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Response Analysis of Root and Leaf Physiology and Metabolism under Drought Stress in Rice

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Abstract The study reveals the complex adaptive mechanisms of plants in response to water stress by deeply analyzing the physiological and molecular responses of rice roots and leaves under drought conditions. In terms of morphological structure adjustment, the root system optimizes water absorption by increasing length and root hair density, as well as adjusting growth strategies; Leaves reduce water evaporation by reducing surface area and adjusting stomatal density. At the molecular level, both roots and leaves exhibit similar and different gene expression patterns, involving pathways such as dehydration responsive element binding (DREB) signaling. Future research needs to address issues such as the interaction between root systems and soil microorganisms, differences in root systems among different rice varieties, and the molecular mechanisms of photosynthesis and transpiration. Through advanced molecular biology and genetic techniques, the search for new drought resistance genes is expected to provide scientific basis for drought tolerance breeding. Deeply exploring the molecular interaction network between roots and leaves will better elucidate the mechanism of rice's drought resistance and provide important support for the sustainable development of global agriculture.

Keywords Rice (*Oryza sativa* L.); Drought response; Roots; Metabolize; Molecular mechanisms

Rice (*Oryza sativa* L.) is one of the major food crops in the world, occupying an important position in the dietary structure of the world's population. However, with the continuous intensification of climate change and the frequent occurrence of extreme weather events such as droughts, rice production has faced serious challenges. In this context, it is particularly urgent and important to delve into the physiological and metabolic responses of rice under drought stress, especially the response mechanisms of roots and leaves.

The impact of drought on the growth of rice is obvious. As an aquatic plant, rice has a great demand for water, and insufficient water supply under drought conditions can directly affect its growth and development. As the main organ for plants to absorb and conduct water, the root system inevitably undergoes a series of adjustments in arid environments to adapt to water scarce environments. In addition, as photosynthetic organs, the drought stress on leaves will also lead to changes in photosynthesis and transpiration, thereby affecting plant growth and yield.

The importance of rice in world food security cannot be ignored. It is the main source of food for many countries around the world, providing staple food for billions of people. However, due to the uncertainty of global climate change, the volatility of rice production continues to increase, which puts greater pressure on the food supply chain. Therefore, in-depth research on the physiological and metabolic responses of rice under drought conditions is of great strategic significance for ensuring food security and improving rice yield (Chicago et al., 2019).

This study will focus on exploring the response mechanism of rice to drought, and deeply analyze the physiological and metabolic adjustment processes of roots and leaves. By systematically synthesizing existing research results, we aim to comprehensively understand the stress response mechanism of rice under drought stress, and provide theoretical support for future drought tolerant breeding. In addition, by revealing the physiological and metabolic regulatory networks of rice roots and leaves under drought conditions, we hope to provide scientific basis for formulating corresponding agricultural management measures and ultimately achieve the goal of improving rice drought resistance.

In addition, this study will systematically explore the response mechanisms of rice roots and leaves under drought conditions, which not only helps to enhance our understanding of rice drought resistance, but also provides concrete and strong support for addressing the challenges of global climate change to food security. By deeply analyzing the adjustment strategies of rice roots and leaves under drought stress, we are expected to provide innovative solutions for future rice breeding and agricultural production.

1 Drought Response of Rice Roots

1.1 Adjustment of Root Structure

In the context of drought pressure on rice, its root system exhibits a series of complex and targeted changes to cope with water scarce environments. Firstly, it is worth noting the changes in root morphology of rice under drought conditions. Research has shown that rice can significantly adjust its root structure in water deficient environments. The length of the root system may increase in order to search deeper for water sources in the soil, while the overall biomass and surface area of the root system may also change to improve the efficiency of water absorption (Bartlett et al., 2022).

