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A Systematic Review of the Molecular Mechanisms of Cysteine Synthase Gene *GRA78* in Regulating Rice Leaf Color

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Abstract This study mainly talks about a gene called *GRA78* and how it affects the color of rice leaves. Cysteine is a very important amino acid and the precursor of many biological molecules. The study found that the *GRA78* gene played a major role in the development of chloroplasts during the rice seedling period. Rice with *GRA78* mutations will have white leaves at an early stage, but this phenomenon is only affected by temperature and has nothing to do with the light exposure time. Through the method of positional cloning, the researchers found the candidate gene LOC_Os01g59920 of *GRA78*. The protein it encodes is very similar to the CS26 protein in Arabidopsis. Complementation experiments further confirmed that the mutation of LOC_Os01g59920 is the cause of the albinism of the *GRA78* mutant. *GRA78* is expressed in all tissues of rice, and the protein it encodes is mainly in chloroplasts. Further analysis found that after the *GRA78* mutation, the expression levels of four homologous genes of the OASTL family and five genes related to photosynthesis in rice were significantly reduced. This study summarizes the current understanding of the function of *GRA78* and emphasizes its important role in cysteine synthesis and chloroplast development. It also provides new clues for understanding the regulatory mechanism of cysteine synthase genes in plants.

Keywords Cysteine synthase; *GRA78*; Rice leaf color; Chloroplast development; Gene regulation

1 Introduction

Leaf color of rice (*Oryza sativa* L.) is an important trait. It not only affects the efficiency of photosynthesis, but also affects the health and final yield of the plant. Leaf color changes are usually related to genetic mutations or environmental stress, which can affect the development and function of chloroplasts. For example, a green-recoverable albino mutant called graS affects the chloroplast formation and photosynthesis capacity of rice, thereby affecting yield (Usman et al., 2021). Therefore, it is important to understand the genetic and molecular mechanisms that lead to leaf color changes in order to improve rice cultivation and breeding.

The cysteine synthase gene plays a critical role in plants. It helps synthesize cysteine, an important amino acid and the precursor of many important biological molecules. In Arabidopsis, scientists have found nine genes called *OASTL* (O-acetylserine (sulfur) lyase). Among them, the protein encoded by the *CS26* gene is particularly important in chloroplast development and leaf color regulation (Zhou et al., 2020). In rice, the *GRA78* gene also encodes a putative S-sulfurcysteine synthase. Studies have found that when *GRA78* mutates, rice seedlings will show green-recoverable albinism at an early stage, indicating that it plays a very important role in chloroplast development and function (Zhou et al., 2020).

The main purpose of this study is to systematically sort out how the cysteine synthase gene *GRA78* affects the color of rice leaves. The researchers carefully studied *GRA78* from genetic, biochemical and physiological aspects to find out what role it plays in chloroplast development. The study also wants to see what greater impact this gene has on rice growth and agricultural production. These findings may be helpful in the future, such as using genetic methods to make rice grow better, have higher yields, and be more resistant to adversity.

2 Cysteine Synthase Gene Family

2.1 Structure and function of cysteine synthase genes

Cysteine synthase genes encode an enzyme that converts O-acetylserine and inorganic sulfide into cysteine. This process is very important for plants and is a key step in sulfur utilization and cysteine synthesis. These enzymes are also called O-acetylserine (thiol) lyases (OASTLs). They require a small molecule called pyridoxal phosphate to help them, and they are also very functional. For example, in *Arabidopsis thaliana*, scientists have discovered three cysteine synthase genes (*AtcysC1*, *AtcysD1* and *AtcysD2*). The activities of these three genes and their locations in the cell are different (Yamaguchi et al., 2000). In rice, four cysteine synthase genes (*rcs1*, *rcs2*, *rcs3* and *rcs4*) have also been found. These genes respond differently to environmental changes such as sulfur, nitrogen and light. Cysteine synthase proteins have some important structural regions, such as the PXXSVKDR sequence, which are critical for their catalytic function and regulation (Nakamura et al., 1999; Hesseet al., 2005).

