

Physiological Mechanisms of Photosynthesis and Antioxidant System in Rice under High Temperature Stress

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Abstract Rice (*Oryza sativa*), as one of the major global food crops, faces threats to its growth and yield due to climate change, particularly high-temperature stress. This study aims to delve into the physiological mechanisms of rice photosynthesis and antioxidant systems under high-temperature stress conditions. The objective is to analyze how rice responds to high-temperature pressure and understand its adaptive mechanisms. By synthesizing and analyzing data related to rice photosynthesis and antioxidant systems under high-temperature stress, the study summarizes the physiological responses of rice to high temperature, including the adverse impacts on growth and yield, as well as changes in relevant physiological parameters. Furthermore, the study discusses the regulation of photosynthesis and the mechanisms of the antioxidant system under high-temperature conditions, with particular emphasis on the variations in antioxidant enzyme activities and the importance of antioxidant substances in protecting plants from oxidative damage. The significance of this research lies in enhancing our understanding of the adaptability of rice to climate change, providing crucial insights for improving rice resistance to high-temperature stress.

Keywords Rice (*Oryza sativa*); Reproductive organ development; Gene editing technology; Sustainable agriculture; Food safety

Climate change poses a huge challenge to global agriculture and food production, and high temperature stress is one of the increasingly serious problems. As global temperatures rise, crops face more frequent and intense high temperature events, among which rice (*Oryza sativa*), as one of the most important food crops in the world, has been severely affected (Xu et al., 2021). Rice is the main food source for hundreds of millions of people around the world, so it is critical to understand and address the impact of heat stress on rice yields and global food security.

The impact of high temperature on rice is not only reflected in yield, but also includes key physiological processes such as photosynthesis and antioxidant systems. This article aims to deeply explore the physiological mechanisms of photosynthesis and antioxidant systems in rice under high temperature stress conditions, with a view to providing agricultural scientists, researchers, and farmers with important insights on how to improve high temperature stress resistance in rice. This study will focus on the physiological response of rice to high temperature stress. The impact of high temperature on rice growth and development is complex and multi-faceted, including reduced yield, shortened growth period, reduced photosynthetic efficiency, etc. These effects will also be discussed in detail to reveal how high temperature can affect rice growth and development. How to damage rice growth.

Photosynthesis is a key process for plant growth and yield. High temperature stress may lead to leaf damage, photosystem obstruction and insufficient supply of photosynthetic substrates. In-depth study of the impact of high temperature on rice photosynthesis, analysis of how high temperature disrupts photosynthesis, and discussion of the role of rice in The adjustment mechanism is particularly important when dealing with high temperature and pressure.

In terms of antioxidant system, this research will pay special attention to the oxidative stress reaction caused by high temperature stress. High temperature may cause oxidative damage, accumulate reactive oxidative substances, and threaten the stability of chloroplasts. It will study how rice resists through antioxidant enzymes and

antioxidant substances. oxidative stress to maintain cellular homeostasis. Through transcriptomic research, we can understand the gene expression patterns of rice under high temperature stress, especially genes related to photosynthesis and antioxidant systems, which helps to identify potential high temperature resistance genes and provides a basis for breeding improvement.

In addition, this study will also propose a series of potential strategies to improve high temperature stress resistance in rice, which include methods of plant breeding and genetic improvement, suggestions for agricultural management practices, and new technologies and innovative methods in improving high temperature stress resistance in rice. By deeply studying the physiological mechanisms of rice under high temperature stress, we can better understand its adaptability and resistance. This research is critical to ensuring the stability and sustainability of global food supplies, while also helping to address the challenges of climate change to the agricultural industry. We expect this review to provide valuable insights and directions for solving the problem of high temperature stress in rice.

1 Physiological Response of Rice to High Temperature Stress

1.1 Effects of high temperature stress on rice growth and yield

High temperature stress is one of the main factors that decreases rice yield. Under high temperature conditions, the development of the reproductive organs of rice is inhibited, including the formation of inflorescences and spikelets, the development of pollen, and the fertilization process. Impairment of these reproductive processes directly results in a reduction in grain quantity and quality. In addition, high temperatures can also cause abnormal development of embryos, endosperm and ovules, further reducing the yield per ear. High temperature stress can also cause premature plant senescence, resulting in immature grains. The combined impact of these factors has led to a significant decline in rice yields, posing a major challenge to agricultural systems and global food supply (Pickson et al., 2021).

High temperature stress can shorten the growth period of rice. Generally, high temperature accelerates the growth and development process, but it also reduces the quality and function of reproductive organs. According to research, the maximum temperature exceeding 35°C is the temperature causing high temperature stress in rice. Among the 17 days of high temperature treatment, the maximum temperature exceeded 35 °C on 14 days, and the maximum temperature exceeded 40 °C on 9 days. The average daily maximum temperature of high temperature treatment reached 40.16 °C, while the average daily maximum temperature of normal temperature control was 30.6 °C (Figure 1) (Miao et al., 2017).

