

Feature Review

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Genetic Basis of Rice Grain Shape and Palatability: A Genome-Wide Study Review

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Abstract The genetic basis of grain shape and palatability of rice is complex, involving multiple genes and QTLs. The combination of Genome-wide association study (GWAS) and functional genomics has greatly improved researchers' understanding of these traits. GWAS has identified important loci and candidate genes that regulate grain shape, including *GS3*, *GW5*, and *qSW5*, and discussed natural variation and artificial selection of these key genes, which play a critical role in the formation of grain size and quality during evolution. This paper highlights the importance of allelic combination and haplotype analysis in understanding the genetic structure of grain shape and palatability, and these findings provide a strong framework for future rice breeding programs to improve grain yield and quality. This paper is expected to provide a comprehensive review of the genetic basis of rice grain shape and palatability through genome-wide analysis, and to identify key genes and quantitative trait loci (QTLs) that influence these traits, thereby offering valuable insights for rice breeding programs.

Keywords Rice grain shape; Quantitative trait loci (QTLs); Genome-wide association study (GWAS); Genetic variation; Rice breeding

1 Introduction

Rice (*Oryza sativa* L.) is a staple food for over half of the world's population, making its yield and quality critical for global food security. Among the various factors influencing rice quality, grain shape and palatability are paramount. Grain shape, which includes attributes such as grain length, width, and thickness, significantly affects both the yield potential and market value of rice (Wang et al., 2012; Jahani et al., 2013; Niu et al., 2020). Palatability, encompassing taste, texture, and overall eating quality, is equally important for consumer acceptance and marketability.

Grain shape is controlled by multiple QTLs and genes, making it a complex trait to study and manipulate. Advances in genomics and molecular biology have facilitated the identification of numerous QTLs and genes associated with grain shape, providing valuable insights for rice breeding programs aimed at improving both yield and quality (Huang et al., 2013; Zheng et al., 2015; Nawaz et al., 2015). Recent advancements in high-throughput sequencing technologies and genomics have further elucidated the genetic basis of these traits (Zhang et al., 2020).

GWAS have become a powerful tool for uncovering the genetic basis of complex traits in rice, including grain shape and palatability. The 3 000 Rice Genomes Project (3K RGP) has been instrumental in this regard, enabling the discovery of valuable genetic variants and resources for grain weight and shape (Niu et al., 2020; Niu et al., 2021). Through GWAS, researchers have identified numerous QTLs and candidate genes that play crucial roles in determining grain shape and quality (Huang et al., 2016; Niu et al., 2020; Meng et al., 2022). For instance, recent studies have identified several novel QTLs and candidate genes associated with grain weight and shape, such as *qTGW3.1*, *qTGW9*, *qTGW11*, *qGL4/qRLW4*, *qGL10*, and *qRLW1* (Niu et al., 2020; Niu et al., 2021). These

findings have provided a deeper understanding of the genetic mechanisms underlying these traits and have highlighted the potential for molecular breeding to enhance rice grain yield and quality (Niu et al., 2021; Chen et al., 2021).

Recent GWAS have identified key genetic factors influencing rice grain shape and chalkiness, traits critical to quality and market value. Wang et al. (2023) conducted a GWAS on Xian (*indica*) rice accessions, revealing significant QTLs and candidate genes linked to these traits. These findings provide valuable genetic markers for breeding programs focused on enhancing grain shape and reducing chalkiness, offering a pathway to improve both consumer satisfaction and marketability. A study using the *indica* rice Multiparent Advanced Generation Intercross (MAGIC) population revealed several key loci associated with grain size traits, such as grain length, width, and thickness. The study conducted by Ponce et al. (2020) employed GWAS and identified significant QTLs, including *qGL4* (grain length) and *qGW7* (grain width), providing valuable genetic targets for improving grain size and quality in rice breeding programs. Similarly, Gong et al. (2023) discussed elite genes like *GS3* and *qSW5*, which are crucial for improving grain size and quality, and how molecular breeding techniques such as marker-assisted selection (MAS) and genomic selection (GS) have been applied to incorporate these traits into high-quality rice varieties.

