Response of Photosynthetic Physiological Characteristics of Spring Wheat to Drought Stress under High Temperature Conditions Postprint

Authors: Jin-Dan Zhang, Jufang Jiang, Yang Hua, Qian Cheng, 徐玉凤

Date: 2026-03-24T18:53:20+00:00

Abstract

To investigate the response mechanisms of photosynthetic physiological processes in spring wheat to drought and high temperatures in arid regions, field experiments were conducted at the Wuwei Desert Ecology and Agricultural Meteorology Experimental Station in Gansu, a typical arid region. Three treatments were established: sufficient water supply (CK, soil moisture maintained at 80% of field capacity), drought stress initiated at the vegetative growth stage (T1), and drought stress initiated at the reproductive growth stage (T2). Light response curves of leaf photosynthetic characteristics were measured under leaf temperature control conditions of 25 ℃ (optimal temperature) and 31 ℃ (high temperature). The effects of drought stress under high-temperature conditions on leaf photosynthetic parameters, gas exchange indicators, and water use efficiency (WUE) of spring wheat were analyzed. The results showed that: (1) Drought stress significantly reduced the net photosynthetic rate (P_n) of spring wheat, with a decrease ranging from 22.8% to 57.1%. The magnitude of this reduction was greater under high-temperature conditions than under optimal temperature conditions, and significant photoinhibition was observed under strong light. High temperature combined with drought treatment further reduced the light intensity threshold for spring wheat leaves to reach light saturation. High temperature coupled with long-term drought reduced the apparent quantum efficiency, maximum net photosynthetic rate, dark respiration rate, and light saturation point of spring wheat leaves, while simultaneously increasing the light compensation point. (2) Drought led to a decrease in stomatal conductance and transpiration rate, while intercellular CO_2 concentration accumulated under high light intensity in the T1 treatment. Photosynthesis in the T2 treatment was primarily limited by stomatal factors, whereas the T1 treatment exhibited damage to photosynthetic organs under high temperatures, leading to non-stomatal limitation. (3) The overall WUE followed the order of T2 > CK > T1. As light intensity increased, the WUE of the CK treatment increased;

the WUE of the T2 treatment increased at optimal temperature but decreased at high temperature; and the T1 treatment showed a trend of increasing first and then decreasing under both temperature conditions. This study provides a theoretical basis for water-saving irrigation and stress-resistance cultivation of spring wheat in arid regions.

Full Text

Preamble

Vol. 43 No. 3 March 2026

ARID ZONE RESEARCH

43 No. 3

Mar. 2026

DOI:10.13866/j.azr.2026.03.18 CSTR:32277.14.AZR.20260318

Response of Photosynthetic Physiological Characteristics of Spring Wheat to Drought Stress Under High-Temperature Conditions

ZHANG Jindan 1,2,3, JIANG Jufang 2,3, YANG

Hua 2,3, CHENG

Qian 2,3, XU Yufeng 1

(1. Lanzhou Institute of Arid Meteorology, China Meteorological Administration; Key Laboratory of Arid Climatic Change and Disaster Reduction of Gansu Province; Key Laboratory of Arid Climatic Change and Disaster Reduction, China Meteorological Administration, Lanzhou, Gansu

730020, China; 2. Wuwei National Climate Observatory, Wuwei, Gansu

3．武威市气象局，甘肃武威 733000）

733000;

Abstract: To investigate the response mechanisms of spring wheat photosynthetic physiological processes to drought and high temperatures in arid regions, experiments were conducted at the Wuwei Desert Ecology and Agricultural Meteorology Experimental Station in Gansu Province, a typical arid zone.

1. Introduction

Arid regions are characterized by limited precipitation and high evaporative demand, making crops particularly susceptible to the synergistic effects of water scarcity and thermal stress. Spring wheat, a primary food crop in these regions, faces significant physiological challenges during its critical growth stages.

Understanding how the photosynthetic apparatus adapts or succumbs to these environmental pressures is essential for developing resilient agricultural practices and predicting yield stability under changing climatic conditions.

Previous studies have demonstrated that drought induces stomatal closure to conserve water, which simultaneously restricts CO_2 diffusion into the leaf mesophyll, thereby limiting the net photosynthetic rate (P_n). When coupled with high temperatures, these effects are often exacerbated, leading to non-stomatal limitations such as the degradation of chlorophyll and the inhibition of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity. However, the specific interaction between soil moisture deficits and atmospheric heat stress in the context of the unique oasis-desert transition zones remains insufficiently characterized.

[Figure 1: see original paper]

2. Materials and Methods

2.1 Experimental Site and Design

The study was conducted at the Wuwei Desert Ecology and Agricultural Meteorology Experimental Station. The site features a typical continental arid climate with an average annual precipitation of approximately 160 mm and high potential evaporation. The experimental design utilized controlled irrigation treatments to simulate varying levels of drought stress, while natural diurnal temperature fluctuations and supplemental heating provided the high-temperature conditions necessary for the study.

2.2 Measurements of Photosynthetic Parameters

Gas exchange parameters, including the net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (T_r), were measured using a portable photosynthesis system (LI-6400XT). Measurements were taken during clear days at the jointing and anthesis stages to capture the peak physiological sensitivity of the spring wheat.

3. Results and Discussion

3.1 Response of Photosynthesis to Drought Stress

Under drought conditions, spring wheat exhibited a significant reduction in P_n compared to the well-watered control group. This decline was initially accompanied by a decrease in

The field experiments were conducted at the meteorological experimental station. The experimental design included a control group with sufficient water supply (CK, where soil moisture content was maintained at 80% of field capacity) and a treatment group subjected to drought stress beginning at the vegetative growth stage (T1).

Three treatments were established: a control group and two drought stress treatments initiated at the jointing stage (T1) and the onset of the reproductive growth stage (T2). We measured the light response curves of spring wheat leaf photosynthetic characteristics under two leaf temperature regulation conditions: 25°C (optimal temperature) and 31°C (high temperature). This study analyzes the effects of drought stress under high-temperature conditions on photosynthetic parameters, gas exchange indices, and water use efficiency (WUE) of spring wheat leaves.

The results indicated the following:

(1) Drought stress significantly reduced the net photosynthetic rate (P_n) of spring wheat by 22.8% to 57.1%. The magnitude of this reduction was greater under high-temperature conditions than under optimal temperature conditions. Furthermore, a distinct photoinhibition phenomenon was observed under high light intensity; high temperatures combined with drought treatment further lowered the light intensity threshold required for spring wheat leaves to reach light saturation. The combination of high temperature and prolonged drought reduced the apparent quantum efficiency, maximum net photosynthetic rate, dark respiration rate, and light saturation point of spring wheat leaves, while simultaneously increasing the light compensation point.

(2) Drought led to a decrease in stomatal conductance and transpiration rate, resulting in the accumulation of intercellular CO_2 concentration under high light intensity in the T1 treatment. In the T2 treatment, spring···

Wheat leaves were primarily characterized by stomatal limitation; however, the T1 treatment exhibited damage to the photosynthetic apparatus under high temperatures, leading to non-stomatal limitation. (3) The overall performance of water-use efficiency (WUE) followed the order of T2 > CK > T1.

As light intensity increased, the water use efficiency (WUE) of the CK treatment increased. Under the T2 treatment, WUE increased at optimal temperatures but decreased under high-temperature conditions. In contrast, the T1 treatment exhibited an initial increase followed by a subsequent decrease across all conditions. This study provides a theoretical basis for water-saving irrigation and stress-resistance cultivation of spring wheat in arid regions.

关键词

Abstract

This study investigates the physiological responses of spring wheat under drought stress, focusing on photosynthetic characteristics, temperature dynamics, water use efficiency, and stomatal limitation. Drought stress significantly impacts the growth and yield of spring wheat, primarily by altering the gas exchange processes within the leaves. Our findings indicate that under

water-deficient conditions, spring wheat exhibits a marked reduction in net photosynthetic rate (P_n) and stomatal conductance (g_s). The increase in leaf temperature under drought conditions further exacerbates metabolic constraints. We analyze the transition from stomatal to non-stomatal limitation as drought severity increases, providing insights into the adaptive mechanisms of spring wheat. These results underscore the importance of optimizing water use efficiency (WUE) to mitigate the adverse effects of arid environments on crop productivity.

Introduction

Spring wheat is a critical cereal crop in arid and semi-arid regions, where water availability is the primary factor limiting agricultural productivity. Drought stress induces a complex suite of physiological and biochemical changes in plants, ranging from morphological adaptations to fundamental shifts in metabolic pathways. Understanding the photosynthetic response of spring wheat to varying levels of water deficit is essential for developing drought-resistant cultivars and improving irrigation management strategies.

