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Response of photosynthesis to light and CO_2 concentration in spring wheat under progressive drought stress

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Abstract

Background Global climate change significantly affects photosynthesis in spring wheat. However, the successive dynamic effects of multiple environmental interactions on photosynthesis in spring wheat have been inadequately investigated. This study conducted pot control experiments to determine photosynthesis characteristics, namely light and CO_2 response curves, in spring wheat under progressive drought stress.

Results Progressive drought stress caused all parameters of the light response curve to decrease logistically and all parameters of the CO_2 response curve to change exponentially. There were noticeable thresholds for these parameter changes. The ability of spring wheat to utilize light was weakened by progressive drought stress. Under all drought levels, the reduction in photosynthetic capacity was greater under strong light than under weak light. The effects on CO_2 utilization and the corresponding photosynthetic capacity depended on the drought level and CO_2 concentration. The optimal light intensity (I_{opt}) for spring wheat showed a logistic decreasing trend under progressive drought stress. Unexpectedly, the optimal atmospheric CO_2 concentration (CO_{2opt}) remained at 800 μmol·mol^{-1} under drought stress, which was less severe than extreme drought.

Conclusions Our results showed that progressive drought stress, combined with different environmental factors, had distinct impacts on the photosynthetic efficiency and carbon assimilation capacity of spring wheat, providing a basis for rational carbon and water resource utilization in spring wheat under climate change.

Keywords Progressive drought stress, Mechanistic model, Photosynthesis response curve, Optimal light intensity, Optimal atmospheric CO_2 concentration

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Background

Photosynthesis is the process by which organisms use light energy to convert carbon dioxide and water into organic matter, making it one of the most important biochemical processes on Earth [1, 2]. It not only provides energy for plants and other organisms but also participates in the global energy and material cycle, which is essential for maintaining the atmospheric carbon–oxygen balance and ecosystem stability.

Plant photosynthesis is influenced by its own genetic characteristics. In addition, external environmental factors have an important impact on it [3, 4]. As a primary source of energy, light is one of the most important environmental factors for plant growth [5, 6] and provides energy for photosynthesis [7]. Before the light saturation point, the photosynthetic rate increases with increasing light intensity, but after this point, the photosynthetic rate does not change. Light inhibition occurs and photosynthetic function is significantly reduced when plants are exposed to strong light for a long time [8]. CO_2 provides the raw material for photosynthesis [9], and increasing its concentration significantly increases the photosynthetic rate of plants. However, long-term exposure to high CO_2 concentrations has varying effects on photosynthesis during plant growth. Certain species enhance carbon assimilation via photosynthetic induction, while others exhibit a minimal response [10]. Insufficient amounts of water, a raw material for photosynthesis, indirectly decreases the photosynthetic rate in many ways, for example, by reducing the stomatal conductance of leaves, which affects the entry of CO_2 into leaves; by reducing mesophyll conductance, which hinders CO_2 transfer within leaves; by inhibiting the carboxylation ability of mesophyll cells; by damaging photosynthetic organs; and by accelerating starch hydrolysis in leaves, which slows the output of photosynthetic products [11–14]. These pathways are the main causes of the decrease in the photosynthetic rate during different soil moisture stages.

Influenced by human activities, the global environment is undergoing climate change characterized by global warming. The global atmospheric CO_2 concentration increased from 280 ppm before the Industrial Revolution to more than 413.2 ppm in 2020 and is increasing at a rapid rate of more than 2.1 ppm per year [15, 16]. Climate warming due to an increase in greenhouse gases, such as CO_2, has led to extreme weather and climate events, such as drought, which has changed in intensity, frequency, and duration over the last few decades in regions worldwide [17, 18]. This trend is expected to persist and intensify. Crops in arid and semi-arid regions will inevitably face the dual challenges of progressive drought stress and elevated atmospheric CO_2 concentrations due to global climate change. This will severely affect the carbon assimilation processes of crops and the functions of terrestrial ecosystems [19]. Therefore, investigating the photosynthetic response mechanisms of crops to global environmental changes is crucial for ensuring food security and developing strategies to adapt to and mitigate adverse effects in arid and semi-arid regions.

The photosynthesis–light response curve reflects the change in the plant photosynthetic rate with increasing and decreasing light intensity, and the CO_2 response curve reflects the response of the photosynthetic rate to variations in the CO_2 concentration. Based on these curves, the corresponding photosynthetic physiological parameters can be determined. These parameters play important roles in determining the operation status, photosynthetic capacity, and photosynthetic efficiency of photosynthetic organs and the extent to which they are affected by environmental changes [20]. Research has shown that water stress in plants decreases the characteristic parameters of the light response curve, such as the maximum net photosynthetic rate, apparent quantum efficiency, and light saturation point [21, 22]. However, the dark respiration rate may exhibit opposite trends depending on the species [22, 23]. For spring wheat, a staple crop growing in the arid and semi-arid regions of northwest China, it is unclear whether the responses of these characteristics to water stress are consistent with previous studies.

When conducting drought-related experiments, studies have often focused on several discrete points that represent different drought levels. It leads to a lack of understanding of the successive dynamic changes in response parameters when soil water continues to decline during drought development. The superposition of external environmental factors has an interactive impact on photosynthesis. For example, in plants, elevated CO_2 levels may mitigate oxidative damage caused by drought stress to some extent and significantly alleviate the negative effects of drought stress on the photosynthetic rates [24]. But the frequent occurrence of stress diminishes such positive effects [25], with severe drought stress causing such positive effects to disappear [26]. However, the impact of drought stress on the photosynthetic response of plants to changes in CO_2 concentrations remains poorly understood. In addition, the physiological parameters of photosynthesis display an obvious threshold effect between different drought stress stages during soil water reduction. Thus, progressive drought can be divided into different intensity levels [11]. The threshold effects under the combined influence of multiple factors warrant further investigation.

