

## Key Genes and Loci Impacting Yield and Quality in Rice Genome

Xuelian Jiang, Yeping Han ✉

Institute of Life Sciences, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China

✉ Corresponding email: [yeping.han@jicau.edu.cn](mailto:Yeping.han@jicau.edu.cn)

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**Abstract** In this study, the main genes and quantitative trait loci that affect rice yield and quality were discussed, and the genes that are important for yield-related traits and the genes that affect food quality were discussed. This study also highlights the mechanisms of action, regulatory networks, and pathways of control of these genes. The successful application of gene editing and traditional breeding in the cultivation of high yield and high quality rice varieties was illustrated through the case study. In addition, the study examines the integration of genomic, transcriptome, and phenotypic data, as well as the role of advanced techniques such as genome-wide association studies (GWAS) and genome selection (GS). Despite significant progress in response, challenges remain, including technical limitations and the need for more comprehensive bioinformatics tools. This study aims to provide a theoretical basis for future directions in rice genomics, highlighting the potential of CRISPR/Cas9 and other gene-editing technologies to further enhance rice breeding programs.

**Keywords** Rice (*Oryza sativa*); Rice genome; Rice genomics; Yield; Grain quality; Quantitative trait loci (QTLs); Gene editing

### 1 Introduction

Rice (*Oryza sativa*) is a cornerstone of global agriculture and food security, serving as a staple food for more than half of the world's population (Zuo and Li, 2014; Zeng et al., 2017). The significance of rice extends beyond its role as a primary food source; it is also a critical model organism for studying the genomics of monocotyledons and agroecosystems (Raghuvanshi et al., 2010; Li et al., 2018). As the global population continues to grow, with projections indicating an increase of 3 billion people over the next 30 years, the demand for rice is expected to rise substantially (Wing et al., 2018). This escalating demand underscores the urgent need to enhance rice yield and quality to ensure food security and meet the nutritional needs of billions of people worldwide (The 3 000 Rice Genomes Project, 2014).

The advent of rice genomics has revolutionized our understanding of this vital crop, providing unprecedented insights into its genetic makeup and the regulatory mechanisms underlying key agronomic traits (Marathi et al., 2012; Zeng et al., 2017; Li et al., 2018). The sequencing of the rice genome has unveiled a wealth of information, including over 32,000 genes, regulatory elements, and DNA markers, which are instrumental in molecular analysis and genetic enhancement (Raghuvanshi et al., 2010). Functional genomics research has led to the identification and cloning of thousands of genes associated with important traits such as yield, grain quality, and resistance to biotic and abiotic stresses (Jiang et al., 2012; Zuo and Li, 2014; Li et al., 2018). These advancements have paved the way for the development of new rice varieties with improved yield potential and quality, contributing to sustainable agricultural practices and food security (Marathi et al., 2012; Xu et al., 2016; Zeng et al., 2017; Xu et al., 2021).

This study will highlight the progress made in understanding the genetic basis of important agronomic traits and the application of genomic technologies in rice breeding. The scope of this study encompasses the identification of novel genomic regions, quantitative trait loci (QTLs), and the integration of multi-omic data to enhance yield prediction and crop improvement strategies. Ultimately, this study aims to elucidate the potential of rice genomics in addressing the challenges of global food security and advancing the development of high-yield, superior-quality rice varieties.

## 2 Overview of Rice Genomics

### 2.1 History of rice genome sequencing

The history of rice genome sequencing began with the recognition of rice as a model system for crop genomics studies. Early efforts focused on analyzing genome-wide genetic variation to understand gene functions in agronomic traits and to generate data and resources for rice research. The completion of high-quality reference genome sequences marked a significant milestone, enabling the development of sequencing-based genotyping and genome-wide association studies (GWAS) (Huang et al., 2013). The availability of high-quality rice genome sequences has accelerated functional genomic research, including the creation of large mutant libraries and global expression profiles of genes throughout the rice life cycle (Jiang et al., 2012).