The morphological adjustment of rice root system is not an isolated behavior, but a part of its growth adaptation strategy. For example, drought stress is one of the common environmental pressures during rice growth, and plants adapt to this challenge by adjusting their root structure. When facing drought conditions, rice roots exhibit significant adaptive changes, with one significant adjustment being the formation of root sheaths. The formation of root sheaths is considered a strategy for plants to cope with water stress, providing a protective mechanism by wrapping the root tips to slow down water loss. This structural adjustment is an important physiological response of rice to drought environments (Abdalla et al., 2021).

However, the formation of root sheaths is accompanied by a decrease in plant biomass. Although the root sheath helps to slow down water loss to a certain extent, it also has a negative impact on the overall growth of plants. This may be because the formation of root sheaths requires plants to consume additional energy and resources, thereby slowing down the progress of other growth activities. This reduction in biomass may affect the yield and overall drought resistance of rice (Figure 1).

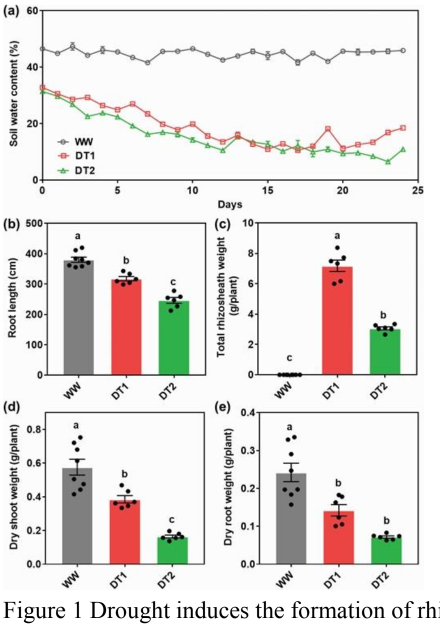

Figure 1 Drought induces the formation of rhizosheaths in rice but decreases plant biomass

Note: a: Daily SWC under different irrigation treatments; b: Total root length; c: Total rhizosheath weight; d: Dry shoot weight; e: Dry root weight of rice after irrigation treatments for 24 days; a~e: Data are the means±SE, bars with different letters were significantly different at P<0.05; WW: Well-watered; DT1: drought treatment I; DT2: drought treatment II (Lei et al., 2023)

Therefore, while studying the adjustment of rice root structure, it is necessary to deeply understand the balance relationship between root sheath formation and biomass. This helps to comprehensively evaluate the adaptive strategies of rice under drought conditions and provides guidance for future breeding work and agricultural management. By conducting in-depth research on these physiological and morphological changes, we can better understand the ecological adaptability of rice under drought stress, providing scientific support for improving its drought tolerance.

The growth adaptation strategy of the root system also involves adjusting the vertical and horizontal distribution of the root system. When there is more water in the deep soil, rice roots may grow deeper to better utilize potential water sources. On the contrary, in situations where the surface soil moisture is relatively abundant, the root system may be more distributed in the surface to quickly absorb available water. This dynamic adjustment helps rice to more flexibly utilize water resources in the soil under drought conditions.

As a result, rice roots exhibit multi-level structural adjustments and growth adaptation strategies when facing drought stress. These adjustments aim to optimize water absorption, improve water use efficiency, and enable plants to better adapt to arid environments. A deep understanding of the changes in root morphology and growth adaptation strategies is of great significance for developing drought resistant rice varieties and formulating agricultural water management policies.

1.2 Root physiological response

Rice roots exhibit complex and coordinated physiological responses under drought conditions, with important aspects including root water absorption and regulation of nutrients. Under drought stress, rice roots maintain growth and survival by adjusting water absorption and nutrient uptake.

It is crucial for rice roots to regulate water absorption under drought conditions. In order to adapt to the water scarce environment in the soil, the roots may optimize water absorption by adjusting the growth and distribution of root hairs. In addition, rice may adjust the osmotic pressure inside and outside the cells to adapt to different soil moisture conditions by regulating the osmotic regulation mechanisms of the root system, such as the synthesis and secretion of osmotic regulating substances. These physiological responses help rice maintain water balance more effectively under drought conditions, ensuring normal growth and development.