Therefore, pot water-control simulation experiments were conducted in this study to investigate how progressive drought stress influences the photosynthetic efficiency of spring wheat under varying light intensities and CO_2 concentrations. The artificial light sources and external CO_2 small steel gas cylinders were used to establish different light intensity and CO_2 concentration gradients. We hypothesized that (1) progressive drought stress causes the photosynthetic parameters of spring wheat to decrease in response to light intensity and CO_2; (2) as drought severity increases, light and CO_2 utilization and corresponding photosynthetic capacity gradually diminish; and (3) the optimal light intensity and optimal CO_2 concentration of spring wheat decrease under progressive drought stress. The results of this study provide a theoretical foundation for the rational and efficient utilization of resources, such as carbon, water, and light, by spring wheat when considering global climate change.

Methods

Experiment site

The experiment was conducted at two sites. The Dingxi Arid Meteorology and Ecological Environment Field Science Experiment Base of the China Meteorological Administration (35°35' N, 104°37' E, 1896.7 m) belongs to the semi-arid climate zone of the Loess Plateau. In this region, precipitation is relatively scarce (approximately 386 mm annually), with high evaporation rates and a relatively dry climate. Agricultural production is constrained by water availability, but rain-fed agriculture is practiced in these areas. The Wuwei Desert Ecology and Agricultural Meteorological Experiment Station of Gansu Province (37°53' N, 102°53' E, 1534.8 m) belongs to the arid climate zone of the Loess Plateau. Precipitation is extremely scarce here, and evaporation is tremendously high, resulting in a particularly dry climate. Agricultural production is severely constrained by water availability and typically relies on irrigation. The two experimental stations were previously described by Chen et al. [11].

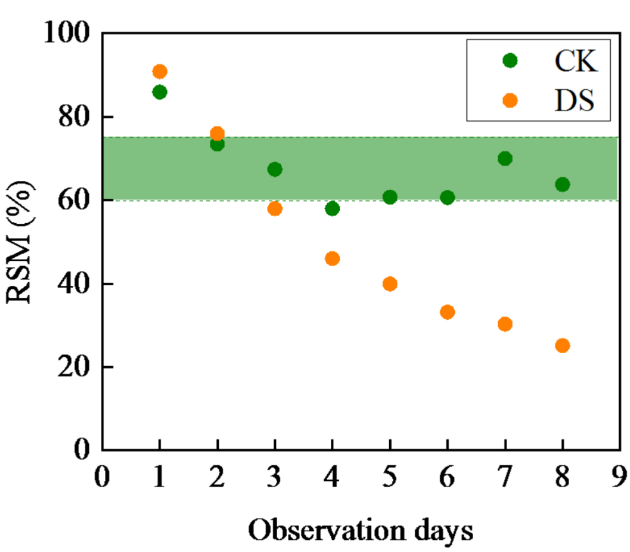

Fig. 1 Changes in the relative soil moisture (RSM) during the observation period. CK represents the control. DS represents drought stress. The green-shaded area represents the 95% confidence interval of CK

Experimental design

The controlled pot experiments were conducted with spring wheat as the experimental material in this study. The two experimental varieties used were "Dingxi Xin 24" (at Dingxi Station) and "Yongliang 4" (at Wuwei Station). Photosynthesis–light response curves were observed in 2015 (at Dingxi Station) and 2017 (at Wuwei Station), and the CO_2 response curves were observed in 2017 and 2021 (all at Dingxi Station). Soil in the pots was collected from the field at a depth of 0–30 cm, dried, sieved, mixed with fertilizer and placed in cylindrical pots (29 cm in diameter, 45 cm in depth). The weights of empty pots (W_p) and pots filled with dry soil (W_d) were measured using a balance with 0.01 g accuracy. The plants were broadcasted for sowing in mid- or late March, with approximately 30 seeds per pot (0.9 g) and a seeding depth of 5 cm.

Two water treatments were used in the experiments. (1) Progressive drought stress (DS): the pots were shaded and not watered during the observation period. (2) Control (CK): the pots were watered to the field capacity daily at dusk. Field capacity here was determined by an internal standard protocol of the Meteorological Bureau of Gansu Province, China. Each treatment had three replicates. Prior to the experiment observation, all plants were uniformly watered to ensure normal growth. When it came to the critical water demand period of spring wheat, jointing stage to the heading stage [27], water control and observation commenced. Until the photosynthesis rate of the DS group approached 0, the observation ended. Soil moisture was monitored daily by weighing at dusk. The soil water status during the observation period is shown in Fig. 1, which was drawn using Origin 9.0.

Observations

Photosynthesis–light response curve. Measurements were recorded daily from 8:30 am to 12:00 pm using an LI-6400 portable photosynthesis measuring system (Li-cor, Lincoln, NE, USA) equipped with a red–blue LED light source (6400-02B). The temperature was set to 25 °C. The ambient CO_2 concentration was set to 400 $\mu mol \cdot mol^{-1}$, and the light intensity was set to 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The youngest fully expanded leaves were measured after induction for 30 min. The parameters of photosynthetic active radiation (PAR) were set to 0, 15, 30, 60, 120, 200, 300, 600, 900, 1200, 1500, 1800, and 2100 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Photosynthesis–CO_2 response curve. The same settings as those for the light response curve were used during induction. After 30 min, the CO_2 concentration in the sample chamber was set to 400, 200, 100, 50, 400, 600, 800, 1000, and 1200 μmol mol^{-1} using an external small steel cylinder, and then, the observations began.

Soil moisture. The total weight of the pot was measured daily and recorded as the wet weight (W_w) after water control. The relative soil moisture (RSM) was calculated according to the following formula: RSM = ((W_w-W_d)/(W_d-W_p))/$\theta_f \times 100\%$, where θ_f is the field capacity.