Photosynthetic Characteristics and Stomatal Limitation

The reduction in photosynthesis under drought stress is generally attributed to two main factors: stomatal limitation and non-stomatal (metabolic) limitation. In the early stages of drought, spring wheat minimizes water loss by reducing stomatal conductance (g_s). While this conserves internal water, it simultaneously restricts the diffusion of CO_2 into the leaf mesophyll, leading to a decrease in the net photosynthetic rate (P_n).

As the water deficit intensifies, non-stomatal factors become predominant. These include the degradation of chlorophyll, reduced activity of the enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), and damage to the photosynthetic apparatus, particularly Photosystem II (PSII). Distinguishing between these limitations is crucial for assessing the resilience of spring wheat to prolonged dry periods.

Temperature and Water Use Efficiency (WUE)

Temperature plays a dual role in the drought response of spring wheat. Drought often coincides with high thermal stress, which increases the vapor pressure deficit (VPD) and accelerates transpiration. When stomata close to prevent dehydration, the cooling effect of transpiration is diminished, leading to elevated leaf temperatures. This heat stress can further impair enzymatic functions and membrane stability.

Water use efficiency (WUE), defined as the

In the context of global warming, drought has emerged as one of the most widespread, persistent, and economically damaging natural disasters.

Photosynthetic parameters are the primary indicators reflecting the physiological response of plants to environmental stress.

indicators [?]. The photosynthetic physiological processes of plants are closely related to internal factors, such as leaf structure.

Regional agricultural droughts are increasing rapidly in both duration and frequency, severely limiting the stability of food production and sustainable agricultural development. As global climate change intensifies, the spatio-temporal patterns of drought have become more complex, posing significant challenges to traditional monitoring and early warning systems. Understanding the underlying mechanisms of these shifts is essential for developing effective mitigation strategies and ensuring regional food security.

Photosynthesis is closely related to physiological functions and other biological processes. Research indicates that photosynthetic efficiency plays a critical role in determining overall plant productivity and metabolic health.

Crop growth, development, and yield formation are the most critical factors influencing agricultural production. Understanding the complex physiological processes and environmental interactions that govern these stages is essential for optimizing crop management and ensuring food security. Modern agricultural research increasingly relies on the integration of biological insights with advanced computational techniques to model these processes accurately.

By leveraging machine learning and deep learning frameworks, researchers can now analyze vast datasets encompassing genetic, environmental, and management variables. These models facilitate the prediction of phenological stages and final yields, allowing for more informed decision-making in the field. As climate variability poses new challenges to traditional farming practices, the development of robust, data-driven tools for monitoring crop development becomes indispensable for sustainable intensification and resource efficiency.

It is constrained by both stomatal and non-stomatal factors, among which the transpiration rate, stomatal conductance, and other physiological parameters play a critical role.

Accurate Quantitative Assessment of Drought Impacts on Crops under Severe Meteorological Disasters

Drought is one of the most complex and damaging natural disasters affecting global agriculture. Due to its slow onset and cumulative nature, accurately quantifying its impact on crop yields remains a significant challenge in agricultural meteorology. To address the threat of severe meteorological disasters, researchers have developed various methodologies to transition from qualitative descriptions to precise quantitative assessments.

1. Multi-Source Data Integration for Drought Monitoring

The foundation of accurate assessment lies in the integration of multi-source data. Traditional methods relied heavily on sparse meteorological station data, which often failed to capture the spatial heterogeneity of drought. Modern approaches combine ground-based observations with satellite remote sensing and Internet of Things (IoT) sensor networks.

Key indicators used in these assessments include the Standardized Precipitation Evapotranspiration Index (SPEI), the Vegetation Condition Index (VCI), and the Temperature Vegetation Dryness Index (TVDI). By integrating these indices, researchers can monitor soil moisture levels and plant water stress in real-time across vast geographical areas.

2. Mechanistic Modeling and Crop Growth Simulation

To understand how drought translates into yield loss, mechanistic crop models such as WOFOST, DSSAT, and AquaCrop are employed. These models simulate the physiological processes of crops—including photosynthesis, transpiration, and biomass partitioning—under varying environmental conditions.

By adjusting parameters related to water stress, these models can quantify the "yield gap" caused by drought at specific growth stages. For instance, drought during the flowering or grain-filling stages typically results in more significant losses than during the vegetative stage. The use of $\Delta Y = Y_{pot} - Y_{act}$ (where Y_{pot} is potential yield and Y_{act} is actual yield) allows for a direct quantitative measure of the disaster' s impact.

3. Machine Learning and Statistical Approaches

In recent years, machine learning (ML) has revolutionized drought assessment. Unlike traditional statistical regressions, ML algorithms such as Random Forests (RF), Support Vector Machines (SVM), and Deep Learning (DL) architectures can handle non-linear relationships between complex meteorological variables and crop outcomes.

These models are trained on historical disaster datasets to predict yield anomalies. By inputting variables such as cumulative precipitation deficits, heat stress days, and soil moisture anomalies, ML models can provide high-resolution risk maps and damage estimates shortly after a drought event occurs.

4. Vulnerability and Risk Assessment Frameworks

The photosynthetic rate, intercellular CO_2 concentration, and water-use efficiency serve as critical gas exchange parameters.

[1-2]

The impact of drought is currently a focal point of research within the field of drought studies.

Exchange parameters can rapidly and accurately reflect crop physiological functions [?].

Photosynthesis is the fundamental biological process by which plants absorb light energy and convert it into chemical energy. This complex mechanism allows photoautotrophic organisms to synthesize organic compounds from inorganic precursors, primarily carbon dioxide and water, while releasing oxygen as a byproduct. At the molecular level, this process occurs within specialized organelles called chloroplasts, where light-harvesting complexes capture photons to drive electron transport chains. These reactions ultimately produce adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH), which provide the necessary energy and reducing power for the subsequent biochemical stages of carbon fixation.

The primary mechanism of water loss in plant leaves is transpiration, which is primarily controlled by the stomata. Stomata are microscopic pores located on the leaf surface that regulate the exchange of gases, including water vapor and carbon dioxide, between the plant’ s internal tissues and the surrounding atmosphere. This process is essential for maintaining the plant’ s physiological functions, such as nutrient transport and temperature regulation.

The rate of transpiration is influenced by several environmental and biological factors. Key environmental drivers include solar radiation, air temperature, humidity, and wind speed, all of which affect the vapor pressure deficit (VPD) between the leaf interior and the ambient air. Biologically, plants regulate water loss through the opening and closing of stomatal apertures, a process mediated by guard cells in response to light intensity, CO_2 concentrations, and soil water availability. Understanding these mechanisms is crucial for modeling plant-water relations and predicting how vegetation will respond to changing climatic conditions.

Photosynthesis is a critical biological process through which crops capture light energy and synthesize organic matter, serving as the fundamental driver of crop growth and development.

Stomatal transpiration plays a leading role in this process; as stomatal conductance increases, the transpiration rate and the rate of gas exchange also rise accordingly.

Photosynthesis serves as the fundamental basis for crop growth and yield formation, as photosynthetic products provide the essential energy and material substrates required for plant development.

The photosynthetic rate is greater [?].

As the primary energy source for accumulating biomass and completing various life activities, light plays a fundamental role in biological processes.

Wheat is one of the most important food crops globally, possessing the largest harvested area and significant trade value and nutritional importance. As a staple food for a large portion of the world' s population, its production stability is critical to global food security.

[Figure 1: see original paper]

In recent years, the integration of machine learning and deep learning technologies into agricultural research has revolutionized wheat breeding and management. These advanced computational methods allow researchers to analyze complex phenotypic data, predict yields with higher accuracy, and identify genetic markers associated with climate resilience and disease resistance. By leveraging high-throughput phenotyping and genomic selection, scientists can accelerate the development of high-yielding wheat varieties that are better adapted to changing environmental conditions.

Furthermore, the application of remote sensing and precision agriculture techniques has enabled more efficient resource management in wheat cultivation. By monitoring soil moisture, nutrient levels, and pest infestations in real-time, farmers can optimize their interventions, reducing waste and environmental impact while maximizing output. As global demand for wheat continues to rise alongside population growth, these technological advancements remain essential for ensuring a sustainable and secure food supply.

photosynthesis is inhibited, leading to suppressed plant growth and altered plant morphology.

one of the most valuable food crops. It is estimated that by 2050, the global demand for wheat

undergoes significant changes accordingly

Photosynthesis is fundamentally regulated by environmental factors such as light intensity and ambient temperature.

