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Dissecting Complex Traits in Rice: Insights from Recent GWAS Findings

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Abstract GWAS has been proven to be a useful tool that helps promote the genetic improvement of rice. This study introduces several commonly used GWAS methods in rice, summarizes the latest GWAS achievements such as key loci related to grain size, drought resistance and protein content, and analyzes the traits related to yield through specific cases. These findings provide references for subsequent gene function verification and actual breeding. In the future, if GWAS can be combined with genomic selection and functional genomics, it is expected to accelerate the breeding of rice varieties with excellent agronomic traits.

Keywords Genome-wide association studies (GWAS); Rice (*Oryza sativa* L.); Complex traits; Agronomic improvement; Genetic loci

1 Introduction

Rice (*Oryza sativa* L.) is the main food crop for more than half of the global population, and its yield and quality are crucial to food security. The genetic structure of rice is complex, involving traits such as yield, flowering time, and grain quality. These traits are usually jointly controlled by multiple genes and are also affected by the environment (Huang et al., 2010; Huang et al., 2011). To cultivate high-yield and stress-resistant rice varieties, it is necessary to first clarify the genetic basis of these complex traits, which is very important for responding to the growing demand for food (Aloryi et al., 2022; Ashfaq et al., 2023).

Wang et al. (2019) demonstrated that GWAS could scan the entire genome to identify single nucleotide polymorphisms (SNPs) loci related to certain traits and recognize the key regions that affect phenotypic differences. This method has achieved success in various crops such as rice and is helpful for understanding the genetic background of some important agronomic traits (Zhong et al., 2021). Singh et al. 's research in 2022 found that the resolution and accuracy of GWAS have been significantly enhanced with the development of high-throughput sequencing technology and the improvement of statistical methods, making it easier to identify candidate genes and conduct functional studies.

GWAS is very useful for understanding how complex traits such as yield, quality and disease resistance of rice are inherited (Huang et al., 2010; Wang et al., 2019). Huang et al. (2011) and Aloryi et al. (2022) have identified many important loci related to traits such as rice yield and flowering time through GWAS in their early studies and in recent years. These achievements have made the genetic structure of rice clearer and also provided more direction when choosing good varieties with molecular markers. Zuo and Li (2014) hold that it can be easier to breed new rice varieties that are both high-yielding and disease-resistant through these findings.

This study summarizes the latest achievements of GWAS in rice, with a focus on its performance in the study of the genetics of complex traits. It introduces some methods used in GWAS and elaborates on the important loci and candidate genes that have been discovered so far and their roles in rice breeding and genetic research. This study hopes that GWAS can bring more help to ensuring global food security.

2 Methodology of GWAS in Rice

2.1 Key GWAS approaches in rice research

The traditional GWAS method involves conducting intensive genetic testing on many different rice individuals to identify genetic changes related to certain traits. However, this method requires testing a large number of samples and has a relatively high cost. To improve efficiency, new methods such as extreme-phenotype GWAS (XP-GWAS) have been developed. This method only detects individuals with particularly outstanding manifestations, which can save a lot of work and also identify important variations related to traits (Yang et al., 2015). PrediXcan reveals the underlying molecular mechanism by predicting the expression of genes and correlating these prediction results with traits (Gamazon et al., 2015). GCTA can be used to estimate the extent to which SNPS affect traits.

2.2 Data collection and phenotyping

To better identify SNPS related to agronomic traits, researchers usually sequence many local rice varieties to establish high-density haplotype maps. Huang et al. (2010) sequenced 517 local varieties and identified approximately 3.6 million SNPS in total. These data helped researchers analyze 14 different agronomic traits and explain approximately 36% of the phenotypic differences. Phenotypic determination in this process involves meticulous measurement of traits to ensure the authenticity and reliability of the data. This comprehensive approach enables scientists to effectively match genetic variations with trait expressions, providing a lot of useful information for rice breeding (Wang et al., 2019; Huang et al., 2024).

2.3 Genotyping techniques and data analysis pipelines

The second-generation genome sequencing technology is commonly used nowadays, which can provide very dense genetic information. Exome sequencing will focus on detecting genes and the regions around them. This method helped identify approximately 940 000 variations in the study of corn by Yang et al. in 2015. A similar method can also be used in the study of rice. When analyzing data, researchers usually use a variety of statistical methods to process and interpret this massive amount of information. GCTA can estimate the genetic relationships among individuals and the explanatory power of SNPS. Yang et al. (2011) and Zhang et al. (2019) demonstrated that multilocus analysis methods such as mrMLM and FASTmrEMMA could overcome some problems of traditional single-point analysis by considering the population structure and the influence of multiple genes.