This review aims to summarize the key genetic factors influencing rice grain shape and palatability; highlight the advancements in genome-wide association studies and their contributions to understanding these traits; identify potential candidate genes and QTLs that could be targeted for future rice breeding programs; and discuss the implications of these findings for improving rice yield and quality through molecular breeding. By providing a comprehensive overview of the genetic determinants of rice grain shape and palatability, we seek to inform and guide future research and breeding efforts aimed at enhancing the quality and marketability of rice.

2 Rice Grain Shape: Genetic and Phenotypic Characteristics

2.1 Definition and assessment of grain shape

Rice grain shape is a critical agronomic trait that significantly influences both the yield and quality of rice (Bai et al., 2010). Grain shape is typically defined by several parameters, including grain length (GL), grain width (GW), and grain thickness (GT). These dimensions are used to determine specific grain shape indices, such as the grain length-to-width ratio (L/W), which is often used to classify rice as long, medium, or short-grained. Grain shape plays a crucial role in determining the rice variety's market category and consumer preference, as it affects both cooking properties and aesthetic appeal. These parameters are measured using digital calipers or specialized image analysis software. Advanced phenotyping tools now allow for the high-throughput collection of grain shape data, improving the accuracy of trait analysis in breeding programs. Researchers also employ QTL mapping and GWAS to identify the underlying genetic factors that influence grain shape, aiding in the selection of optimal traits for breeding. (Huang et al., 2013; Niu et al., 2021; Meng et al., 2022).

2.2 Importance of grain shape in consumer preference and market value

Grain shape is a major determinant of rice market value and consumer preference. Different markets and cultures have varying preferences for grain shape, which can influence the commercial success of rice varieties. For example, long and slender grains are often preferred in South Asian markets, while shorter and rounder grains may be favored in East Asian markets. Grain shape also significantly affects market value. Longer and slender grains tend to fetch higher prices in international markets due to their appearance and cooking qualities. The aesthetics of rice, including the uniformity of grain shape, contribute to its overall visual appeal and marketability. Studies show that grain shape is often a key criterion in rice grading and pricing (Fitzgerald et al., 2009; Wang et al., 2023). The appearance, processing quality, and palatability of rice are all affected by grain shape, making it a crucial factor in rice breeding programs aimed at meeting consumer demands (Lu et al., 2013; Misra et al., 2018; Angira et al., 2022).

2.3 Genetic determinants of grain shape

The genetic basis of rice grain shape is complex and involves multiple genes and QTLs. Advances in genomics have facilitated the identification of numerous QTLs and candidate genes associated with grain shape. Advances

in genomics have facilitated the identification of key genes such as *GS3*, *GW5*, and *qSW5*, which play significant roles in determining grain shape (Niu et al., 2020; Meng et al., 2022). Recent studies have also identified new QTLs and candidate genes through GWAS, further expanding researchers' understanding of the genetic architecture underlying grain shape. For example, GWAS has uncovered QTLs such as *qTGW3.1*, *qTGW9*, and *qGL4*, which are involved in regulating grain size and shape (Feng et al., 2016; Zhou et al., 2019; Niu et al., 2021). Moreover, advanced populations such as the MAGIC have provided deeper insights into the genetic diversity governing grain traits (Ponce et al., 2020), enabling the discovery of multiple alleles that contribute to grain shape variation. The integration of these genetic insights into breeding programs holds promise for the development of rice varieties with optimized grain shapes tailored to specific market preferences (Misra et al., 2018; Kang et al., 2021).

3 Palatability of Rice: Factors and Attributes

3.1 Defining rice palatability and its importance in breeding programs

Rice palatability refers to the sensory attributes that determine the acceptability and preference of rice by consumers. These attributes include texture, flavor, appearance, and aroma which together create the overall eating experience. A key component affecting palatability is the amylose content, which significantly influences the texture of cooked rice. Higher amylose content results in firmer, less sticky rice, while low amylose varieties tend to be softer and more adhesive (Misra et al., 2018). Textural attributes such as adhesiveness, hardness, springiness, and cohesiveness are vital in determining how rice feels in the mouth, making texture one of the most critical aspects of palatability (Huang et al., 2013). In addition to texture, aroma plays a significant role in consumer preference, especially in aromatic rice varieties such as Jasmine and Basmati. These varieties possess 2-acetyl-1-pyrroline (2-AP), a compound that imparts a distinct, appealing fragrance (Buttery et al., 1983). The integrated value of organoleptic evaluation, which includes luster and tenderness, also plays a crucial role in determining the overall palatability of rice (Wan et al., 2004).

