

# Systematic Analysis of QTLs for Rice Yield and Quality: From Mapping to Application

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**Abstract** Rice (*Oryza sativa* L.) is a major food crop crucial to global food security, and its yield and quality are the most important traits for improvement. This study examines the quantitative trait loci (QTL) associated with rice yield and quality, details their localization, mechanism, and application in breeding programs, and explores the historical development of QTL mapping techniques, from traditional two-parent hybridization to advanced methods such as genome-wide association studies (GWAS). The genetic mechanisms and regulatory pathways of key QTLs affecting yield components such as grain number, panicle length, biomass, grain size, amylose content, aroma and other quality traits were discussed. By analyzing previous studies, this study highlights the successful identification and application of these QTLs in the breeding of high-yield and high-quality rice varieties, and illustrates how QTL data can be integrated into breeding strategies through marker-assisted selection (MAS) and genomic selection (GS). The purpose of this study is to provide some scientific basis for the next research.

**Keywords** Rice yield; Rice quality; Quantitative trait loci (QTL); Marker-assisted selection (MAS); Genomic selection (GS)

## 1 Introduction

Rice (*Oryza sativa* L.) is a staple food for more than half of the world's population, providing 60%~70% of the daily caloric intake for over two billion Asians alone (Marathi et al., 2012). The global demand for rice continues to rise due to population growth, urbanization, and changing dietary preferences. Ensuring high rice yield and quality is crucial for global food security, especially in the face of challenges such as climate change, water scarcity, and limited arable land (Sandhu and Kumar, 2017). Enhancing rice yield and quality not only addresses food shortages but also contributes to economic stability and poverty alleviation in rice-dependent regions (Miura et al., 2011).

Quantitative trait loci (QTL) are genomic regions that contribute to the variation in complex traits such as yield, drought tolerance, and grain quality in rice. The identification and mapping of QTLs have revolutionized plant breeding by enabling the precise selection of desirable traits through marker-assisted selection (MAS) (Selamat and Nadarajah, 2021; Aloryi et al., 2022). QTL mapping involves the use of various genetic populations and high-throughput sequencing technologies to locate specific genomic regions associated with target traits (Miura et al., 2011). Meta-QTL analysis further refines these regions, providing stable and robust QTLs that are consistent across different genetic backgrounds and environments (Aloryi et al., 2022). This approach has been instrumental in identifying key genes and regulatory networks that control important agronomic traits, thereby facilitating the development of high-yielding and stress-tolerant rice varieties (Sandhu and Kumar, 2017).

The aim of this study is to provide a comprehensive analysis of QTLs related to rice yield and quality, from their initial localization to their practical application in breeding programs. In this study, we reviewed the current status of QTL research related to rice yield and quality, highlighted the main research results in recent years, discussed the methods and techniques of QTL localization and meta-QTL analysis, and emphasized their advantages and limitations. In different studies, identify consistent genomic regions and candidate genes associated with yield and quality traits, and explore the practical application of QTL in marker-assisted selection and genetic engineering of improved rice varieties. By synthesizing the latest research and providing

insights into the practical applications of QTLs, this study aims to contribute to the ongoing efforts to enhance rice yield and quality, thereby supporting global food security and sustainable agricultural practices.

## 2 QTL Mapping in Rice

### 2.1 Historical development and milestones in QTL mapping

The journey of QTL mapping in rice has seen significant advancements over the past few decades. Initial efforts focused on constructing genetic maps using simple sequence repeats (SSR) and other molecular markers. For instance, a study on recombinant inbred lines (RILs) derived from the popular rice hybrid KRH-2 utilized SSR loci to construct a genetic map spanning 294.2 cM, identifying 22 QTLs related to yield and its associated traits (Kulkarni et al., 2020). The development of high-density genetic maps, such as those created by the Rice Genome Project (RGP), has been pivotal. These maps have facilitated the identification of QTLs for various agronomic traits, including yield, disease resistance, and abiotic stress tolerance. The integration of multiple studies through meta-analysis has further refined our understanding, revealing consensus regions and candidate genes across different rice species (Swamy and Sarla, 2011).