The antioxidant system plays a crucial role in the drought response of rice roots. Due to oxidative stress caused by drought conditions, the root system may experience the accumulation of reactive oxygen species such as oxygen free radicals, leading to lipid peroxidation of cell membranes and protein oxidative damage. To combat this oxidative stress, rice roots activate the antioxidant system, including enzymes such as superoxide dismutase (SOD), peroxidase (POD), and ascorbic acid peroxidase (APX). The increased activity of these enzymes helps to clear intracellular reactive oxygen species, maintain cellular redox balance, and thus slow down or alleviate oxidative damage to roots (Bouabdelli et al., 2022).

During this process, the physiological response of rice roots is not only a stress-induced adjustment, but also a survival strategy to combat drought stress. By regulating water absorption and nutrient uptake, as well as activating the antioxidant system, rice roots exhibit strong adaptability under drought conditions, providing physiological support for their survival and growth in harsh environments. A deeper understanding of the mechanisms underlying these root physiological responses can provide a theoretical basis for developing drought resistant rice varieties and offer more sustainable solutions for agricultural production.

1.3 Molecular level root response

The molecular level response of rice roots is a key link in their resistance to drought stress, involving changes in gene expression and regulation of water channel genes. A deeper understanding of these molecular level reactions can help reveal the adaptive mechanisms of rice under drought conditions. Under drought stress, the gene expression in rice roots undergoes significant changes. This change is a direct response to environmental pressure, and by adjusting the expression levels of specific genes, plants can better adapt to arid environments. Some genes related to stress response, water regulation, and antioxidant activity may be activated, initiating a series of physiological processes to enhance the root system's resistance to drought. Meanwhile, some growth and development related genes may be suppressed to regulate the growth rate of plants and better adapt to water limited conditions.

For example, previous studies have found that the decrease in plant hydraulic conductivity (Kplant) of rice under drought conditions is mainly due to the decrease in soil root interface hydraulic conductivity (Ki), as Ki is more sensitive to drought than root and stem hydraulic conductivity, and the soil root interface contributes more than 40% of the overall plant hydraulic resistance to the two crops (Yang et al., 2023) (Figure 2).

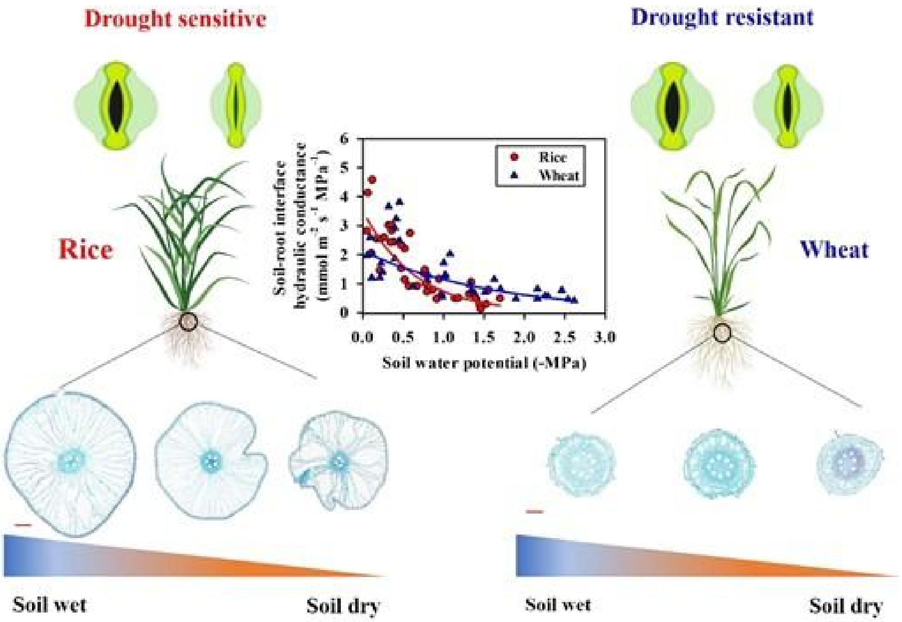

Figure 2 The mechanism of the plasticity of root morphology and anatomy in regulating plant drought resistance (Yang et al., 2023)