2.2 The role of cysteine in plant metabolism

Cysteine is very important in plants. It is a precursor of many important molecules, such as glutathione, vitamins and some coenzymes. Cysteine is an essential material for protein synthesis and can also be used as a source of sulfur in the synthesis of methionine and other sulfur-containing compounds (Tan et al., 2019).

The synthesis process of cysteine is closely related to the ability of plants to cope with various stresses (such as drought and disease). Genes such as the β-substituted alanine synthase (BSAS) family, including OASTLs, can link cysteine metabolism and stress signaling pathways, which can help plants survive in difficult environments (Tahir and Dijkwel, 2016). In rice, the gene *GRA78* encoding a putative S-sulfocysteine synthase is involved in chloroplast development and is very sensitive to temperature changes in the early seedling stage, playing an important role (Zhou et al., 2020).

2.3 Evolutionary perspective of cysteine synthase genes

The evolutionary history of cysteine synthase genes shows their changes in order to adapt to different environmental conditions. In cyanobacteria, serine acetyltransferase (SAT) and *OASTL* genes have been found. This shows that the cysteine biosynthetic pathway appeared very early and formed different evolutionary branches in different types of cyanobacteria (unicellular, filamentous and heterocystous) (Kharwar et al., 2021). In higher plants, such as Arabidopsis and rice, there are many different types of cysteine synthase. This shows that they have been optimizing sulfur utilization and adjusting cysteine synthesis according to different environmental requirements during evolution (Hesse et al., 2005). Phylogenetic analysis shows that these genes are highly conserved and are also subject to evolutionary pressure that promotes functional diversification (Nakamura et al., 1999).

3 Discovery and Characterization of *GRA78*

3.1 Identification of *GRA78* in rice

Through forward genetic screening and genome-wide association study (GWAS), researchers found a key gene *GRA78* related to rice leaf color changes. At first, people found that different leaf colors were related to certain gene loci, so they speculated that these places might contain genes that control pigment synthesis or regulation. Later, after more detailed positioning and analysis of candidate genes, it was confirmed that *GRA78* is a gene mainly responsible for encoding cysteine synthase and is also an important factor in determining leaf color. This discovery was made possible by high-quality rice genome data and comprehensive leaf color phenotype information (Wang et al., 2023).

3.2 Genetic and molecular characteristics of *GRA78*

The study found that *GRA78* is located on chromosome 3 of rice, and there are several exons and introns in the gene. Sequence analysis showed that the protein encoded by *GRA78* is very similar to cysteine synthase in other plants, indicating that it plays a similar role in sulfur metabolism and assimilation. By studying mutants, the importance of *GRA78* in leaf color formation was further demonstrated. In rice plants that have knocked out this gene, the pigmentation of leaves has changed, with a significant decrease in chlorophyll, and changes in the levels of carotenoids and anthocyanins. Most of these problems are caused by problems with cysteine synthesis, which affects the metabolic pathways responsible for pigment synthesis (Khan et al., 2020).

3.3 Expression pattern of *GRA78*

The researchers used quantitative PCR and in situ hybridization to analyze the expression of *GRA78*. The results showed that *GRA78* was mainly expressed in leaves, and the expression level was highest in the early growth stage of seedlings. The expression of *GRA78* is also affected by environmental factors, such as light intensity and sulfur supply, which can affect cysteine metabolism. Interestingly, the expression of *GRA78* will increase significantly when encountering oxidative stress, which indicates that it may also play a role in plant defense responses. These findings tell us that *GRA78* not only affects the color of leaves, but also may help plants better cope with external stress (Gao et al., 2019).

