

Review and Progress

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GWAS Reveals Progress in Genes Related to Rice Yield and Quality Yu Wang

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Abstract This study reviews the application progress of genome-wide association analysis (GWAS) in the study of genes related to rice yield and quality. This study further discusses the potential role and development direction of GWAS in rice breeding, especially its application prospects in precision breeding, multi-trait improvement, and adaptation to climate change. The importance of further understanding the rice genome, including studies of non-coding regions and epigenetic modifications, and the role of these studies in promoting the development of rice breeding technology are also discussed. In addition, this study also analyzed the challenges and opportunities facing rice genetic breeding, and pointed out that combining modern genetics technology, especially GWAS and gene editing technology, can effectively meet the challenges of improving disease resistance and meeting global food demand. Through GWAS analysis, researchers can accurately identify key genetic markers and genes related to rice yield and quality, providing a scientific basis for the cultivation of high-yield and high-quality rice varieties.

Keywords Genome-wide association studies (GWAS); Rice breeding; Yield improvement; Quality improvement; Genetic markers

Rice (*Oryza sativa* L.) is one of the major global food crops, providing a staple food for most of the world's population. As the population grows and living standards improve, the demand for rice yield and quality continues to increase. However, traditional breeding methods have been unable to meet the growing demand. Therefore, it is particularly important to find new breeding methods and strategies to improve rice yield and quality.

GWAS is a method to explore the relationship between genes and traits by comparing large-scale genotypic and phenotypic data. With the continuous development and cost reduction of sequencing technology, the application of GWAS in the agricultural field has received widespread attention and application. Especially in the field of crop genetics, GWAS has become an important tool for research, providing a new way to analyze the genetic basis of complex traits.

In the field of rice, GWAS has successfully revealed many genes related to yield and quality. By analyzing large-scale rice germplasm resources and phenotypic data, researchers have identified many genes that have important effects on rice yield, resistance, and quality. The discovery of these genes provides new genetic resources and theoretical basis for rice breeding, helps to speed up the breeding process and improve breeding efficiency.

This study aims to review the research progress of genome-wide association analysis (GWAS) in revealing genes related to rice yield and quality. This study will introduce the importance of rice yield and quality and the limitations of traditional breeding methods in meeting the needs. The basic principles and application status of GWAS in the agricultural field were further introduced in detail , especially its application in rice genetic breeding (Fang et al. 2017). The existing research results, including published GWAS articles and discovered genes related to yield and quality , will be used to predict the potential role and future development direction of GWAS in rice genetic breeding. Through research and analysis, we will comprehensively understand the application progress of GWAS in rice genetic breeding, provide reference and inspiration for future research, and also provide new ideas and methods for improving rice yield and quality.



1 The importance of Rice Yield and Quality

As one of the three major food crops in the world, rice plays an irreplaceable and important role. It plays an important role in global food production. First of all, rice is one of the main sources of food for humans around the world, especially in Asia. Rice is indispensable on the table of almost every family. Asia is the main production and consumption region of rice, accounting for almost 70% of global rice production.

Rice is also one of the main economic sources of many developing countries. Many residents in rural areas rely on rice cultivation as their main source of livelihood, which directly affects the economic status and social stability of these areas. In addition, the importance of rice is not only reflected in food security, but also in environmental protection and ecological balance. As a typical aquatic crop, rice plays a vital role in maintaining the balance of wetland ecosystems.

The yield and quality of rice have a direct and profound impact on rice cultivation and market value. Yield is one of the key factors that determines the economic benefits of rice cultivation. High-yield rice means more harvest per unit area, which can meet the food needs of a larger population and improve farmers' income and living standards. It can be seen that planting high-yielding rice varieties is of great economic significance to farmers and can also promote economic development in rural areas (Bauchet et al., 2017a).

The quality of rice directly affects consumers' taste and nutritional value, which in turn affects market competitiveness and price. High-quality rice has good taste, color and edible value, and can meet consumers' demands for food quality, so it is more popular in the market. High-quality rice may also receive higher sales prices, bringing greater economic returns to growers. Therefore, rice growers usually choose rice varieties that have both high yield and high quality to improve the economic benefits and market competitiveness of planting (Bauchet et al., 2017b).