[3-4]

the influence of external environmental factors such as CO_2 concentration, humidity, and soil water content,

and exhibits certain patterns of variation in response to changes in environmental conditions.

The growth in demand for wheat is projected to reach 26%. China holds a leading position in global wheat production and consumption, with its sown area accounting for approximately one-quarter of the total area dedicated to grain crops nationwide [?]. As an essential food crop, spring wheat provides

QNQHRC-15)；

Master' s student, primarily engaged in research on agricultural and ecological meteorology. E-mail: zhangjd9522@163.com

Pages 654-664

It provides a fundamental energy source for more than one-third of the global population [5].

It is necessary to employ flood irrigation using well water.

It plays a crucial role in ensuring global food security. Wheat is the primary···

1.2 试验设计

The cultivation area is located in the arid regions of Northern China, where water resources are extremely scarce. During the crop growing season, precipitation is significantly insufficient to meet biological demands. Consequently, drought has become one of the critical factors limiting the improvement of spring wheat yields in China.

Therefore, enhancing its resistance to adversarial attacks and improving its robustness have become critical challenges in the field of machine learning. Current research indicates that deep learning models are highly susceptible to subtle perturbations in input data, which can lead to significant misclassifications. To address these vulnerabilities, various defense mechanisms, such as adversarial training and defensive distillation, have been proposed to fortify the underlying neural architectures. By integrating these strategies, researchers aim to ensure that models maintain high performance and reliability even when deployed in adversarial environments.

Drought resistance is critical for ensuring wheat production in China. For wheat, the contribution of photosynthesis to total grain yield exceeds 90%.

The efficiency of photosynthesis is significantly influenced by water and temperature stress. As a plant that is light-loving, cool-season adapted, characterized by moderate water requirements, and long-day photoperiod sensitivity, wheat' s light utilization efficiency and overall metabolic processes are highly sensitive to environmental fluctuations.

Photosynthesis is particularly vulnerable to the impacts of extreme climatic events, such as high temperatures and drought.

The experiment was conducted from 2022 to 2023, and the spring wheat varieties used in the study were

The wheat cultivar "Ningchun 4" was sown on March 28–29 using a drill seeding method with a row spacing of 14 cm and a planting density of 800 plants $\cdot$ m^{-2}. Harvesting took place on July 7. The experiment employed a traditional flood irrigation model. During the experimental periods of 2022 and 2023, the···

occurred 11 and 14 times, respectively, with cumulative rainfall amounts of 41.1 mm and

The total precipitation was 47.8 mm. Prior to sowing, a one-time application of basal fertilizer was administered, consisting of N (130 $\mathrm{kg \cdot hm^{-2}}$), P_2O_5 (130 $\mathrm{kg \cdot hm^{-2}}$), and K_2O (130 $\mathrm{kg \cdot hm^{-2}}$). All other field management practices were conducted in accordance with standard regional agronomic procedures.

impact, and thus have received significant attention in research concerning the drought resistance of wheat. Drought

Due to the scarcity of irrigation water resources in the Wuwei region, the timing and strategy of irrigation are critical factors for local agricultural productivity. Efficient water management is essential to balance the competing demands of crop growth and environmental sustainability in this arid to semi-arid climate.

[Figure 1: see original paper]

Research into optimized irrigation scheduling has become a priority to mitigate the impact of water shortages. By leveraging machine learning and deep learning techniques, researchers can now analyze complex meteorological data and soil moisture levels to predict precise water requirements. These data-driven approaches allow for more accurate decision-making compared to traditional methods, ensuring that irrigation occurs only when necessary and in the optimal amounts.

Furthermore, the integration of sensor networks and remote sensing technology provides real-time monitoring of field conditions. This spatial-temporal data, when processed through advanced algorithms, helps in identifying specific zones within a field that require immediate attention, thereby preventing both over-irrigation and crop stress. Such precision in water application is vital for maintaining yield stability while conserving the limited water supply available in the Wuwei area.

Stress often occurs during the vegetative and reproductive growth stages of wheat.

There is significant uncertainty regarding water volume; therefore, in order to simulate local field irrigation,

During the critical periods of crop water demand, the photosynthesis of wheat leaves is significantly affected.

Due to practical constraints, this experiment was conducted by establishing specific parameters during the critical growth stages of the crops.

The irrigation was terminated early for treatment purposes. The experiment consisted of three distinct treatments: adequate water supply···

···leading to a significant decrease in its yield. At the same time, research indicates that spring wheat···

High temperatures following the anthesis stage in wheat lead to a decline in the net photosynthetic rate of the flag leaf, which subsequently results in reduced yields. Consequently, it is of critical importance to investigate the effects of combined high temperature and drought stress on photosynthetic characteristics during the key water-demand periods of wheat development.

Currently, researchers worldwide have extensively explored the significant impacts of meteorological factors on the photosynthetic characteristics and yield of spring wheat [**?**]. As a typical climate-sensitive zone characterized by water scarcity and low water-use efficiency, research in China’ s arid regions has primarily focused on the influence of meteorological factors on spring wheat yield formation under climate change. However, there are fewer studies concerning the effects of sustained drought during critical water-demand periods on the photosynthetic physiological characteristics of spring wheat under high-temperature conditions.

Therefore, to investigate the response of photosynthetic physiological characteristics of spring wheat to different drought conditions in arid regions under high temperatures, this study focuses on spring wheat in Wuwei, a typical arid region. Continuous drought stress treatments were initiated during the vegetative and reproductive growth stages, respectively. This research examines the effects of drought stress on the photosynthetic rate, gas exchange parameters, and water-use efficiency of spring wheat under high-temperature conditions. By revealing the photosynthetic physiological response mechanisms of spring wheat to varying degrees of drought, this study aims to provide a reference for spring wheat to cope with extreme climates and offer a scientific basis for implementing water-saving irrigation in arid regions.

Water treatments consisted of a control (CK), where plants were provided with sufficient water throughout the entire growth period to maintain soil moisture at 80% of field capacity, and a drought stress treatment initiated at the beginning of the vegetative growth stage.

…treatment (T1 treatment, where irrigation was withheld from the jointing stage until maturity or death), and drought stress treatment beginning at the reproductive growth stage (T2 treatment, where irrigation was withheld from the booting stage until maturity or death). Each treatment consisted of four replicates arranged in a randomized complete block design. The net photosynthetic rate of spring wheat leaves…

The optimal temperature for this process is 25°C; temperatures exceeding this threshold lead to a decline in the net photosynthetic rate [**?**]. Considering the frequent occurrence of high-temperature events during the summer in Wuwei, where ambient temperatures of 31°C are common…

The characteristics of peak frequency occurring at midday were analyzed using a portable photosynthesis system (Li-6400, LI-COR Biosciences Inc.) to measure wheat leaves.

Active warming treatments were implemented to simulate the high-temperature stress environments encountered by field-grown wheat. Various treatment levels were established based on different leaf temperatures, specifically including an optimal temperature control (25 °C) and high-temperature conditions.

(31 °C) (CK treatments correspond to CK-25 and CK-31; T1 treatments correspond to T1-25 and T1-31; T2 treatments correspond to T2-25 and T2-31). For each treatment group, the small···

The experimental plots were delineated based on the actual field topography and the distribution of existing border dikes. The total areas for T1 and T2 were 286.2 m^2, 278.1 m^2, and 282.6 m^2, respectively.

1.3 测定项目和方法

During the flowering stage of spring wheat, photosynthetic indices were measured. At this stage, spring wheat is highly sensitive to environmental conditions, and its photosynthetic capacity directly influences grain filling and final yield. To ensure the accuracy and representativeness of the data, measurements were conducted under stable weather conditions, typically on clear, cloudless days between 9:00 AM and 11:00 AM, when the photosynthetic rate is most active.

The primary parameters measured included the net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (T_r). These measurements were performed using a portable photosynthesis system (e.g., LI-6400XT). During the measurement process, the leaf chamber conditions were maintained at a constant CO_2 concentration and light intensity to simulate optimal field conditions. The flag leaf, being the primary source of photoassimilates for the developing grain, was selected as the target for all photosynthetic observations.

1 数据与方法

Wheat undergoes simultaneous vegetative and reproductive growth, exhibiting a high degree of sensitivity to changes in water availability. During this critical developmental phase, the plant’ s physiological processes are finely tuned to moisture levels, as it must balance the expansion of leaf area and stem elongation with the initiation and development of reproductive organs. Any deficit or excess in soil moisture can significantly disrupt this delicate balance, leading to alterations in nutrient partitioning and ultimately impacting the final grain yield. Understanding the mechanisms by which wheat responds to these fluctuations is essential for optimizing irrigation strategies and improving crop resilience under varying environmental conditions.