The regulation of water channel gene expression by rice roots under drought conditions is an important mechanism to ensure effective water absorption by plants. This involves water channel proteins, such as aquaporins in the aquaporin family. Under drought stress, rice roots may regulate the expression of water channel proteins to control water absorption and transportation. On the one hand, the upregulation of aquaporins may increase cell membrane permeability and promote water entry into cells. On the other hand, it is possible to reduce the expression of water channel proteins by regulating the negative regulators of certain water channel proteins, in order to limit water loss (Wu et al., 2020).

These molecular level root responses constitute an important component of rice's adaptability under drought conditions. By delving into these molecular mechanisms, we can better understand the stress response of rice in arid environments, providing strong guidance for future breeding work. Understanding the changes in gene expression in rice roots and the regulation of water channel genes is expected to provide more in-depth and precise strategies for developing more drought tolerant rice varieties. This will help improve the adaptability of rice and better respond to extreme climate events brought about by global climate change.

2 Drought Response of Rice Leaves

2.1 Changes in leaf physiological characteristics

Rice leaves undergo complex physiological changes under drought stress, including adjustments in water use efficiency and changes in photosynthesis and transpiration. These adjustments are survival strategies adopted by plants to more effectively maintain growth and survival in environments with limited water.

The adjustment of water use efficiency is one of the important physiological characteristics of rice leaves under drought conditions. Water use efficiency refers to the biomass produced by plants under unit water conditions, which is the ratio of photosynthetic products to transpiration loss. In arid environments, rice leaves may reduce water loss by adjusting stomatal opening and epidermal conductance. In addition, plants may also improve photosynthetic efficiency by adjusting physiological and molecular responses, thereby more effectively utilizing limited water resources.

The changes in photosynthesis and transpiration are another significant physiological feature of rice leaves under drought stress. In situations of water scarcity, plants may reduce stomatal conductance, slow down transpiration, and lower the rate of water loss. This adjustment helps to maintain leaf water balance and prevent excessive water loss. However, this may also lead to a decrease in photosynthesis, as stomatal closure restricts the entry of CO2 and affects the process of photosynthesis. Therefore, rice leaves may balance the relationship between photosynthesis and transpiration by adjusting the expression of photosynthetic enzymes and other related genes to maximize growth and survival (Buckley, 2019).

The changes in physiological characteristics of these leaves indicate that rice has adopted a series of physiological adjustments under drought conditions to adapt to environments with limited water. Understanding the molecular mechanisms and physiological processes of these adjustments can help us better understand the response mechanisms of plants to drought and provide theoretical support for future drought tolerance breeding. In depth research on the adjustment of water use efficiency and changes in photosynthesis and transpiration of rice leaves will provide strong scientific basis for formulating more effective drought management strategies in rice.

2.2 Leaf metabolic regulation

Rice leaves undergo complex metabolic regulation under drought stress, involving changes in carbon metabolism and accumulation of antioxidant substances, which are key physiological responses of plants in response to drought conditions. Under drought conditions, the carbon metabolism of rice leaves undergoes significant changes. Under limited water conditions, plants may adjust their carbon metabolism pathways to adapt to changes in photosynthesis and carbon fixation. Usually, plants adjust enzyme activity, such as regulating the activity of RuBisCO enzyme to improve carbon fixation efficiency. In addition, plants may also adjust sugar metabolism pathways to maintain a balance between energy and carbon. This may include increasing sugar accumulation as a reserve of energy and signaling molecules to maintain normal growth and metabolic activity under drought conditions.