### 2.2 Techniques and methodologies for QTL mapping

QTL mapping methodologies have evolved from traditional linkage analysis to more sophisticated approaches. Early studies relied on phenotyping and genotyping information to identify QTLs, as demonstrated by the identification of major effect QTLs for traits like total grain yield and panicle length using SSR markers (Figure 1) (Kulkarni et al., 2020). The advent of genotyping-by-sequencing (GBS) has significantly enhanced the resolution and precision of QTL mapping. For example, GBS was used to develop high-density linkage maps in rice, identifying stable QTLs for grain yield under drought stress (Figure 2) (Yadav et al., 2019). Another innovative approach, QTL-seq, combines whole-genome resequencing with bulked segregant analysis, allowing rapid identification of QTLs by comparing DNA from populations with extreme trait values (Takagi et al., 2013). Dynamic QTL mapping, which considers the temporal expression of traits, has also been employed to study protein content and index in rice, revealing stage-specific QTLs (Zheng et al., 2011).

### 2.3 Tools and software for QTL mapping

The advancement of QTL mapping has been supported by the development of various tools and software. High-density genetic maps and consensus maps have been instrumental in QTL identification and meta-analysis (Swamy and Sarla, 2011). Software like QuLine has been used to simulate breeding strategies and demonstrate the application of identified QTLs in rice quality improvement (Wang et al., 2007). The integration of QTL mapping with functional genomics, as seen in the construction of rice function maps, has provided deeper insights into the genetic control of agronomic traits (Ishimaru et al., 2001). These tools have not only facilitated the identification and validation of QTLs but also enabled their application in marker-assisted selection (MAS) and breeding programs.

## 3 Key QTLs for Rice Yield

### 3.1 Major QTLs associated with yield components

Quantitative Trait Loci (QTL) mapping has identified several major QTLs associated with yield components in rice. For instance, a study using an F<sub>2</sub> and F<sub>3</sub> population derived from an indica-indica cross identified 44 QTLs across nine chromosomes, including QTLs for the number of panicles, number of filled grains, total number of spikelets, spikelet fertility, 1 000-grain weight, grain weight per plant, plant height, and panicle length. Another study using a recombinant inbred line (RIL) population derived from the rice hybrid KRH-2 identified 22 QTLs, with major QTLs for total grain yield per plant (qYLD3-1), panicle weight (qPW3-1), plant height (qPH12-1), flag leaf width (qFLW4-1), and panicle length (qPL3-1) (Kulkarni et al., 2020).

### 3.2 Mechanisms of action

The mechanisms by which these QTLs influence yield components often involve complex genetic interactions and environmental factors. For example, the QTLs identified in the F<sub>2</sub> and F<sub>3</sub> populations showed significant QTL×environment interactions, suggesting that the expression of these QTLs can be influenced by environmental conditions. Similarly, the QTLs identified in the RIL population also exhibited significant

epistatic interactions, indicating that the effects of these QTLs can be modified by interactions with other loci (Kulkarni et al., 2020). Furthermore, a study on reciprocal introgression lines revealed that QTLs for grain yield and its components are influenced by genetic background and environment, with some QTLs showing strong genetic background effects (Wang et al., 2014).