Sterility and early seedling growth are major components of seedling vigor. Prolonged temperature increases reduce the germination potential of seeds, resulting in reduced germination rates and seedling vigor (Figure 2). The optimal growth temperature for rice in the seedling stage is 25 ~ 28°C. Heat stress (42 ~ 45°C) in the seedling stage will cause increased water loss, yellowing of leaves, damage to seedling and root growth, and even death of seedlings. The resistance of rice to HS in the seedling stage varies with different genetic backgrounds. After exposure to HS (45°C for 72 h), seedlings of the japonica rice variety Nipponbare almost completely withered, whereas seedlings of the indica rice variety HT54 could tolerate up to 48°C for 79 h. Plants treated with HS at the tillering stage showed various morphological symptoms, such as leaf wilting, curling and yellowing, and reduced tiller number and biomass. Under HS (40°C day/35°C night) for 15 days, the panicle number and total yield per plant of rice were about 35% lower than those under 28°C. The impact of HS on tillers and panicle number in japonica rice is more serious than that in indica rice. The number of tillers under HS is often used as a marker for selecting heat-tolerant rice varieties (Xu et al., 2021).

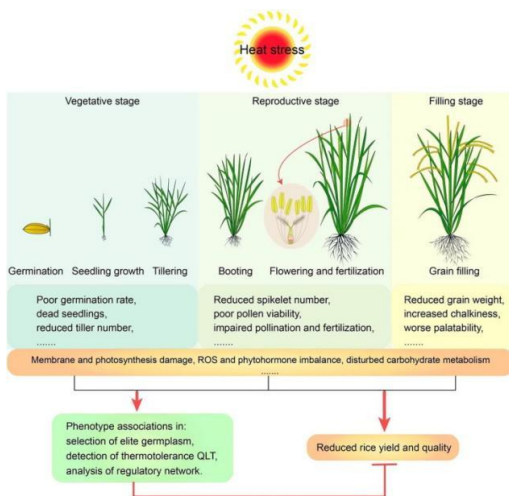


Figure 1 Morphological and physiological characteristics of rice under heat stress (Xu et al., 2021)

High temperature stress has a negative impact on rice leaves, which are the main organs for photosynthesis. However, under high temperatures, leaves are damaged, manifesting as chlorosis, wilting, scorch, and necrosis. Damage to these leaves reduces the efficiency of photosynthesis, resulting in inefficient conversion of light energy into biomass, thereby affecting yields. At the same time, leaf damage also reduces leaf surface area, reduces photosynthetic potential, and exacerbates yield decline (Gautam et al., 2022).

High temperature is usually accompanied by drought or high-temperature evaporation, which intensifies the degree of water stress. Under high-temperature conditions, rice is more likely to lose water, which increases the risk of dehydration of the plant. Dehydration affects the root system's ability to absorb water and nutrients, limiting plant growth. At the same time, under high temperature conditions, the transpiration rate of plants increases, resulting in a large amount of water loss. This water stress not only reduces yield, but also makes plants more susceptible to osmotic stress, adversely affecting cell stability.

High temperature stress will also affect the absorption and transportation of nutrients in rice. Key nutrients, such as nitrogen, phosphorus and potassium, are crucial for the normal growth of rice. However, under high temperature conditions, the root structure and function of plants are damaged, limiting the absorption of these elements. In addition, high temperatures may interfere with the transport of these elements, resulting in uneven nutrient distribution, affecting plant health and yield. These effects further exacerbate the adverse effects of high temperature stress on rice yield.

1.2 Temperature-sensitive stages of rice and classification of high-temperature stress

The growth and development of rice have different sensitivities to temperature at different growth stages. The seedling stage of rice is usually within the first few weeks after emergence. Seedlings at this stage are particularly sensitive to high temperatures because their growth points and reproductive organs have not yet been fully developed. Leaves are susceptible to sunburn in hot conditions, especially in full sunlight. When the rice seedling stage encounters continuous high temperatures and lack of water in the rice field, the vigorously growing rice seedlings in the early stage enter the state of ear differentiation in advance. The ears will be heading around 12 to 15 days after transplanting, and the ears will be obviously weak. In production, this is called "banding". "Fetal transplanting", if not handled in time, will affect the growth and development of other tillers, and in severe cases, the yield will be reduced by 20% to 40%.

The tillering stage is a critical period when rice begins to form side tillers and reproductive organs. High temperature stress may lead to a reduction in the number of tillers, which directly affects yield. In addition to tillering, high temperatures may also affect the development of inflorescences, thereby affecting subsequent fertilization and grain development. In this case, high temperature may lead to the formation of empty spikes or damage to some spikelets (Wang et al., 2017).

In the early heading stage, the rice plant is preparing to enter the reproductive stage, forming inflorescences and flowering. High temperature stress may cause delayed or abnormal heading, thereby affecting the success rate of fertilization. This may result in empty ears or insufficient fertilization, thus reducing yield. High temperature stress may also affect the flowering process of rice. Under high temperature conditions, pollen may be damaged, reducing pollen viability and affecting fertilization. Decreased pollen quality and quantity is a key factor in yield reduction caused by high temperature stress.