Photosynthesis model selection

Light response model. Ye et al. mechanistic model [4] is used to fit the photosynthesis–light response curve of C3, C4, and CAM plants under any environmental conditions (including extreme environments) and demonstrates the light inhibition phenomenon in plants (for details, please see http://photosynthetic.sinaapp.com/index.html). The initial slope of the light response curve (α_p), light compensation point (I_c), dark respiration rate (R_d), apparent quantum efficiency (AQY), maximum net photosynthetic rate (A_{max-I}), and corresponding saturation light intensity (I_{sat}) can be obtained using this model. Therefore, it has been widely cited and applied [28–30]. Based on these advantages, we used this model to simulate the light response curves of spring wheat and obtain related parameters. Among the light response parameters, A_{max-I} represents the maximum photosynthetic capacity. Both α_p and AQY are important indicators for evaluating photosynthetic efficiency and are related to the ability of photosynthetic pigment molecules to absorb photons. The difference between them is that α_p refers to the ability of photosynthetic pigment molecules to convert light energy into chemical energy after photons are absorbed during the initial stage of photosynthesis, in theory. However, AQY refers to the same ability but during the process of photosynthesis and, in practice, after being influenced by other factors. This makes AQY a more important indicator for practical applications. Compared to A_{max-I}, AQY reflects the photosynthetic capacity of plants under weak light conditions [31]. I_{sat} reflects strong light utilization, and I_c reflects the plant's ability to use weak light [32]. A smaller I_c value indicates a stronger ability to utilize weak light, and the greater the difference between I_{sat} and I_c, the stronger the ability of plants to use light. R_d reflects the respiration rate of plants under dark conditions. The lower R_d, the less respiration consumes, and the more conducive it is to photosynthetic product accumulation.

CO_2 response model. The CO_2 response model for photosynthesis from the same website was selected to simulate the CO_2 response curve. Because this study focused on the change in the net photosynthetic rate with the atmospheric CO_2 concentration (C_a) but not with the CO_2 concentration in leaves, C_a was used in the model instead of the intercellular CO_2 concentration (C_i). The parameters obtained were the initial slope of the atmospheric CO_2 concentration response curve (α_a), the CO_2 compensation point (C_{ac}), the photorespiration rate (R_{ap}), the maximum net photosynthetic rate (A_{amax-C}), and the corresponding saturation CO_2 concentration (C_{asat}). A_{amax-C} reflects the maximum photosynthetic capacity of plants under high atmospheric CO_2 concentration, and α_a is the initial CO_2 utilization efficiency, reflecting the photosynthetic capacity under low atmospheric CO_2 concentrations. C_{ac} reflects the ability of plants to use low CO_2 concentrations, and C_{asat} reflects the ability of plants to use high CO_2 concentrations. R_{ap} has the same meaning as R_d.

Determination of the optimal light intensity (I_{op}) and optimal CO_2 concentration (CO_{2op})

Under appropriate conditions, the photosynthesis–light response curve and CO_2 response curve of plants can generally be divided into two stages. Under theoretical conditions, photosynthetic rate first increases with the increasing light intensity or CO_2 concentration, and after reaching a certain threshold, the curve reaches the saturation point and enters a stable stage. However, in practice, C3 crops often fail to reach the saturation light intensity when the light intensity exceeds 2100 μmol·m^{-2}·s^{-1}, and the curve continues to increase slowly. For growers, the maximum photosynthetic rate corresponding to I_{sat} or C_{asat} is not the goal. Instead, a relatively high photosynthetic rate is pursued to limit unnecessary energy consumption. Therefore, an economically relatively optimal value needs to be determined. By analyzing the curve fit of the observed data, this study revealed that when the photosynthetic rate reached 90% A_{max}, all curves entered a relatively stable stage. Therefore, the corresponding light intensity or CO_2 concentration at 90% A_{max} was set as I_{opt} and CO_{2opt}, respectively.

Data analysis

The 99% confidence interval of the CK dataset for each parameter was determined using SPSS statistical software (version 19.0, IBM Electronics). Principal component analysis (PCA), curve fitting, and plotting were performed using Origin 9.0.

Results

Photosynthesis–light response curve parameters

The photosynthesis–light response curve parameters for spring wheat decreased to different degrees due to progressive drought stress. Under sufficient soil moisture, all parameters fluctuated around the mean value (Fig. 2). When the soil water was deficient, the parameters decreased with decreasing RSM. Critical thresholds were observed for parameter declines during progressive drought stress. Additionally, the threshold value at which all parameters began to decrease was slightly greater than