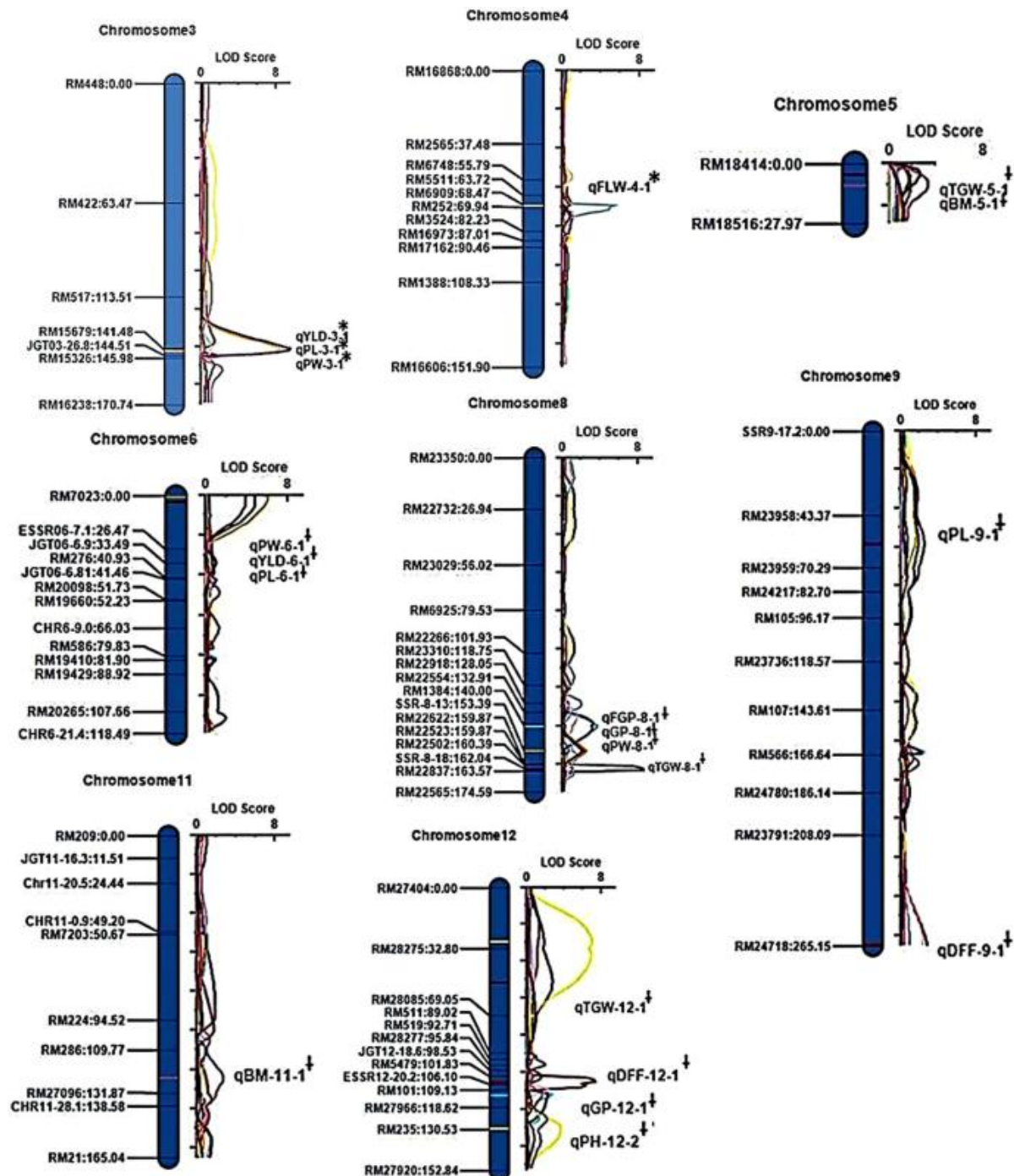


Figure 1 QTL-marker linkage map of selected chromosomes along with the identified QTLs when QTL mapped with 105 RILs and 126 SSR markers (Adopted from Kulkarni et al., 2020)

Image caption: The names and position of markers in centi morgan (cM) are given on left side and LOD scores with peaks are presented on right side of chromosomes. Major effect QTLs are denoted with asterisk (\*) and minor effect QTLs are denoted with † symbol (Adopted from Kulkarni et al., 2020)