So, when rice leaves face drought stress, they will accumulate more antioxidant substances. Due to the oxidative stress caused by drought, excessive accumulation of reactive oxygen species occurs. Rice leaves alleviate oxidative stress by adjusting the synthesis and accumulation of antioxidant substances. Antioxidants include superoxide dismutase (SOD), peroxidase (POD), ascorbic acid peroxidase (APX), etc. These enzymes can clear free oxygen radicals in cells, protect cell membranes, proteins, nucleic acids, and other biomolecules from oxidative damage (Wang et al., 2018).

These changes in metabolic regulation constitute important physiological characteristics of rice leaves under drought conditions. By adjusting carbon metabolism pathways, plants can more effectively utilize limited water resources and protect cells from oxidative damage by accumulating antioxidant substances. This adaptation strategy helps rice maintain basic growth and survival functions in arid environments. Deeply understanding the mechanisms of metabolic regulation not only helps to understand the physiological response of rice to drought, but also provides scientific basis for developing rice varieties with better drought tolerance.

2.3 Molecular level leaf response

The response of rice leaves under drought conditions involves complex molecular level regulation, including regulation of leaf gene expression and activation of signal transduction pathways. These molecular level regulatory mechanisms are key components for plants to respond quickly and accurately to drought stress.

Drought stress can trigger the regulation of gene expression in rice leaves, which is a direct response to environmental pressure. By changing the expression level of specific genes, plants can quickly adapt to drought environments (Wang et al., 2019). In the leaves, a series of genes related to drought resistance may be activated or suppressed. This may include genes encoding dehydratin response elements, transcription factors, and signaling molecules, whose expression regulation directly participates in the plant's stress response to drought. Through the regulation of gene expression, rice leaves can initiate a series of physiological processes to enhance their drought resistance.

For example, previous studies on Yangdao 6 and Shanyou 63 have shown that compared to normal water conditions, the leaf water content of Yangdao 6 and Shanyou 63 did not significantly decrease under 10% PEG drought stress, but significantly decreased under 20% and 30% drought stress. They decreased by 5% and 2% under 20% PEG stress, and by 7% and 6% under 30% PEG stress, respectively. Both under normal water conditions and drought stress, the water content of Yangdao 6 is lower than that of Shanyou 63 (Figure 3).

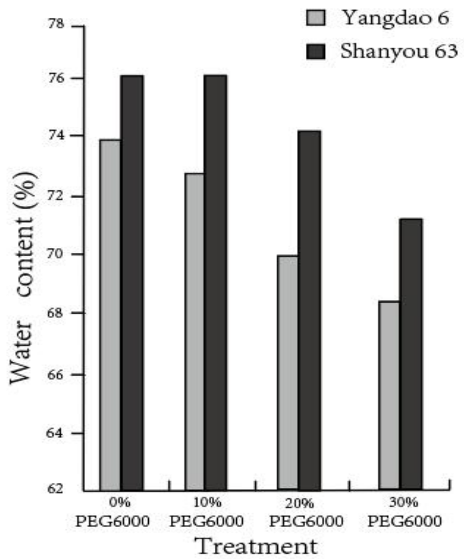

Figure 3 Effects of drought stress on leaf water content (Ding et al., 2014)

Leaves may activate signal transduction pathways under drought conditions to more effectively transmit drought signals. Signal transduction pathways are a series of complex biochemical and molecular events that involve interactions between molecules such as protein kinases, kinase substrates, and transcription factors. In leaves, dehydration hormone signaling pathways, protein kinase cascade reactions, and other key signaling networks may be involved. The activation of these signal transduction pathways helps plants perceive drought signals more quickly and trigger corresponding physiological and biochemical responses to improve their drought resistance.

These molecular level leaf response mechanisms provide strong support for the survival of rice under drought stress. By regulating gene expression and activating signal transduction pathways, rice leaves can more flexibly cope with drought stress, achieving survival and growth in arid environments. A deep understanding of these molecular level regulatory mechanisms will provide a crucial scientific basis for developing rice varieties with stronger drought resistance and formulating agricultural management strategies.