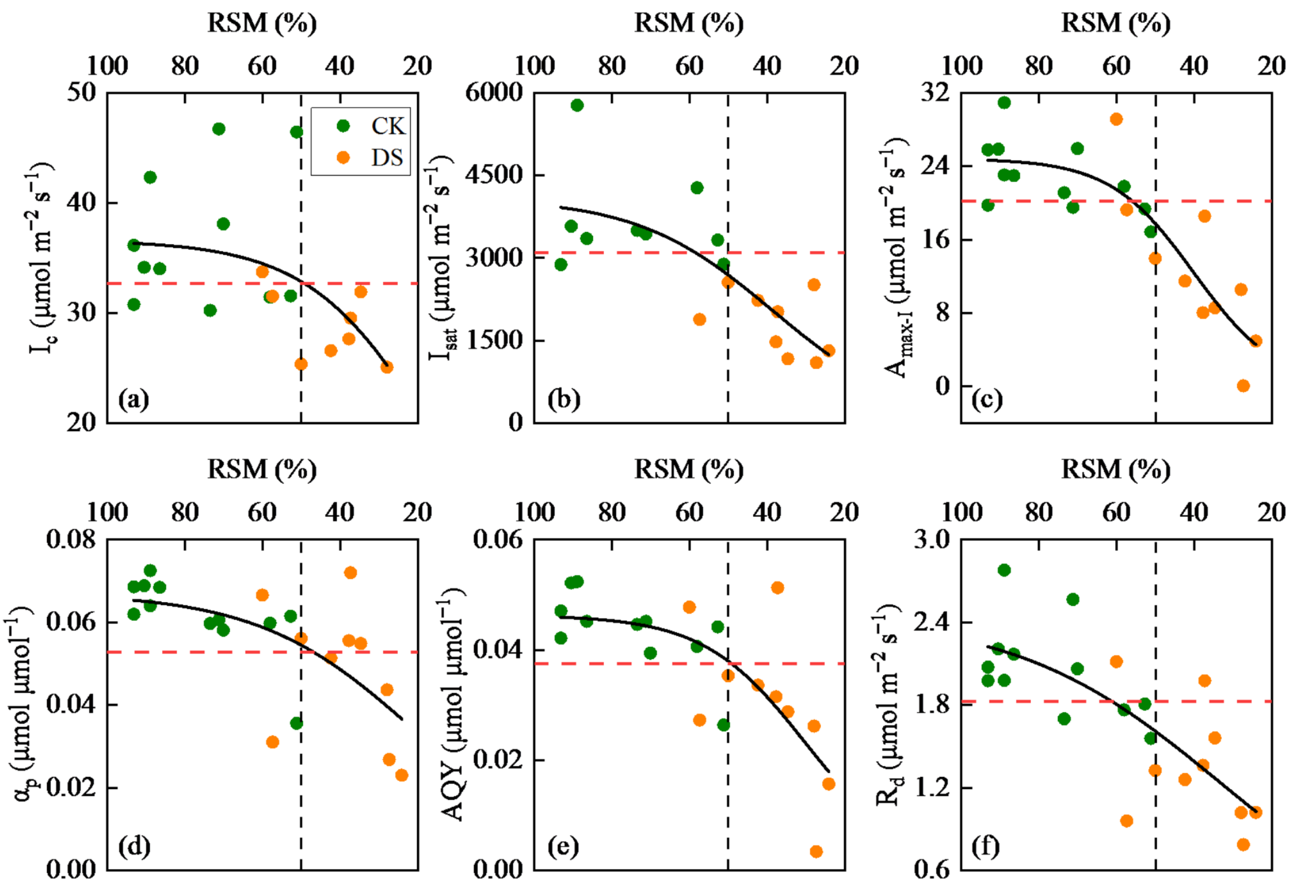

Fig. 2 Changes in photosynthesis–light response curve parameters ((**a**) I_c, (**b**) I_{sat}, (**c**) A_{max-I}, (**d**) α_p, (**e**) AQY, (**f**) R_d) of spring wheat under progressive drought stress. CK represents the control. DS represents drought stress. The solid black line represents the fitted curve derived from the logistic regression model. The solid dashed line represents the reference line (50% RSM). The red dashed line represents the lower 99% confidence interval of CK

Table 1 Relationships between the photosynthesis–light response curve parameters of spring wheat and RSM

Parameter	Fitted Equation	Adjusted R^2	F	Significance
I_c	$y=\frac{36.61}{1+e^{-0.06(x-15.04)}}$	0.3	215.4	0.000**
I_{sat}	$y=\frac{4091.58}{1+e^{-0.06(x-38.62)}}$	0.6	74.1	0.000**
A_{max-I}	$y=\frac{24.82}{1+e^{-0.09(x-40.14)}}$	0.8	169.2	0.000**
α_p	$y=\frac{0.07}{1+e^{-0.05(x-20.49)}}$	0.4	176.9	0.000**
AQY	$y=\frac{0.05}{1+e^{-0.08(x-30.2)}}$	0.6	137.3	0.000**
R_d	$y=\frac{2.45}{1+e^{-0.04(x-32.91)}}$	0.6	181.6	0.000**

Note: Symbol ** indicates level of significance at $P<0.01$

50% RSM. By fitting the relationship between the parameters and the RSM, the logistic model showed the best fitting effect, reaching a very significant level ($P<0.01$) (Table 1). Based on the fitted equation, the values of I_c, I_{sat}, A_{max-I}, α_p, AQY, and R_d decreased by 10.09, 26.68, 22, 11.62, 12.93, and 21.65%, respectively, when RSM was 50%, by 17.38, 42.01, 45.76, 21.13, 27.87, and 32.31%, respectively, when RSM was 40%, and by 28.19, 57.69, 69.4, 32.95, 47.28, and 43.52%, respectively, when RSM was 30%. Regardless of the drought development stage, A_{max-I} and I_{sat} were most affected by drought stress, followed by R_d, AQY, and α_p. I_c was least affected by drought stress. This indicates that progressive drought stress continuously reduced the photosynthetic capacity of spring wheat. The adverse effects on photosynthesis were greater under strong light than under weak light at all drought stages. Progressive drought stress enhanced the ability of spring wheat to use weak light but weakened its ability to use strong light, and the latter was more effective than the former. This indicates that drought stress shifted the use of light energy toward the weak light area and narrowed the range of available light energy, weakening spring wheat's ability to utilize light resources. In addition, the consumption of dark respiration was reduced, which had a certain compensatory effect on photosynthetic products. The changes in these parameters reflect the adverse impact of progressive drought stress on the photosynthetic response of spring wheat to light intensity.

Photosynthesis–CO_2 response curve parameters

Progressive drought stress had varying effects on the parameters of the photosynthesis–CO_2 response curve for spring wheat. The CK parameters changed little and mainly fluctuated (Fig. 3). When spring wheat was subjected to progressive drought stress, A_{amax-C}, α_a, and R_{ap} decreased with decreasing RSM after about 50% RSM. However, C_{ac} increased with decreasing RSM after about 30% RSM. C_{asat} showed little difference between DS and CK when the RSM was greater than 25% and decreased when the RSM was slightly greater than 20%. The exponential model provided the best fit for the relationships of all parameters with RSM, achieving statistical significance ($P < 0.01$) (Table 2). Based on the fitted equation, the values of C_{ac}, A_{amax-C}, α_a, and R_{ap} decreased by −3.93, 12.04, 11.41, and 6.92%, respectively, when RSM was 50%, by −11.38, 25.83, 28.91, and 17.73%, respectively, when RSM was 40%, and by −78.91, 54.45, 71.14, and 46.06%, respectively, when RSM was 30%. When 50, 40, and 30% RSM were considered as mild, moderate, and severe drought, respectively, A_{amax-C} was most affected under mild drought, and α_a was most affected under moderate drought. C_{ac} was most affected under severe drought but was least affected in the previous drought stage. Drought generally had little effect on C_{asat}, only decreasing under extreme drought conditions. This analysis showed that progressive drought stress caused the photosynthetic capacity of spring wheat to decrease under different CO_2 concentrations. High CO_2 concentrations had a stronger weakening effect on the photosynthetic capacity under