### 2.2 Current state of rice genomic resources

In the post-genomic era, significant progress has been made in defining the rice transcriptome and epigenome, as well as in gene discovery through forward and reverse genetic approaches. The rice genome contains more than 32,000 genes, regulatory elements, repeat DNA, and DNA markers, which have opened new horizons for molecular analysis and genetic enhancement (Raghuvanshi et al., 2010). Functional genomic resources have rapidly accumulated, including full-length cDNAs for both indica and japonica rice, and sequences from resequencing large numbers of diverse germplasm accessions. These resources have greatly facilitated gene cloning and the identification of genes controlling agriculturally useful traits such as yield, grain quality, and resistance to biotic and abiotic stresses (Jiang et al., 2012).

### 2.3 Advances in sequencing technologies and their impact on rice genomics

The advent of next-generation high-throughput DNA sequencing technologies has revolutionized rice genomics. These technologies have enabled the development of sequencing-based genotyping and GWAS, significantly advancing rice genetics research (Huang et al., 2013). Deep sequencing methods, such as massively parallel signature sequencing (MPSS) and sequencing-by-synthesis (SBS), have provided comprehensive analyses of the rice transcriptome, identifying many differentially expressed genes that may affect grain quality traits (Venu et al., 2011). These advances have also facilitated the identification of quantitative trait loci (QTLs) and the molecular characterization of genes involved in yield traits, enhancing researchers' understanding of the regulation of these traits (Huang et al., 2009; Xing and Zhang, 2010).

The integration of next-generation sequencing with genomic selection and marker-assisted selection (MAS) has proven effective in improving grain yield and quality. For instance, the use of well-characterized major QTLs through introgression and gene pyramiding has shown success in enhancing yield, particularly under abiotic stress conditions (Guo and Ye, 2014). Additionally, haplotype analysis of key genes governing grain yield and quality traits has revealed significant variations and superior haplotypes (Figure 1), suggesting the potential for developing next-generation tailor-made rice varieties (Abbai et al., 2019).

## 3 Key Genes and Loci Affecting Yield

### 3.1 Major genes and QTLs related to yield

Rice yield is a complex trait influenced by multiple quantitative trait loci (QTLs) and genes. Among the significant QTLs, *DEP1* and *Ghd8* have been extensively studied for their roles in enhancing grain yield. The *DEP1* locus, identified as a major QTL, influences panicle architecture by enhancing meristematic activity, leading to a reduced length of the inflorescence internode and an increased number of grains per panicle, thereby boosting grain yield (Huang et al., 2009). Another critical QTL, *Ghd8*, has pleiotropic effects on grain yield, heading date, and plant height. *Ghd8* regulates key genes such as *Ehd1*, *RFT1*, and *Hd3a*, which are involved in flowering and tillering, ultimately increasing the number of grains per plant (Yan et al., 2011).

### 3.2 Mechanisms of action

The mechanisms by which these QTLs and genes affect yield are diverse and intricate. The *DEP1* locus encodes a phosphatidylethanolamine-binding protein-like domain protein. A gain-of-function mutation in this protein enhances meristematic activity, resulting in a more compact panicle structure with a higher grain count (Huang et al., 2009). On the other hand, *Ghd8* encodes the *OsHAP3* subunit of a CCAAT-box binding protein

complex. This gene modulates the expression of other genes involved in flowering and tillering, such as *MOC1*, which controls tillering and branching. By up-regulating *MOC1*, *Ghd8* increases the number of tillers and branches, leading to a higher grain yield (Yan et al., 2011).