The grain filling period is the period when rice grains are enlarged and substantial. High temperature stress may cause the development of grains to be blocked, affecting the size and quality of the grains. In addition, high temperatures may cause uneven expansion of the seeds, causing some of the seeds to become smaller or hollow.

Understanding the different types and classifications of high temperature stress can help to better address this challenge. Sustained high temperature stress refers to rice being exposed to high temperature conditions for a long time, which may cover multiple growth stages. In this case, the impact of high temperature on yield is usually severe, as it can cause damage to multiple reproductive and growth processes. For example, high temperatures may occur continuously during the seedling and tillering stages, resulting in significant yield reductions.

Cyclic high temperature stress refers to high temperature events occurring at specific growth stages, but not necessarily continuously. For example, high temperatures may be exposed to rice during the tillering or heading stages, while temperatures at other stages may be relatively low. In this case, the effects of high temperatures focus on specific reproductive or growth processes. Understanding the cyclical nature of this high temperature stress helps to take targeted management measures (Schneider et al., 2020).

Rice usually grows under cooler nighttime temperatures, but if nighttime temperatures rise, the temperature difference between day and night will decrease. This is also considered a form of high temperature stress as it affects the normal growth and development of rice. Rice usually photosynthesizes at night, taking advantage of periods of low temperatures to maximize light energy utilization. If temperatures rise at night, plants may suffer during this critical process, affecting yields.

1.3 Physiological changes of rice under high temperature

With the intensification of global climate warming, high temperature stress has become one of the most important stress factors restricting the security of world food production. It is predicted that by 2040, high temperatures will significantly reduce global food production. Therefore, mining high-temperature resistance gene resources, elucidating the molecular mechanism of high-temperature resistance, and cultivating new high-temperature resistant crop varieties have become major issues that need to be overcome (Song Youjin et al. , 2021) .

High temperature stress limits photosynthesis in rice leaves. Damaged leaves cannot effectively utilize light energy for photosynthesis, resulting in reduced carbon fixation. In addition, stomatal closure is one of the plant's responses to high temperatures, which reduces the entry of CO₂ and further reduces the rate of photosynthesis. Therefore, rice biomass accumulation is limited under high temperature conditions.

It is a common phenomenon that the rice seed setting rate decreases under high temperature and rainy weather. Especially after heavy rain days, the rice seeds in the lodging fields are immersed in water for a long time, and the rice absorbs water, which further promotes germination on the ear. The performance of different varieties in the same area is different. Some varieties are relatively resistant to high temperatures, and the yield reduction is obviously not much; the seed setting rate of varieties with large ears is more obvious than that of varieties with small ears. The high-temperature response of rice at different stages will be reflected in the development of growing points. If the early high-temperature drought is not treated, the growth will be slow, the leaves will twist and lose water, and then dry up and die.

Post-harvest testing of rice in hot and dry weather during the heading period shows that the 1,000-grain weight is generally reduced. Varieties with high 1,000-grain weight have a significant reduction, while varieties with low

1,000-grain weight have a relatively small reduction. For example, the chalky grain rate and chalkiness of rice in Sichuan and Chongqing in 2022 are significantly higher than in 2021, and the polished rice rate is also significantly lower. Rice mills are less willing to purchase local rice, and there are also findings in the rice milling that year, 100 kg of rice can only yield about 50 kg of whole rice, and the taste has also deteriorated (Jin et al., 2022).

High temperature stress adversely affects the development of rice reproductive organs such as inflorescences, spikelets, and pollen. High temperatures may lead to reduced inflorescences, abnormal pollen development, and abnormalities in the fertilization process. These changes directly affect the quantity and quality of grains, resulting in reduced yields. These physiological changes are interrelated and jointly affect the growth and yield of rice under high temperature conditions. Understanding these changes is crucial for developing high temperature stress management strategies and developing high temperature resistant rice varieties.

2 Changes in Photosynthesis under High Temperature Stress

2.1 Effect of high temperature stress on key enzymes

Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase) is a key enzyme involved in the carbon fixation process in photosynthesis. It is widespread in plants, algae and some bacteria. The effect of high temperature stress on Rubisco enzyme can affect the growth and productivity of plants and other photosynthetic organisms, because Rubisco plays a key catalytic role in photosynthesis (Yuan et al., 2018).

High temperature may cause the activity of Rubisco to decrease. This is because high temperature may cause protein denaturation and affect the three-dimensional structure of Rubisco, thereby reducing its affinity for the substrate (ribulose-1,5-bisphosphate). Rubisco's substrate specificity for oxygen and carbon dioxide may also be affected by high temperatures, causing the enzyme to mistakenly use oxygen for the reaction instead of carbon dioxide, producing an oxidation reaction instead of a carbon fixation reaction, which is called photorespiration.