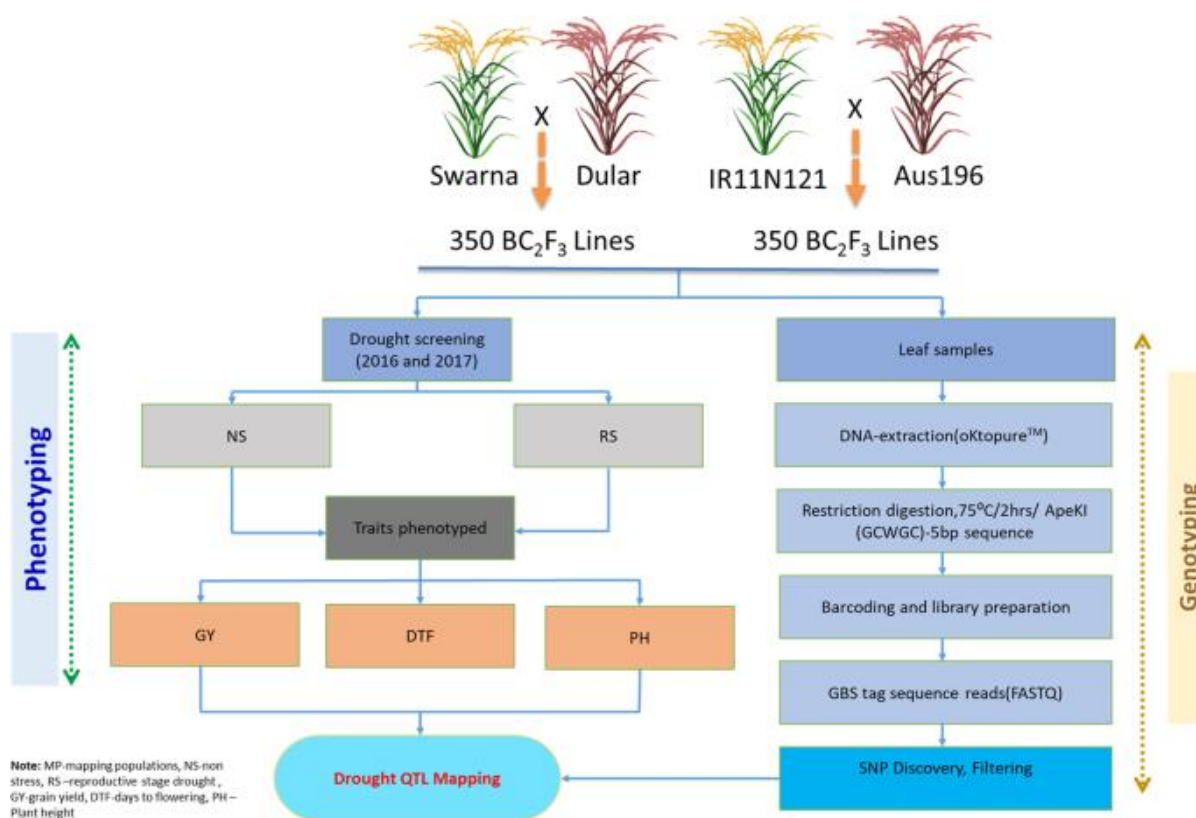


Figure 2 Integration of GBS derived high density SNPs and multi-season phenotyping data for mapping of drought QTLs in rice (Adopted from Yadav et al., 2019)

### 3.3 Case studies

Several studies highlight the practical applications of these QTLs in rice breeding. For instance, the identification of QTLs for yield components in the F<sub>2</sub> and F<sub>3</sub> populations has facilitated the development of rice varieties with improved yield stability across different environments. In another case, the validation of QTLs through SNP genotyping in the RIL population has enabled the identification of novel major effect QTLs with better resolution and precision, which can be utilized in the development of superior rice hybrids (Figure 3) (Kulkarni et al., 2020). Additionally, the use of meta-analysis to integrate QTL data from multiple studies has led to the identification of consensus QTL regions and candidate genes, which can be targeted for marker-assisted selection (MAS) to improve rice yield (Swamy and Sarla, 2011).

## 4 Key QTLs for Rice Quality

### 4.1 Major QTLs associated with grain quality traits

Grain quality in rice is influenced by several quantitative trait loci (QTLs) that govern traits such as grain length, grain width, chalkiness, and milling quality. Notable QTLs identified for these traits include qGL5, qPGWC-5 and qHR. qGL5 is associated with grain length and is located on chromosome 5. It has been shown to significantly influence the grain length to width ratio (LWR) and grain thickness (GT) (Gao et al., 2016). qPGWC-5 is found on chromosome 5, this QTL controls the percentage of grain with chalkiness (PGWC), a critical trait affecting the visual quality of rice grains (Gao et al., 2016). qHR is linked to head-rice yield (HR), a key milling quality trait. It has been mapped in recombinant inbred lines (RILs) derived from a cross of L-204 and 01Y110, showing consistent expression across multiple environments (Nelson et al., 2012).

### 4.2 Mechanisms of action

The mechanisms by which these QTLs influence grain quality traits involve various genetic and molecular pathways. qGL5 affects grain length by regulating cell division and elongation in the developing grain. The alleles at this locus contribute to variations in grain dimensions, which are crucial for market preferences and processing quality (Gao et al., 2016). The action of qPGWC-5 involves the regulation of starch synthesis and

deposition within the grain endosperm. Variations at this locus can lead to differences in the chalkiness of the grain, impacting its appearance and cooking quality (Gao et al., 2016). qHR for head-rice yield influences the structural integrity of rice kernels during milling. It likely affects the physical properties of the grain, such as kernel hardness and resistance to breakage, which are essential for maintaining high milling yields (Nelson et al., 2012).