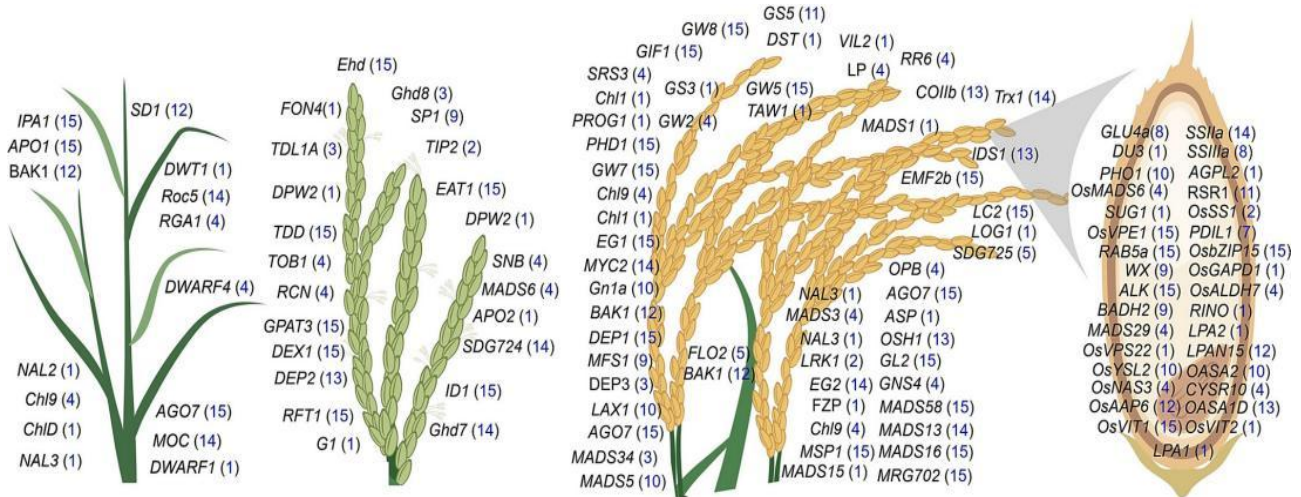


Figure 1 Haplotype analysis of 120 cloned key genes associated with major grain yield and quality related traits in rice (Adopted from Abbai et al., 2019)

Image caption: The chosen 120 genes were previously functionally characterized and were reported to govern/regulate several major grain yield (87 genes) and quality related traits (33 genes) such as tiller number, flowering, panicle architecture, lodging resistance, single plant yield, grain amylose content, grain Fe and Zn concentration, grain size etc. For all these genes haplotype analysis was conducted and the numbers in blue within brackets indicates the number of haplotypes for that particular gene in the 3K RG panel. Interestingly, more than 75% of the genes had haplotypes ranging from 2 to 15 among the 3024 lines. This is a gold mine for the identification of superior haplotypes and utilizing the same in developing elite versions of rice via *haplotype-based breeding* (Adopted from Abbai et al., 2019)

### 3.3 Case studies

Several studies highlight the practical applications of these QTLs in rice breeding. For instance, the *DEP1* allele has been widely introduced into Chinese high-yielding rice varieties, demonstrating its significant impact on increasing grain yield (Huang et al., 2009). Similarly, the *Ghd8* QTL has been utilized in breeding programs to develop rice varieties with improved yield and adaptability to different environmental conditions. The ectopic expression of *Ghd8* in Arabidopsis also revealed its conserved function in flowering regulation, further validating its role in yield enhancement (Yan et al., 2011).

Moreover, advanced breeding techniques such as CRISPR-Cas9 have been employed to edit multiple QTLs simultaneously, including *OsGS3*, *OsGW2*, and *OsGn1a*, which are known to negatively regulate grain size, width, weight, and number. This multiplex editing approach has resulted in significant yield increases in elite rice varieties, demonstrating the potential of combining multiple QTLs for rapid yield improvement (Zhou et al., 2018).

## 4 Key Genes and Loci Affecting Quality

### 4.1 Grain quality traits and their genetic basis

Grain quality in rice is a multifaceted trait influenced by various genetic factors. Key quality attributes include grain size, shape, amylose content, and cooking properties. Recent advances in genomics have enabled the identification of numerous quantitative trait loci (QTLs) and genes associated with these traits. For instance, a genome-wide association study identified 123 significant loci related to grain quality traits, highlighting the complex genetic architecture underlying these attributes (Yu et al., 2022). Additionally, haplotype analysis of key genes governing grain quality traits has revealed significant variations, providing insights into the genetic basis of these traits (Abbai et al., 2019).

#### 4.2 Mechanisms of action

The mechanisms by which these genes and loci influence grain quality are diverse. For example, the *DEP1* locus, which is associated with grain yield, also impacts grain quality by altering panicle architecture and grain number (Huang et al., 2009). Another significant gene, *Ghd8*, has pleiotropic effects, influencing not only grain yield but also plant height and heading date, thereby indirectly affecting grain quality (Yan et al., 2011). The genetic basis of quality traits such as fragrance and cooking temperature has been elucidated through re-sequencing and transcriptome analysis, demonstrating the role of specific genes in determining these attributes (Henry, 2021).