Rubisco is the main enzyme for carbon fixation in photosynthesis, and the decrease in its activity may lead to a decrease in carbon fixation efficiency. This will further weaken the efficiency of photosynthesis and affect the photosynthetic capacity of rice. Rubisco enzyme is the key rate-limiting enzyme in the photosynthetic dark reaction stage. When the temperature and CO₂ concentration increase, the total activity and protein content of Rubisco enzyme are affected. Under the current atmospheric CO₂ concentration, the decrease in Rubisco enzyme activity when the temperature increases has been verified in many plants, including rice (Yuan et al., 2018). The decrease in activity of Rubisco enzyme under high CO₂ concentration is not its own inactivation (Rubisco enzyme is still active at 50 degrees) but the decrease in the activation of Rubisco activating enzyme (RCA) caused by changes in ATP energy state (Figure 2).

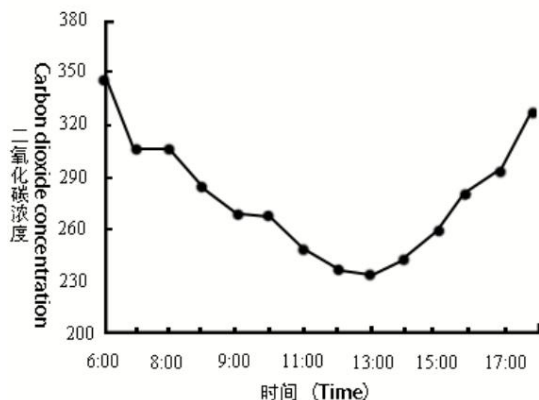


Figure 2 Diurnal changes in intercellular CO concentration in rice (Wen et al., 2019)

Not only that, Rubisco is also a key carbon-fixing enzyme in photosynthesis, and the reduction of its activity may

lead to a decrease in the overall photosynthetic rate. This affects the plant's fixation of carbon dioxide, slowing the plant's growth and development. Some plants and microbes may have adapted Rubisco's structure to adapt to high-temperature environments through evolution. Some heat-tolerant plants may have Rubisco isoenzymes that are more stable to high temperatures, thereby slowing down the negative impact of temperature on their activity.

The main effect of high temperature stress on Rubisco is the reduction of its activity, which may lead to abnormal photosynthesis and restriction of plant growth. This is an important consideration for plant productivity in agriculture and ecosystems in situations such as global warming.

High temperature stress has multiple adverse effects on the rice photosystem, including damage to structure and function, decomposition of photosynthetic substrates, stomatal closure, ROS accumulation, leaf damage, and instability of photosystem proteins. These changes jointly lead to a decrease in photosynthetic efficiency, which is one of the key factors leading to reduced rice yield due to high temperature stress. Therefore, it is crucial to study how to improve the adaptability of rice to photosynthetic systems under high temperatures and to take corresponding management measures.

2.2 Effect of high temperature stress on photosynthetic substrates

High temperature stress has many effects on the photosynthetic substrates of rice, directly affecting the efficiency of photosynthesis and the growth of rice. High temperature stress promotes the decomposition of photosynthetic substrates, especially glucose and sucrose. These substrates are products of photosynthesis and are used to supply the plant's energy needs and carbon fixation. However, under high temperature conditions, enzyme activity increases, causing these substrates to be broken down into metabolites more quickly, reducing the carbon source available for growth and development. This has a direct impact on rice growth (Yan et al., 2011).

Starch granules in rice leaves store carbon during photosynthesis to feed periods when photosynthesis is inactive. However, under high temperature conditions, the degradation rate of starch granules increases, which reduces the amount of starch accumulation. This results in rice lacking sufficient carbon sources to maintain growth and development at night or when photosynthesis is limited.

Under high temperature conditions, the production of ATP and NADPH in the photosynthesis chain is inhibited. This is because high temperatures cause damage to the electron transport chain, reducing the production of ATP and NADPH. These two are the key energy and reducing power required to maintain photosynthesis and carbon fixation, and their reduction further reduces the efficiency of photosynthesis.

High temperature stress causes oxidative stress in leaves, impairing the redox balance. This affects the production and utilization of a variety of photosynthetic substrates. In addition, oxidative stress can also lead to oxidative damage, reducing enzyme activity and the stability of photosynthetic substrates. Under high temperatures, rice may adjust the allocation of carbon sources, allocating more carbon to stress response and defense mechanisms and reducing carbon sources for growth and yield. This change may result in growth restrictions because rice is unable to fully utilize carbon sources to support normal growth processes.

2.3 Changes in physiological parameters related to photosynthesis at high temperatures

Under high temperature stress conditions, the photosynthesis-related physiological parameters of rice undergo significant changes, and these changes are directly related to plant growth and yield. One key change is a decrease in photosynthetic rate. Research shows that in high-temperature environments, the photosynthetic rate of rice leaves is significantly reduced. This is due to insufficient supply of CO₂ due to closed stomata, which limits the carbon fixation process. At the same time, stomatal closure caused by high temperature also leads to stomatal restriction, making it impossible for rice to maintain normal gas exchange, exacerbating the problem of reduced CO₂ utilization efficiency (Yuan et al., 2018).