Rice yield and quality play a vital role in rice cultivation and market value. High yield can increase farmers' income and the level of economic development in rural areas, while high quality can meet consumer demand and improve the market competitiveness and price of rice. Rice growers and agricultural managers need to comprehensively consider yield and quality factors, select appropriate rice varieties, and adopt appropriate planting management measures to achieve a win-win situation of economic and social benefits.

2 Overview of GWAS

2.1 Basic principles and methods of GWAS

Genome -wide association studies (GWAS) are a method to explore the relationship between genes and traits by comparing large-scale genotype data and phenotypic data. The basic principle is to find out by correlating genotype data of large- scale single nucleotide polymorphisms (SNP) markers with phenotypic data of target traits (such as yield, quality, etc.) Genes or gene regions associated with the trait of interest.

Genome-wide association analysis is an effective method for locating complex quantitative traits. This analysis does not require the construction of a family group. Using natural populations, multiple traits can be analyzed simultaneously to find SNP sites associated with traits, and then find candidates associated with traits. interval (Chopra et al., 2017).

We obtain candidate functional genes through GWAS analysis, we can select individuals with different traits from the research materials, perform qRT-PCR analysis on the candidate genes, and verify them through differences in gene expression. This analysis method is simple and fast, and is a commonly used verification method in analysis.

Cotton population evolution + genome-wide association analysis published in 2017 is a good example. The author identified a candidate gene *AIL6* related to cotton lint fraction through GWAS analysis, and then selected TM-1 plants with low cotton lint fraction. Compared with ZMS12 plants with high cotton lint content, the expression level of this gene in different samples was analyzed by qRT-PCR. It was found that the expression level of this gene in TM-1 at 10 to 20 days of ovule development was about 10 times higher than that in ZMS12 (Figure 1) (Fang et al., 2017).



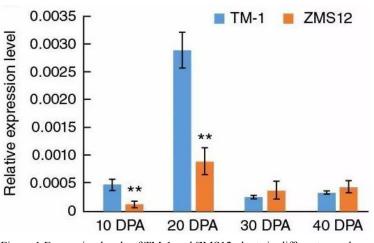


Figure 1 Expression levels of TM-1 and ZMS12 plants in different samples

2.2 Application of GWAS in plant genetics

genome-wide association analysis (GWAS) in plant genetics has made significant progress and plays an important role in analyzing the genetic basis of complex traits, discovering new genes, and analyzing genetic variation. GWAS can help identify genes or genetic variants associated with target traits through large-scale genotypic and phenotypic data. In plant genetics research, these target traits may include important agronomic traits such as yield, quality, resistance, and stress tolerance. Currently, two commonly used technologies for detecting SNPs include gene chips and direct resequencing. Candidate genes or genetic variants of these traits can be accurately located through GWAS, providing an important reference for subsequent functional research and genetic improvement.

GWAS can help resolve the genetic basis of complex traits. Many plant traits are jointly regulated by multiple genes, and each gene may only contribute to a small part of the trait. Through high-resolution analysis of the whole genome, GWAS can reveal the joint action modes and genetic mechanisms of these genes, helping us better understand the genetic basis of complex traits.

In addition, GWAS can also discover new genes and genetic variants. Traditional genetic analysis methods often require prior knowledge or specific hypotheses, while GWAS can comprehensively explore the association between the genome and phenotype without restrictions, thereby discovering new genes and genetic variants.

2.3 Advantages and limitations of GWAS in rice genetics research

Genome-wide association studies (GWAS) have become an important methodology in rice genetics research, which uses statistical means to find genetic variations associated with specific traits in the genome sequences of different individuals. This method has significant advantages in analyzing the genetic basis of complex traits. GWAS can identify genetic markers related to important rice traits on a genome-wide scale, such as yield, disease resistance, and stress tolerance. This is of great significance to rice breeding because it can help breeders quickly locate key genes that affect target traits.

Compared with traditional genetic mapping methods, GWAS does not require a priori information about genes or traits, which enables it to discover new trait-related genes in unknown genetic backgrounds. Many rice traits, such as yield and disease tolerance, are complex traits controlled by multiple genes. GWAS can reveal the genetic mechanisms behind these complex traits and provide a powerful tool for understanding the genetic basis of traits (Yano et al., 2019).