3 Compare the differences in response between roots and leaves

3.1 Differences in morphological structure between roots and leaves

When rice faces drought conditions, its roots and leaves exhibit significant morphological differences, which play an important role in the plant's adaptability to drought. Firstly, from the comparison of morphological structures, the root system and leaves exhibit different adjustment strategies under drought conditions.

In terms of root system, rice may exhibit more significant morphological changes. Under drought stress, the main changes in the root system include an increase in root length, adjustments in the number of lateral roots, and changes in the growth and distribution of root hairs. These adjustments help the root system to explore soil moisture more deeply and increase the surface area for absorbing water and nutrients. In contrast, the morphological changes of leaves are relatively small, which may mainly manifest as wrinkling, curling, or reduction of leaves to reduce transpiration and water loss.

The morphological differences between roots and leaves directly affect the performance of plants in drought resistance. For example, under drought conditions, rice roots typically increase in length to search deeper for water sources in the soil. In addition, it may increase the number and length of lateral roots to expand the water absorption area. The root system may enhance the water absorption capacity of the soil by adjusting the density and length of root hairs. At the same time, the adjustment of leaf morphology reduces water transpiration and reduces water loss. This synergistic adjustment of roots and leaves can be seen as a stress response of plants in the face of drought stress (Sarabi et al., 2019).

The differences in morphological structure have a significant impact on drought resistance. Reasonable adjustment of root system structure can enable plants to better obtain water and nutrients, thereby improving drought resistance. The adjustment of leaf morphology slows down water transpiration rate, reduces water loss, and helps plants maintain water balance under drought conditions. Therefore, the differences in morphological structure enable plants to adapt more flexibly to different soil moisture conditions, enhancing their survival ability in arid environments.

When comprehensively analyzing the differences in the morphological structure of roots and leaves, it is necessary to pay attention to the variations under different varieties and ecological environments. Meanwhile, examples or tables can be used to demonstrate the comparison and adjustment of root and leaf morphology of rice under drought conditions, in order to more intuitively illustrate the impact of these differences on plant drought tolerance. This comparison helps to gain a deeper understanding of the adaptive strategies of rice in the face of drought stress.

3.2 Differences and Similarities in Physiological Processes

The root system and leaves play complementary yet differentiated physiological roles in water regulation. The root system is mainly responsible for the absorption and supply of water in the soil, while the leaves regulate water transpiration and gas exchange through stomata. Under drought conditions, roots and leaves exhibit some common responses, but there are also significant differences.

Under drought stress, the root system aims to maximize the exploration of water resources in the soil by adjusting the growth and distribution of root hairs, as well as adjusting the root structure. This adaptation strategy aims to increase the surface area of the root system to improve the efficiency of water absorption. On the other hand, by adjusting the opening and closing of stomata, leaves limit the transpiration of water and reduce water loss. The adjustment of leaf morphology may include reducing leaf surface area, adjusting stomatal density and distribution to reduce water evaporation on the surface.

However, the differences between roots and leaves in water regulation are mainly reflected in their functional division of labor. The main task of the root system is to absorb and supply water from the soil, while the leaves focus more on regulating transpiration to maintain water balance. This difference enables plants to respond more harmoniously to drought stress throughout the entire water transport system, ensuring effective water utilization and allocation (Corso et al., 2020).

The antioxidant system is a crucial physiological process in both roots and leaves, used to combat oxidative stress and maintain cellular redox balance. The similarities and differences in antioxidant systems in roots and leaves reflect their specific adaptability in plant resistance to drought stress.

The antioxidant system in the root system mainly alleviates oxidative stress by regulating the activity of related enzymes. For example, enzymes such as superoxide dismutase (SOD), peroxidase (POD), and ascorbic acid peroxidase (APX) are activated in the root system to eliminate excessive oxygen free radicals and protect cell membranes and other biomolecules from oxidative damage.