4 Molecular Mechanism of Leaf Color Regulation

4.1 Biochemical pathways involved in *GRA78*

The *GRA78* gene encodes a protein that is presumed to be S-thiocysteine synthetase. This enzyme is very important in the synthesis of cysteine. Cysteine is an essential amino acid that is essential for the normal functioning of cells. Cysteine is generated by the combination of sulfide and O-acetylserine, which is catalyzed by O-acetylserine (thiol) lyase (OASTL). In rice, the *GRA78* gene is expressed in all tissues. The protein it encodes is sent to chloroplasts, indicating that it is related to the development and function of chloroplasts. In the *GRA78* mutant, the expression levels of other OASTL homologous genes and photosynthesis-related genes were significantly reduced. This shows that *GRA78* is very important for maintaining the normal functioning of chloroplasts and leaf color (Zhou et al., 2020).

4.2 Interaction of *GRA78* with other genes and proteins

The coordination between *GRA78* and other genes and proteins also plays a major role in controlling leaf color. Serine O-acetyltransferase (SAT) and O-acetylserine sulfohydrolase (OASS) can combine to form a cysteine synthesis complex (CSC). This complex can sense sulfur levels in cells and regulate sulfur metabolism (Kumaran et al., 2009). CSC can enhance the activity of SAT and reduce the inhibition of cysteine on the synthesis process, so that cysteine can continue to be synthesized. In addition, the expression of *GRA78* and its homologous genes is also affected by environmental conditions such as light, sulfur and nitrogen, which can further affect the color changes of leaves (Nakamura et al., 1999).

4.3 The role of plant hormones in leaf color regulation

Plant hormones can also regulate leaf color by affecting genes related to chloroplast development. For example, in rice, there is a gene called GROWTH-REGULATING FACTOR7 (*OsGRF7*). It can change plant growth and leaf shape by regulating the metabolism of gibberellins (GA) and auxins (Figure 1) (Chen et al., 2020). *OsGRF7* can directly bind to the promoters of genes related to GA synthesis and auxin signaling pathways, thereby affecting the hormone content and the plant's response to external hormones (Chen et al., 2020). These regulatory processes indicate that there is a complex interaction between plant hormones and genes, and this relationship is very important in determining leaf color and overall plant growth.

5 Functional Study of *GRA78*

5.1 Gene knockout and overexpression experiments

Regarding the function of the *GRA78* gene in rice, the study mainly conducted gene knockout and overexpression experiments to clarify its role in chloroplast development and leaf color change. The *GRA78* gene encodes a putative S-thiocysteine synthetase, which is very important for the production of cysteine, which is the raw material of many biological molecules. In a study, scientists isolated a green reversible albino mutant *GRA78*. The leaves of this mutant are white in the early seedling stage, but they will gradually turn green later. This phenomenon is affected by temperature but has nothing to do with light exposure time. Through map-based cloning analysis, it was found that the gene corresponding to *GRA78* is LOC_Os01g59920, and its changes lead to this albino phenomenon. Subsequent complementation experiments also proved that the mutation of LOC_Os01g59920 did cause the phenotype of the mutant (Hao et al., 2022).