At the same time, GWAS also has many limitations. For example, GWAS may produce false positive results, that is, certain genetic markers that are not related to the trait are mistakenly considered to be related to the trait. This requires researchers to adopt strict statistical correction methods to reduce the occurrence of false positives. For less frequent genetic variants, GWAS may have difficulty detecting their association with traits because the effects of these rare variants may require very large sample sizes to be detected. The genetic background diversity of rice



germplasm resources may affect the results of GWAS. If the sample contains individuals with widely varying genetic backgrounds, it may increase the difficulty of identifying genetic variation associated with a trait.

Due to the global demand for high crop yields, elucidating the genetic control of rice architecture is critical. Rice structure is a complex trait affected by plant height, tillers, and panicle morphology, and is an important agronomic trait that determines yield. However, the complexity of this trait makes it difficult to elucidate the molecular mechanism.

3 Progress in GWAS Research on Rice Yield-related Genes

3.1 Yield-related genes identified by GWAS

Genome-wide association studies (GWAS) have been widely used to identify genes associated with rice yield. Yield is a complex trait that is affected by multiple genes, including genes that control sub-traits such as plant height, tillering (tillering), grain size, grain number, and maturity period.

For example, the Gn1a gene affects the grain number of rice. It encodes a cytokine oxidase that affects the number of inflorescence branches and thus the number of grains in rice. The discovery of Gn1a helps to understand the genetic mechanism of rice yield formation and provides target genes for improving rice yield through molecular breeding. GS3 is one of the main genes that control rice grain size. Its different allelic variations are related to differences in grain length, thereby affecting rice yield. The discovery of the GS3 gene provides the possibility to regulate grain size through molecular breeding; DEP1 gene and The panicle density of rice is related. Its allelic variation affects the panicle structure of rice, thereby affecting yield. Specific DEP1 mutations can lead to a denser panicle structure, increase the number of grains, and increase yield; the Ghd7 gene affects the maturity period and yield of rice. It is one of the important genes that controls the length of the rice growth cycle and can regulate the flowering time and grain number of rice. Different Ghd7 allelic variations can lead to different growth cycles and yield performances, which are extremely important for the development of rice varieties adapted to different planting environments; and the qSW5 gene affects the grain width and thousand-grain weight of rice. Variations in this gene can lead to significant changes in grain morphology, thereby affecting yield (Song et al., 2015).

The discovery of these genes not only deepens our understanding of the genetic basis of rice yield, but also provides specific targets for improving rice varieties through molecular breeding techniques. Through the yield-related genes identified by GWAS, researchers can edit or select specific genes to develop new rice varieties with higher yields and stronger adaptability. However, it is worth noting that the phenotypic effects and environmental interactions of these genes need to be considered in the actual breeding process to ensure the success of variety improvement.

3.2 Functions and regulatory mechanisms of these genes

The Gn1a gene is a key gene that controls rice grain number. It encodes a cytokine oxidase (cytokinin oxidase/dehydrogenase, CKX), which is responsible for decomposing cytokines. Cytokines are a type of plant hormones that play an important role in plant growth, development and tillering. Gn1a affects tiller number and inflorescence development by regulating the levels of cytokines, thereby indirectly affecting grain number. The lower the expression level of the Gn1a gene, the lower the activity of decomposing cytokines, and the higher the concentration of cytokines, which promotes the formation of more tillers and inflorescences, thereby increasing the number of grains. The GS3 gene mainly affects rice grain size and is a pleiotropic gene. Its different allelic variations are related to significant differences in grain length. The GS3 gene encodes a protein containing a membrane-binding domain that controls the final size of the grain by negatively regulating cell proliferation in the early stages of rice grain development. Certain allelic variations of GS3 may reduce its function, leading to increased cell division activity, thereby producing larger grains (Weng et al., 2018).