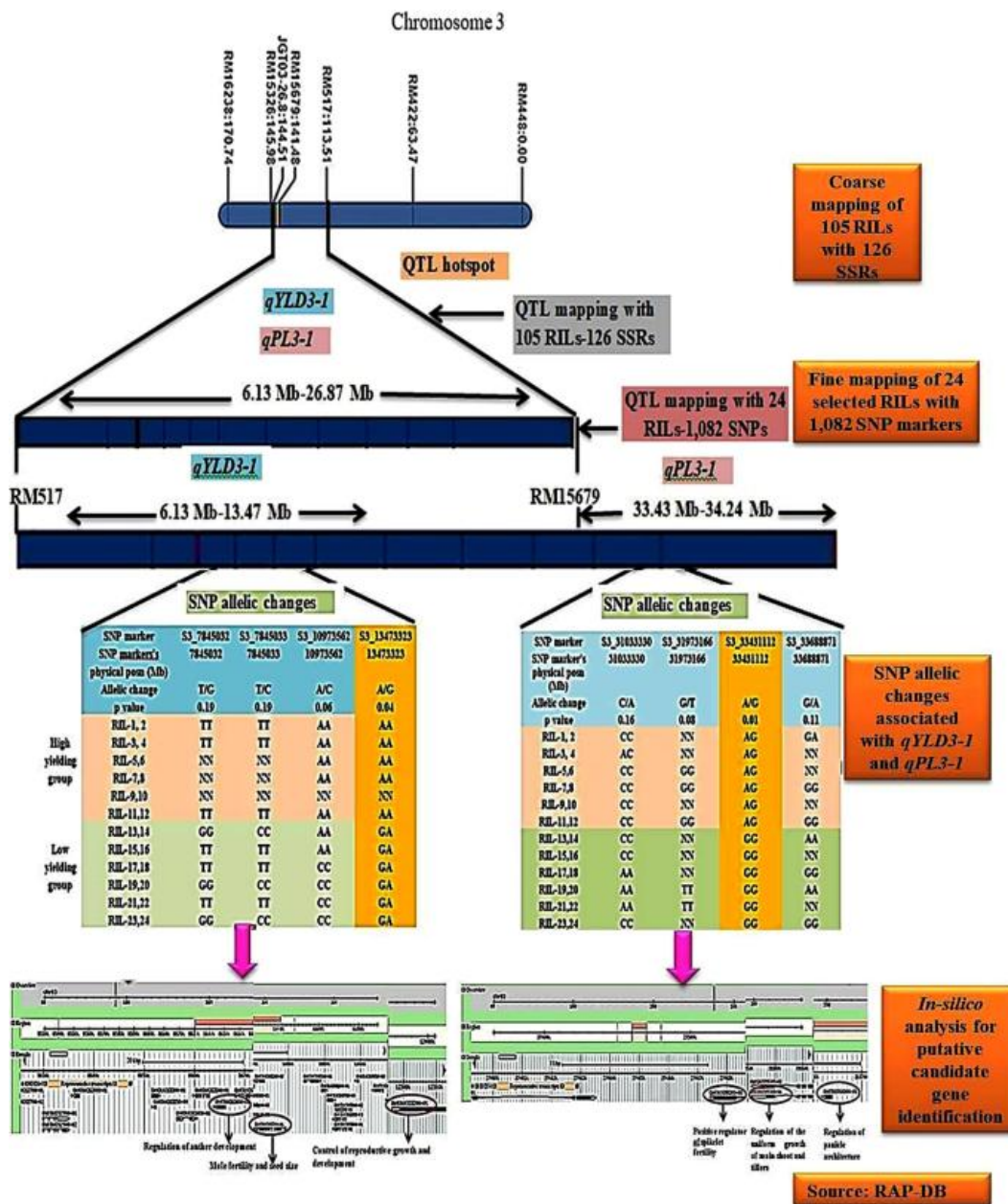


Figure 3 Scheme of fine mapping of YLD and PL QTLs on chromosome 3 with 24 selected RILs and 1 082 SNP markers (Adopted from Kulkarni et al., 2020)

Image caption: Significant SNP changes highlighted in yellow (Adopted from Kulkarni et al., 2020)