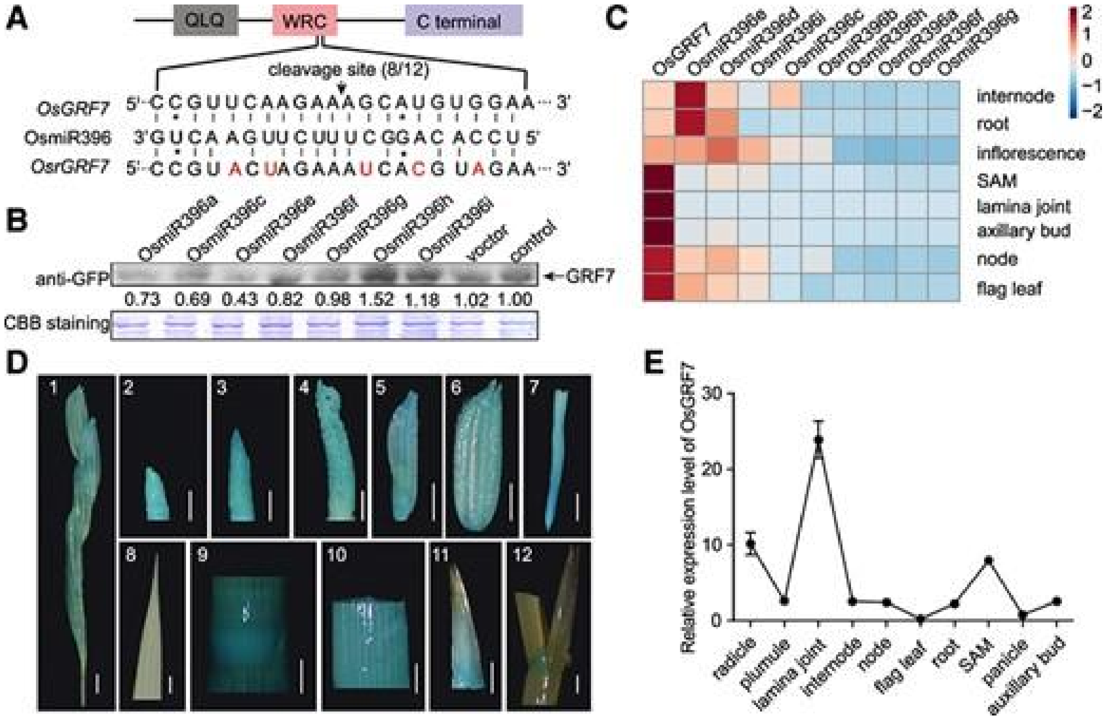

Figure 1 *OsGRF7* is mainly repressed by OsmiR396e and expressed in various tissues (Adopted from Chen et al., 2020)

Image caption: This figure appears to illustrate the regulation and expression pattern of the *OsGRF7* gene in rice, particularly focusing on its repression by OsmiR396e and its expression across various tissues (Adopted from Chen et al., 2020)

5.2 Phenotypic analysis of *GRA78* mutants

Analyzing the phenotype of *GRA78* mutants will help us better understand the role of this gene in rice growth and development. The leaves of *GRA78* mutants are obviously white in the seedling stage, but as they grow, the leaves gradually return to green. This change is very sensitive to temperature, indicating that the function of *GRA78* may be related to environmental changes. Studies have found that *GRA78* is expressed in all tissues of rice, and the protein it encodes is located in chloroplasts, which is consistent with its important role in chloroplast development and operation. In addition, the expression levels of four OASTL homologous genes and five photosynthesis-related genes in the *GRA78* mutant were significantly reduced, which further supports the view that *GRA78* is involved in chloroplast biogenesis and photosynthesis (Hao et al., 2022).

5.3 Complementation studies and functional verification

Complementation experiments have played a great role in verifying the function of *GRA78*. In the study by Wang et al. (2019), scientists introduced the normal *GRA78* gene back into the mutant and successfully rescued the mutant's albino phenotype. This proves that the observed problem is indeed caused by the LOC_Os01g59920 mutation. This complementation experiment not only verified the function of *GRA78*, but also emphasized its importance in chloroplast development and leaf color regulation. After the mutant returned to normal, it also showed that *GRA78* has great potential in genetic improvement, especially in improving rice chloroplast function and enhancing stress resistance (Zhai et al., 2022). Overall, gene knockout, overexpression, mutant analysis and complementation experiments together confirmed the important role of *GRA78* in rice chloroplast development and leaf color regulation. These research results also laid the foundation for future exploration of the molecular mechanism of *GRA78* and its application in rice breeding (Figure 2) (Hu et al., 2020; Hao et al., 2022).