Palatability is a critical factor in rice breeding programs because it directly impacts consumer acceptance and market value. Breeding for improved palatability involves selecting desirable textural properties and other sensory attributes that meet consumer preferences. The identification of QTLs associated with palatability traits enables breeders to use marker-assisted selection to develop rice varieties with enhanced eating quality (Wan et al., 2004; Tang et al., 2005). Consistently producing rice varieties with improved palatability not only increases consumer satisfaction but also boosts economic returns for farmers and producers, making it a critical focus in modern rice breeding (Wan et al., 2004; Huang et al., 2013; Misra et al., 2018).

3.2 Genetic factors influencing palatability

The genetic basis of rice palatability is complex and involves multiple genes and QTLs. Studies have identified several QTLs that influence various aspects of rice palatability, such as amylose content, adhesiveness, and other textural properties. A GWAS identified significant QTLs on chromosome 6 that are associated with amylose content and adhesiveness, which are key determinants of rice texture and palatability (Misra et al., 2018). Additionally, QTLs for luster, tenderness, and the integrated value of organoleptic evaluation have been mapped to specific regions on chromosomes 6 and 8, indicating their importance in rice quality improvement (Wan et al., 2004). The identification and validation of these QTLs provide valuable resources for breeding programs aimed at enhancing rice palatability (Wan et al., 2004; Tang et al., 2005; Misra et al., 2018).

4 Methodologies in Genome-Wide Studies of Rice

4.1 GWAS

GWAS are a powerful tool used to identify genetic loci associated with specific traits in rice. This method involves scanning the entire genome for single nucleotide polymorphisms (SNPs) that occur more frequently in individuals with a particular trait. For instance, a study utilized multiple GAPIT models and high-density SNP chip DNA markers (Figure 1) to identify QTLs associated with grain shape and size in rice. The study revealed significant associations between SNP markers and QTLs for grain length, width, and thickness across various chromosomes, explaining a substantial portion of the phenotypic variance (Kabange et al., 2023). Another study

combined linkage mapping with GWAS to identify QTLs governing rice grain shape and weight, highlighting the co-detection of several QTLs on chromosomes 3, 5, and 12 (Kang et al., 2020). Wang et al. (2023) performed GWAS on 137 *indica* rice accessions, identifying 195 significant SNP-trait associations and revealing six key QTLs linked to grain quality traits.