### 4.3 Case studies

Several studies have demonstrated the practical applications of these QTLs in rice breeding programs. In a study involving recombinant inbred lines derived from Gang46B and K1075, the qGL5 and qPGWC-5 QTLs were identified and shown to significantly affect grain length, width, and chalkiness. These findings have been utilized to improve grain appearance quality in rice breeding programs (Gao et al., 2016). The qHR QTL was mapped in a population derived from a cross between L-204 and 01Y110. This QTL has been used to enhance

head-rice yield in elite Western U.S. rice germplasm, demonstrating its potential for improving milling quality in commercial rice varieties (Nelson et al., 2012). The identification of QTLs such as qGL5 and qPGWC-5 has facilitated marker-assisted selection (MAS) in rice breeding. By incorporating these QTLs into breeding programs, researchers have been able to develop rice varieties with superior grain quality traits, meeting both domestic and international market demands (Nelson et al., 2012; Gao et al., 2016). These studies highlight the importance of understanding the genetic basis of grain quality traits and the application of QTL mapping in the development of high-quality rice varieties.

## **5 Integration of QTL Mapping and Breeding**

### **5.1 Combining QTL mapping with traditional breeding strategies**

Combining QTL mapping with traditional breeding strategies has proven to be a powerful approach to enhance rice yield and quality. Traditional breeding methods, which rely on phenotypic selection, can be significantly improved by incorporating QTL mapping to identify genomic regions associated with desirable traits. This integration allows breeders to make more informed decisions and accelerate the development of high-yielding, stress-resistant rice varieties. For instance, QTL-seq, a method involving whole-genome resequencing of DNA from bulked populations, has been successfully applied to identify QTLs for important agronomic traits such as partial resistance to rice blast disease and seedling vigor (Takagi et al., 2013). Additionally, the use of advanced backcross QTL analysis and introgression lines has facilitated the exploitation of major QTLs from less adapted germplasms, such as landraces and wild relatives, to improve grain yield under abiotic stress conditions (Guo and Ye, 2014).

### **5.2 Use of marker-assisted selection (MAS) and genomic selection (GS)**

Marker-assisted selection (MAS) and genomic selection (GS) are two advanced breeding techniques that leverage QTL mapping data to enhance the efficiency and accuracy of breeding programs. MAS involves the use of DNA markers linked to target traits to select individuals carrying desirable alleles, thereby accelerating the breeding process (Huang and Hong, 2024). This method has been effectively used to integrate major genes or QTLs with large effects into widely grown rice varieties, improving traits such as disease resistance and stress tolerance (Jena and Mackill, 2008). On the other hand, GS uses genome-wide markers to predict the breeding value of individuals, allowing for the selection of superior genotypes based on their genetic potential rather than phenotypic performance alone. GS has shown promise in improving breeding efficiency for complex traits like grain yield, plant height, and flowering time, with prediction accuracies ranging from 0.31 to 0.63 depending on the trait and statistical model used (Spindel et al., 2015).

### **5.3 Challenges and solutions in integrating QTL data into breeding programs**

Integrating QTL data into breeding programs presents several challenges, including the complexity of quantitative traits, the need for high-resolution mapping, and the variability of QTL effects across different genetic backgrounds and environments. One major challenge is the accurate identification and validation of QTLs with significant effects on target traits. Advances in next-generation sequencing and meta-analysis techniques have helped address this issue by increasing mapping resolution and narrowing down QTL regions, making them more suitable for MAS and fine mapping (Swamy and Sarla, 2011). Another challenge is the effective utilization of QTL data in breeding programs, which requires careful consideration of the genetic architecture of traits and the development of efficient selection schemes. Practical guidelines derived from theoretical and empirical studies can guide the design of efficient marker-assisted gene introgression and pyramiding schemes, ensuring the successful application of QTL data in breeding programs (Francia et al., 2005; Guo and Ye, 2014).

## **6 Challenges and Future Directions**

### **6.1 Current limitations in QTL mapping and application**

Despite significant advancements in QTL mapping for rice yield and quality, several limitations persist. One major challenge is the complexity of quantitative traits, which are often controlled by multiple genes with small effects, making it difficult to identify and manipulate individual QTLs effectively (Takagi et al., 2013).