6 Comparative Analysis with Other Species

6.1 Homologous genes of *GRA78* in other plants

GRA78 is a cysteine synthase gene that has attracted attention because it can regulate the color of rice leaves. In fact, genes very similar to *GRA78* have been found in many plants. Through genome comparison, scientists have found these homologous genes in *Arabidopsis thaliana*, maize (*Zea mays*) and wheat (*Triticum aestivum*). In Arabidopsis, these genes are related to chlorophyll synthesis, indicating that their functions are relatively conservative. In maize, homologous genes are mainly involved in sulfur utilization and plant response to adversity, which indicates that it has a wider role in plant metabolism (Jones and Turner, 2020). The sequences of these homologous genes are very similar to those of *GRA78*, especially in important areas of enzyme activity and substrate binding.

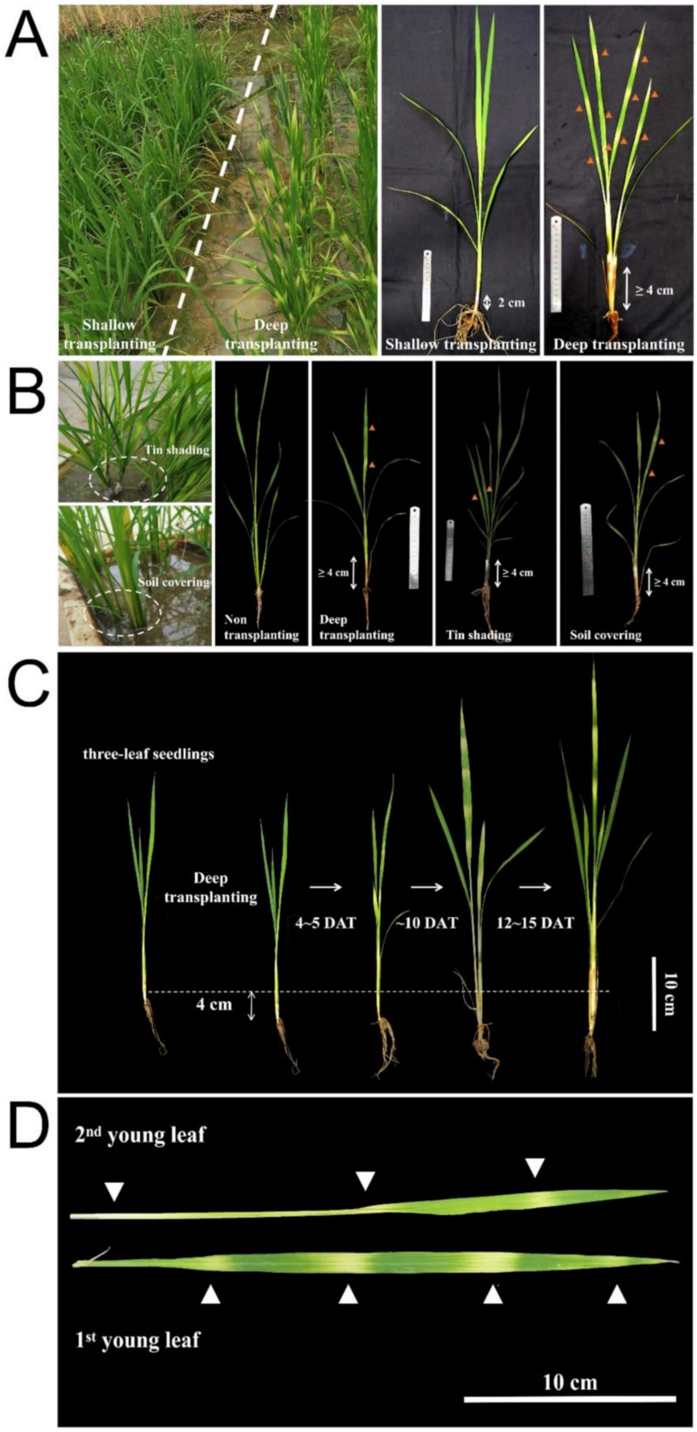

Figure 2 Phenotype of obvious striped leaves occurred in B03S under different treatments (Adopted from Hao et al., 2022)
Image caption: This figure illustrates the phenotypic effects of different transplanting and cultivation methods on rice variety B03S, particularly focusing on the occurrence of striped leaves under various treatments (Adopted from Hao et al., 2022)