DEP1 gene is related to rice panicle density, and specific allelic variations can significantly affect panicle structure and grain number. *The DEP1* gene encodes a signal transduction component involved in regulating plant branching patterns. Rice with enhanced *DEP1* allelic variation exhibits a denser panicle structure, which is



achieved by promoting the formation of branch points and increasing the number of branches, thereby improving grain yield.

Ghd7 controls the maturity period and yield of rice and is an important gene that affects the growth cycle and flowering time. The *Ghd7* gene encodes a protein containing a CCCH-type zinc finger protein domain that controls flowering time and maturity by regulating photoperiodic responses. The activity of Ghd7 is affected by day length. Under long-day conditions, *Ghd7* is highly expressed, delaying flowering time, extending the growth cycle, and increasing grain yield.

The qSW5 gene affects the grain width and thousand-grain weight of rice, and is closely related to grain morphology and yield. *The qSW5* gene encodes a protein of unknown function that regulates grain width by affecting cell expansion in early stages of grain development. Specific allelic variations can lead to an increase in grain width, which in turn affects thousand-grain weight and overall yield.

3.3 Impact and potential applications of related genes on rice yield

Genetic improvement of rice yield is key to global food security. Relevant genes identified through genome-wide association studies (GWAS) provide important molecular targets for improving rice yield. The impact of these genes on rice yield is mainly reflected in the control of plant height, tiller number, grain size, grain number, and maturity period.

Gn1a gene directly affects the number of inflorescence branches and grain number of rice by encoding a cytokine oxidase. A higher number of inflorescence branches means more potential seed setting locations, potentially increasing final grain yield. Through molecular marker-assisted selection (MAS) or gene editing technology (such as CRISPR/Cas9), efficient *Gn1a* allelic variations can be introduced into rice varieties with high yield or other excellent agronomic traits to increase their yield.

Different allelic variations of the *GS3* gene affect the length and volume of grains, thereby affecting yield. Larger kernels usually mean higher thousand-kernel weight, which is one of the key factors in increasing yields. Precisely regulating *GS3* allelic variation can optimize grain size, and combined with the improvement of other yield-related traits, it is expected to significantly increase the overall yield of rice (Song et al., 2015).

DEP1 gene directly affects the number of grains by affecting the density of the panicle structure. Rice varieties with specific *DEP1* variants exhibit higher panicle density and increased grain number. Selecting or introducing favorable *DEP1 mutations* through gene editing during breeding can increase the panicle density of rice, thus increasing the yield per plant.

The *Ghd7* gene controls the length of the growth cycle, affecting flowering time and seed number. Different allelic variations of this gene can regulate the adaptability and yield traits of rice. By regulating the expression of the *Ghd7* gene, rice varieties can be developed to adapt to different planting seasons and environmental conditions, while optimizing yield traits.

qSW5 gene affects grain width, thereby affecting thousand-grain weight and yield. Variations in this gene can lead to significant changes in grain morphology. Using the variation of the qSW5 gene, breeding strategies can be used to adjust grain size, optimize thousand-grain weight, and increase rice yield.

In practical applications, these genes do not act in isolation, but interact to form a complex network, which together determine the final yield of rice. Therefore, modern rice breeding not only focuses on the improvement of a single gene, but also achieves comprehensive improvement of rice yield and other agronomic traits by integrating a combination of multiple beneficial genes and using multi-gene editing technology. In addition, considering the impact of environmental factors on rice traits, breeding strategies need to incorporate ecological and climate models to ensure that improved rice varieties can exhibit excellent yield and stability under different environmental conditions.



4 Application of GWAS in Rice Renetic Breeding

4.1 Methods and strategies for genetic improvement of rice using GWAS

GWAS is a highly efficient strategy that relies on the analysis of genomic information and phenotypic data from large genetic resources to identify genes or genetic markers associated with important agronomic traits. This method can not only reveal the genetic basis of complex traits, but also provide accurate molecular targets for the improvement of rice varieties.

Collect rice germplasm resources with a wide range of genetic backgrounds, including wild species, landraces and improved varieties. The genetic diversity of these germplasm resources is the basis of GWAS analysis and can improve the coverage and accuracy of association analysis. Conduct detailed phenotypic evaluation of the collected germplasm resources, including yield, disease resistance, stress tolerance, grain quality and other agronomic traits. The accuracy and reproducibility of phenotypic data are crucial for subsequent GWAS analysis.