On the other hand, high temperature stress also caused changes in chlorophyll fluorescence parameters. For example, chlorophyll maximum photochemical efficiency (Fv/Fm) is often used to assess PSII health. Under high temperature conditions, the Fv/Fm value of rice leaves decreased, suggesting damage to the structure and function

of PSII, which may be related to stomatal closure caused by high temperature and oxidative stress caused by heating of leaves (Table 1).

Table 1 Changes in various physiological parameters of rice under high temperature stress

Physiological parameters	Changes under high temperature stress
Photosynthetic rate	Descending, affected by pore closure and insufficient CO ₂ supply
Stomatal limitation	Increase, leading to a decrease in CO ₂ utilization efficiency
Chlorophyll fluorescence parameters	FV/FM reduction, reflecting damage to PSII structure and function
Impairment of PSII	Structure and function may be affected by high temperature stress
Photorespiration	Increase as a response to the impact of insufficient CO ₂ supply

Photosystem II (PSII) is also a key change under high temperature stress . Studies have found that in high temperature environments, the structure and function of PSII may be damaged, leading to the interruption of photosynthesis. This includes denaturation of proteins and loss of photosynthetic pigments, which in turn affects the stability of the electron transport chain.

3 Functions and Changes of Antioxidant System

3.1 The role of antioxidant enzymes in high temperature stress

When rice faces high temperature stress, antioxidant enzymes play a key protective role, helping plants maintain intracellular redox balance and reduce the degree of oxidative damage. An important antioxidant enzyme is superoxide dismutase (SOD) , which can catalyze the reduction of superoxide anions and prevent the accumulation of this harmful oxidative substance. Under high temperature conditions, the activity of SOD in rice usually increases significantly to cope with oxidative stress. Studies have found that the increase in SOD activity in rice leaves after high temperature treatment helps remove excess superoxide anions, thereby maintaining the integrity and function of cell membranes.

Another important antioxidant enzyme is peroxidase (POD), which is involved in removing hydrogen peroxide and other substances in cells. Under high temperature stress, POD activity in rice often shows an upward trend, which helps slow down oxidative damage to cell membranes. Research shows that the increase in POD activity in rice under high temperature conditions synergizes with the antioxidant system to help maintain a stable redox state in cells and reduce the damage caused by oxidative stress.

CAT (Catalase) is another antioxidant enzyme whose main function is to break down hydrogen peroxide into water and oxygen. Studies have found that the activity of CAT in rice will also significantly increase under high temperature stress, which helps to remove reactive oxygen species such as hydrogen peroxide and protect cells from oxidative damage. Experimental data show that after high temperature treatment, the increase in CAT activity in rice is closely related to alleviating oxidative stress in leaves and maintaining the integrity of the chloroplast structure (Kang et al., 2021) .

In addition, ascorbate peroxidase (APX) is also a key antioxidant enzyme in rice under high temperature stress. Studies have shown that high temperature treatment leads to an increase in APX activity in rice. Its main function is to remove hydrogen peroxide produced in cells and prevent cell damage caused by oxidative stress. Experimental data show that under high temperature stress conditions, the activity of APX in rice leaves increases significantly, which helps maintain intracellular redox balance and reduce oxidative damage caused by high temperature.

3.2 Accumulation of antioxidant substances and protection of chloroplasts from oxidative damage

In the context of high temperature stress in rice, plants respond to oxidative stress by accumulating antioxidant substances, thereby protecting chloroplasts from oxidative damage. Ascorbic acid (a scorbate, Asc) is a key antioxidant substance . The content of ascorbic acid in rice increases significantly under high temperature stress. Ascorbic acid, as a non-enzymatic antioxidant, can directly neutralize reactive oxygen species and prevent oxidative damage to chloroplasts. Experimental data show that the increase in ascorbic acid content in rice leaves after high temperature treatment is closely related to slowing down lipid peroxidation of the chloroplast

membrane and maintaining the stability of the chloroplast structure (Lee et al., 2000).

Another important antioxidant substance is glutathione (GSH). Studies have found that under high temperature stress conditions, the accumulation of glutathione in rice also shows an upward trend. Glutathione participates in the reduction of oxidized proteins. For example, reduced glutathione removes intracellular hydrogen peroxide by reducing the activity of catalase, thus protecting chloroplasts from oxidative stress damage. Experimental data show that the increase in glutathione content in rice leaves under high temperature stress is closely related to maintaining the integrity of the chloroplast membrane and the oxidation degree of antioxidant proteins.

The accumulation of these antioxidant substances is closely related to their protective role in rice against high temperature stress. By maintaining intracellular redox balance and reducing the damage caused by oxidative stress, it provides key support for the physiological adaptability of rice. An in-depth understanding of the regulatory mechanisms of these antioxidant substances is expected to provide a theoretical basis for improving rice resistance to high temperature stress.

3.3 Response mechanism of antioxidant system to high temperature stress

Under high temperature stress, rice regulates antioxidant enzyme activity to remove excess reactive oxygen species and maintain intracellular red oxygen balance. Among them, enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) play key roles in this process. Experimental results show that the activities of these antioxidant enzymes in rice leaves significantly increased after high temperature treatment, thereby enhancing resistance to oxidative stress (Pang et al., 2021).

