments increased, while the light compensation point (LCP) and dark respiration (Rd) decreased, indicating that elevated CO2 concentration can effectively enhance the light energy conversion efficiency and utilization range, thereby improving the photosynthetic capacity of winter wheat. As soil water content decreased, the light compensation point (LCP) and dark respiration rate (Rd) of winter wheat increased, whereas the apparent quantum efficiency ( ), light saturation point (LSP), and maximum net photosynthetic rate (Pnmax) decreased. This suggests that although winter wheat can partially offset the effects of drought stress by increasing initial photosynthetic efficiency, drought stress nonetheless reduces its photosynthetic capacity.

Additionally, increased CO2 concentration can mitigate part of the photosynthetic capacity reduction in winter wheat induced by drought stress.

Full Text

Response Mechanism of Photosynthetic Characteristics of Winter Wheat to CO2 Concentration and Soil Water Content

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Abstract

Photosynthesis serves as a crucial indicator of plant environmental responses. By fitting light response curves to quantify photosynthetic characteristics, we can elucidate the physiological mechanisms underlying plant acclimation and adaptation to different growth conditions. This study measured light response curves of flag leaves during the grain-filling stage of winter wheat under four treatment conditions using a Li-6400 portable photosynthesis system. Five models—rectangular hyperbolic model (RHM), non-rectangular hyperbolic model (NRHM), rectangular hyperbolic modified model (RHMM), exponential model (EM), and modified exponential model (MEM)—were employed to fit the light response data and analyze the effects of different CO2 concentrations and soil water contents on winter wheat photosynthetic characteristics. The results demonstrated that the rectangular hyperbolic modified model produced fitted values for both the light response curves and associated parameters that closely matched measured values, showing the best overall performance. As CO2 concentration increased, apparent quantum efficiency ( ), light saturation point (LSP), and maximum net photosynthetic rate (Pnmax) increased under all water treatments, while light compensation point (LCP) and dark respiration rate (Rd) decreased. This indicates that elevated CO2 effectively enhances light energy conversion efficiency and expands the range of light utilization, thereby improving photosynthetic capacity. Conversely, as soil water content decreased, LCP and Rd increased while , LSP, and Pnmax decreased. Although winter wheat can partially offset drought stress effects by increasing initial photosynthetic efficiency, drought stress still reduces photosynthetic capacity. Furthermore, increased CO2 concentration can compensate for the photosynthetic capacity reduction caused by drought stress.

Keywords: Winter wheat; Elevated CO2 concentration; Drought stress; Photosynthetic light-response model; Photosynthetic capacity

Introduction

Due to excessive fossil fuel consumption and deforestation, atmospheric CO2 concentration has been increasing at a rate of 1.5–2.0 mol · mol ^{1} annually [1], reaching 407.7 mol · mol ^{1} in 2016 [2] and projected to reach 700 mol · mol ^{1} by the end of the 21st century [3]. Along with rising greenhouse gas emissions, global climate change has altered precipitation patterns and increased regional drought frequency [4]. Winter wheat (*Triticum aestivum* L.), a C3 plant, is particularly sensitive to CO2 concentration changes. In the North China Plain, where rainfall during the winter wheat growing season can only meet one-third of the crop' s water requirements [5], investigating photosynthetic response curves and characteristics under varying CO2 concentrations and soil water contents holds significant importance.

Photosynthesis directly reflects plant responses to environmental conditions, and determining photosynthetic light response curves is essential for understanding plant photosynthetic traits. Through curve fitting analysis, important photosynthetic parameters can be estimated, including apparent quantum efficiency ( ), light compensation point (LCP), light saturation point (LSP), maximum net photosynthetic rate (Pnmax), and dark respiration rate (Rd). Numerous studies have shown that elevated CO2 concentration effectively increases plant Pnmax [6] and LCP [7], while decreasing soil water content reduces Pnmax, , and LCP [8-9]. Various models have been developed to study light response curves, with the rectangular hyperbolic model and non-rectangular hyperbolic model being most widely applied [10-14]. However, these two models cannot directly calculate light saturation intensity. Ye et al. [15-17] proposed a modified rectangular hyperbolic model that overcomes these limitations and can simulate photoinhibition phenomena. Zhang et al. [18] demonstrated that the exponential model provides more reasonable estimates of LSP and Pnmax for *Phyllostachys pubescens*. Chen et al. [19-20] applied the modified exponential model to analyze *Mirabilis jalapa*, sorghum, and barley, showing its accuracy in calculating saturation light intensity and maximum net photosynthetic rate for both C3 and C4 plants.