3 Key Findings from Recent GWAS in Rice

3.1 Genetic loci associated with yield-related traits

Huang et al. (2011) analyzed 950 rice varieties from around the world and identified 32 new loci related to flowering time and 10 grain traits, indicating that the larger the sample size, the easier it is to discover useful genetic variations. In 2021, Zhong et al. used 529 core rice varieties and identified multiple SNPS related to grain length, width, thickness, 1000-grain weight and yield per plant. This study employed both single-site and multi-site methods and discovered a total of 20 recurrent quantitative trait nucleotides (QTNs). These traits of rice yield are very complex and are controlled by many different genes together.

Kumar et al. (2021) specifically studied the performance of rice under high night temperature conditions and identified several important SNPS related to panicle length and the number of spikelets per panicle. These two traits are crucial components of biomass and harvest index. The discovery of these loci has given us a new understanding of how these traits are inherited under stress conditions.

3.2 Loci related to stress resistance traits

Guo et al. (2018) conducted a GWAS study on 507 rice germplasms and identified 470 loci related to drought resistance, some of which were at the same location as the drought-resistant QTL previously found (Figure 1). Selamat and Nadarajah's research in 2021 identified several relatively stable drought-resistant QTLS in different rice varieties and environments. They also discovered some key genes such as ABI5 and aquaporin PIP 1-2, which play significant roles in the drought resistance response of rice.