Rice responds to oxidative stress by increasing the accumulation of antioxidant substances under high temperature stress conditions. For example, the levels of glutathione (GSH) and ascorbic acid (Asc) increased significantly. These antioxidant substances can neutralize reactive oxygen free radicals and reduce oxidative damage. Experimental data showed that the contents of GSH and Asc in rice leaves after high temperature treatment were significantly increased compared with the control group, indicating a positive response to antioxidant stress (Table 2).

Table 2 Changes in antioxidant content of rice leaves under high temperature stress

Processing Group	Glutathione content (μmol/g fresh weight of leaves)	Ascorbic acid content (μmol/g fresh weight of leaves)
Control group	8.2	2.5
High temperature treatment group	15.6	5.83.2
High temperature treatment group	10.3	3.2

Together, these examples and data reveal the response mechanism of the rice antioxidant system to high temperature stress. By regulating antioxidant enzyme activity and accumulating antioxidant substances, rice can maintain intracellular redox balance and reduce oxidative damage under high temperature conditions. Provides important physiological support for survival in inhospitable climatic environments. This in-depth understanding provides a theoretical basis for cultivating rice varieties with greater resistance to high temperatures in the future.

4 Potential Strategies to Improve Resistance to High Temperature Stress in Rice

4.1 Methods of plant breeding and genetic improvement

In order to improve the resistance of rice under high temperature stress conditions, scientists and agricultural researchers use a variety of methods, including traditional breeding, molecular marker-assisted breeding, gene editing technology, collection and preservation of genetic resources, and the application of biotechnology. These approaches are discussed in detail below to better understand how to improve rice resistance to high temperature stress.

Traditional breeding methods are a classic way to improve rice. It involves selecting and breeding parents with high temperature resistance and then introducing these traits into new varieties through crossing. This requires

patience and time, as multiple generations of selection and breeding are required to ensure that the desired resistance traits are stably passed on to future generations. Traditional breeding methods can also be combined with other technologies, such as selective markers, to more effectively screen candidate varieties with high temperature resistance.

Molecular marker-assisted breeding is a modern method that allows more precise screening of plants with target resistance genes. By analyzing the plant's DNA, breeders can identify individuals with high-temperature resistance genes, thus speeding up the breeding process. This approach can help reduce breeding cycles and increase the chances of successful breeding because it allows the selection of promising parents that have been validated at the molecular level.

Recent gene editing technologies (such as CRISPR-Cas9) provide new tools for plant genetic improvement. Using these techniques, researchers can precisely edit plant genes to increase their resistance to high temperatures. This method has the advantages of speed, accuracy, and customization, but it also requires strict supervision to ensure the safety and sustainability of its application (Fiaz et al., 2019) .

In the process of improving rice, collecting and preserving rich genetic resources is crucial. These resources include wild species, local species and wild relatives. They may have useful genes related to high temperature resistance that could be used in breeding efforts. Therefore, protecting and studying these genetic resources is very important to improve the high temperature resistance of rice.

However, with the application of traditional breeding, molecular marker-assisted breeding, gene editing technology, collection and preservation of genetic resources, and biotechnology, the high temperature resistance of rice has been continuously improved . These methods can be used alone or in combination to breed rice that is more adaptable to high temperatures. environment-friendly rice varieties, thereby increasing yields and food security.

4.2 Recommendations for agricultural management practices

To better cope with high temperature stress, agricultural management practices play a key role in improving rice's high temperature resistance. Some key agricultural management recommendations will be explored in detail below to help farmers and agricultural practitioners better manage rice production under high temperature conditions. These suggestions will help mitigate the adverse effects of high temperature stress on rice yield and quality.

Selecting rice varieties that are adapted to high temperature environments is the first step in agricultural management. Farmers should choose varieties that have been bred and improved to handle high temperatures. These varieties usually show better heat resistance and can maintain higher yield and quality under high temperature conditions. Adjustment of planting time can help circumvent the effects of high temperature stress. Farmers can choose to grow rice during the cooler seasons to mitigate the adverse effects of high temperatures on growth. In addition, choosing the right season can also avoid the adverse effects of high temperatures on rice flowering and fruiting.

Good irrigation management is critical to maintaining rice growth under high temperature conditions , ensuring adequate water supply but not over-irrigating to avoid flooding and heat stress. The optimization of the irrigation system can improve water use efficiency and reduce the waste of water resources (Xu et al., 2020). In hot weather, shading can help reduce soil and plant surface temperatures. This can be achieved by erecting awnings or planting trees where appropriate. Shade can reduce the impact of high temperature stress on rice and improve the comfort of the growing environment.

Under high temperature conditions, rice is susceptible to various pests and diseases. Farmers should adopt appropriate pest management measures to protect rice from pests and diseases. This can be accomplished by using pesticides or employing biological control methods.