#### 4.3 Case studies

Several related studies illustrate the practical applications of these genetic discoveries. For instance, the identification of superior haplotypes for genes like *GS5* and *GW2* (Figure 2), which influence grain size and shape, has enabled the development of rice varieties with improved grain quality (Abbai et al., 2019). Another study demonstrated the use of marker-assisted selection (MAS) to introgress major QTLs for grain quality traits, resulting in rice varieties with enhanced cooking and nutritional properties (Guo and Ye, 2014). Furthermore, the integration of genomic tools in breeding programs has facilitated the selection of desirable alleles from wild relatives, contributing to the improvement of grain quality in cultivated rice (Henry, 2021).

### 5 Integrative Approaches in Rice Genomics

#### 5.1 Combining genomic, transcriptomic, and phenotypic data

Integrating genomic, transcriptomic, and phenotypic data has become a cornerstone in modern rice genomics. This approach allows researchers to bridge the gap between genotype and phenotype, providing a comprehensive understanding of the genetic basis of important agronomic traits. The advent of next-generation sequencing technologies has significantly advanced this field, enabling high-throughput genotyping and transcriptome analysis. For instance, resequencing of rice genomes has facilitated the identification of genetic variations that correlate with phenotypic traits, thereby enhancing our understanding of gene functions in agronomic contexts (Huang et al., 2013). Additionally, combining these datasets helps in the accurate prediction of trait performance, which is crucial for breeding programs aimed at improving yield and quality (Yu et al., 2022).

#### 5.2 Use of genome-wide association studies (GWAS) and genomic selection (GS)

Genome-Wide Association Studies (GWAS) and Genomic Selection (GS) are pivotal tools in rice genomics. GWAS enables the identification of significant loci associated with traits of interest by scanning the genome for marker-trait associations. For example, a study identified 67 significant loci for yield and agronomic traits and 123 loci for grain quality traits in hybrid rice, demonstrating the power of GWAS in uncovering genetic determinants of complex traits (Yu et al., 2022). On the other hand, GS uses genome-wide markers to predict the breeding value of individuals, thus accelerating the breeding process. Studies have shown that GS models, especially those informed by GWAS, can significantly improve prediction accuracy for various traits, including grain yield and plant height (Spindel et al., 2015; Spindel et al., 2016). The integration of GWAS and GS has been shown to enhance the efficiency of breeding programs by providing a robust framework for selecting superior genotypes (Spindel et al., 2015).

#### 5.3 Role of bioinformatics and computational tools in rice genomics

Bioinformatics and computational tools play a crucial role in managing and analyzing the vast amounts of data generated in rice genomics. Tools like GAPIT (Genomic Association and Prediction Integrated Tool) have been developed to boost the power and accuracy of GWAS and genomic prediction. These tools implement advanced statistical models and algorithms to handle the complexity of genomic data, thereby improving the reliability of association studies and prediction models. For instance, GAPIT version 3 includes multiple loci test methods and enhanced GP/GS methods, which significantly increase the capacity to analyze big genomic data and improve computing speed (Wang and Zhang, 2020). The use of such bioinformatics tools is essential for the

effective integration of genomic, transcriptomic, and phenotypic data, ultimately facilitating the discovery of key genes and loci impacting rice yield and quality.

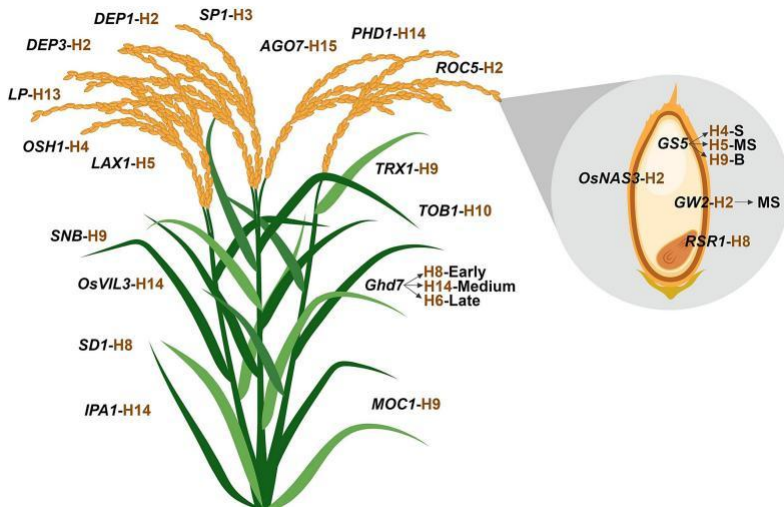


Figure 2 The tailored rice with superior haplotypes for grain yield and quality (Adopted from Abbai et al., 2019)