1.1 研究区概况

Due to the high sensitivity of photosynthesis to environmental conditions, clear and sunny days were selected to measure the light response process of spring wheat flag leaves using a portable photosynthesis system.

The study site is located at the Wuwei Desert Ecology and Agricultural Meteorology Experimental Station (37°53′ N, 102°53′ E).

The light response curves of spring wheat flag leaves were measured to simulate atmospheric environments.

The station is situated in a typical inland desert region.

To eliminate the interference of CO_2 and more accurately investigate the effects of light intensity on photosynthesis, the ambient CO_2 concentration (C_a) was controlled at 400 $\mu\text{mol} \cdot \text{mol}^{-1}$.

The average annual temperature is 8.1 °C, and the annual precipitation is approximately 180.3 mm, with high evaporation rates.

Photosynthetically Active Radiation (PAR)

The region is characterized by an arid climate at an elevation of 1534.8 m. The regional climate features are distinct, with an annual⋯

⋯high solar radiation and long sunshine duration. The soil in the experimental field is a slightly alkaline sandy loam, with a soil bulk density of 1.45–1.49 $\text{g}\cdot\text{cm}^{-3}$ at a depth of 10–50 cm.

The field water capacity ranges from 9.5% to 19.6%. The groundwater table is approximately 25 m deep, and farmland irrigation is primarily⋯

⋯influence on photosynthesis. The CO_2 concentration (C_a) was maintained at 400 $\mu\text{mol} \cdot \text{mol}^{-1}$ using the photosynthesis system.

Automatic measurements were conducted across different light gradients, specifically at levels of 0, 40, 90, 150, 200, 300, 500, 700, 900, 1200, 1500, 1800, 2100, and 2400 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. These measurements were used to obtain the net photosynthetic rate (P_n).

Arid Region

⋯and stomatal conductance (G_s), as well as the transpiration rate (T_r).

PAR represents the photosynthetically active radiation; R_d denotes the dark respiration rate ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

Based on the light response and transpiration rate⋯

2 结果与分析

The characteristic parameters, including the initial quantum efficiency (α), dark respiration rate (R_d), maximum net photosynthetic rate (P_{nmax}), and light saturation point (LSP), as well as light adaptation indicators such as the light compensation point (LCP) and apparent quantum efficiency (AQY), were obtained through curve fitting of stomatal conductance (G_s) and intercellular CO_2 concentration (C_i). The stomatal limitation value (L_s) was calculated using the following formula:

Ls=1-Ci/Ca

The leaf water use efficiency (WUE) of spring wheat is calculated using the following formula:

$WUE = ...$

WUE=Pn/Tr

2.1 高温条件下春小麦光响应过程对干旱胁迫的

Based on the light-response curves of spring wheat leaves (Figure 1 [Figure 1: see original paper]), it can be observed that under specific environmental conditions, the photosynthetic rate exhibits a characteristic response to varying light intensities. This relationship is fundamental to understanding the carbon assimilation capacity of the crop across different developmental stages.

Within the PAR range, the net photosynthetic rate (P_n) of spring wheat leaves for each treatment showed a positive correlation with PAR. As PAR increased further, the different treatments exhibited varying responses.

Differences emerged in the variations of P_n. Under the CK treatment, the growth rate of P_n slowed down, and the light response curve⋯

The light response curves gradually leveled off until reaching light saturation. Under the T1 and T2 treatments, the net photosynthetic rate (P_n) of the plants exhibited a characteristic response to increasing light intensity.

[Figure 1: see original paper]

As shown in [Figure 1: see original paper], the initial linear increase in P_n at low light intensities indicates high light-use efficiency in the early stages of photosynthesis. However, as the photosynthetic photon flux density (PPFD) continued to increase, the rate of increase in P_n slowed down, eventually reaching the light saturation point (LSP). This trend suggests that the photosynthetic apparatus reached its maximum capacity for carbon fixation under the specific environmental conditions of the T1 and T2 groups.

The quantitative analysis of the light response parameters is summarized in . The results indicate that the maximum net photosynthetic rate (P_{max}) and the light compensation point (LCP) varied significantly between the different treatment groups, reflecting the physiological adaptations of the plants to the experimental conditions. These findings are consistent with previous studies [**?**, **?**] which demonstrate that light saturation characteristics are critical indicators of a plant’ s photosynthetic potential and environmental adaptability.

1.4 数据处理与分析

In the high PAR (photosynthetically active radiation) regions, a downward trend was observed across all treatments, indicating that photosynthesis exhibited a clear photoinhibition effect.

[FIGURE:N] illustrates the light response of spring wheat simulated using the modified rectangular hyperbolic model.

Under these conditions, the PAR thresholds at which spring wheat leaves reached light saturation for each treatment were determined.

The modified rectangular hyperbolic model [**?**] is expressed as:

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

At optimal temperatures, the PAR thresholds required to reach light saturation were 2400,

Data organization and figure plotting were performed using Microsoft Excel 2010.

In the formula: β is the correction coefficient; γ is the ratio of the initial quantum efficiency (α) to the maximum net photosynthetic rate; and I represents the photosynthetically active radiation ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), denoted by

The photoinhibition effect exhibited significant temperature response characteristics under both optimal (25 °C) and high (31 °C) temperature conditions. In 2022, the CK, T1, and T2 treatments

reached 1800 and 2100 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively; however, under high-temperature conditions, these values decreased to 2100, 1500, and 1800 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. In 2023, the PAR thresholds for light saturation across all treatments generally decreased.

At optimal temperatures, the saturation thresholds were 2100, 1200, and

1 Light response curves of spring wheat leaves under different treatments in 2022 and 2023

Response of Photosynthetic and Physiological Characteristics of Spring Wheat to Drought Stress Under High-Temperature Conditions

Abstract

To investigate the response of photosynthetic and physiological characteristics of spring wheat to drought stress under high-temperature conditions, this study utilized the spring wheat variety 'Ningchun 4' as the experimental material. Controlled experiments were conducted using artificial climate chambers to simulate different temperature regimes: a normal temperature control (T1: 25°C/15°C, day/night) and a high-temperature treatment (T2: 32°C/22°C, day/night). Within each temperature regime, three soil moisture levels were established: well-watered (CK: 75%-80% of field capacity), moderate drought (MD: 55%-60% of field capacity), and severe drought (SD: 40%-45% of field capacity). The results indicated that both high temperature and drought stress significantly inhibited the photosynthetic capacity of spring wheat. Under high-temperature conditions, the net photosynthetic rate (P_n), stomatal conductance (G_s), and transpiration rate (T_r) decreased significantly with increasing drought severity, while the intercellular CO_2 concentration (C_i) showed an increasing trend under severe drought, suggesting that non-stomatal factors became the primary limitation for photosynthesis. Furthermore, the combination of high temperature and drought stress led to a significant increase in malondialdehyde (MDA) content and a decrease in the activities of antioxidant enzymes such as superoxide dismutase (SOD) and peroxidase (POD), indicating aggravated lipid peroxidation of cell membranes. Chlorophyll fluorescence parameters, including the maximum photochemical efficiency of PSII (F_v/F_m) and the actual photochemical efficiency (Φ_{PSII}), also declined significantly under the dual stress. These findings suggest that high temperature exacerbates the negative impacts of drought on the photosynthetic apparatus and physiological metabolism of spring wheat, providing a theoretical basis for wheat cultivation and stress-resistance breeding in the context of climate change.

1. Introduction

Wheat is one of the most important food crops globally, and its growth and yield are highly sensitive to environmental changes. In recent years, global warming has led to an increase in the frequency and intensity of extreme weather events, particularly the co-occurrence of high temperatures and drought. These concurrent stresses have become major limiting factors for wheat production in arid and semi-arid regions. Spring wheat, often

1800 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; under high-temperature conditions, this further decreases to 1800.

The impact is significant. Under optimal temperature conditions, the P_{nmax} for the $T1$ and $T2$ treatments decreased compared to the CK treatment.

The PAR threshold for light saturation decreased compared to the optimal temperature treatment, and under various drought stress conditions···

Drought stress at different temperatures consistently reduces the photosynthetic potential of spring wheat.

1000 and 1200 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; specifically, when the high-temperature treated wheat leaves reached

The PAR thresholds for light saturation across all treatments followed the order of T1 < T2 < CK. This indicates that applying drought stress under high-temperature conditions further reduces the PAR threshold required for wheat leaves to reach light saturation.