Although many studies have examined the effects of elevated CO2 and drought stress on crop photosynthesis, few have used different light response models to analyze the interactive effects of CO2 and soil moisture on photosynthetic characteristics. This study employed five models to fit winter wheat light response curves under different CO2 concentrations and soil water contents, aiming to identify the most suitable model for different growth conditions and to analyze the photosynthetic response patterns of winter wheat to these environmental factors, thereby providing a theoretical basis for high-yield, low-water-consumption wheat production under future climate scenarios.

Materials and Methods

Experimental Site and Design The experiment was conducted at the Luancheng Agro-ecosystem Experimental Station of the Chinese Academy of Sciences (37°53 N, 114°41 E), located in the central Taihang Mountain Piedmont Plain. The region features a semi-arid, semi-humid monsoon climate with scarce precipitation during the winter wheat growing season, averaging only 100 mm in normal years [21]. Two water treatment plots were established: suitable water condition (~75% field capacity) and drought stress (~55% field capacity). Each plot measured 5 m × 10 m, with 1.5 m isolation walls installed between plots to prevent lateral water exchange.

The experimental material was winter wheat cultivar ‘Kenong 199’ , sown on October 17, 2015 and harvested on June 5, 2016. Plants were grown in 60 cm row spacing with phosphate diammonium fertilizer applied at 562.5 kg · hm ^{2} during the growing season. Four treatments were established based on CO2 concentration and soil water content: (1) 400 mol · mol ^{1} CO with suitable water (W1); (2) 750 mol · mol ^{1} CO with suitable water (W2); (3) 400 mol · mol ^{1} CO with drought stress (D1); and (4) 750 mol · mol ^{1} CO with drought stress (D2).

Data Collection From May 10 to May 24, 2016 (grain-filling stage), measurements were taken on clear days between 9:00–11:30 AM using a Li-6400 portable photosynthesis system (Li-Cor Inc., USA) with an LI-6400-02B artificial light source. Atmospheric relative humidity was maintained at approximately 60% and temperature at 25 °C. Photosynthetically active radiation (PAR) gradients were set at 1500, 1400, 1200, 1000, 800, 600, 400, 200, 150, 100, 50, 20, and 0 mol · m ^{2} · s ^{1}, with CO concentrations set at 400 and 750 mol · mol ^{1}. To ensure consistent experimental conditions, three uniformly growing wheat plants were selected for flag leaf measurements in each treatment.

Light Response Curve Models Five light response curve models were employed:

1. **Rectangular Hyperbolic Model (RHM)** [22]:

$$P_n = \frac{\alpha I \cdot P_{nmax}}{\alpha I + P_{nmax}} - R_d$$

where P_n is net photosynthetic rate (mol · m ^{2} · s ^{1}), α is apparent quantum efficiency (mol · mol ^{1}), I is photon flux density (mol · m ^{2} · s ^{1}), P_{nmax} is maximum net photosynthetic rate (mol · m ^{2} · s ^{1}), and R_d is dark respiration rate (mol · m ^{2} · s ^{1}). This model has no extreme values and thus cannot directly estimate light saturation intensity.

2. **Non-Rectangular Hyperbolic Model (NRHM)** [22]:

$$P_n = \frac{\alpha I + P_{nmax} - \sqrt{(\alpha I + P_{nmax})^2 - 4\theta\alpha I \cdot P_{nmax}}}{2\theta} - R_d$$

   where θ is the convexity of the non-rectangular hyperbola and other parameters are as defined in Eq. (1). Like RHM, this model has no extreme values and cannot directly estimate light saturation intensity.

3. **Rectangular Hyperbolic Modified Model (RHMM)** [23]:

$$P_n = \frac{\alpha I}{1 + \beta I} \cdot \frac{1}{1 + \gamma I} - R_d$$

   where β and γ are model correction coefficients and other parameters are as defined in Eq. (1). This model has extreme values and can directly calculate LSP, LCP, and P_{nmax}.