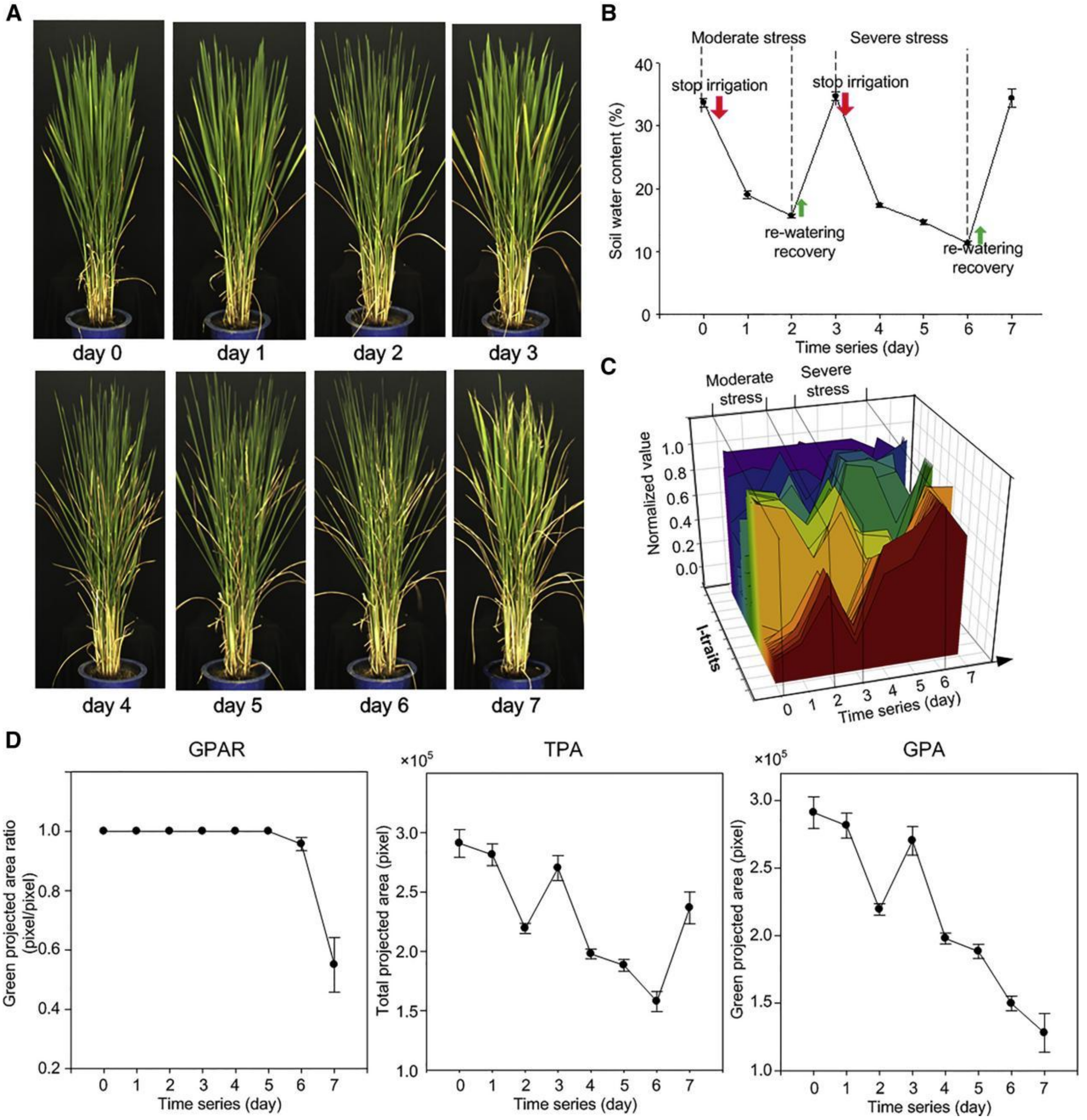


Figure 1 Drought Response Monitored by 51 I-Traits Measured by RAP (Adopted from Guo et al., 2018)

Image caption: (A) Raw images of a rice variety (Swarna) measured at eight time points during progressive drought stress and rewatering; (B) Soil water content measured by TDR at eight time points. Two rounds of drought stress were applied to three plants of the rice variety Swarna. Based on soil water content, the number of days of drought stress, and the stay-green level of the stressed plants after rewatering, the levels of stress, i.e. “moderate stress” (2 days for the first round of stress) and “severe stress” (3 days for the second round of stress), were determined. Error bars indicate the SE based on three biological replicates; (C) Normalized value of 51 i-traits during progressive drought stress and rewatering. The range of values at eight time points for each i-trait was transformed to 0-1 by linear normalization. y=(x-min)/(max-min) where x, y, max, and min represent raw data, normalized data, maximum, and minimum, respectively.; (D) Three temporal patterns of i-traits (GPAR, TPA, and GPA) during progressive drought stress and rewatering. GPAR, green projected area ratio; TPA, total projected area; GPA, green projected area. Error bars indicate the SE based on three biological replicates (Adopted from Guo et al., 2018)

GWAS also played a significant role in identifying the genetic loci related to the disease resistance of rice. Huang et al. (2011) and Wang et al. (2019) hold that although there is no specific research on disease resistance at present, if the GWAS results are combined with the information of functional genomes, it is still possible to discover some key variations related to disease resistance traits.

Researchers have identified many gene loci related to salt tolerance in rice through GWAS, including some important positions that affect the Na^+/K^+ ratio and other salt tolerance indicators. Kumar et al. (2015) found in the study of 220 rice germplasm that the Saltol region on chromosome 1 was regarded as the main gene region affecting salt tolerance at the seedling stage. Kumar et al. (2021) also identified sites related to the heat tolerance of rice under stress conditions of high nocturnal temperatures.

3.3 Identification of genes influencing nutritional quality

GWAS was used to study which genes in rice affect the content of proteins and minerals and to identify the gene loci related to amylose and starch composition in rice. Wang et al. (2019) demonstrated in their study that it is still possible to identify some candidate genes that affect nutritional quality by combining the results of GWAS with the information of functional genomes. Huang et al. (2010) argued that the wide application of GWAS in the genetic research of rice indicates that there have been many advancements in understanding the genetic mechanisms of traits such as amylose and the gene loci related to starch composition in rice.

3.4 Mechanistic insights from GWAS into complex trait control

Guo et al. (2018) demonstrated in their study that the combination of high-density haplotype maps and functional genomic information is helpful for researchers to identify the key variations behind these traits, facilitating a better understanding of their genetic structure. Confirming the functions of these key genes through subsequent experiments also makes it clearer how these traits are controlled. Wang et al. (2019) and Kumar et al. (2021) demonstrated that these findings lay the foundation for formulating more targeted and efficient rice breeding methods.

4 Case Study: Dissecting Yield-Related Traits through GWAS

4.1 Selection of specific yield-related traits

The traits such as the number of grains per panicle (GPP), 1000-grain weight (KGW), and the number of tillers per plant (TP) are often selected for focused research because they together determine how much rice a rice plant can produce (Su et al., 2021). Traits such as grain length (GL), grain width (GW), grain thickness (GT), and 1000-grain weight (TGW) will affect the quality and yield of rice (Zhong et al., 2021). Selecting these traits for study is beneficial for a more comprehensive understanding of the genetic factors of yield, thereby formulating more targeted breeding strategies.