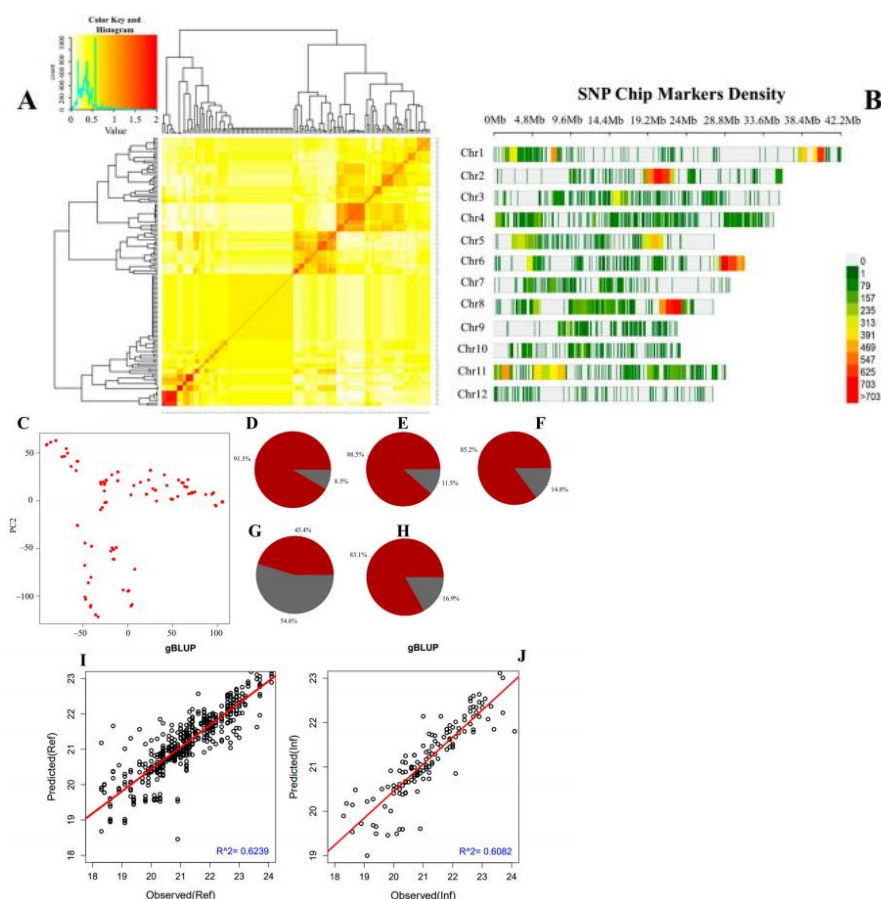


Figure 1 Kinship matrix, marker density, PCA, heritability, and genome selection results (Adopted from Kabange et al., 2023)

Image caption: (A) heat map showing the relatedness or the level of co-ancestry of the population, (B) density map of SNP Chip DNA markers, (C) principal component analysis (PCA), (D) narrow sense heritability of grain length, (E) grain width, (F) grain thickness, (G) grain length-to-width ratio, (H) thousand-grain weight, and (I, J) results of the genome selection analysis that predict the genomic estimated breeding value (GEBV) of individuals in the RIL population in the reference group (Ref) and the inference group (Inf) (Adopted from Kabange et al., 2023)

4.2 QTL mapping

QTL mapping is a method used to identify regions of the genome that are associated with quantitative traits (Chen et al., 2016). This approach involves crossing two parent lines with contrasting traits and analyzing the progeny to identify genetic markers linked to the traits of interest. By correlating these traits with molecular markers, QTLs are identified, which pinpoint regions of the genome contributing to the variation in traits. For example, a study using recombinant inbred lines (RILs) derived from a cross between two Iranian rice cultivars identified seven QTLs associated with grain appearance and quality traits on chromosomes 1, 6, 9, and 12 (Bazrkar-Khatibani et al., 2019). Another study focused on fine mapping a major QTL, *qGL1.3*, for grain length and weight, narrowing it down to a 350 kb region on chromosome 1 (Zhou et al., 2019). Additionally, QTL-seq, a rapid mapping technique using whole-genome resequencing of DNA from bulked populations, has been successfully applied to identify QTLs for traits such as seedling vigor and resistance to rice blast disease (Takagi et al., 2013). Advanced techniques like high-density SNP arrays and next-generation sequencing have improved the resolution of QTL mapping, enabling more precise identification of candidate genes involved in rice trait development (Huang et al., 2010).

4.3 Whole-genome sequencing (WGS) and analysis

WGS provides a comprehensive approach to understanding the genetic basis of traits by sequencing the entire genome of an organism. This method identifies all genetic variations, including SNPs, insertions, deletions, and structural variants. In rice, WGS has been used to dissect the genetic basis of grain shape and quality traits. For instance, a study employed WGS to fine-map the *gw-5* gene, which controls grain width and length-width ratio, to a 49.7 kb region on chromosome 5 (Wan et al., 2008). Another study used WGS to identify novel QTLs for grain shape, such as *qLG2*, *qWG2*, and *qLG8* and fine-mapped them to small genomic intervals (Wang et al., 2020). These studies highlight the power of WGS in providing detailed insights into the genetic architecture of complex traits in rice. Jiang et al. (2019) utilized WGS to identify a novel allele, *gs9-1*, which controls grain shape in rice. Their work highlighted the use of WGS to create segregating populations and gene pools, ultimately revealing genetic variations for traits such as grain length, width, and grain weight. By integrating these methodologies, researchers can gain a deeper understanding of the genetic basis of rice grain shape and palatability, ultimately aiding in the development of rice varieties with improved traits.