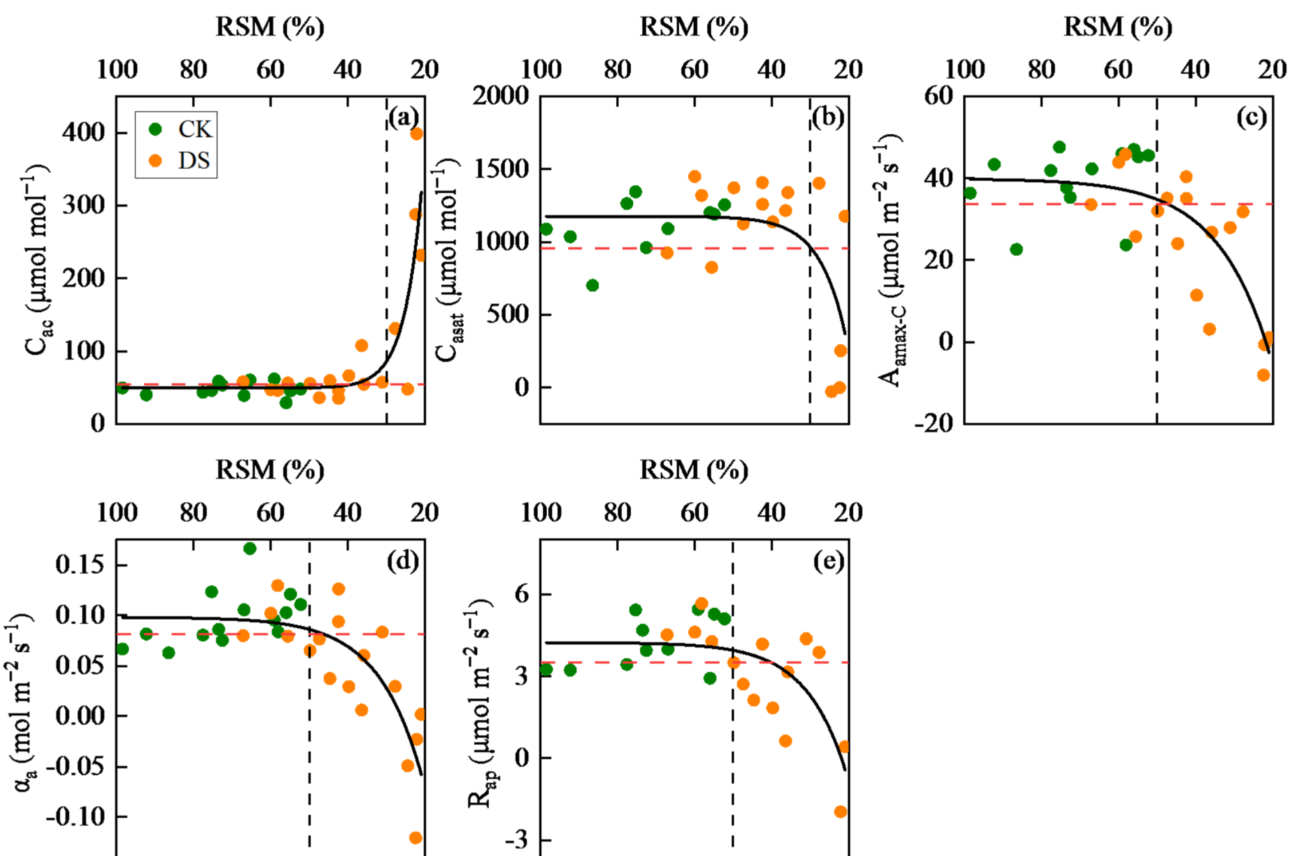

Fig. 3 Changes in photosynthesis–CO_2 response curve parameters ((**a**) C_{ac}, (**b**) C_{asat}, (**c**) A_{amax-C}, (**d**) α_a, (**e**) R_{ap}) of spring wheat under progressive drought stress. CK represents the control. DS represents drought stress. The solid black line represents the fitted curve derived from the exponential model. The solid, dashed line represents the reference line (30 or 50% RSM). The red dashed line represents the upper or lower 99% confidence interval of CK

Table 2 Relationships between the photosynthesis–CO_2 response curve parameters of spring wheat and RSM

Parameter	Fitted Equation	Adjusted R^2	F	Significance
C_{ac}	$y = 27104.36e^{\frac{-x}{4.54}} + 49.46$	0.7	39.0	0.000**
C_{asat}	$y = -17536.31e^{\frac{-x}{6.8}} + 1176.26$	0.4	6.4	0.000**
A_{amax-C}	$y = -195.65e^{\frac{-x}{13.69}} + 39.89$	0.6	20.8	0.000**
α_a	$y = -0.99e^{\frac{-x}{11.35}} + 0.1$	0.6	25.6	0.000**
R_{ap}	$y = -35.1e^{\frac{-x}{10.37}} + 4.24$	0.5	11.5	0.000**