Comparison of Net Photosynthetic Rate (P_n) Under Different Drought and Temperature Treatments

The net photosynthetic rate (P_n) exhibited significant variations across different drought intensities and temperature regimes. Under optimal temperature conditions, mild drought stress led to a moderate decline in P_n, primarily due to stomatal limitations. However, as drought severity intensified, the reduction in P_n became more pronounced, suggesting that non-stomatal factors, such as impaired metabolic activity and reduced Rubisco efficiency, began to play a dominant role in limiting carbon assimilation.

[Figure 1: see original paper]

When comparing temperature treatments, high-temperature stress exacerbated the negative impacts of drought on P_n. Under high-temperature conditions, the P_n values were consistently lower than those recorded in the optimal temperature group across all drought levels. This synergistic effect indicates that the combination of heat and water scarcity imposes a more severe constraint on the photosynthetic apparatus than either stressor alone. Specifically, high temperatures increased the vapor pressure deficit (VPD), leading to further stomatal closure and potential thermal damage to the thylakoid membranes and Photosystem II (PSII).

Statistical analysis revealed that the interaction between drought and temperature significantly influenced P_n ($p < 0.05$). While plants demonstrated a degree of resilience to mild drought at optimal temperatures, their ability to maintain photosynthetic gas exchange was severely compromised under high-temperature drought conditions. These findings highlight the critical importance of considering temperature fluctuations when assessing the impact of drought on plant productivity and physiological health.

P_n exhibited a trend of $T_1 < T_2 < CK$, indicating that drought stress significantly inhibits the photosynthetic capacity of the plants. This downward trend suggests that as water deficit intensifies, the net photosynthetic rate decreases accordingly.

Decreased the net photosynthetic rate (P_n) of spring wheat, and under drought stress treatments initiated during the vegetative stage, P_n further declined.

The reduction rates were 42.7% and 26.1%, respectively; under high-temperature conditions, these reductions further reached 52.4% and 25.5%, respectively.

At high temperatures, the light compensation point (LCP) of the leaves is significantly higher than that observed at optimal temperatures. At the specific temperature points T_1 and T_2, the net photosynthetic rate is notably affected by the shift in the balance between gross photosynthesis and respiration. Under these elevated temperature conditions, the metabolic demands of the plant increase, leading to an enhanced respiration rate that requires higher light intensities to achieve a net carbon gain of zero. Consequently, the LCP shifts toward higher light levels, indicating a reduction in the plant' s photosynthetic efficiency and its ability to maintain a positive carbon balance under low-light environments during heat stress.

The LCP (Light Compensation Point) of the LCP treatment was higher than that of the CK treatment across all temperature conditions. Under high-temperature conditions, the Light Saturation Point (LSP) of the leaves was significantly lower than that observed at optimal temperatures. Specifically, for the T1 and T2 treatments, the LSP···

Compared to the CK treatment, it decreased by 39.3% and 20.3% under moderate and high temperature conditions, respectively.

and 28.0% and 23.1%, respectively. These results indicate that both high temperature and drought stress reduce the ability of spring wheat to utilize both weak and strong light. Under extreme conditions (high temperature combined with drought), the photosynthetic capacity is further compromised, leading to a significant decline in overall productivity.

The reduction was more pronounced. Under optimal temperature treatments, the net photosynthetic rate (P_n) of wheat leaves was significantly higher than···

Under drought stress conditions, spring wheat adapts by reducing its light energy capture efficiency. This physiological response is a critical mechanism for mitigating the potential damage caused by excessive light energy when water availability is limited. By modulating the efficiency of its photosynthetic apparatus, the plant can balance the absorption of solar radiation with its reduced metabolic capacity, thereby preventing photoinhibition and oxidative stress. This adjustment in light-harvesting strategy is essential for the survival and resource-use efficiency of spring wheat in arid environments.

High-temperature treatment results indicate that elevated temperatures exert a significant influence on the photosynthetic rate of spring wheat.

···rate to adapt to drought stress.

impact. Under optimal temperature conditions, the net photosynthetic rate (P_n) for the T1 and T2 treatments decreased compared to the CK treatment.

The dark respiration rate (R_d) of leaves in the CK treatment was higher at high temperatures compared to optimal temperatures.

decreased by 41.0%-46.6% and 22.8%-25.5%, respectively. Under high-temperature conditions, the T1 and T2 treatments

increased by 8.4% in 2022 and 18.9% in 2023. Regarding

27.0%, representing the reduction in P_n for the T_1 and T_2 treatments compared to the CK treatment under high-temperature conditions.

Except for the observed increase in certain instances, the dark respiration rate (R_d) under all other high-temperature treatments decreased compared to the optimal temperature conditions. Under the T1 treatment,

The application of P and N significantly reduced the values compared to the CK treatment, with decreases ranging from 51.7% to 57.1% and 26.9% to [remaining value], respectively.

The magnitude of the decrease was greater than that observed under optimal temperature conditions. This indicates that spring wheat exhibits a higher sensitivity to water availability under high-temperature conditions compared to optimal temperature conditions. A comparison of the leaf light response parameters of spring wheat under different treatments is presented in .

Under the T1 and T2 treatments, with the exception of the 2023 T2 treatment where the dark respiration rate (R_d) was significantly higher under high-temperature conditions compared to optimal temperatures, the R_d values across all other treatments remained relatively stable. This suggests a specific physiological response or potential stress threshold being reached under the combination of the T2 treatment and extreme heat during that particular year.

Compared to the CK treatment, the R_d values under the T2 treatment were lower; at the optimal temperature, the reductions were⋯

38.5% and 18.4%, respectively; under high-temperature conditions, these reductions were 46.6% and 23.2%, respectively. These results indicate that under high-temperature conditions, sufficient moisture can promote the activity of spring wheat leaves.

High-temperature treatment leads to a decrease in the apparent quantum efficiency (AQE) of spring wheat leaves compared to optimal temperature conditions.

The metabolic activity of spring wheat leaves increases, characterized by an elevated dark respiration rate. Conversely, under drought stress, the physiological activity of spring wheat leaves is significantly altered.

low, with an average decrease of 10.6%, indicating that high temperatures reduce the leaf area of spring wheat.

activity is inhibited, the dark respiration rate of the leaves decreases, and early long-term drought

The average reductions at optimal temperatures were 46.3% and 24.0%, respectively, while at high temperatures, they were

2.2 高温条件下春小麦叶片气体交换参数对干旱

The inhibitory effect of drought stress on the ability of leaves to utilize weak light is more pronounced. Furthermore, drought stress···

2.2.1 气孔导度（Gs）春小麦叶片气孔导度的光反

The capacity to utilize weak light. The apparent quantum efficiency (AQE) in the T1 and T2 treatments was lower than that of the CK treatment.

The degree of inhibition was relatively high.

were 56.9% and 30.7%, respectively. This indicates that compared to optimal temperatures, drought stress under high-temperature conditions

response to stress

The earlier the onset of stress and the longer its duration, the more pronounced the effects became.

The response is shown in Figure 2 [Figure 2: see original paper]. There were distinct differences in the response patterns of stomatal conductance (G_s) to photosynthetically active radiation (PAR) across the various treatments.

Under high-temperature conditions, the average maximum net photosynthetic rate (P_{nmax}) of the leaves was significantly lower than under optimal temperatures, with a reduction of 20.2%. This demonstrates the significant impact of temperature on P_{nmax}.

differences; under different temperature regimes, the G_s of the CK treatment showed a continuous increasing trend as PAR increased, with the rate of increase being initially rapid before slowing down. In contrast, the G_s in the T1 and T2 treatments exhibited an initial rapid increase.

1 Photosynthetic light-response parameters of spring wheat leaves under different treatments

CK-25 T1-25 T2-25

CK-31 T1-31

T2-31

CK-25 T1-25 T2-25

CK-31 T1-31 T2-31

Apparent Quantum Efficiency $AQE/(\mu\text{mol} \cdot \mu\text{mol}^{-1})$

Maximum Net Photosynthetic Rate $P_{nmax}/(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$

LSP/(μmol • m-2 • s-1)

LCP/(μmol • m-2 • s-1)

Dark respiration rate R_d / $(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$

Arid regions

2 Response curves of stomatal conductance in spring wheat leaves under different treatments in 2022 and 2023

long, showing a trend of continuous decrease after reaching its peak. Under high-temperature conditions, the values at various locations

The degree of decline was more pronounced than under optimal temperature conditions, indicating that temperature fluctuations have a stronger impact on Tr

The Gs under these treatments were all lower than those under optimal temperature conditions. When $PAR > 500 \ \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$

The influence is relatively significant. Tr followed the order of $CK > T2 > T1$; under optimal temperature, $T1$ and

At this time, the Gs of spring wheat under different temperatures followed the order of CK being the largest, followed by $T2$, and then $T1$

2.2.2 胞间 CO（C

Analysis of the light response curves of intercellular CO_2 concentration (C_i) in spring wheat leaves revealed distinct patterns across treatments.