5 Key Findings on the Genetic Basis of Grain Shape

5.1 Major genes and QTLs identified

Research on the genetic basis of rice grain shape has led to the identification of over 400 QTLs associated with key traits, including grain length (GL), grain width (GW), and grain thickness (GT). Several major genes, such as *GS3*, *GW5*, and *qSW5*, play significant roles in determining these grain characteristics (Huang et al., 2013; Niu et al., 2020). Meng et al. (2022) conducted a GWAS that identified 39 important QTLs related to grain shape traits such as GL, GW, and grain length to width ratio (GLWR) (Figure 2). In addition, novel QTLs such as *qTGW3.1*, *qTGW9*, and *qTGW11* for grain weight, and *qGL4/qRLW4*, *qGL10*, *qGL11*, and *qRLW1* for grain shape were discovered (Niu et al., 2020). GWAS have also mapped several QTLs associated with grain shape, including those located on chromosomes 2, 3, and 6, which have been linked to variations in grain length and width (Wang et al., 2021; Wang et al., 2023). The identification of QTLs like *qGL-7a*, *qGL-8*, and *qGL-11a* further expands the genetic resources available for breeding programs (Kang et al., 2021). Fine mapping efforts have also pinpointed major QTLs such as *qGL1.3*, which significantly influence grain length and weight (Zhou et al., 2019).

5.2 Functional analysis of grain shape genes

Functional analysis of grain shape genes has provided valuable insights into their roles in rice development. The gene *GS3* has been identified as a major determinant of grain length, while *GW5* influences grain width (Meng et al., 2022). The functional annotation of these genes has revealed their involvement in various biochemical pathways that regulate cell division and expansion in the grain (Meng et al., 2022). *GS3* acts as a negative regulator of grain length by inhibiting cell proliferation and elongation in the developing panicle (Fan et al., 2006). Another study identified candidate genes such as *Os03g0186600* and *Os09g0544400*, which are predicted to play roles in grain shape regulation through gene-based association and haplotype analyses (Niu et al., 2020). The gene *ORF3* (LOC_Os07g42410) was found to control the ratio of grain length to width, with a single nucleotide deletion causing a frameshift mutation that affects grain shape (Shang et al., 2020). These functional analyses are crucial for understanding the molecular mechanisms underlying grain shape and for developing targeted breeding strategies.

5.3 Comparative genomics of grain shape

Comparative genomics has been instrumental in identifying conserved and unique genetic elements influencing grain shape across different rice varieties. Studies have shown that QTLs such as *qLWR-12c/qGW-12* are consistently detected across multiple environments, indicating their stable genetic effects (Kang et al., 2021). Comparative analysis of QTLs identified through linkage mapping and GWAS has revealed co-detection of QTLs like *qGLE-12-1* and *qGLE-12-2*, which govern grain length and width (Kang et al., 2020). Additionally, the identification of overlapping QTLs such as *qGS7*, which is consistent with *GL7/GW7*, highlights the conserved genetic basis of grain shape traits (Chen et al., 2021). These comparative genomics approaches not only provide valuable insights into the evolutionary conservation and divergence of grain shape genes but also facilitate the transfer of beneficial traits across different rice cultivars. The integration of genomic data from various sources

enhances our understanding of the genetic architecture underlying grain shape and aids in the development of improved rice varieties with desirable grain characteristics.

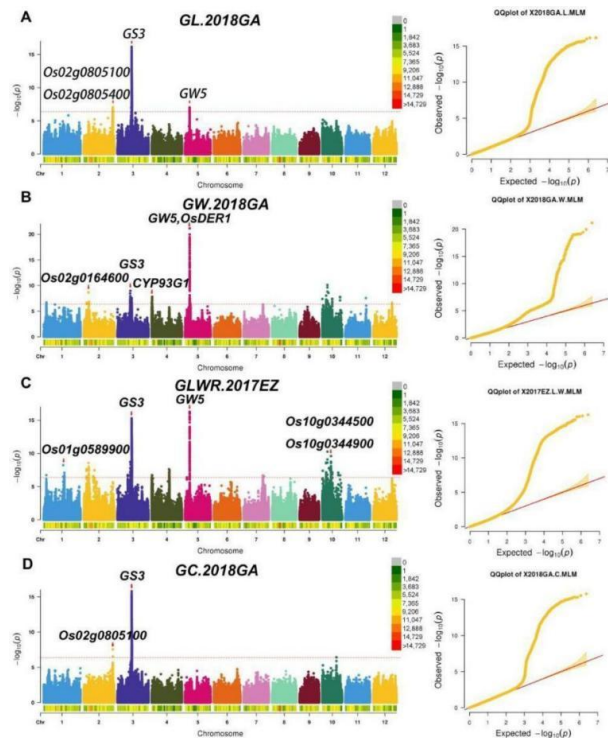


Figure 2 Manhattan plot and Q-Q plot (Adopted from Meng et al., 2022)