Additionally, the accuracy of QTL mapping can be hindered by environmental interactions and the genetic background of the populations used, leading to inconsistent results across different studies and environments (Wan et al., 2005; Prince et al., 2015). The resolution of QTL mapping is another limitation, as traditional methods often result in large confidence intervals, making it challenging to pinpoint the exact location of the QTLs (Swamy and Sarla, 2011). Furthermore, the integration of QTLs into breeding programs is still limited, with few QTLs successfully utilized in marker-assisted breeding (MAB) due to the complexity of trait inheritance and the need for precise validation (Prince et al., 2015).

### **6.2 Need for multi-environment trials and large-scale validation**

To overcome the limitations of QTL mapping, there is a critical need for multi-environment trials and large-scale validation. Multi-environment trials help in understanding the stability and consistency of QTLs across different environmental conditions, which is essential for developing robust rice varieties (Wan et al., 2005; Bernier et al., 2009). Large-scale validation involves testing the identified QTLs in diverse genetic backgrounds and environments to confirm their effects and utility in breeding programs (Prince et al., 2015; Kulkarni et al., 2020). This approach can help in identifying QTLs with broad adaptability and significant impact on yield and quality traits. Additionally, the use of advanced genotyping techniques, such as SNP genotyping and whole-genome resequencing, can enhance the precision and resolution of QTL mapping, facilitating the identification of candidate genes and their functional validation (Takagi et al., 2013; Kulkarni et al., 2020).

### **6.3 Future trends and potential breakthroughs in QTL research**

Future trends in QTL research are likely to focus on integrating high-throughput phenotyping and genotyping technologies to improve the accuracy and efficiency of QTL mapping. The use of next-generation sequencing (NGS) and genome-wide association studies (GWAS) can provide deeper insights into the genetic architecture of complex traits and identify novel QTLs with significant effects (Takagi et al., 2013). Additionally, the development of advanced statistical models and bioinformatics tools can enhance the analysis of QTL data, allowing for more precise mapping and better understanding of gene interactions (Liu et al., 2013). Another potential breakthrough is the application of gene editing technologies, such as CRISPR/Cas9, to directly manipulate QTLs and validate their functions, paving the way for targeted breeding strategies (Wan et al., 2006). Furthermore, the integration of QTL mapping with systems biology approaches can provide a holistic understanding of the molecular networks underlying complex traits, leading to the development of superior rice varieties with improved yield and quality (Wang et al., 2007).

## **7 Concluding Remarks**

The systematic analysis of quantitative trait loci (QTLs) for rice yield and quality has revealed significant insights into the genetic control of these complex traits. Various studies have identified numerous QTLs associated with yield-related traits, such as grain yield, panicle length, and plant height, as well as quality traits like head rice yield, amylose content, and chalkiness degree. For instance, research has shown that near isogenic lines (NILs) are effective in fine-mapping and cloning target QTLs, leading to the identification of 20 QTLs directly affecting rice grain yield. Additionally, meta-analysis has helped narrow down initial yield QTLs, making them more suitable for marker-assisted selection (MAS). The use of recombinant inbred lines (RILs) and other advanced populations has further validated these QTLs, enhancing the precision of genetic mapping.

Systematic QTL analysis is crucial for the genetic improvement of rice yield and quality. By identifying and validating QTLs, researchers can better understand the genetic architecture of these traits, which is essential for effective breeding programs. The integration of QTL mapping with advanced genomic tools, such as whole-genome resequencing (QTL-seq), has streamlined the identification of QTLs, making the process faster and more efficient. This systematic approach allows for the precise selection of favorable alleles, which can be combined to enhance both yield and quality traits in rice. The application of identified QTL-marker associations in breeding programs has already shown promising results in improving traits like amylose content and chalkiness degree.

The findings from systematic QTL analysis have several implications for future research and breeding programs. First, the continuous discovery and validation of QTLs will provide a robust genetic foundation for developing high-yielding and high-quality rice varieties. Future research should focus on fine-mapping and cloning additional QTLs, as well as understanding their molecular mechanisms. Second, the integration of QTL analysis with other genomic tools, such as genome-wide association studies (GWAS) and genomic selection, will further enhance the efficiency of breeding programs. Finally, breeding programs should adopt a holistic approach that considers both yield and quality traits, ensuring that new rice varieties meet the demands of both farmers and consumers. The use of advanced breeding techniques, such as marker-assisted selection and genomic selection, will be instrumental in achieving these goals.

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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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