Combining these agricultural management recommendations, farmers and agricultural practitioners can better prepare for and cope with rice production under heat stress conditions. By selecting adaptive varieties, adjusting planting time, optimizing irrigation, adopting shading measures, improving soil quality, and managing pests and diseases, rice's high temperature resistance can be improved and yields and food security can be maintained.

4.3 Application of new technologies and innovative methods in improving rice resistance to high temperature stress

With the advancement of science and technology, new technologies and innovative methods continue to emerge, providing new ways to improve rice resistance to high temperature stress. The application of these new technologies and innovative methods in rice high temperature stress resistance will be discussed in sections below.

Emerging high-temperature stress screening platforms allow researchers to simulate high-temperature conditions to better understand rice's response mechanisms. These platforms can control temperature and humidity in the laboratory to help researchers study the effects of high temperature stress on rice and evaluate the high temperature resistance of different varieties. This helps to quickly screen out rice varieties with better high temperature resistance.

The development of genomics and transcriptomic technologies allows researchers to comprehensively understand gene expression changes in rice under high temperature stress. By analyzing gene and transcript data, researchers can identify key genes associated with high temperature resistance. This provides strong support for breeding efforts, allowing researchers to select and improve high temperature resistance genes in a targeted manner.

Gene editing technologies (such as CRISPR-Cas9) provide unprecedented precision and efficiency for rice genetic improvement. Researchers can use these techniques to directly edit rice genes to increase its resistance to high temperatures. This includes deleting genes that negatively affect high temperature resistance or inserting foreign genes with high temperature resistance properties. This method has the potential to accelerate the breeding process and create rice varieties that are more resistant to high temperatures (Huang et al., 2018).

Research has found that the interaction between rice and some symbiotic microorganisms can enhance its high temperature resistance. These microorganisms can promote the growth of rice, improve its nutrient absorption, and increase its antioxidant capacity. Therefore, methods that utilize beneficial microorganisms, such as inoculation or soil amendment, can help improve rice's ability to survive high temperature conditions.

Smart agriculture technologies, such as sensors, remote sensing and data analytics, can provide tools to monitor and manage rice production in real time. These technologies can help farmers better understand heat stress and take timely measures to mitigate its effects. New technologies and innovative methods provide a wide range of options for improving resistance to high temperature stress in rice. Through the application of high temperature stress screening platform, genomics and transcriptomics, gene editing technology, interaction between rice and symbiotic microorganisms, and smart agricultural technology, rice breeding and management can be accelerated and the yield and resistance of rice in high temperature environment can be improved. The comprehensive application of these methods will help cope with the high temperature challenges brought about by climate change and maintain food security.

5 Conclusion

This study reveals the complex response mechanism of the photosynthetic and antioxidant systems of rice under high temperature stress conditions. We found that high temperature stress significantly reduced the photosynthetic efficiency of rice, resulting in damage to the photosystem and insufficient supply of photosynthetic substrates. At the same time, the antioxidant system plays a key role in resisting oxidative stress and protecting chloroplasts from oxidative damage under high temperature conditions. The upregulation of antioxidant enzyme activity and the accumulation of antioxidant substances are important components in maintaining the physiological balance of rice.

High temperature stress causes significant negative effects on rice yield and quality, which is of importance in

global food security issues. Photosynthesis is one of the key factors for rice growth and yield, and the antioxidant system is an important defense mechanism for rice to cope with high temperature stress. A thorough understanding of the changes and interactions of these two physiological mechanisms is critical for developing high temperature-resistant rice varieties and improving agricultural sustainability.

In order to further improve the resistance of rice to high temperature stress, future research can focus on more detailed research on gene regulatory networks and signaling pathways, which will help reveal the deeper mechanisms of photosynthesis and antioxidant systems, especially those related to high temperature. Interactions between resistance-related genes and proteins are key.

Emerging gene editing technology and molecular marker-assisted breeding can also be used to introduce high-temperature resistance-related genes more quickly and accurately. In addition, new high-temperature resistance genes can be discovered through extensive screening of genetic resources. Future research should also explore integrated management methods, including planting time adjustment, irrigation management, pest and disease control, and soil improvement, to maximize rice productivity under high temperature conditions.

Therefore, research on the photosynthesis and antioxidant systems of rice under high temperature stress will not only help increase rice yield, but also contribute to global food security. Future research and practice should continue to work on uncovering mechanisms, developing new resistant varieties and improving agricultural management to cope with the high temperature challenges brought by climate change. These efforts will make important contributions to sustainable agriculture and food supply.