4. **Exponential Model (EM)** [24]:

$$P_n = P_{nmax}(1 - e^{-\alpha I/P_{nmax}}) - R_d$$

   where all parameters are as defined in Eq. (1). This function also has no extreme values. Light saturation intensity is estimated as the light intensity corresponding to $P_n = 0.90P_{nmax}$ [25].

5. **Modified Exponential Model (MEM)** [20]:

$$P_n = \alpha(1 - \beta e^{-\gamma I})e^{-\varepsilon I} - R_d$$

   where α, β, γ, and ε are model coefficients and other parameters are as defined in Eq. (1).

To evaluate model performance, relative error (RE) was calculated as:

$$RE = \frac{|y - y_i|}{y} \times 100\%$$

where y and y_i are measured and fitted values of light response curve parameters, respectively. Smaller RE indicates better fit.

Results

Model Performance in Fitting Light Response Curves As shown in [Figure 1: see original paper], the rectangular hyperbolic model provided satisfactory fits for the W2 treatment but showed substantial deviations from measured values for W1, D1, and D2 treatments. Specifically, when PAR ranged from 600–1000 mol · m ^{2} · s ^{1}, fitted values for D1 and D2 were significantly lower than measured values. Moreover, when photoinhibition occurred in W1, D1, and D2 treatments (where net photosynthetic rate reached saturation and subsequently declined due to excess light energy [26]), the fitted values continued to increase, failing to capture the photoinhibition phenomenon. Similar patterns were observed for the non-rectangular hyperbolic model and exponential model, which also could not simulate photoinhibition because these three models are asymptotic functions without extreme values, causing estimated photosynthetic rates to increase indefinitely with PAR. In contrast, the rectangular hyperbolic modified model provided excellent fits for all treatments, with fitted values closely matching measured values and successfully capturing photoinhibition in W1, D1, and D2 treatments. The modified exponential model also simulated photoinhibition well for most treatments but showed substantial deviations between fitted and measured values for the D2 treatment.

Comparison of Fitted Parameters Photosynthetic parameters include apparent quantum efficiency ( ), light compensation point (LCP), light saturation point (LSP), maximum net photosynthetic rate (P_{nmax}), and dark respiration rate (R_d). Comparisons between fitted and measured values across treatments are presented in . Overall, the rectangular hyperbolic modified model provided the best parameter estimates, while other models showed large discrepancies for most parameters despite occasional close matches for individual parameters.

Apparent quantum efficiency ( ) is a key indicator of photosynthetic light energy conversion efficiency, with values of 0.04–0.07 typical for healthy field-grown plants [27]. As soil water content decreases, declines [28], while elevated CO2 enhances photosynthetic capacity, leading to increased values. Among the models, the rectangular hyperbolic model significantly overestimated , whereas other models produced more realistic estimates. For LSP estimation, the rectangular hyperbolic and non-rectangular hyperbolic models use linear equation solving methods that substantially underestimate LSP compared to measured values [15-17,29], consistent with many previous studies. The exponential model employs an arbitrary threshold of $0.9P_{nmax}$ [25] to estimate LSP, a method lacking biological significance that also failed to solve LSP for the D1 treatment. Both rectangular hyperbolic and non-rectangular hyperbolic models overestimated P_{nmax} compared to measured values [15-16,30-31]. Although the modified exponential model could simulate photoinhibition, its fitted parameters deviated substantially from measured values, resulting in poorer performance than the rectangular hyperbolic modified model.

To further quantify model deviation, relative error analysis was performed. As shown in [Figure 2: see original paper], the rectangular hyperbolic modified model produced the smallest relative errors across all parameters and treatments, with particularly excellent performance for P_{nmax} and LSP. The other four models showed small relative errors only for certain parameters but could not achieve satisfactory overall performance.

Effects of CO2 Concentration and Soil Water Content on Photosynthesis Given its superior performance, the rectangular hyperbolic modified model was selected to analyze the effects of CO2 concentration and soil water content on flag leaf photosynthesis during the grain-filling stage. As shown in [Figure 3: see original paper], when PAR was below 400 mol · m^{2} · s^{1}, P_n in all treatments responded sensitively and increased rapidly with PAR. Above 400 mol · m^{2} · s^{1}, the rate of increase gradually slowed. However, when PAR exceeded 1000 mol · m^{2} · s^{1}, differential responses emerged among treatments. For D1 and D2 treatments, P_n reached light saturation at approximately 1100 mol · m^{2} · s^{1}, while W1 treatment saturated at approximately 1300 mol · m^{2} · s^{1}, after which P_n declined with increasing PAR, indicating photoinhibition. In contrast, W2 treatment showed no light saturation, with P_n continuing to increase across all PAR levels, demonstrating that elevated CO2 significantly enhances light use efficiency and promotes photosynthesis.