Use high-throughput sequencing technology to sequence the entire genome of germplasm resources to obtain high-density genotype data. This includes genetic variation information such as single nucleotide polymorphisms (SNPs) and insertions and deletions (InDels). Perform quality control on the obtained genotype data, including removing low-quality sequences, correcting sequencing errors, filling in missing genotype data, etc., to ensure the accuracy of subsequent analysis.

Use statistical methods to analyze the association between genotypic and phenotypic data and identify genetic markers or gene regions that are significantly associated with specific agronomic traits. This step may involve a variety of statistical models to control for the effects of population structure and genetic background. Based on the GWAS analysis results, combined with gene annotation information and bioinformatics tools, candidate genes associated with traits are screened out. Further use methods such as gene expression analysis and functional verification experiments to determine the key regulatory genes of traits.

For example, after GWAS obtains candidate functional genes, the function of the genes can also be verified through transgene overexpression. For example, in the association analysis of rice, the author found that the gene LOC_Os01g62780 affects the heading time of rice, so the gene sequence containing haplotypes A and B was introduced into Nipponbare containing haplotype A (Figure 2). The results showed that the phenotype of plants transferred to haplotype A did not change, while the heading stage of plants transferred to haplotype B became later. This proves that the LOC_Os01g62780 gene is a gene that controls rice heading time (Yano et al., 2016).

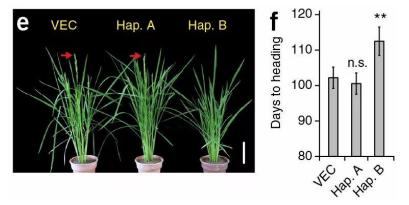


Figure 2 Effect of LOC_Os01g62780 gene on rice heading time (Yano et al., 2016)

Based on the key genes or genetic markers identified by GWAS, develop efficient molecular markers, such as SNP markers, simple sequence repeat (SSR) markers, etc. In the process of rice breeding, these molecular markers are used for efficient genetic background screening and rapid selection of target traits, significantly improving breeding efficiency and accuracy.

For important genes identified by GWAS, gene editing technologies such as *CRISPR/Cas9* can be used to precisely modify specific sites in the rice genome to directly create new varieties with excellent agronomic traits.



For multiple genes that affect complex traits, the agronomic traits of rice can be comprehensively controlled through a multi-gene simultaneous editing strategy to achieve comprehensive improvements in yield, quality and stress resistance.

Conduct field trials and quality evaluation of rice materials improved through molecular marker-assisted selection or gene editing to ensure that the selected new varieties have excellent agronomic traits and adaptability. Evaluate the performance of new varieties in different ecological environments to ensure their broad adaptability and stable yield performance.

The use of GWAS for rice genetic improvement is a systematic process, involving the entire chain from gene discovery to variety improvement. With the rapid development of genomics, bioinformatics, and molecular biotechnology, this strategy provides unprecedented accuracy and efficiency for rice breeding, and is expected to bring more high-yielding, high-quality, and stress-resistant rice in the near future. New rice varieties.

4.2 The role of GWAS in breeding material selection, molecular marker-assisted selection and predictive breeding

GWAS play a crucial role in modern plant breeding, especially in the selection of breeding materials, marker-assisted selection (MAS), and predictive breeding. By analyzing the correlation between genotype and phenotype, GWAS can efficiently identify genes and genetic markers related to important agronomic traits, providing scientific basis for precise breeding decisions.

GWAS can help breeders identify individuals carrying favorable alleles in a wide range of germplasm resources. By analyzing the association between genetic diversity and specific traits in different rice varieties or wild species, GWAS reveals the genetic basis of trait formation and provides a basis for the optimization of germplasm resources. Genetic markers associated with superior agronomic traits identified through GWAS can be used as tools for selecting high-performance breeding materials. These markers help breeders identify potential excellent varieties at the initial screening stage, thereby shortening the breeding cycle and improving breeding efficiency.