Compared to the CK treatment, the T2 treatment showed reductions of 39.2% and 25.3%, respectively. Under high-temperature conditions,

reductions of 48.5% and 27.0% were observed, indicating that drought stress further intensifies the impact on transpiration rate (T_r) under high-temperature conditions.

The analysis (Figure 3 [Figure 3: see original paper]) shows that in the low photosynthetically active radiation (PAR) region, the C_i of spring wheat leaves varies with PAR.

2.2.4 Stomatal Limitation Value (L_s)

As shown in Figure 5 [Figure 5: see original paper], in the low PAR region, the rate of decline slowed down under both temperature levels, manifesting as a relatively stable and gradual decrease.

C_i rose rapidly with increasing light intensity. As PAR continued to increase, the control (CK) treatment

exhibited a specific trend. In the high PAR range, C_i showed an increasing trend with the increase of PAR for the T1 and T2 treatments.

L_s continued to rise slowly, while L_s decreased under drought treatments (T1, T2), with the downward trend in the T1 treatment being more pronounced.

The variations in C_i for the CK and T2 treatments were characterized by CK-25 $>$ CK-31 and T2-25 $>$ T2-31.

L_s followed the patterns of CK-25 $<$ CK-31, T1-25 $<$ T1-31, and T2-25 $<$ T2-31. For the T1 treatment, L_s was

sharply decreasing as PAR increased; subsequently, as PAR further increased, the CK treatment at both temperature levels

showed an increasing trend, which was particularly evident for the T1 treatment in 2023. The difference in the T2-31 treatment was relatively small. Under different temperature treatments, the differences between CK and T2

treatments regarding C_i were minor. Under optimal temperature conditions, the C_i of the CK treatment was 16.5% higher than that of the T1 treatment, while under high-temperature conditions, it was 10.6% higher.

2.2.3 Transpiration Rate (T_r)

The T_r of spring wheat leaves under different treatments is shown in Figure 4 [Figure 4: see original paper].

In the low PAR region, the L_s of spring wheat leaves for all treatments under both optimal and high-temperature conditions

was more pronounced than in the T2 treatment. Comparing the changes in L_s under different temperatures,

under optimal and high-temperature conditions, L_s increased by 46.2% and 27.0%, respectively, compared to the CK treatment, while the difference in the T2 treatment was not significant.

2.3 高温条件下春小麦叶片水分利用效率对干旱

Response to Stress

As shown, in the low PAR (photosynthetically active radiation) region, the transpiration rate (Tr) of leaves across all treatments increased rapidly.

Analysis of the light response characteristics of water use efficiency (WUE) in spring wheat leaves was conducted.

As PAR increased, the Tr of the CK (control) treatment under optimal temperature conditions exhibited a gradual increase.

The analysis of these characteristics is illustrated in Figure 6 [Figure 6: see original paper]. In the low PAR range, the spring wheat across all treatments showed specific patterns.

The treatments exhibited a downward trend across different temperatures, particularly under high-temperature conditions.

As PAR continued to increase, the growth rate of WUE for the CK and T2 treatments slowed down under optimal temperature conditions, tending toward stabilization.

Under high-temperature conditions, there was a slow downward trend, whereas for the T1 and T2 treatments, a gradual increase was observed.

WUE improved significantly as PAR intensified. As PAR increased further, distinct variations emerged between the groups.

Zhang Jindan et al.: Response of Photosynthetic Physiological Characteristics of Spring Wheat to Drought Stress under High-Temperature Conditions

3 Response curves of intercellular CO2 concentration in spring wheat leaves under different treatments in 2022 and 2023

4 Response curves of transpiration rate in spring wheat leaves under different treatments in 2022 and 2023

Arid Regions

5 Response curves of stomatal limitation value in spring wheat under different treatments in 2022 and 2023

6 Response curves of leaf water use efficiency in spring wheat under different treatments in 2022 and 2023

Zhang Jindan et al.: Response of Photosynthetic Physiological Characteristics of Spring Wheat to Drought Stress Under High-Temperature Conditions

In the case of a gentle slope, the T1 treatment first increased rapidly to its maximum value and then gradually decreased. During

It was observed that under high-temperature conditions, sufficient moisture promoted an increase in R_d, reflecting leaf

Only the CK treatment showed a diminishing increase in WUE, tending toward stability, while the T2 and T1 treatments

Continuous drought under high-temperature conditions significantly inhibited leaf activity, prompting the plants to

In the high PAR region, the WUE of the T1 treatment was smaller than that of both the CK and T2 treatments.

The "conservative" adaptation mechanism further confirms that spring wheat, when facing extreme environments,

WUE was significantly lower than under optimal temperature conditions.

strategies to maintain the balance between survival and growth [**?**, **?**, **?**].

In the high PAR region, WUE followed the order of T2 > CK > T1; under high-temperature conditions,

metabolic activity is enhanced; conversely, drought stress caused a decrease in R_d, indicating that high

WUE first increased and then decreased across all treatments, with the magnitude of the decrease in the T1 treatment being greater than that in the T2 treatment.

maintain carbon accumulation by reducing respiratory consumption, forming a "metabolic-saving"

The difference between the CK treatment and the T2 treatment was not significant. Under high-temperature conditions, all treatments

tended to down-regulate light energy capture and carbon consumption when facing extreme environments to main-

3 讨论

Influence of Parameters

In this section, we analyze the impact of various hyperparameters on the performance of the proposed model. Understanding how these parameters influence the learning process is critical for optimizing the model's stability and predictive accuracy.

First, we examine the effect of the learning rate on the convergence behavior. A higher learning rate may lead to rapid initial progress but often results in oscillations around the local minima, potentially preventing the model from reaching an optimal state. Conversely, an excessively small learning rate significantly increases the computational cost and risks trapping the optimization process in suboptimal plateaus. Our empirical results suggest that an adaptive learning rate strategy provides the most robust performance across different datasets.

Furthermore, the regularization parameter plays a vital role in balancing the trade-off between bias and variance. By adjusting the strength of the penalty term, we can effectively control the model complexity to prevent overfitting. As shown in , increasing the regularization coefficient initially improves generalization on the test set; however, beyond a certain threshold, the model begins to suffer from underfitting, as evidenced by a simultaneous decrease in both training and validation accuracy.

Finally, we investigate the sensitivity of the model to the dimensions of the latent space. The dimensionality of the hidden layers determines the capacity of the network to capture intricate patterns within the data. While a larger latent space allows for the representation of more complex features, it also necessitates a larger volume of training data to avoid the curse of dimensionality. Our analysis indicates that the optimal parameter configuration is highly dependent on the specific characteristics of the input features and the overall scale of the dataset.

3.1 高温条件下干旱胁迫对春小麦光响应过程的

Photosynthesis is a physiological process in crops that is highly sensitive to environmental changes. As the fundamental mechanism for biomass accumulation and yield formation, it serves as a critical indicator of plant health and productivity. Variations in external factors—such as light intensity, temperature, carbon dioxide concentration, and water availability—directly modulate photosynthetic efficiency. Understanding the intricate relationship between these environmental drivers and photosynthetic responses is essential for optimizing crop management and predicting agricultural outcomes under shifting climatic conditions.

The physiological processes of plants, particularly under multiple stress conditions, involve highly complex response mechanisms [**?**]. The results of this study demonstrate that under two distinct drought treatment conditions, spring wheat exhibits significant photoinhibition of the net photosynthetic rate (P_n). Furthermore, the observed decline in P_n was accompanied by⋯

The reduction in P_n followed the order of T1 > T2 > CK. This indicates that drought stress initiated during the vegetative growth stage exerts a more significant inhibitory effect on P_n compared to drought stress initiated at the onset of the reproductive growth stage.

Transpiration rate, stomatal conductance, and intercellular CO_2 concentration are critical indicators reflecting the intensity of plant photosynthesis. In wheat leaves, water loss occurs primarily through transpiration, with stomatal transpiration playing a dominant role. Consequently, both the transpiration rate and the photosynthetic rate increase as stomatal conductance rises. Generally, drought stress leads to a decrease in stomatal conductance and the closure of stomata, which results in a reduced transpiration rate and potential damage to photosynthetic organs. Current research indicates that the reduction in photosynthetic rate under drought stress is co-regulated by both stomatal and non-stomatal factors. Specifically, photosynthesis is primarily limited by stomatal factors under mild drought conditions, whereas under severe drought, the limitation shifts to non-stomatal factors, which are influenced by the photosynthetic capacity of mesophyll cells.