Image caption: (A) 2018 GA's GL Manhattan and Q-Q images. (B) 2018 GA's GW Manhattan and Q-Q images. (C) 2017 EZ's GLWR Manhattan and Q-Q images. (D) 2018 GA's GC Manhattan and Q-Q images. The red arrow indicates the location of the gene. In the upper right corner is the SNP density indicator band, and different colors represent different SNP distribution densities. Gongan/GA, Ezhou/EZ (Adopted from Meng et al., 2022)

6 Key Findings on the Genetic Basis of Palatability

6.1 Major genes and QTLs identified

Recent studies have identified numerous QTLs and genes associated with rice grain shape and palatability, with several key genes cloned and fine-mapped, such as *GS3*, *GW5*, and *qSW5* (Huang et al., 2013). GWAS have revealed several novel QTLs, such as *qTGW3.1*, *qTGW9*, and *qTGW11* for grain weight, and *qGL4/qRLW4*, *qGL10*, *qGL11*, and *qRLW1* for grain shape (Niu et al., 2020). Additionally, 39 important QTLs were identified in a study involving 623 *indica* rice cultivars, including three cloned genes (*GS3*, *GW5*, *OsDER1*) and seven new candidate genes (Meng et al., 2022). Another study identified 38 significant loci for grain shape-related traits, with key genes like *GS3* and *qGL3* on chromosome 3, and *TGW6* and *GW6a* on chromosome 6 (Lv et al., 2019).

6.2 Functional analysis of palatability genes

Functional analysis of these genes has provided insights into their roles in determining grain shape and palatability. For example, the gene *qGL1.3*, a major QTL for grain length, was fine-mapped to a 350 kb region on chromosome 1, elucidating significant phenotypic variation in grain length and weight (Zhou et al., 2019). Similarly, the QTL cluster *qLWR-12c/qGW-12* was validated across multiple environments, with candidate genes identified within a 431 kb interval (Kang et al., 2021). These functional analyses are crucial for understanding the biochemical pathways and molecular mechanisms underlying grain shape and palatability.

6.3 Comparative genomics of palatability traits

Comparative genomics has been instrumental in identifying and validating QTLs across different rice populations and environments. For instance, a study using a doubled haploid population and Kompetitive Allele-Specific PCR (KASP) markers identified QTLs like *qGLE-12-1* and *qGLE-12-2* on chromosome 12, and *qGTE-3-1* on chromosome 3, which were co-detected by both linkage mapping and GWAS (Kang et al., 2020). Another study

utilized a high-density genetic map with 3 203 Bin markers to detect 91 QTLs for grain shape, with 64 forming 15 clusters, and three new QTLs identified (Kang et al., 2021). These comparative studies highlight the genetic diversity and stability of palatability traits across different genetic backgrounds and environmental conditions.

7 Integrative Analysis of Grain Shape and Palatability

7.1 Correlation between grain shape and palatability

Grain shape is a critical determinant of rice quality, influencing both yield and consumer preferences. Traits such as grain length, width, and roundness are closely associated with sensory properties like softness, stickiness, and overall mouthfeel (Huang et al., 2013). Long, slender grains tend to be less sticky and firmer after cooking, which may appeal to consumers in regions where rice is served as individual grains. Conversely, shorter, rounder grains are often associated with softer textures and higher stickiness, characteristics that contribute to the palatability preferred in other cultural contexts (Misra et al., 2018). Studies have shown that grain shape, including traits such as GL, GW, and length-width ratio (LWR), significantly impacts the palatability of rice. The identification of QTLs associated with grain shape in high-yielding rice varieties has provided insights into the genetic factors that contribute to both yield and quality (Kang et al., 2020; Kang et al., 2021; Meng et al., 2022). Moreover, the grain shape impacts the water absorption rate during cooking, which directly affects the final texture and taste of the rice (Feng et al., 2016). The correlation between grain shape and palatability is further supported by the discovery of pleiotropic effects of certain QTLs, which affect multiple traits including grain shape and eating quality (Ogawa et al., 2018; Wang et al., 2023). This suggests that breeding programs targeting grain shape improvements can simultaneously enhance rice palatability.