Image caption: the findings of this study could be employed to develop a designer rice genotype comprising superior haplotype combinations of the target genes such as *MOC1-H9* & *IPA1-H14* for higher tiller number, *Ghd7-H8* & *TOB1-H10* for early, *Ghd7-H14* & *OsVIL3-H14* for medium duration, *Ghd7-H6*, *SNB-H9* & *TRX1-H9* for late flowering, *DEP3-H2*, *DEP1-H2* & *SP1-H3* for long panicles, *SD1-H8* for semi-dwarf nature, *LAX1-H5*, *OSH1-H4* & *LP-H13* resulting in increased panicle branching, *PHD1-H14*, *AGO7-H15* & *ROC5-H2* for high yield, along with *GS5-H4* for slender, *GS5-H5* & *GW2-H2* for medium slender, *GS5-H9* for bold grains, *RSR1-H8* for intermediate amylose content and *OsNAS3-H2* for increased Fe and Zn concentration in grains, B: Bold grain; MS: Medium slender type grain; S: Slender type grain (Adopted from Abbai et al., 2019)

## 6 Challenges and Future Directions

### 6.1 Current limitations in rice genomics research

Despite significant advancements in rice genomics, several limitations persist. One major challenge is the complexity of rice yield traits, which are controlled by multiple quantitative trait loci (QTLs) and influenced by various environmental factors. This complexity makes it difficult to pinpoint specific genes responsible for yield improvements (Xing and Zhang, 2010; Guo and Ye, 2014). Additionally, while high-quality genome sequences are available, the functional characterization of many genes remains incomplete, limiting our understanding of their roles in agronomic traits (Delseny et al., 2001; Xing and Zhang, 2010). The slow genetic progress in breeding programs, despite technological innovations, further highlights the gap between genomic research and practical applications in crop improvement (Guo and Ye, 2014).

### 6.2 Technological and methodological challenges

Technological and methodological challenges also hinder progress in rice genomics. High-throughput sequencing technologies have revolutionized the field, but the integration of these data into breeding programs is still in its infancy (Huang et al., 2013). Marker-assisted selection (MAS) has shown promise, yet its application is often limited to a few target QTLs, and the success rate in improving complex traits like yield remains modest (Guo and Ye, 2014). Moreover, the development of advanced mapping populations and the identification of single nucleotide polymorphisms (SNPs) have enhanced genetic analysis, but the translation of these findings into practical breeding strategies is still challenging (Fukuoka et al., 2010). The need for more efficient and cost-effective genotyping methods is also a significant barrier (Kumar et al., 2017).

### 6.3 Future trends and potential breakthroughs

Looking ahead, several trends and potential breakthroughs could address these challenges. The continued development of next-generation sequencing technologies and genome-wide association studies (GWAS) will likely enhance our understanding of the genetic basis of complex traits and facilitate the identification of key

genes and loci (Huang et al., 2013). Functional genomics, including transcriptome and epigenome analysis, will play a crucial role in bridging the gap between genotype and phenotype, enabling more precise manipulation of genetic traits (Raghuvanshi et al., 2010). Additionally, the integration of genomics with advanced breeding techniques, such as genomic selection and gene editing, holds promise for accelerating the development of high-yielding, resilient rice varieties (Fukuoka et al., 2010). The use of well-characterized major QTLs through introgression and gene pyramiding is expected to improve grain yield, particularly under abiotic stress conditions (Guo and Ye, 2014). Finally, the establishment of comprehensive genomic databases and the development of bioinformatics tools will support more efficient data analysis and application in breeding programs (Delseny et al., 2001; Xing and Zhang, 2010). By addressing these challenges and leveraging emerging technologies, the future of rice genomics research holds great potential for significant advancements in yield and quality improvement.

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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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