Note: Symbol ** indicates level of significance at $P < 0.01$

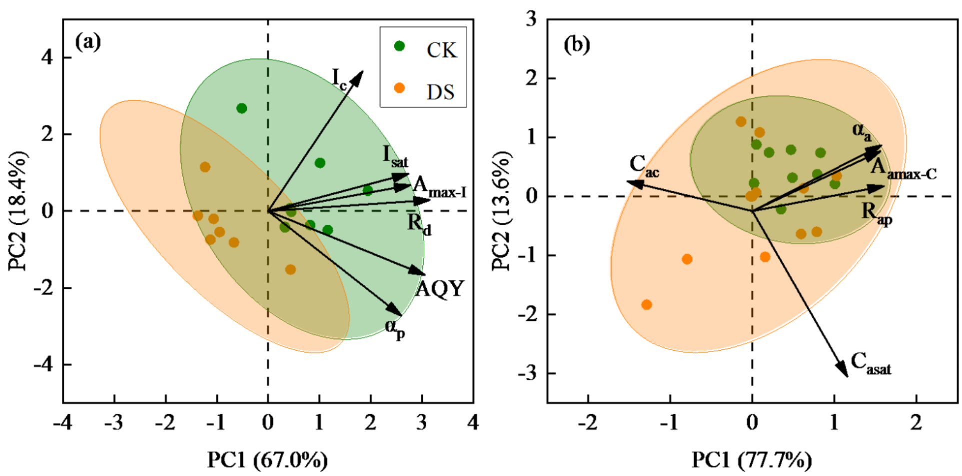

Fig. 4 PCA of the photosynthesis–light (**a**) and CO_2 (**b**) response curve parameters of spring wheat under progressive drought stress. CK represents the control. DS represents drought stress. The filled ellipses represent 95% confidence intervals

mild drought, and low CO_2 concentrations had a stronger weakening effect on the photosynthetic capacity under more severe drought. Less severe drought stress had no effect on the ability of spring wheat to use CO_2. However, severe drought weakened its ability to use low CO_2 concentrations, and extreme drought weakened its ability to use high CO_2 concentrations. The change in dark respiration had a beneficial effect on photosynthetic products. These results show that progressive drought stress has significant adverse effects on the photosynthetic response of spring wheat to the atmospheric CO_2 concentration.

PCA of photosynthesis response parameters

CK and DS samples exhibited distinct clustering within their respective groups for the light response parameters (Fig. 4(a)), and there was a clear boundary between the two groups. CK had good performance in the positive part of PC1, and DS had good performance in the negative parts of PC1 and PC2, indicating that there were certain differences between the two groups. However, the DS samples all fell within the 95% confidence interval of CK, and the directions of the confidence ellipses were the same, indicating that the difference between the groups was not significant; that is, the decreased amplitude of every parameter was basically equal under different drought intensities. In other words, the linearity of the light response curve exhibited certain but not significant changes under progressive drought stress. The angles between parameters were less than 90°, indicating positive correlations. I_{sat}, A_{max-I}, and R_d had relatively high correlations, indicating that they were similarly affected by drought. The correlation between α_p and AQY was relatively high, and these variables were similarly affected by drought. The loadings showed that the variable that contributed the most to PCA1 was R_d, followed by AQY and A_{max-I} and then by I_{sat}, α_p, and I_c.

Figure 4(b) shows that the confidence ellipse of CK was transverse and that of DS was oblique. Most DS samples fell within the 95% confidence interval of CK, but a few were outside due to the influence of C_{ac} and C_{asat}, resulting in a significant difference between the two groups. The correlation between A_{amax-C} and α_a was extremely high, and those between them and R_{ap} were high. These results indicate that these three parameters were similarly affected by progressive drought stress. However, C_{asat} was differently affected, and C_{ac} was oppositely

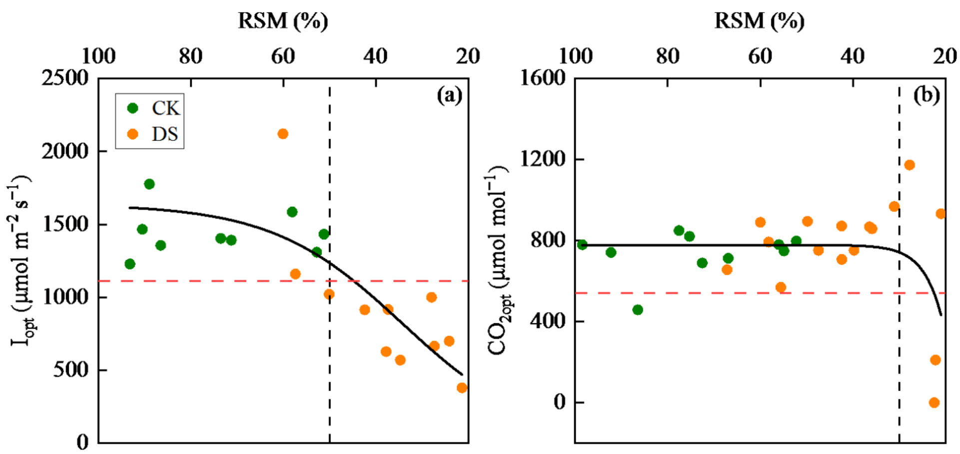

Fig. 5 Changes in I_{opt} (**a**) and CO_{2opt} (**b**) during photosynthesis in spring wheat under progressive drought stress. CK represents the control. DS represents drought stress. The solid black line represents the fitted curve. The solid dashed line represents the reference line (30 or 50% RSM). The red dashed line represents the lower 99% confidence interval of the dataset larger than 60% RSM in CK

Table 3 Relationships between I_{op} and CO_{2op} during photosynthesis for spring wheat and RSM

Parameter	Fitted Equation	Adjusted R^2	F	Significance
I_{opt}	$y = \frac{1638.79}{1+e^{-0.07(x-34.21)}}$	0.7	130.1	0.000**
CO_{2opt}	$y = -65107.03e^{\frac{-x}{4}} + 778.15$	0.2	2.2	0.137

Note: Symbol ** indicates level of significance at $P < 0.01$

affected. The loadings showed that the contributions of the parameters to PCA1 were similar to those of the light response parameters. R_{ap} had the largest loading, followed by α_a and A_{max-C}. C_{asat} and C_{ac} had the smallest.