The antioxidant system in leaves also plays a crucial role, but exhibits different characteristics in certain aspects. Due to the fact that leaves face the external environment more directly, their antioxidant system may be more flexible and respond quickly to oxidative stress caused by drought. The antioxidant enzymes in leaves may undergo more complex regulation to adapt to physiological activities such as photosynthesis and gas exchange.

3.3 Comparison at the molecular level

At the molecular level, the gene expression of roots and leaves exhibits certain similarities and differences, reflecting their different physiological roles and adaptation strategies in response to drought stress. Research has shown that there are similarities in the expression patterns of some genes in roots and leaves, especially those related to antioxidant and dehydrating hormone responses. The common regulation of these genes may be an important component of plant adaptation to oxidative stress and drought.

However, there are also significant differences in gene expression between roots and leaves. In the root system, there may be some genes whose expression is more strongly regulated to adapt to changes in soil moisture. For example, the root system may exhibit stronger water sensing and regulatory gene expression changes to more sensitively perceive and respond to soil water conditions. On the contrary, in leaves, gene regulation may focus more on adjusting genes related to photosynthesis and transpiration to minimize water loss (Corso et al., 2020).

The regulation of signaling pathways in roots and leaves also shows some similarities and differences, and the dehydratin signaling pathway is one of the main signaling pathways for plants to combat drought. Both roots and leaves are involved in the regulation of dehydratin responsive elements, transcription factors, and other key molecules to initiate a series of stress responses.

The root system, signal transduction pathways may focus more on the perception and regulation of soil moisture, including water sensors in root tip cells and hormone regulation related to water signaling. At the same time, in leaves, signal transduction pathways may place greater emphasis on stomatal regulation and photosynthetic response. Although there are some differences in signal transduction pathways, the signal transduction systems of roots and leaves work together to form the overall response mechanism of plants to drought conditions. This synergistic effect enables plants to adjust various physiological processes more flexibly at the molecular level to adapt to the different perceptual needs of different parts for drought. Such meticulous regulation helps plants more effectively cope with drought stress in complex environments.

4 Outlook

By comprehensively analyzing the response mechanisms of rice roots and leaves under drought conditions, we can see that plants exhibit multi-level and multifaceted physiological and molecular adjustments when facing water stress. The root system improves its water absorption capacity through changes in its morphological structure; Leaves reduce water loss by adjusting physiological characteristics such as photosynthesis and transpiration. At the molecular level, the synergistic regulation of gene expression and signaling pathways constitutes a comprehensive response network of rice to drought stress. This synergistic effect ensures that plants can quickly and effectively transmit drought signals between different tissues to maximize drought tolerance.

Although we have made some key findings, there are still some unclear issues that need to be addressed. Understanding the mechanism of interaction between rice roots and soil microorganisms, as well as the differences in root morphology and physiological characteristics among different rice varieties, will help to better understand the details of root systems in water absorption. In addition, further in-depth research is needed on the molecular mechanisms underlying the regulation of photosynthesis and transpiration.

Future research can focus on the early perception mechanisms of drought in plants, revealing how water signals are transmitted in different tissues. Utilizing advanced molecular biology and genetic techniques to explore new drought resistance genes and regulatory factors, in order to accelerate the process of drought tolerance breeding. Deeply exploring the molecular interaction network between roots and leaves is expected to provide new scientific basis for further improving drought tolerance in rice.

Rice roots and leaves exhibit a synergistic and independent response strategy under drought stress. The synergistic effect of morphological structure adjustment, gene expression regulation, and signal transduction pathways enables rice to adapt more flexibly to different drought environments. Future research should focus on addressing unresolved issues, delving deeper into molecular mechanisms, and utilizing this knowledge to support the cultivation of more drought tolerant rice varieties and the development of more effective agricultural management strategies. This research direction will help improve rice yield and food security, and address the challenges posed by climate change to agriculture. In the future, we hope to make greater contributions to the sustainable development of global agriculture by conducting in-depth research on the drought response mechanism of rice.

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