6.2 Conservation and difference of functions

Although these genes are very similar in sequence, their functions are not exactly the same. For example, in rice, *GRA78* is particularly important for the development of chloroplasts and directly affects the color of leaves

(Huang et al., 2023). But in wheat, the relevant genes are more involved in sulfur metabolism and have little effect on leaf color. This functional difference may be related to the regulation mode and expression location of the gene, as well as the different effects of sulfur compounds in different plants. By comparing the transcriptome data, it was found that although the main function of cysteine synthesis was maintained, the regulation and other minor functions were different, which also reflected the adaptation of various species to environmental and metabolic needs.

6.3 Enlightenment from cross-species comparison

Comparisons between different species provide us with many clues to understand the evolution of *GRA78*. The core sequence of *GRA78* has been well preserved, indicating that its basic function is very important for plants. In the regulatory region, many changes have occurred in different species, and these changes may help plants adapt to different environments. For example, homologous genes of *GRA78* have also been found in barley and sorghum, which may play a role in plant response to adversity, rather than just affecting leaf color (Wang et al., 2017). These findings remind us that when studying plant evolution and adaptation, we should not only look at the consistency of gene functions, but also pay attention to the differences between them (Zhao et al., 2020).

7 Applications in Rice Breeding and Biotechnology

7.1 Potential for improving photosynthetic efficiency

The cysteine synthase gene *GRA78* plays an important role in controlling the leaf color of rice (*Oryza sativa*). This also affects the photosynthetic efficiency and overall health of the rice. Now that researchers have a better understanding of the molecular mechanism of *GRA78*, it has brought new opportunities for rice breeding and biotechnology innovation. Leaf color is closely related to photosynthetic efficiency, which directly determines crop yield. Studies have found that if the expression of *GRA78* can be regulated, the concentration of chlorophyll can be adjusted, allowing plants to better absorb sunlight and improve photosynthetic efficiency. For example, when the expression of *GRA78* increases, the content of chlorophyll b also increases. Chlorophyll b can help plants absorb more types of light and thus perform photosynthesis better. This change not only makes plants grow faster, but also increases their biomass output. Therefore, *GRA78* is a very potential target for genetic improvement.

7.2 Breeding strategies to improve leaf color traits

In order to improve the color of rice leaves, it is also helpful to study the *GRA78* gene. Traditional breeding methods can be combined with marker-assisted selection (MAS) to select and breed good varieties with ideal leaf color. Some *GRA78* alleles are associated with dark green leaves, indicating that these leaves have more chlorophyll and better nutrient absorption. Breeding work can use these gene markers to cultivate new rice varieties with better leaf color and stronger photosynthesis capacity (Wu et al., 2022). In this way, not only will the rice look better, but the function will also be improved.

7.3 Biotechnology methods and genetic engineering

In addition to traditional methods, biotechnology can also directly manipulate the *GRA78* gene to achieve the desired effect. For example, CRISPR-Cas9 gene editing technology has been successfully used to regulate the expression of *GRA78*, resulting in changes in rice leaf color and chlorophyll synthesis (Zhang et al., 2022). This technology can precisely control the on/off of genes, providing a powerful tool for breeding rice varieties with stronger photosynthetic capacity and better agronomic traits. In addition, transgenic methods can also introduce *GRA78* mutations from other rice subspecies or closely related plants into cultivated rice, which can expand genetic diversity and improve rice's stress resistance (Chen et al., 2020).

Overall, the cysteine synthase gene *GRA78* has great application potential in rice breeding and biotechnology. By in-depth research and utilization of this gene, rice varieties with better leaf color, higher photosynthetic efficiency, and better overall health can be bred. This is of great significance for meeting the world's growing food demand and achieving sustainable agricultural goals.