Genetic markers identified by GWAS provide powerful tools for MAS. Breeders can use these markers to directly select for specific traits, especially those for which phenotypic identification is difficult or costly, such as disease resistance, stress tolerance, etc. During the background selection (background purification) process, MAS can ensure that genomic regions other than target traits can quickly return to the state of the superior parent, thereby accelerating the breeding process and reducing undesirable cumulative linkage effects.

The genotype-phenotype association information provided by GWAS can be used to build prediction models that can predict the trait performance of unphenotyped individuals. Predictive breeding uses this information to evaluate the performance of potential breeding materials without field testing, significantly saving time and resources. By integrating GWAS results and other genetic information, predictive breeding can optimize mating design and selection strategies and improve breeding efficiency. For example, by predicting the phenotypic performance of different genome combinations, breeders can selectively select the most promising hybrid combinations, thereby improving the success rate of breeding and the performance of innovative varieties.

The applications of GWAS in breeding material selection, MAS and predictive breeding complement each other and jointly promote the precision and efficiency of plant breeding. The genetic markers and genes identified through GWAS not only accelerate the screening and optimization process of breeding materials, but also provide reliable molecular tools for MAS and make predictive breeding possible, which greatly enhances the accuracy and predictability of breeding. With the genome sequencing

Ming et al. (2023) explored the role of cis-regulatory variation in rice domestication and breeding and its impact on panicle shape traits by analyzing young panicle (1-2 mm) transcriptome data of 275 representative rice varieties. The researchers analyzed the transcriptome data of 275 representative rice varieties at the young panicle (1-2 mm) stage of branch stem and spikelet primordium differentiation. They conducted transcriptome breadth association analysis (TWAS) on three key panicle traits, namely the number of spikelets in the panicle (SPP), the



number of primary branches and panicle length, and their gene expression levels, and found 4 results respectively. 1 755 844 and 6 839 genes significantly associated with these traits. These significant genes discovered through TWAS include not only many key genes known to be involved in panicle development, but also a large number of new regulatory factors that may play an important role in panicle development (Figure 3).

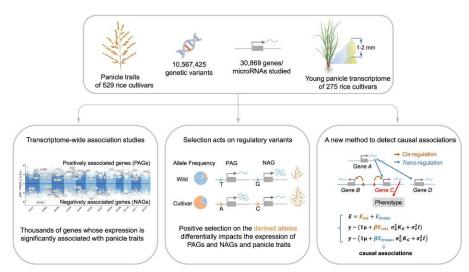


Figure 3 Transcriptome data of the panicle stage during the differentiation stage of rice branch stems and spikelet primordia (Mao et al., 2023)

4.3 The role of GWAS in promoting rice yield and quality improvement

Genome-wide association studies (GWAS) play a crucial role in improving rice yield and quality, providing an efficient method to unlock the genetic potential of rice. Through this method, researchers can identify key genetic markers and genes related to yield and quality, accelerate the process of rice breeding, and improve the accuracy and efficiency of breeding.

In terms of rice yield improvement, GWAS allows breeders to accurately identify genetic variations related to yield, including genes that control traits such as plant height, tiller number, and grains per panicle. For example, through GWAS, researchers have successfully identified multiple key genes that affect rice yield, such as *Gn1a*, *GS3*, *DEP1*, etc. The discovery of these genes has directly promoted the breeding of high-yielding rice varieties. In addition, GWAS also reveals the complex genetic network behind yield traits, providing scientific basis for precise manipulation of genetic resources, allowing breeding work to be carried out in a more targeted manner (Song et al., 2015).

In terms of quality improvement, GWAS has helped breeders gain a deeper understanding of the genetic basis that controls rice quality, including rice grain shape, endosperm texture, protein content, and disease resistance. By identifying the genes associated with these traits, breeders can more precisely select for favorable alleles, thereby creating rice varieties that are both high-yielding and of good quality. For example, different allelic variations of the *Waxy* gene have an important impact on amylose content, which is directly related to the stickiness and taste of rice. The application of GWAS makes it possible to improve the quality of rice based on specific consumer needs.