7.2 Combined GWAS and QTL studies

The integration of GWAS and QTL mapping has proven to be a powerful approach to identifying genetic determinants of grain shape. The use of a combined linkage mapping and GWAS strategy has led to the identification of several QTLs that govern rice grain shape and weight, with significant contributions to phenotypic variation (Kang et al., 2020). Similarly, haplotype-based GWAS has been effective in evaluating multiple QTLs with small effects on grain shape, providing high-accuracy QTL detection (Ogawa et al., 2018). These integrative studies have not only identified novel QTLs but also validated known ones, thereby enhancing our understanding of the genetic architecture of grain shape (Niu et al., 2020; Kabange et al., 2023; Wang et al., 2023). For example, studies by Misra et al. (2018) and Yano et al. (2016) employed combined GWAS and QTL strategies, identifying key loci such as *GS3*, *GW5*, and *qGL3* that regulate grain length and width. Additionally, Chen et al. (2016) highlighted the use of integrative mapping for discovering pleiotropic QTLs influencing both grain shape and chalkiness. These insights pave the way for more precise marker-assisted selection in rice breeding programs, improving grain quality and yield.

7.3 Case studies of successful breeding programs

Several breeding programs have successfully utilized the findings from GWAS and QTL studies to develop rice varieties with improved grain shape and palatability. The identification of major QTL clusters and candidate genes has facilitated the breeding of high-yielding rice varieties with desirable grain shapes (Chen et al., 2021; Kang et al., 2021). In Japan, the JAM population has been used to identify QTLs for grain shape, leading to the development of rice lines with optimized grain traits for better eating quality (Figure 3) (Ogawa et al., 2018). Additionally, the validation of QTLs in different populations and environments has provided robust genetic markers for marker-assisted selection (MAS), enabling the production of rice varieties with consistent quality and yield (Zhou et al., 2019). Ashikari and Matsuoka (2006) highlighted the successful application of QTL pyramiding in rice breeding, focusing on combining multiple QTLs to enhance grain shape, yield, and other agronomic traits. Their work demonstrated how integrating various QTLs related to grain size and quality can lead to the development of superior rice varieties. These case studies highlight the practical applications of genetic research in rice breeding programs aimed at enhancing both grain shape and palatability.

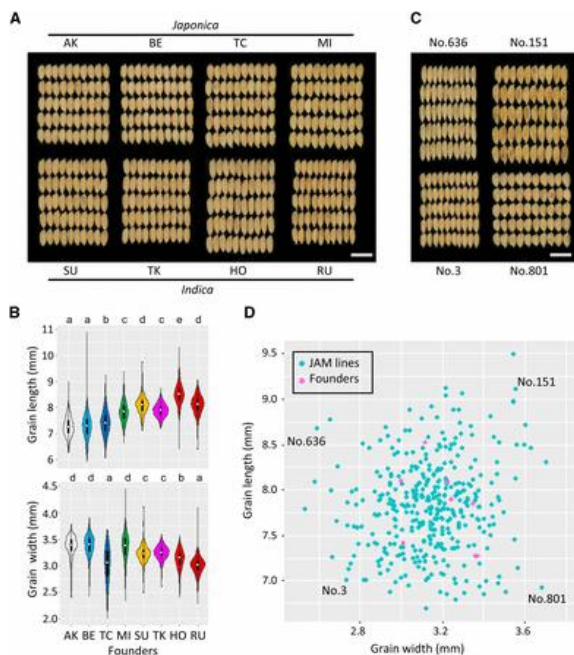


Figure 3 Grain length and width of the eight founders and JAM lines (Adopted from Ogawa et al., 2018)

