

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

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Date: 2017-11-09T00:00:00+00:00

Abstract

Photosynthesis is an important indicator for measuring plant responses to the environment, and by fitting light-response curves to quantify photosynthetic characteristics, the self-regulation and adaptation mechanisms of plants under different growth environments can be revealed from the perspective of physiological mechanisms. In this study, the Li-6400 portable photosynthesis system was used to measure the light-response curves of flag leaves at the grain-filling stage of winter wheat under four different treatment conditions, 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), and the effects of different CO₂ concentrations and soil water contents on the photosynthetic characteristics of winter wheat were analyzed. The results showed that the Modified Rectangular Hyperbola Model produced fitted values for both the light-response curves and light-response curve parameters of winter wheat under various treatments that were relatively close to the measured values, exhibiting the best fitting performance; with increasing CO₂ concentration, the apparent quantum efficiency (Φ_{app}), light saturation point (LSP), and maximum net photosynthetic rate (P_{nmax}) of winter wheat under various water treatments increased, while the light compensation point (LCP) and dark respiration (R_d) decreased, that is, elevated CO₂ concentration can effectively increase the light energy conversion efficiency and light energy utilization range of winter wheat, and enhance its photosynthetic capacity; with decreasing soil water content, the light compensation point (LCP) and dark respiration rate (R_d) of winter wheat increased, but the apparent quantum efficiency (Φ_{app}), light saturation point (LSP), and maximum net photosynthetic rate (P_{nmax}) decreased, that is, although winter wheat can offset some effects of drought stress by increasing initial photosynthetic efficiency, drought stress still reduces the photosynthetic capacity of

winter wheat; furthermore, increased CO₂ concentration can offset part of the photosynthetic capacity reduction in winter wheat caused 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 responses to environmental conditions. By fitting light response curves to quantify photosynthetic characteristics, we can elucidate the regulatory and adaptive mechanisms of plants under different growth conditions from a physiological perspective. This study measured the 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—the 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 the effects of different CO₂ concentrations and soil water contents on winter wheat photosynthetic characteristics were analyzed. 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, yielding the best overall fit. As CO₂ concentration increased, the apparent quantum efficiency (Φ_{app}), light saturation point (LSP), and maximum net photosynthetic rate (P_{nmax}) of winter wheat increased under all water treatments, while the light compensation point (LCP) and dark respiration rate (R_d) decreased. This indicates that elevated CO₂ concentration effectively enhances the light energy conversion efficiency and utilization range while improving the photosynthetic capacity of winter wheat. Conversely, as soil water content decreased, LCP and R_d increased, whereas Φ_{app} , LSP, and P_{nmax} decreased. This suggests that although winter wheat can partially offset drought stress effects by increasing initial photosynthetic efficiency, drought stress still reduces its photosynthetic capacity. Furthermore, increased CO₂ concentration can compensate for the photosynthetic capacity decline caused by drought stress.

Keywords: Winter wheat; CO concentration enhancement; Drought stress; Photosynthetic light-response model; Photosynthetic capacity

1.1 Experimental Site and Methods

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. Two water treatment plots were established: suitable water conditions (approximately 75% field capacity) and drought stress conditions (approximately 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 (*Triticum aestivum* L.) cultivar ‘Kenong 199’, sown on October 17, 2015, and harvested on June 5, 2016. Wheat was planted in rows spaced 60 cm apart, with 562.5 kg · hm⁻² of diammonium phosphate applied during the growing season. Four treatments were established based on different CO₂ concentrations and soil water contents: (1) 400 mol · mol⁻¹ CO₂ with suitable water (W1); (2) 750 mol · mol⁻¹ CO₂ with suitable water (W2); (3) 400 mol · mol⁻¹ CO₂ with drought stress (D1); and (4) 750 mol · mol⁻¹ CO₂ with drought stress (D2). Measurements were taken during the wheat grain-filling stage from May 10 to May 24, 2016, on clear days between 9:00 and 11:30 AM using a Li-6400 portable photosynthesis system (Li-Cor Inc., USA) equipped with an LI-6400-02B artificial light source. During measurements, atmospheric relative humidity was approximately 60%, temperature was set at 25 °C, and photosynthetically active radiation (PAR) gradients (mol · m⁻² · s⁻¹) were set at 1,500, 1,400, 1,200, 1,000, 800, 600, 400, 200, 150, 100, 50, 20, and 0. CO₂ concentrations were set at 400 mol · mol⁻¹ and 750 mol · mol⁻¹. To ensure consistent experimental conditions across treatments, three wheat plants with uniform growth were selected for flag leaf measurements in each treatment group.

1.2 Light Response Curve Models

The following light response curve models were employed:

Rectangular Hyperbolic Model (RHM):

$$P_n = \frac{\alpha I P_{n \max}}{\alpha I + P_{n \max}} - R_d \quad (1)$$

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), $P_{n \max}$ is maximum net photosynthetic rate (mol · m⁻² · s⁻¹), and R_d is dark respiration rate

($\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). This model is an asymptotic function without extreme values, thus it cannot directly estimate light saturation intensity.