The impact of drought on the photosynthetic characteristics of spring wheat is particularly significant, indicating that both the timing of drought onset and its duration play critical roles in determining the physiological response of the crop.

impact on overall performance [?]. The present study demonstrates that the stomatal conductance of spring wheat,

has a critical impact on the overall performance

area development and stomatal conductance, exacerbating irreversible damage to the photosynthetic apparatus.

The transpiration rates followed the order of T1 < T2 < CK. Under the T1 treatment, the intercellular CO_2 concentration (C_i) of spring wheat···

Furthermore, as a cool-season crop, the photosynthetic system of spring wheat is highly sensitive to temperature.

C_i shows an increasing trend. This study suggests that drought occurring at the onset of the reproductive growth stage···

Early drought may significantly impact plant growth and development by affecting leaf physiological processes and structural characteristics. When plants encounter water scarcity during their early growth stages, they often undergo a series of adaptive responses to mitigate the negative effects of environmental stress. These responses include the regulation of stomatal conductance to reduce water loss through transpiration, which simultaneously limits the intake of carbon dioxide and subsequently reduces the rate of photosynthesis.

Furthermore, early drought can alter leaf morphology and anatomy. Plants may develop smaller leaves with higher stomatal density or thicker cuticles as a strategy to enhance water-use efficiency. Such structural modifications are critical for survival but often come at the cost of reduced biomass accumulation. Understanding these mechanisms is essential for predicting how vegetation will respond to increasingly frequent and severe drought events under changing climatic conditions.

The photosynthetic process is extremely sensitive to changes in temperature [?]. Under high-temperature conditions (31 °C), the photosynthetically active radiation (PAR) threshold for the light saturation point across all treatments was lower than those observed under optimal temperature conditions (25 °C). Furthermore,

Drought stress further reduced this threshold, particularly within the T1 treatment group.

The reduction in P_n was more pronounced under these conditions, and the magnitude of the decrease in P_n for the T1 and T2 treatments was further expanded compared to the optimal temperature conditions. This indicates that high temperatures not only directly weaken photosynthetic efficiency but also enhance the inhibitory effects observed in these treatments.

increased the sensitivity of spring wheat to water stress and lowered the tolerance threshold of spring wheat to drought stress, resulting in a synergistic "high temperature-drought" inhibitory effect.

lower than the T2 and CK treatments. Furthermore, in the high PAR (Photosynthetically Active Radiation) region, the T1 treatment exhibited⋯

The primary mechanism underlying the decline in photosynthesis in spring wheat under drought stress is stomatal limitation. However, when drought stress begins during the vegetative growth stage and persists with high intensity over a long duration, the photosynthetic organs of the spring wheat sustain damage. This damage acts as a non-stomatal factor that further exacerbates the constraints on photosynthesis. Consequently, intercellular CO_2 is prevented from fully participating in the photosynthetic process, leading to its gradual accumulation within the cells. As a result, the intercellular CO_2 concentration exhibits an upward trend [**?**]. Temperature is⋯

One of the critical environmental factors affecting crop growth, it not only regulates the physiological processes of plants but also significantly influences their developmental stages and overall yield. In the context of agricultural science, understanding the multifaceted impact of this factor is essential for optimizing cultivation strategies and enhancing food security.

Recent advancements in machine learning and deep learning have provided researchers with robust tools to analyze the complex interactions between environmental variables and crop performance. By leveraging high-dimensional datasets, these computational approaches can identify patterns that traditional statistical methods might overlook, thereby offering more precise predictions of crop behavior under varying conditions.

The photosynthetic mechanisms of plants may face limitations in carbon assimilation and a reduction in Photosystem II (PSII) activity. Under these conditions, the efficiency of the Calvin cycle is often restricted by a decrease in the activity of key enzymes or a reduction in the regeneration of ribulose-1,5-bisphosphate (RuBP). Simultaneously, the light-harvesting complex and the reaction center of PSII may undergo photoinhibition, leading to a decline in the maximum quantum yield (F_v/F_m) and the effective photochemical efficiency (Φ_{PSII}). Such physiological responses indicate that environmental stressors can disrupt the balance between light energy absorption and metabolic utilization, ultimately impacting the overall biomass accumulation and growth of the organism.

The level of enzyme activity within a plant alters the physiological and biochemical reactions of the crop.

The dual pressure of performance degradation

rate, it also directly affects the transpiration water loss of the leaves and the opening of the stomata.

[18-20]

Photoresponsive characteristic parameters can effectively characterize the photosynthetic mechanisms of plants. These parameters serve as critical indicators for understanding how plants utilize light energy and adapt to varying environmental conditions. By analyzing these characteristics, researchers can gain deeper insights into the efficiency of light capture, energy conversion, and the overall metabolic health of the plant.

closed state, thereby further influencing the photosynthetic physiological processes of the crop [**?**].

mechanisms governing the response to environmental changes [**?**]. The results of this study demonstrate that, relative to the optimal temperature

The results of this study indicate that when the temperature rises to 31 °C, the elevated temperature significantly affects the physiological processes under investigation. This thermal threshold appears to be a critical point beyond which observed biological or physical responses deviate from baseline conditions. Furthermore, the data suggest that sustained exposure to 31 °C may lead to accelerated reaction rates or potential thermal stress, depending on the specific system being analyzed. These findings underscore the importance of monitoring temperature fluctuations in maintaining the stability of the experimental environment.

Under high-temperature conditions, drought stress significantly limits the growth and productivity of spring wheat in arid and semi-arid regions. This environmental constraint poses a substantial challenge to food security, as the synergistic effect of heat and water scarcity exacerbates physiological damage to the crop. Specifically, these stressors impair photosynthetic efficiency, disrupt metabolic processes, and lead to premature senescence, ultimately resulting in severe yield reductions. Understanding the mechanisms by which spring wheat responds to these concurrent stresses is essential for developing resilient cultivars and optimizing irrigation strategies in vulnerable agricultural zones.

This increases the leaf stomatal saturation vapor pressure, thereby accelerating the rate of leaf transpiration.

The ability to utilize light energy in both standard and high-intensity light zones is specifically manifested in high-temperature environments.

rate, the significant loss of cellular water triggers plant defense mechanisms, causing

Under drought stress conditions, the apparent quantum efficiency (AQE) of spring wheat···

Stomatal closure leads to a decrease in stomatal conductance, which subsequently reduces the intercellular CO_2 concentration within the leaf.

The significant decrease indicates that the capacity for capturing and converting weak light is impaired. Furthermore, the decline in the light saturation point reflects that the photosystem becomes highly susceptible to damage or inhibition under high photosynthetically active radiation (PAR).

An increase in the stomatal limitation value led to an insufficient supply of CO_2, which ultimately inhibited the photosynthetic rate of spring wheat.

reached light saturation and exhibited earlier photoinhibition, particularly during the vegetative growth stage.

3.3 高温条件下干旱胁迫对春小麦叶片水分利用

Impact of Long-term Drought Stress and Extreme Environments on Light Utilization Capacity

Long-term drought stress significantly alters the physiological and biochemical processes of plants, particularly affecting their capacity for light energy utilization. Under extreme environmental conditions, the balance between light absorption and the metabolic requirements of the plant is disrupted, leading to potential photoinhibition or permanent damage to the photosynthetic apparatus.

Physiological Responses to Drought Stress

When plants are subjected to prolonged water deficits, the primary response is the closure of stomata to minimize transpirational water loss. While this mechanism preserves internal water status, it simultaneously restricts the diffusion of CO_2 into the leaf mesophyll. This reduction in intercellular CO_2 concentration limits the dark reactions of photosynthesis, specifically the Calvin cycle, thereby reducing the consumption of ATP and NADPH generated during the light-dependent reactions.

As the duration of drought increases, the accumulation of excess excitation energy becomes a critical challenge. If the absorbed light energy exceeds the capacity of the plant to utilize it for carbon fixation, it can lead to the formation of reactive oxygen species (ROS). These radicals cause oxidative damage to the D1 protein in the Photosystem II (PSII) reaction center, further reducing the efficiency of light energy conversion.

Adaptation Mechanisms in Extreme Environments

Plants have evolved several photoprotective mechanisms to cope with the high-light and low-water conditions characteristic of extreme environments. One of the most vital processes is non-photochemical quenching (NPQ), which allows the plant to dissipate excess light energy safely as heat. This process involves the xanthophyll cycle, where pigments such as violaxanthin are converted to zeaxanthin to facilitate energy dissipation.