Through GWAS, researchers can not only identify the impact of a single gene on rice traits, but also reveal the interactions and regulatory networks between multiple genes, providing new strategies for comprehensive trait improvement in rice. For example, by comprehensively considering multiple genes that affect yield and quality, breeders can improve varieties more effectively and achieve balanced selection of multiple traits. The application of GWAS in rice breeding has greatly improved the scientific nature and efficiency of breeding, not only accelerated the development of high-yield and high-quality rice varieties, but also provided powerful molecular tools for rice genetic improvement. With the continuous advancement of genome sequencing technology and the continuous optimization of data analysis methods, the role of GWAS in improving rice yield and quality will be



further strengthened (Wang et al., 2015).

5 Outlook

GWAS has become a key technology in the field of rice genetic breeding, and its role in revealing the genetic basis of complex traits and accelerating the process of genetic improvement has become increasingly prominent. In the future, the application of GWAS is expected to be further expanded and deepened, especially when combined with the latest genome editing technologies, such as the CRISPR/Cas system, to achieve precise improvement of specific traits. In addition, with the improvement of computing power and advancement of statistical methods, GWAS can process larger data sets and improve the accuracy and efficiency of association analysis. In rice breeding, GWAS is expected to promote the transformation from the improvement of single traits to the improvement of comprehensive traits in multiple traits and environments, providing strong support for cultivating rice varieties that are adaptable to climate change and have high and stable yields.

Athorough understanding of the rice genome is critical to uncovering its complex genetic and phenotypic diversity. With the development of high-throughput sequencing technology and the reduction of costs, the comprehensive analysis of the rice genome will be more in-depth, including the study of non-coding regions, epigenetic modifications, and interactions between genes. This not only helps to discover new functional genes and regulatory elements, but also reveals the regulatory mechanism of gene expression and the impact of genetic variation on complex traits. In addition, a comprehensive understanding of the rice genome will promote the development of precision breeding technology, achieve efficient utilization of rice genetic resources, and provide a solid foundation for the continuous improvement of rice yield and quality (Song et al., 2015).

The main challenges facing rice genetic breeding include adapting to climate change, improving disease resistance and meeting growing food demand. Faced with these challenges, modern genetic techniques such as GWAS provide new opportunities. Through GWAS, breeders can more accurately identify genetic variations associated with key traits, accelerating the development of resistant varieties and improvement of yield traits. In addition, combining genomic selection (GS) and predictive breeding, trait improvement can be carried out in a wider range of genetic backgrounds, improving the efficiency and adaptability of breeding. At the technical level, the application of artificial intelligence and machine learning will further optimize the analysis process and accuracy of GWAS, and promote the development of rice genetic breeding in a more precise and efficient direction.

GWAS and its combination with other modern biotechnologies will open up new paths for rice genetics and breeding, facing both challenges and huge opportunities. Future research needs to continue to explore innovative breeding strategies and technologies based on an in-depth understanding of the rice genome to achieve dual improvements in rice yield and quality and meet the needs of global food security.

References

Bauchet G., Grenier S., and Samson N., 2017a , Identification of major loci and genomic regions controlling acid and volatile content in tomato fruit: Implications for flavor Improvement, New Phytologist, 215(1). <u>https://doi.org/10.1111/nph.14615</u>

Bauchet G., Grenier S., and Samson N., 2017b, Use of moderm tomato breeding germplasm for deciphering the genetic control of agronomical traits by genome wide associa-tion study, Theoretical & Applied Genetics, 130(5): 875-889. https://doi.org/10.1007/s00122-017-2857-9

Chopra R., Burow G., and Burke J.J., 2017. Genome-wide as-sociation analysis of seedling traits in diverse Sorghum germplasm under thermal stress, BMC Plant Biology, 17(1): 12.

https://doi.org/10.1186/s12870-016-0966-2

Fang L., Wang Q., and Hu Y., 2017, Genomic analyses in cotton identify signatures of selection and loci associated with fiber quality and yield traits, Nature genetics, 49(7): 1089-1098.

https://doi.org/10.1038/ng.3887

Fang L., Wang Q., Chen J.D., Liu B.L., Zhang Z.Y., Guan X.Y., Chen S.Q., Zhou B.L., Mei G.F., Sun J.L., Pan ZE., He S.P., Xiao S.H., Shi W.J., Gong W.F., Liu J.G., Ma J., Cai C.P., Zhu X.F., Guo W.Z., Du X.M., and Zhang T.Z., 2017, Genomic analyses in cotton identify signatures of selection and loci associated with fiber quality and yield traits, Nature Genetics, 49: 1089-1098. <u>https://doi.org/10.1038/ng.3887</u>