Non-Rectangular Hyperbolic Model (NRHM):

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

where θ is the convexity of the non-rectangular hyperbola, and other parameters are as defined in Equation (1). Like the rectangular hyperbolic model, this is also an asymptotic function without extreme values, preventing direct estimation of light saturation intensity.

Rectangular Hyperbolic Modified Model (RHMM):

$$P_n = \frac{\alpha I}{1 + \beta I + \gamma I^2} - R_d \quad (3)$$

where β and γ are model correction coefficients, and other parameters are as defined in Equation (1). This model has extreme values and can directly calculate light saturation point, light compensation point, and maximum net photosynthetic rate from Equation (3).

Exponential Model (EM):

$$P_n = P_{n \max}(1 - e^{-\alpha I/P_{n \max}}) - R_d \quad (4)$$

where all parameters are as defined in Equation (1). This function also lacks extreme values; light saturation intensity is estimated by assuming the light intensity corresponding to $P_n = 0.90P_{n \max}$ as the saturation point.

Modified Exponential Model (MEM):

$$P_n = \alpha I e^{-\beta I} + \gamma I - R_d \quad (5)$$

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

To better evaluate the agreement between fitted and measured light response curve values, relative error (RE) was defined as:

$$RE = \frac{|y - y_i|}{y} \times 100\% \quad (6)$$

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

2.1 Comparison of Model Fits to Light Response Curves

As shown in [Figure 1: see original paper], the rectangular hyperbolic model provided a reasonable fit for the light response curve of winter wheat under the W2 treatment. However, for W1, D1, and D2 treatments, fitted values differed substantially from measured values. When PAR ranged from 600 to 1,000 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, the model underestimated values for D1 and D2 treatments. Furthermore, when winter wheat under W1, D1, and D2 treatments exhibited photoinhibition—where net photosynthetic rate gradually declined after reaching saturation due to excess light energy—the fitted values continued to increase, failing to capture the photoinhibition phenomenon. Figures 1b and 1d reveal that the non-rectangular hyperbolic model and exponential model produced similar fitting results to the rectangular hyperbolic model, showing good performance for W2 but inability to simulate photoinhibition under W1, D1, and D2 treatments. This limitation arises because these three models are asymptotic functions without extreme values, causing estimated net photosynthetic rates to increase continuously with PAR. In contrast, Figure 1c demonstrates that the rectangular hyperbolic modified model provided excellent fits for all treatments, with fitted values closely matching measured values and successfully capturing photoinhibition under W1, D1, and D2 treatments. Figure 1e shows that while the modified exponential model performed well for W2 and could simulate photoinhibition across treatments, it produced substantial deviations between fitted and measured values for the D2 treatment.

2.2 Comparison of Fitted Parameters for Winter Wheat Light Response Curves

Light response curve parameters include apparent quantum efficiency (ϕ), light compensation point (LCP), light saturation point (LSP), maximum net photosynthetic rate ($P_{n\max}$), and dark respiration rate (R_d). Comparisons between fitted and measured values across models are presented in . Comprehensive comparison reveals that the rectangular hyperbolic modified model provided the best parameter fits across all treatments, while other models showed large discrepancies between fitted and measured values for most parameters, despite occasional close matches for individual parameters. Apparent quantum efficiency (ϕ) is a key indicator of photosynthetic light energy conversion efficiency; under field conditions, values for healthy plants typically range from 0.04 to 0.07, decreasing with soil water content and increasing with CO_2 concentration due to the fertilization effect enhancing photosynthetic capacity. Among the models, the rectangular hyperbolic model substantially overestimated ϕ values, whereas other models produced more realistic estimates. The rectangular hyperbolic and non-rectangular hyperbolic models calculate LSP by solving linear equations, yielding fitted values far below measured values—a finding consistent with numerous studies. The exponential model estimates LSP using the light intensity corresponding to 0.9 $P_{n\max}$, a method lacking biological significance and introducing artificial bias, and it failed to solve for LSP under D1 treatment.

Both rectangular and non-rectangular hyperbolic models overestimated P_{nmax} compared to measured values, consistent with previous research. Although the modified exponential model could simulate photoinhibition, its fitted parameters deviated substantially from measured values, resulting in poorer overall performance than the rectangular hyperbolic modified model.

To further quantify deviations between fitted and measured values, relative error analysis was performed on light response curve parameters. Smaller relative errors indicate closer agreement and higher fitting precision. As shown in [Figure 2: see original paper], the rectangular hyperbolic modified model produced small relative errors for all parameters across treatments, with the smallest overall fitting error and values closest to measurements, particularly for P_{nmax} and LSP. The remaining four models showed small relative errors only for isolated parameters, failing to achieve comprehensive fitting quality across all parameters.