Furthermore, long-term stress often triggers structural changes in the photosynthetic machinery. This may include a reduction in the size of the light-harvesting complex (LHC) to decrease the amount of light absorbed, or an increase in the synthesis of antioxidant enzymes like superoxide dismutase (SOD) and peroxidase (POD) to neutralize ROS.

Impacts on Light Use Efficiency (LUE)

The overall light use efficiency (LUE) of a plant community is a function of both the fraction of absorbed photosynthetically active radiation (fAPAR) and the efficiency with which that radiation is converted into biomass. Long-term drought stress typically results in a decline in LUE due to both stomatal and non-stomatal limitations. In extreme environments, the metabolic cost of maintaining cellular integrity and repairing damaged photosynthetic proteins further diverts energy

Impact on Efficiency

The impact on efficiency is a critical consideration in the evaluation of system performance. In the context of machine learning and deep learning frameworks, efficiency typically refers to the relationship between the computational resources consumed and the resulting performance output. When analyzing the efficiency of a proposed method, it is essential to consider both temporal complexity (processing time) and spatial complexity (memory utilization).

The introduction of complex architectural components often leads to a trade-off between model accuracy and computational overhead. For instance, increasing the depth of a neural network or incorporating sophisticated attention mechanisms may improve predictive performance but can simultaneously decrease inference speed and increase the energy consumption of the hardware. Therefore, optimizing the balance between these factors is a primary objective in modern algorithmic design.

Furthermore, efficiency is significantly influenced by the underlying hardware acceleration and the optimization of data pipelines. Effective utilization of parallel processing capabilities, such as those provided by GPUs or TPUs, can mitigate the latency introduced by high-dimensional data transformations. In practical applications, a model that achieves high accuracy but fails to meet real-time processing requirements is often considered inefficient for deployment in production environments.

The inhibitory effect is more pronounced. Changes in the dark respiration rate (R_d) reveal that the crop’ s physiological response to environmental stressors is highly sensitive. Under conditions of elevated atmospheric CO_2 concentrations, the metabolic pathways associated with carbon consumption are significantly altered. Specifically, the observed reduction in R_d suggests a strategic shift in the plant’ s energy allocation, potentially prioritizing biomass accumulation over maintenance respiration.

Furthermore, the interaction between temperature and nutrient availability plays a critical role in modulating these respiratory responses. As shown in , the correlation between R_d and leaf nitrogen content remains robust across different treatment groups, although the magnitude of the response varies. This suggests that while the fundamental mechanisms of dark respiration are conserved, their expression is subject to complex regulatory feedbacks driven by the prevailing microclimate and soil conditions.

[Figure 1: see original paper]

The data further indicate that prolonged exposure to high-stress environments leads to a partial acclimation of the respiratory system. This acclimation is characterized by a gradual stabilization of R_d values, which may mitigate the long-term impact on the overall carbon balance of the ecosystem. Understanding these dynamics is essential for accurately modeling crop yields and carbon sequestration potential in the context of global climate change.

At the leaf scale, water-use efficiency (WUE) is typically defined as the ratio of net photosynthetic rate (A) to transpiration rate (E), expressed as $WUE = A/E$. This metric reflects the amount of carbon fixed by the plant per unit of water lost through transpiration, serving as a critical indicator of the coupling between carbon and water cycles in terrestrial ecosystems. Understanding leaf-level WUE is essential for predicting how vegetation responds to environmental changes, such as increasing atmospheric CO_2 concentrations and varying vapor pressure deficits.

Abstract

Plants have evolved sophisticated adaptation strategies to cope with environmental stress at the level of energy metabolism. This study identifies···

The ratio of the net photosynthetic rate to the transpiration rate (P_n/T_r) [**?**] is used to represent the leaf-level water-use efficiency (WUE) of plants.

Arid Regions

Leaf responses represent a comprehensive reaction to changes in both internal and external environments. Because leaf water utilization involves the absorption, transformation, transport, and utilization of CO_2 and water, it is a complex physiological process.

The intercellular CO_2 concentration and transpiration rate decreased, while the stomatal limitation value increased.

(3) The leaf water use efficiency of spring wheat is co-regulated by temperature and moisture.

A series of biological, physical, and chemical processes lead to the regulation of water-use efficiency (WUE).

co-regulation. Within a certain range of light intensity, water-use efficiency increases with light intensity.

The availability and distribution of water are influenced by a wide range of factors. Specifically, environmental and biological factors play a critical role in determining moisture dynamics.

increases as light intensity rises. Under optimal temperature conditions, as light intensity continues to increase, provided there is an adequate water supply and

Efficiency does not act in isolation; rather, there are often clear interactions and synergies between different types of efficiency. In the context of resource allocation and system performance, these factors frequently exhibit complex interdependencies where the optimization of one metric may influence or constrain another. Understanding these relationships is critical for developing a comprehensive framework for system evaluation, as focusing on a single dimension of efficiency can lead to suboptimal global outcomes.

The increase in Water Use Efficiency (WUE) tended to slow down when drought stress treatments were initiated during the reproductive growth stage. Furthermore,

significant interactions. In this study, under optimal temperature conditions, as the Photosynthetically Active Radiation (PAR) increases, the net photosynthetic rate (P_n) of the leaves exhibits a characteristic response curve. This relationship is typically described by the non-rectangular hyperbola model, which accounts for the light saturation point and the light compensation point.

[Figure 1: see original paper]

As shown in [Figure 1: see original paper], the initial linear increase in P_n at low light intensities reflects the high efficiency of light energy conversion. However, as PAR continues to rise, the rate of increase in P_n diminishes until it reaches a plateau, indicating that the photosynthetic apparatus has become light-saturated. Under these conditions, the maximum net photosynthetic rate (P_{max}) is constrained by the capacity of the Calvin cycle, specifically the regeneration of ribulose-1,5-bisphosphate (RuBP) and the activity of the enzyme Rubisco.

The parameters derived from the light-response curves are summarized in . The data suggest that the light utilization efficiency (α) and the dark respiration rate (R_d) are significantly influenced by the interaction between environmental factors and the physiological state of the plant. Specifically, the quantum yield remains relatively stable within the optimal temperature range but decreases significantly under thermal stress, suggesting a disruption in the electron transport chain within the thylakoid membrane. These findings underscore the importance of considering synergistic effects when modeling carbon assimilation in varying environmental contexts.

The latter exhibited a higher Water Use Efficiency (WUE). Under high-temperature conditions, drought stress occurring at the onset of the reproductive growth stage⋯

increases, the growth rate of Water Use Efficiency (WUE) for both the CK treatment and the T2 treatment slows down, eventually tending to level off.

Under high light intensity, the Water Use Efficiency (WUE) decreases. At both optimal and high temperatures, vegetative growth···

The overall variation of the water use efficiency (WUE) in spring wheat leaves followed the trend of T2 > CK > T1.

Water use efficiency (WUE) decreased across all treatments starting from the onset of drought stress.

At the onset of drought stress treatment, the reduction in soil moisture stimulates the production of new stomata.

References

···characteristics, the T2 treatment resulted in a higher water use efficiency (WUE) in spring wheat. This may be attributed to the reproductive growth stage, where an increase in stomatal density on the leaves occurred alongside a reduction in both stomatal volume and aperture. Consequently, this led to a decrease in stomatal conductance, with the magnitude of the reduction in transpiration rate (Tr) being significantly greater···

na[J]. Meteorological and Environmental Sciences, 2015, 38(1):

Conversely, an increase in water use efficiency can lead to a reduction in root water uptake from the soil. However, under high-temperature conditions, the water use efficiency (WUE) of spring wheat in the T2 treatment began to decline in high light intensity regions.

This suggests that under multi-factor composite stress conditions, non-stomatal limiting factors exert a more prominent inhibitory effect on the net photosynthetic rate (P_n).

At this stage, the CO_2 assimilation rate is more severely affected than the transpiration rate.

Consequently, the physiological metabolic reactions within the crop are altered.

(1) High temperature and drought stress significantly inhibit the leaf photosynthesis of spring wheat.

Impact on water use efficiency [J]. Jiangsu Journal of Agricultural Sciences, 2021, 37(5): 1108-

al Sciences, 2021, 37(5): 1108-1118.]

Stupko V Y, Neshumaeva N A, Pomytkin N S, et al. Climate in fluence on photosynthesis related morphophysiological traits of ence, 2021, 677(5): 052009.

Qi Yue, Zhang Qiang, Hu Shujuan, et al. Response of photosynthetic parameters of spring maize leaves to leaf temperature under drought stress [J]. Journal of Arid Meteorology, 2023, 41(2): 215-222.

exchange parameters. Under conditions of sufficient water supply, the stomatal conductance, transpiration rate,

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