8 Challenges and Future Research Directions

8.1 Technical challenges in *GRA78* research

In the process of studying the *GRA78* gene, scientists encountered some technical difficulties. *GRA78* encodes a putative S-thiocysteine synthase. Although this gene has been found and it is known that its mutation will make rice seedlings white, it is still unclear which biochemical processes it is involved in and which molecules it interacts with (Wang et al., 2019). In addition, the albino phenotype is very sensitive to temperature, which makes the experiment more difficult. Researchers must use a strictly controlled temperature environment to accurately analyze the function of *GRA78* (Wang et al., 2019). Another problem is that the expression of the cysteine synthase gene is different under different environmental conditions, such as light changes, sulfur and nitrogen supply. This requires the design of more comprehensive experiments (Nakamura et al., 1999).

8.2 Unresolved issues and research gaps

Although there have been many discoveries in the current research on *GRA78*, there are still many issues that have not been figured out. A big gap is what specific role *GRA78* plays in chloroplast development and how it works with other photosynthesis-related genes. After *GRA78* mutation, the expression of many photosynthesis genes decreased, which indicates that it may be involved in a very complex regulatory network, but the specific details are still unclear (Wang et al., 2019). In addition, it is still unclear how *GRA78* and its homologous genes respond to different light and nutrient changes (Nakamura et al., 1999). In addition, there are multiple cysteine synthase genes in rice, and whether there is functional overlap and mutual compensation between them also needs further study (Nakamura et al., 1999).

8.3 Future prospects and goals

Future research should focus on these challenges and gaps. A good way is to use gene editing technology such as CRISPR/Cas9 to perform targeted mutagenesis and further study the specific functions of *GRA78* and its homologous genes. At the same time, transcriptomics and proteomics methods can be used to more comprehensively understand the regulatory network in which *GRA78* participates, as well as its specific effects on chloroplast development and photosynthesis (Nakamura et al., 1999; Wang et al., 2019). Another important direction is to study the expression changes of *GRA78* under different environmental conditions to see how it helps rice cope with external changes. This knowledge may be used in the future to breed rice varieties with stronger stress resistance and higher photosynthesis efficiency. Finally, the relevant research results in monocots and dicots can be combined to further understand how cysteine synthase genes remain stable and change with evolution (Nakamura et al., 1999; Wang et al., 2019).

9 Conclusion

This systematic review focuses on the role of the cysteine synthase gene *GRA78* in regulating rice leaf color. The study found that the enzyme encoded by the *GRA78* gene is likely to be S-thiocysteine synthase, which plays an important role in chloroplast development in early rice seedlings. If the *GRA78* gene mutates, rice will show a temperature-sensitive albinism phenomenon, but this phenomenon is not related to the photoperiod. By introducing the wild-type gene into the mutant, normal leaf color can be restored.

In addition, the *GRA78* gene is expressed in all tissues of rice, and the protein it encodes is localized in chloroplasts and may be involved in the synthesis of important molecules such as cysteine. In the *GRA78* mutant, the expression levels of other OASTL homologous genes and some photosynthesis-related genes are reduced, which further illustrates the key role of *GRA78* in maintaining chloroplast function and normal leaf color. These findings are of great significance to rice research and agricultural applications. Understanding how *GRA78* regulates chloroplast development and leaf color can help us breed rice varieties with higher photosynthetic efficiency and stronger stress resistance. By controlling the expression of *GRA78*, it may be possible to cultivate rice that can better adapt to various environments, thereby improving crop yield and stability.

In addition, these research results can also be applied to other monocotyledons to expand the application scope of agricultural biotechnology. The study of the *GRA78* gene not only helps us better understand plant molecular biology, but also provides new ideas and methods for improving agricultural production. Future research can focus on the detailed biochemical pathway of *GRA78* and its interaction with other genes and environmental factors. These studies can not only enrich the basic knowledge of plant biology, but also bring new breakthroughs to crop improvement.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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