4.2 GWAS analysis and identification of key genetic regions

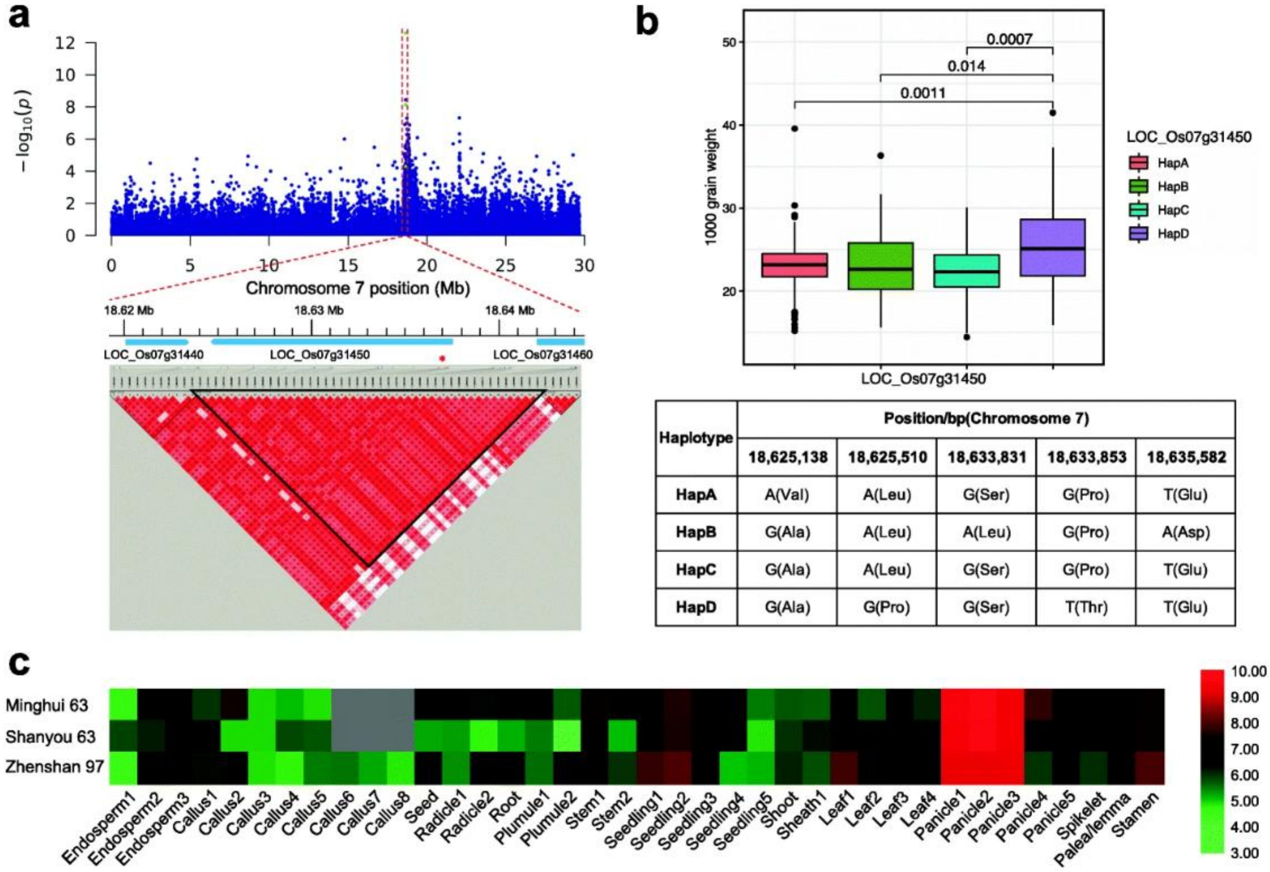
Researchers have discovered many important loci related to yield by analyzing different types of rice varieties. Su et al. (2021) conducted single-site and multi-site GWAS analyses on 529 core rice varieties and identified a total of 20 quantitative trait nucleotides (QTNs) related to yield traits. Another meta-GWAS study identified 3 589 significant loci related to constituent traits, indicating that the genetic structure of rice yield is very complex. In an early study by Huang et al. (2011), 32 new loci related to flowering time and grain-related traits were identified in 950 different rice varieties through a high-density haplotype map.