Klein R.J., Zeiss C., and Chew E.Y., 2005. Complement factor hpolymorphism in age-related macular degeneration, Science, 308(5720): 385-389.



https://doi.org/10.1126/science.1109557

Ma Z., He S., and Wang X., 2018, Resequencing a core collection of upland cotton identifies genomic variation and loci influencing fiber quality and yield, Nature genetics, 50(6): 803-813.

https://doi.org/10.1038/s41588-018-0119-7

Ming L.C., Fu D.B., Wu Z.N., Zhao H., Xu X.B., Xu T.T., Xiong X.H., Li M., Zheng Y., Li G., Yang L., Xia C.J., Zhou R.F., Liao K.Y., Yu Q., Chai W.Q., Li S.J., Liu Y.M., Wu X.K., Mao J.Q., Wei J.L., Li X., Wang L., Wu C.Y., and Xie W.B., Transcriptome-wide association analyses reveal the impact of regulatory variants on rice panicle architecture and causal gene regulatory networks[J]. Nature Communications, 2023, 14(1): 7501. https://doi.org/10.1038/s41467-023-43077-6

Risch N., and Merikangas K., 1998. The future of genetic studies of complex human diseases, Epidemiology, 9(3): 350-354. https://doi.org/10.1097/00001648-199805000-00023

- Song X.J., Kuroha T., Ayano M., Furuta T., Nagai K., Komeda N., Segami S., Miura K., Ogawa D., Kamura T., Su-zuki T., Higashiyama T., Yamasaki M., Mori H., Inukai Y., Wu J., Kitano H., Sakakibara H., Jacobsen S.E., Ashikari M., 2015, Rare allele of a previously unidentified histone H4 acetyltransferase enhances grain weight, yield, and plant biomass in rice, Proc. Natl. Acad. Sci. USA, 112: 76-81. https://doi.org/10.1073/pnas.1421127112
- Tang F.F., Xu F. F., and Bao J. S., 2013, The application of genome-wide association study in genetics and breeding of rice, Journal of Nuclear Agricultural Sciences, 27(5): 598-606. (Tang Fufu, Xu Feifei, Bao Jinsong, 2013, Application of genome-wide association analysis in rice genetic breeding, Journal of Nuclear Agriculture, 27(5):598-606.)
- Tian F., Bradbury P.J., and Brown P.J., 2011, Genome-wide as-sociation study of leaf architecture in the maize nested association mapping population, Nature Genetics, 43(2): 159-62.

https://doi.org/10.1038/ng.746

- Wang Y., Xiong G., Hu J., Jiang L., Yu H., Xu J., Fang Y., Zeng L., Xu E., Xu J., Ye W., Meng X., Liu R., Chen H., Jing Y., Wang Y., Zhu X., Li J., and Qian Q., 2015, Copy number variation at the GL7 locus contributes to grain size diversity in rice, Nat Genet, 47: 944-948. <u>https://doi.org/10.1038/ng.3346</u>
- Weng J., Wan X., Gao H., GuoT., Su N., Lei C., ZhangX., Cheng Z., Guo X., Wang J., Jiang L., Zhai H., and Wan J., 2018, Isolation and initial characterization of GW5, a major QTL associated with rice grain width and weight, Cell Res., 18: 1199-1209. https://doi.org/10.1038/cr.2008.307

Yano K., Yamamoto E., and Aya K., 2016, Genome-wide association study using whole-genome sequencing rapidly identifies new genes influencing agronomic traits in rice, Nature Genetics, 48(8): 927-934.

https://doi.org/10.1038/ng.3596

Yano K.L., Morinaka Y., Wang F.M., and Makoto Matsuoka M., 2019, GWAS with principal component analysis identifies a gene comprehensively controlling rice architecture, PNAS, 116 (42): 21262-21267.

https://doi.org/10.1073/pnas.1904964116