Under identical light conditions, W2 treatment exhibited the highest P_n, while D1 treatment showed the lowest, indicating that both elevated CO2 and increased soil water content enhance net photosynthetic rate and photosynthetic capacity. Notably, when PAR ranged from 200–1300 mol · m^{2} · s^{1}, P_n under D2 treatment was significantly higher than under W1 treatment, suggesting that CO2 effects can exceed soil water effects within certain light intensity ranges and that elevated CO2 can partially compensate for photosynthetic rate reductions caused by water deficit.

Further analysis of photosynthetic parameters revealed that , a critical indicator of light energy conversion efficiency [32], was highest under W2 treatment, similar between W1 and D1 treatments, and lowest under D1 treatment. This demonstrates that both elevated CO2 and adequate soil moisture significantly improve light energy conversion efficiency and maintain high photosynthetic capacity. Maximum net photosynthetic rate (P_{nmax}), representing maximum leaf photosynthetic capacity [33], was highest under W2 treatment, followed by W1, and lowest under D1. Specifically, P_{nmax} increased by 32.77% in W2 compared to W1, while the increase was 48.28% in D2 compared to D1, indicating that CO2 enhancement promotes photosynthetic capacity more effectively under drought stress than under suitable water conditions. Additionally, P_{nmax} decreased by 43% in D1 compared to W1, but only by 24% in D2 compared to W2, further confirming the compensatory effect of elevated CO2 on drought-induced photosynthetic decline.

Light compensation point (LCP) and light saturation point (LSP) reflect a plant' s ability to utilize weak and strong light, respectively [27]. Lower LCP indicates stronger weak-light utilization capacity, while higher LCP indicates stronger strong-light utilization capacity. Dark respiration rate (R_d) reflects metabolic activity [34]. Elevated CO2 in W2 treatment reduced LCP and R_d by 31% compared to W1 while substantially increasing LSP, demonstrating that elevated CO2 expands the range of light utilization, enhances ecological adaptability to light conditions, and reduces metabolic rates, thereby improving photosynthesis—a phenomenon consistent with the "CO2 fertilization effect" reported by Ainsworth et al. [35] and Long et al. [36]. Under drought stress (D1), both

LCP and R_d were lower than in W1, indicating that drought-stressed wheat enhances initial photosynthetic efficiency and reduces physiological metabolism to cope with water deficit [37]. However, LSP and P_{nmax} remained lower than in W1, confirming that although wheat can partially offset water stress through increased initial photosynthetic efficiency, drought stress ultimately reduces photosynthetic capacity.

Discussion

Comparative analysis of the five models (rectangular hyperbolic, non-rectangular hyperbolic, rectangular hyperbolic modified, exponential, and modified exponential) across different CO2 concentrations and soil water contents demonstrated that the rectangular hyperbolic modified model is most suitable for fitting winter wheat light response curves and parameters under all treatment conditions. This model successfully simulated photoinhibition phenomena occurring under low CO2 and low soil water conditions where plants cannot utilize strong light effectively.

Analysis of parameters fitted by the rectangular hyperbolic modified model revealed that elevated CO2 concentration effectively increased , LSP, and P_{nmax} while decreasing LCP and R_d, thereby enhancing light energy conversion efficiency, maximum net photosynthetic rate, light utilization range, and initial photosynthetic efficiency. This confirms that elevated CO2 significantly enhances winter wheat photosynthetic capacity. Under low soil water content, although wheat increased initial photosynthetic efficiency to partially offset drought effects, , LSP, and P_{nmax} remained substantially lower than under suitable water conditions, indicating that drought stress significantly reduces photosynthetic capacity and weakens photosynthesis. Furthermore, elevated CO2 provided compensatory effects against drought-induced photosynthetic decline, with CO2 enhancement being more pronounced under drought stress than under suitable water conditions.

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Note: Figure translations are in progress. See original paper for figures.