Optimal light intensity (I_{opt}) and CO_2 concentration (CO_{2opt})

Progressive drought stress decreased the I_{opt} of spring wheat, and its impact on CO_{2opt} varied under different drought stages. As the optimal values in this study were based on I_{sat} and C_{asat}, I_{opt} and CO_{2opt} showed similar variation characteristics. The decreasing trend in I_{opt} with decreasing RSM followed an 'S' curve, with a threshold around 50% RSM, and was well-fitted by the logistic model ($P < 0.01$) (Fig. 5, Table 3). The latter remained stable from the non-drought to severe drought stages (RSM > 30%) and did not change as drought intensified. Under extreme drought (RSM < 30%), the values varied greatly, and increasing, unchanging, and decreasing cases were observed. Therefore, its trend under worsening drought conditions remained uncertain. The relationship between CO_{2opt} and RSM was fitted by common models, but the fitted effects did not reach a significant level ($\alpha = 0.05$). The exponential model had the best fitted effect among the models. Based on the traditional agricultural drought grades in China, progressive drought was divided into stages, and the value ranges of I_{opt} and CO_{2opt} were obtained at these stages. I_{opt} at 60% RSM and CO_{2opt} at 30% RSM were determined from the mean values of the scatterplot within the range before this point, and I_{opt} at 50, 40, and 30% RSM were calculated from the fitted curve. The final results after these figures were rounded to the nearest 100 are shown in Table 4.

Table 4 I_{opt} and CO_{2opt} during photosynthesis in spring wheat under different drought conditions

Drought level	RSM	I_{opt} (μmol m^{-2} s^{-1})	CO_{2opt} (μmol mol^{-1})
No drought	> 60%	1500	800
Mild drought	50–60%	1200–1500	800
Moderate drought	40–50%	1000–1200	800
Severe drought	30–40%	700–1000	800
Extreme drought	< 30%	< 700	uncertain

Discussion

This study demonstrated that progressive drought stress led to a consistent reduction in light response parameters. This could be explained by a series of shared physiological mechanisms, including stomatal regulation, chlorophyll degradation, enzyme inhibition, and electron transport chain efficiency reduction. Water stress reduces turgor pressure and stomatal closure [33] and limits the supply of CO_2, thereby inhibiting the dark reactions of photosynthesis and decreasing A_{max-I}. Restricting Rubisco enzyme activity and the regeneration capacity further exacerbate this phenomenon. The limitations of Rubisco enzyme activity and the regeneration capacity and the damage to the photosynthetic apparatus caused by increased reactive oxygen species accumulation also exacerbate this phenomenon. Water stress triggers chlorophyll degradation, affects light energy capture and transfer, weakens the light absorption and conversion efficiency of PSII and PSI, and reduces the efficiency of light energy conversion into chemical energy, thus decreasing AQY. As water availability decreases, enzyme conformation changes and activity are suppressed, slowing down enzymatic reaction rates. At the same time, the operational efficiency of the electron transport chain decreases [34], resulting in reduced ATP and NADPH synthesis. An insufficient energy supply weakens metabolic activity. These effects decrease R_d. Under the combined effects of chlorophyll degradation and reduced carbon dioxide, plants cannot perform effective photosynthesis under high light intensity, ultimately decreasing I_{sat}. This study showed that the decrease in R_d was more pronounced than that in AQY, indicating that a lower light intensity is sufficient to achieve a balance between photosynthesis and respiration under drought stress. Thus, I_c is reduced. However, unlike our findings, studies on oriental lily and common reed plants have shown that R_d and I_c increase in response to drought stress [22, 31], indicating that the effects of drought stress on the light response of plants may vary by species. We found that progressive drought stress continuously reduced the photosynthetic capacity of spring wheat, which is consistent with results for winter wheat [35]. The capacity of utilization and corresponding photosynthetic under strong light were more affected than under weak light during progressive drought stress for spring wheat. There are two possible explanations for this. First, under strong light conditions, chlorophyll degradation leads to the insufficient absorption of abundant light energy, affecting light utilization and limiting photosynthesis. In contrast, under weak light conditions, the amount of light energy itself is reduced; thus, the impact is relatively weaker. Second, under strong light conditions, the efficiency of the electron transport chain decreases, resulting in an insufficient supply of energy substances for light utilization. However, under weak light conditions, the load on the electron transport chain is lower. We found that weak light efficiency improved under drought conditions. This may be because drought stress increases the quantity or activity of light-harvesting complexes (such as Light-Harvesting-Complex II) and enhances the synthesis of osmotic adjustment substances (such as proline and soluble sugars) [36]. Thus, the ability to utilize weak light is improved, enabling plant survival under adverse conditions.

When wheat is affected by elevated CO_2, similar to other C3 plants, the primary responses are increased photosynthetic rate (P_n) and light-use efficiency, reduced stomatal conductance and transpiration, improved water-use efficiency, and decreased photorespiration [37–42]. The impact of elevated CO_2 on wheat is positive; however, this changes when considering the impact of drought. Under moderate drought, the effect of elevated CO_2 is positive, but under severe drought, the positive effect disappears. Elevated CO_2 is able to delay the P_n reduction due to drought but not remove it completely [43]. These conclusions are drawn from the response of wheat grown under a high CO_2 concentration for long-term superimposed drought stress. This study shows how wheat that continues to endure drought stress responds to short-term changes in the CO_2 concentration. According to the results, progressive drought stress reduced the photosynthetic capacity of spring wheat, and this effect was not altered by the atmospheric CO_2 concentration. This is primarily because the main physiological mechanisms by which water stress reduces the photosynthetic rate are less influenced by changes in the external CO_2 concentration. Under mild drought conditions, the photosynthetic capacity was more significantly impaired in high CO_2 environments due to the greater impact on the associated physiological mechanisms. In contrast, under more severe drought conditions, the dual limitations of water and CO_2 in low CO_2 environments resulted in a more pronounced reduction in photosynthesis. During drought stress, leaf stomata closure reduces the amount of CO_2 entering the leaves. Spring wheat may require a higher CO_2 concentration gradient between the inside and outside of the leaves to ensure sufficient CO_2 influx and maintain the photosynthetic rate. This may explain why the demand for atmospheric CO_2 remained unchanged under mild drought conditions and only decreased under severe drought stress. This means that the utilization capacity of the CO_2 concentration decreased. At high CO_2 concentrations, a reduction in utilization capacity occurred only under extreme drought conditions.