4.3 Functional validation of key loci

After researchers identify important gene regions related to rice yield through GWAS, they usually conduct some functional verifications such as gene expression analysis, mutant analysis, and map cloning to confirm whether these genes are really effective. Zhong et al. (2021) found that the two candidate genes *LOC_Os09g02830* and *LOC_Os07g31450* would respectively affect grain width (GW) and 1000-grain weight (TGW) (Figure 2). In 2022, Aloryi et al. used meta-QTL analysis to identify 52 candidate genes that might affect grain yield, including some genes encoding cytochrome P450, zinc finger protein and MADs-box protein.

4.4 Implications for rice breeding and future applications

The findings obtained from GWAS and the functional verification of key loci are of great help to rice breeding. Breeding experts can develop molecular markers for marker-assisted selection (MAS) by identifying and confirming those gene regions related to yield, thereby more effectively selecting high-yield varieties. Begum et al. (2015) applied the GWAS results to breeding projects and identified haplotypes that could be used to screen dwarf, early-flowering and high-yielding varieties. Su et al. (2021) held that component traits such as the number of grains per spike (GPP) and the number of tillers (TP), because they have a positive impact on yield, can be regarded as indirect indicators of yield and also provide a basis for designing the ideal plant type. Gene editing tools such as CRISPR/Cas9 may be used in the future to precisely modify these key genes, thereby enhancing the yield potential of rice. If GWAS can be continuously combined with functional genomics and breeding practices, it will bring new hope for cultivating high-yield rice and solving global food problems.



Haplotype	Position/bp(Chromosome 7)				
	18,625,138	18,625,510	18,633,831	18,633,853	18,635,582
HapA	A(Val)	A(Leu)	G(Ser)	G(Pro)	T(Glu)
HapB	G(Ala)	A(Leu)	A(Leu)	G(Pro)	A(Asp)
HapC	G(Ala)	A(Leu)	G(Ser)	G(Pro)	T(Glu)
HapD	G(Ala)	G(Pro)	G(Ser)	T(Thr)	T(Glu)

Figure 2 (a) Local linkage disequilibrium for qTGW-7-1. (b) Box plot of TGW traits about four haplotypes of LOC_Os07g31450. The x-axis represents four haplotypes of LOC_Os07g31450 and the y-axis represents 1000-grain weight. The table below is the detailed information of four haplotypes.(c) Heatmap of the expression pattern of LOC_Os07g31450 in various tissues among three local rice species. The y-coordinate indicates three species and relative expression, and x-coordinate indicates 39 different parts and development stages of rice tissue. Red represents higher gene expression and green indicates lower gene expression level, the gene expression levels are $\log_2$ transformed (Adopted from Zhong et al., 2021)

5 Challenges and Limitations in GWAS for Rice

5.1 Population structure and confounding factors

If the group structure is not handled properly, false associations may arise. Population structure refers to the different subpopulations included in the study. Because they have different ancestors, the frequencies of some alleles are inherently different, and this difference has nothing to do with the traits themselves. Sul et al. (2016) and Sul et al. (2018) indicated that if not distinguished, incorrect results might be obtained. It seems that a certain variation is related to traits, but in fact, it is only due to different population structures. To reduce this impact, scientists have developed hybrid models that can take into account both group structure and kinship during analysis. However, this type of model is rather complex to calculate and not easy to operate (Jiang et al., 2019).

5.2 Limitations in phenotypic data and measurement

Because many traits are rather complex and the measurement requires a very high degree of accuracy, the determination of phenotypes often encounters difficulties. In rice research, traits such as yield, flowering time and grain quality are often influenced by multiple genes and environmental factors, which makes it difficult to obtain unified and accurate data (Huang et al., 2011; Korte and Farlow, 2013). Phenotypic determination in large-scale rice populations is costly and labor-intensive, and may also limit the scale of research. As a result, it becomes difficult to discover those truly useful genetic variations (Yano et al., 2016).

5.3 Environmental variability and its impact on GWAS findings

Changes in conditions such as temperature, humidity, soil type and moisture will all affect the expression of traits and their relationship with genes. Wang et al. (2019) argued that the gene-by-environment interaction (GEI) would make the results of GWAS more difficult to interpret, because the same genetic variation might have different effects in different environments. It is not easy to control these environmental differences. If not, it may lead to inconsistent research results and even be difficult to replicate (Sul et al., 2016).