References

- Fiaz S., Ahmad S., and Noor MA, 2019, Applications of the CRISPR/Cas9 system for rice grain quality improvement: perspectives and opportunities, *International journal of molecular sciences*, 20(4): 888.
<https://doi.org/10.3390/ijms20040888>
- Gautam H., Fatma M., Sehar Z., Iqbal RM, and Nafees AK, 2022, Hydrogen sulfide, ethylene, and nitric oxide regulate redox homeostasis and protect photosynthetic metabolism under high temperature stress in rice plants, *Antioxidants*, 11(8) :1478.
<https://doi.org/10.3390/antiox11081478>
- Huang ZM, Zhou YB, Tang XD, Zhao XH, Zhou ZW, Fu XX, Wang K., Shi JW, Li YF, Fu CJ, and Yang YZ, 2018, Construction of tms5 Mutants in Rice Based on CRISPR/Cas9 Technology, *Acta Agronomica Sinica*, 44(6): 844-851.
<https://doi.org/10.3724/SP.J.1006.2018.00844>
- Jin DY, Xie LY, Zhao HL, LI Y., Han X., He YT, and Lin ED, 2022, Impacts of barnyard grass on photosynthesis and physiology of rice under elevated atmospheric CO₂ concentration, *Nongye Qixiangju (Chinese Journal of Agrometeorology)*, 43(03): 204-214.
- Kang H., Zhu T., Zhang Y., 2021, Elevated CO₂ enhances dynamic photosynthesis in rice and wheat, *Frontiers in Plant Science*, 12: 727374.
<https://doi.org/10.3389/fpls.2021.727374>
- Lee B.H., Won S.H., Lee H.S., Mitsue M., Won-II C., In-Jung K., and Jinki J., 2000, Expression of the chloroplast-localized small heat shock protein by oxidative stress in rice, *Gene*, 245(2): 283-290.
[https://doi.org/10.1016/S0378-1119\(00\)00043-3](https://doi.org/10.1016/S0378-1119(00)00043-3)
- Miao N.Y., Tang S., and Chen W.Z., 2017, Research of nitrogen granular fertilizer alleviating high temperature stress at rice grain filling stage and its physiological mechanism. *Journal of Nanjing Agricultural University (Social Science)*, 40(1): 1-10
- Pickson R.B., He G., and Boateng E., 2021, Impacts of climate change on rice production: evidence from 30 Chinese provinces, *Environment, Development and Sustainability*, (2): 1-19.
<https://doi.org/10.1007/s10668-021-01594-8>
- Pang Y., Hu Y., and Bao J., 2021, Comparative phosphoproteomic analysis reveals the response of starch metabolism to high-temperature stress in rice endosperm, *International Journal of Molecular Sciences*, 22(19): 10546.
<https://doi.org/10.3390/ijms221910546>
- Schneider P., and Asch F., 2020, Rice production and food security in Asian Mega deltas-A review on characteristics, vulnerabilities and agricultural adaptation options to cope with climate change, *Journal of Agronomy and Crop Science*, 206(4): 491-503.
<https://doi.org/10.1111/jac.12415>
- Song YJ, Wu C., and Zhang ZY, 2021, Differential responses of grain yields to high temperature in different stages of reproductive growth in rice, *Shuidao Kexue (Rice Science)*, 35(2): 177.
- Xu GW, Jiangf MM, Lu DK, Zhao XH, 2020, and Chen MC, Optimum combination of irrigation and nitrogen supply form achieving high photosynthetic and

- nitrogen utilization efficiency, *Zhiwu Yingyang yu Feiliao Xuebao (Plant Nutrition and Fertilizer Science)*, 26(7): 1239-1250.
- Xu Y., Chu C., and Yao S., 2021, The impact of high-temperature stress on rice: Challenges and solutions, *The Crop Journal*, 9(5): 963-976.
<https://doi.org/10.1016/j.cj.2021.02.011>
- Xu Y.F, Chu C.C., and Yao S.G., 2021, The impact of high-temperature stress on rice: Challenges and solutions, *The Crop Journal*, 9(5): 963-976.
<https://doi.org/10.1016/j.cj.2021.02.011>
- Yan L., Chen S., and Huang J., 2011, Water regulated effects of photosynthetic substrate supply on soil respiration in a semiarid steppe, *Global Change Biology*, 17(5): 1990-2001.
<https://doi.org/10.1111/j.1365-2486.2010.02365.x>
- Yuan M.M., Zhu J.G., Liu G., and Wang W.L., 2018, Response of diurnal variation in photosynthesis to elevated atmospheric CO₂ concentration and temperature of rice between cloudy and sunny days: a free air CO₂ enrichment study. *Acta Ecologica Sinica*, 38(6): 1897-1907.
<https://doi.org/10.5846/stxb201701230187>
- Wang S.S., Wu K., Qian Q., Liu Q., Li Q., Pan Y.J., Ye Y.F., Liu X.Y., Wang J., Zhang J.Q., Li S., Wu Y.J., and Fu X.D., 2017, Non-canonical regulation of SPL transcription factors by a human OTUB1-like deubiquitinase defines a new plant type rice associated with higher grain yield, *Cell Research*, 27: 1142-1156.
<https://doi.org/10.1038/cr.2017.98>
- Wen X.Y., Lu Q., and Jiang D.A., 2019, Rubisco Activase and Its Regulation on Diurnal Changes of Photosynthetic Rate and the Activity of Ribulose 1, 5-Bisphosphate Carboxylase/Oxygenase (Rubisco), *Chinese J. Rice Sci.*, 15(1):35-40.