The light response parameters of spring wheat exhibited a threshold of 50% RSM during their decline under progressive drought stress, reflecting the balance between water utilization and photosynthesis in plants. When the soil relative humidity fell below 50%, the negative impact of water stress on plant physiological functions became significantly more pronounced, leading to a comprehensive reduction in the plant's ability to utilize light and photosynthetic capacity. This threshold not only illustrates the physiological response mechanisms of plants to drought stress but also provides important scientific insights for agricultural production and ecological management. Among these parameters, I_{sat} and A_{max} decreased more significantly than I_c and AQY. This is primarily because photosynthesis under high light intensity is more dependent on the CO_2 supply and electron transport chain, both of which are highly sensitive to water stress. In contrast, photosynthesis under low light intensity mainly relies on light energy capture and conversion, which is less sensitive to water stress, resulting in a smaller degree of decline [44]. This difference reflects the adaptive responses of plants to drought stress under varying light intensity conditions.

Spring wheat maintains a relatively high photosynthetic capacity under mild water stress through mechanisms such as stomatal regulation and osmotic adjustment, resulting in a slower decline in light response parameters. When water stress reaches a certain threshold (e.g., 50% soil relative humidity), physiological processes, such as stomatal closure and impaired chloroplast function, are significantly suppressed, leading to a rapid decline in light response parameters. Under severe water stress, plants enter a state of wilting or death, and the decline in light response parameters stabilizes, with the photosynthetic capacity no longer significantly decreasing. This process aligns well with the characteristics of the logistic model [11]. Therefore, the logistic model can be used to simulate the impact of water stress on light response parameters. Changes in the CO_2 response parameters due to water stress are better suited to the exponential model, likely because these parameters are influenced by physiological processes and exhibit a gradual decline without a distinct threshold effect. Instead, their decline increases progressively with increasing water stress intensity, making their trends more consistent with the exponential model.

The environmental factors for plant growth have optimal values. Regardless of whether conditions are lower or higher than the optimal value, growth is inhibited, or resources are wasted. Therefore, rationally using these environmental factors and clarifying their optimal values are important for improving plant growth. This study showed that light intensity controlled at approximately 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was appropriate when soil moisture was sufficient, and I_{opt} decreased in a curved trend with decreasing RSM when drought stress occurred (Table 4; Fig. 5). A light intensity of 1200–1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was appropriate in the mild drought stage, and a light intensity less than 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was appropriate in the extreme drought stage. During actual production, especially in controlled environments, the light intensity under different soil water conditions can be controlled according to these values to achieve relatively high photosynthetic product accumulation. When light energy is excessive, the amount received by the photosynthetic structure exceeds what it can use, generating oxygen radicals, inactivating PSII, and causing photoinhibition [8, 45]. Thus, the photosynthetic rate decreases [46, 47], and plant growth and development are inhibited. However, in this study, light inhibition was rarely observed in actual experiments, which may be due to the strong ecological adaptability of spring wheat to light, the measurement error of the observation instrument, or the experimental area. This needs to be confirmed in a follow-up study.

The present study showed that the contemporary atmospheric CO_2 concentration could not meet the needs of spring wheat growth. Only when the current concentration was doubled, that is, approximately 800 $\mu mol \cdot mol^{-1}$, was it more suitable for the growth of spring wheat. At the same time, we found that when drought stress occurred, as long as the drought severity not reach the level of extreme drought, this optimal value did not change. This differs from the expected decrease, which may be attributed to the demand for a difference in CO_2 concentration inside and outside the leaf. Under extreme drought, photosynthesis is extremely unstable due to severe damage to photosynthetic organs. At this time, photosynthesis measurement instruments may be prone to observational errors. These factors eventually lead to a large fluctuation in CO_{2opt}. Therefore, the trend in CO_{2opt} with decreasing soil water under extreme drought conditions could not be determined in this study.

Based on these findings, it is recommended that agricultural producers adopt technologies to preserve soil moisture, such as water-saving irrigation and mulching, in practical production under future climatic conditions. These measures will ensure that spring wheat obtains sufficient water under drought conditions [48], thereby enhancing light energy and CO_2 utilization and improving the photosynthetic capacity of spring wheat. Photosynthesis in spring wheat under sunny days with high light intensity should receive more attention at any drought stress level compared to overcast days with low light intensity. In the future, although atmospheric CO_2 will continue to rise, it will remain at a relatively low level for crops. The more severe the drought, the greater the impact on the carbon assimilation process in spring wheat. To address these issues, measures such as optimizing planting density to maximize light energy utilization and increasing organic fertilizer application or returning straw to the field to enhance soil CO_2 release can be implemented. Breeding crop varieties with strong drought resistance and high light energy and CO_2 utilization efficiency may also be beneficial. For facility agriculture, CO_2 levels can be set to 800 ppm, and soil moisture can be precisely managed using Internet-of-Things technology. Additionally, light intensity can be adjusted to the optimal range based on the results of this study, thereby enabling spring wheat to achieve efficient photosynthesis and a high yield.

Conclusions

In the present study, under progressive drought stress, the changes in the photosynthesis–light and CO_2 response curve parameters of spring wheat were described using logistic and exponential models, respectively. These changes exhibited different thresholds. Drought stress reduced the capacity for light utilization and corresponding photosynthesis in spring wheat, with a greater decline under strong light than under weak light. The capacity of CO_2 utilization and corresponding photosynthesis varied depending on drought severity and the CO_2 concentration. This study identified the optimal light intensity and atmospheric CO_2 concentration for spring wheat under different drought levels. These findings deepened our understanding of drought stress response mechanisms in spring wheat and provided important scientific insights for research on ecosystem carbon cycles, climate change adaptation strategies, and the breeding of drought-resistant varieties.

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Author contributions

F.C. conceived and designed designed the research; F.C. and K.Z. wrote the paper; R.W. provided funding support; S.Y. analyzed the data and edited the paper; H.W. commented and revised the paper; H.Z. and F.Z. modified the language of the manuscript; Y.Q., Y.Y., X.W. and Y.T. performed the experiments. All authors have read and agreed to the published version of the manuscript.

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Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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