2.3 Effects of Different CO₂ Concentrations and Soil Water Contents on Winter Wheat Photosynthesis

Given the superior performance of the rectangular hyperbolic modified model in simulating light response curves and parameters, this model was selected to analyze the effects of different CO₂ concentrations and soil water contents on flag leaf photosynthesis during the grain-filling stage. As shown in [Figure 3: see original paper], when PAR was below $400 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, P_n in all treatments responded sensitively to PAR, increasing rapidly with light intensity. When PAR exceeded $400 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, the rate of P_n increase gradually slowed. However, when PAR surpassed $1,000 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, differential responses emerged due to CO₂ concentration and soil water content variations. Under D1 and D2 treatments, P_n reached light saturation at approximately $1,100 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, after which P_n decreased with increasing PAR, exhibiting photoinhibition. In contrast, under W2 treatment, P_n continued to increase with PAR, showing no light saturation. This demonstrates that elevated CO₂ concentration significantly enhances light use efficiency and promotes photosynthesis in winter wheat. Under identical light conditions, W2 treatment produced the highest P_n , while D1 treatment yielded the lowest, indicating that both elevated CO₂ concentration and soil water content increase net photosynthetic rate and enhance photosynthetic capacity. Notably, when PAR ranged from 200 to $1,300 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, P_n under D2 treatment was significantly higher than under W1 treatment, suggesting that under certain light intensities, CO₂ effects exceed soil water content effects, and increased CO₂ concentration can compensate for photosynthetic rate reductions caused by water deficit.

Further analysis of light response parameters across treatments revealed that Φ_{psII} , a critical indicator of photosynthetic light energy conversion efficiency, was highest under W2 treatment, similar between W1 and D1 treatments, and lowest under D1 treatment. This confirms that elevated CO₂ concentration and soil water content significantly improve light energy conversion efficiency and

maintain high photosynthetic capacity. Maximum net photosynthetic rate (P_{nmax}) represents maximum leaf photosynthetic capacity under given conditions. P_{nmax} was highest under W2 treatment, significantly higher than W1, which in turn exceeded D1 treatment. Specifically, P_{nmax} increased by 32.77% from W1 to W2 treatment, but by 48.28% from D1 to D2 treatment, indicating that CO_2 elevation promotes photosynthetic capacity more strongly under drought stress than under suitable water conditions. Additionally, P_{nmax} decreased by 43% from W1 to D1 treatment, but only by 24% from W2 to D2 treatment, further demonstrating that elevated CO_2 concentration compensates for photosynthetic capacity decline induced by drought stress.

Light compensation point (LCP) and light saturation point (LSP) represent the abilities to utilize weak and strong light, respectively—lower LCP indicates stronger weak-light utilization, while higher LSP indicates stronger strong-light utilization. Dark respiration rate (R_d) reflects metabolic activity levels. Elevated CO_2 concentration in W2 treatment reduced LCP and R_d by 31% compared to W1 treatment, while substantially increasing LSP, indicating that CO_2 enrichment broadens the light intensity utilization range, enhances ecological adaptability to light, reduces metabolic rates, and improves photosynthesis, consistent with fertilization effects reported in the literature. Under drought stress (D1 treatment), LCP and R_d were lower than in W1 treatment, suggesting that drought-stressed wheat enhances weak-light utilization and reduces physiological metabolism to improve initial photosynthetic efficiency. However, LSP and P_{nmax} remained lower than in W1 treatment, indicating that although wheat can partially offset water stress effects through increased initial photosynthetic efficiency, drought stress still significantly reduces photosynthetic capacity.

In summary, comparison of the five models (rectangular hyperbolic, non-rectangular hyperbolic, rectangular hyperbolic modified, exponential, and modified exponential) for fitting light response curves and parameters under different CO_2 concentrations and soil water contents revealed that the rectangular hyperbolic modified model is suitable for all treatments and can effectively simulate photoinhibition under low CO_2 and low soil water conditions. Analysis of parameters fitted by this model demonstrated that elevated CO_2 concentration effectively increases apparent quantum efficiency (Φ_{app}), light saturation point (LSP), and maximum net photosynthetic rate (P_{nmax}) while decreasing light compensation point (LCP) and dark respiration rate (R_d), thereby enhancing light energy conversion efficiency, maximum net photosynthetic rate, light utilization range, and initial photosynthetic efficiency. Although wheat under low soil water content can partially compensate for drought stress effects by increasing initial photosynthetic efficiency, Φ_{app} , LSP, and P_{nmax} remain significantly lower than under suitable water conditions, indicating that drought stress substantially reduces photosynthetic capacity and weakens photosynthesis. Furthermore, elevated CO_2 concentration provides compensatory effects against photosynthetic decline caused by drought stress, with CO_2 enhancement effects on photosynthetic capacity being greater under drought stress than under suitable water conditions.

Acknowledgments

We thank Zhao Yanqian (Hebei GEO University), An Sai (Hebei University of Science and Technology), and Ren Xiaodong (Qinghai Normal University) for their assistance with this experiment.

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