5.4 Integration of GWAS with other genomic tools

If GWAS can be combined with other genomic tools, the results will be clearer and more explanatory. Cai et al. 's research in 2023 indicates that fine positioning technology can take advantage of genetic differences among different varieties, prioritize the study of those variations that might truly play a role, and also reduce errors caused by interference. Using GWAS together with single-cell data or functional genomic information is also useful for a deeper understanding of the biological mechanisms behind these traits. However, Huang et al. (2011) proposed that such comprehensive methods require very complex computing tools and a large amount of detailed data, but these conditions are not always available.

6 Future Prospects of GWAS in Rice Improvement

6.1 Combining GWAS with genomic selection (GS)

GWAS can provide a lot of detailed information about genes and traits. If GS uses this information, it can predict more accurately which varieties are better. The BLUPGA model incorporates the results of GWAS into the genomic relationship matrix and performs more accurately than traditional methods when predicting multiple traits of rice. Using trait marker selection and prediction models that can take into account different environments, there is also better performance in predicting complex traits such as drought resistance. This combination approach can help breed new rice varieties with high yield and stress resistance more quickly, promoting the sustainable development of agriculture.

6.2 Functional genomics and GWAS for trait dissection

Huang et al. (2011) identified many candidate genes related to important agronomic traits by using high-density haplotype maps and sequence-based GWAS. These genes can be verified experimentally for their roles in trait expression. Some important genes found through GWAS were later confirmed in experiments, indicating that this method is very useful in the study of traits (Wang et al., 2019). Scientists can gain a clearer understanding of how traits are regulated by genes through the combination of GWAS and functional genomes, and it also provides the possibility of precisely intervening in key genes in the future.

6.3 Translating GWAS findings into breeding programs

Applying the research results of GWAS to actual rice breeding is an important step for genetic research to truly play a role. Finding gene loci related to important traits provides very useful resources for marker-assisted selection (MAS) and genomic selection (GS) (Huang et al., 2010). Spindel et al. (2015) argued that using the results of GWAS to improve the GS model could make trait prediction more accurate and enhance the efficiency of breeding. Spindel et al. (2016) demonstrated that incorporating the latest GWAS findings into the GS model could further optimize breeding strategies and enable useful new genetic variations to be better integrated into excellent breeding materials. These advancements can shorten the breeding time and enhance the genetic improvement effect of rice.

6.4 Opportunities for enhancing GWAS methodologies in rice

High-density SNP chips and next-generation sequencing technology enable more genotypes to be studied (Korte and Farlow, 2013). Some new statistical methods, such as the mixed model, can reduce false positive results and improve the discovery ability of GWAS. Cortes et al. ’s research in 2021 indicates that future studies can focus more on new directions such as analyzing rare variations and using synthetic association methods, or continue to optimize the GWAS model. If these methodological issues can be resolved, it will make GWAS more accurate, which is helpful for better identifying key variations and gaining a deeper understanding of the genetic structure of complex traits in rice.

7 Conclusion

Genome-wide association studies (GWAS) have advanced people's understanding of the genetic mechanisms of complex traits in rice and have played a significant role in identifying gene loci related to important agronomic traits such as flowering time and grain yield over the past decade. Researchers discovered millions of SNPS through high-density haplotype maps and whole-genome sequencing, and established detailed genetic maps. The combination of GWAS and functional genomics has helped scientists identify many key genes and study their functions, facilitating a deeper understanding of the genetic structure of rice. Statistical methods such as linear mixed models, by considering population structure and other interfering factors, have improved the accuracy and analytical ability of GWAS.

The recent research results of GWAS have had a significant impact on rice breeding. By identifying the genetic variations and loci related to the ideal traits, breeders can select these traits more specifically during the breeding process and accelerate the breeding speed of new varieties. Identifying candidate genes and conducting functional verification have also helped develop more accurate molecular markers and improved the efficiency of marker-assisted selection. Understanding the genetic mechanisms of complex traits enables researchers to regulate multiple genes simultaneously and cultivate rice varieties that are more productive, more stress-resistant and have better nutrition.

Future GWAS studies on rice can expand the diversity of rice germplasm resources, which is useful for better discovering new genetic variations related to traits. Combining multiple omics data such as transcriptomics and metabolomics with GWAS is helpful for understanding the molecular mechanisms behind complex traits from multiple perspectives. The development and use of more complex statistical models can better handle the problems of multi-gene control and the interaction between genes, making the results of GWAS clearer and easier to understand. The application of these research results in rice breeding requires the joint efforts of geneticists, breeding experts and other relevant personnel to ensure that this genetic information is truly useful for increasing rice yield and ensuring food security.

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Conflict of Interest Disclosure

The authors affirm 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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