Image caption: (A) Alignments of 50 grains of each of the four *japonica* cultivars (Akidawara [AK], Bekogonomi [BE], Tachiaoba [TC], and Mizuhochikara [MI]) and four *indica* cultivars (Suweon 258 [SU], Takanari [TK], Hokuriku 193 [HO], and Ruriaoba [RU]) used as founders. Pictures of the grain of each founder were taken individually and then merged. (B) Violin plots of the grain length and width of the founders. They include information on kernel density estimation, quantiles (black boxes), and median values (white circles). Different letters indicate significant differences (Tukey method, $P < 0.05$). (C) Alignments of 50 grains each of four JAM lines showing characteristic features. (D) Scatter plot of average grain length and width for each JAM line and the eight founders. White bars indicate 1 cm (Adopted from Ogawa et al., 2018)

8 Implications for Rice Breeding and Cultivar Development

8.1 Utilizing genetic information in breeding programs

The identification of numerous QTLs and candidate genes associated with rice grain shape and palatability provides a valuable resource for rice breeding programs. The findings of Huang et al. (2013) identify the protein products of 13 genes and the chromosomal locations of 15 fine-mapped QTLs, highlighting the complex potential of genetic information in breeding programs. GWAS have further identified significant QTLs and candidate genes, such as *GS3*, *GW5*, and *OsDER1*, which can be utilized to enhance grain shape and quality (Meng et al., 2022). Additionally, the identification of novel QTLs and candidate genes, such as *qGL-7a*, *qGL-8*, and *qGL-11a*, provides new targets for genetic improvement (Kang et al., 2021). The combination of these genetic insights into breeding strategies not only accelerates the development of rice cultivars with desirable traits but also enables the fine-tuning of specific attributes like grain length, width, and texture. By applying molecular tools such as MAS and GS, breeders can efficiently target these QTLs to produce rice varieties with improved yield, grain shape, and palatability, meeting both agronomic and consumer demands.

8.2 Challenges in breeding for grain shape and palatability

Despite significant advancements in identifying genetic determinants of grain shape and palatability, several challenges remain in breeding programs. One major challenge is the functional characterization of identified genes at the biochemical level, which is essential for understanding their roles in grain development and quality (Huang et al., 2013). While genomic studies have identified numerous genes associated with these traits, translating this information into practical breeding applications requires detailed functional insights. Additionally, the complex genetic architecture of traits such as grain shape and palatability, which are influenced by multiple genes and environmental factors, complicates the breeding process (Wang et al., 2023). The need for high-resolution mapping and validation of QTLs in diverse genetic backgrounds further adds to the complexity (Shang et al., 2020). Moreover, the trade-offs between different agronomic traits, such as yield and quality, present a significant

challenge in developing balanced cultivars (Zhang et al., 2020). Effective breeding programs must carefully manage these compromises to enhance both quality and productivity.

8.3 Future directions in breeding strategies

Future breeding strategies should focus on the integration of advanced genomic tools and techniques to address existing challenges. The use of high-density genetic maps and SNP arrays can enhance the precision of QTL mapping and facilitate the identification of candidate genes (Chen et al., 2021). Multi-locus GWAS approaches offer a comprehensive understanding of the genetic basis of complex traits and identify additional loci influencing grain shape and palatability (Misra et al., 2018). Functional validation of candidate genes through techniques such as CRISPR/Cas9-mediated gene editing can accelerate the development of improved rice cultivars (Ruan et al., 2020). Additionally, the incorporation of MAS and GS in breeding programs can enhance the efficiency and accuracy of selecting desirable traits (Niu et al., 2021). Collaborative efforts between researchers and breeders, along with the utilization of diverse germplasm resources, will be crucial in achieving sustainable improvements in rice grain shape and palatability.

9 Challenges and Future Directions

9.1 Limitations of current GWS

Despite significant advancements in GWAS and the identification of numerous QTLs associated with rice grain shape and palatability, several limitations persist. One major challenge is the complexity of the genetic architecture underlying these traits. Many studies have identified a large number of QTLs, but the functional characterization of these loci remains incomplete. For example, while over 400 QTLs related to rice grain traits have been identified, only a few have been cloned and functionally analyzed (Huang et al., 2013). Additionally, the resolution of GWAS is often limited by the population size and genetic diversity of the samples used, which can result in the identification of broad genomic regions rather than specific causal genes (Niu et al., 2020; Niu et al., 2021). Another limitation is the reliance on single-locus GWAS approaches, which may not capture the full spectrum of genetic variation influencing complex traits like grain shape and texture (Misra et al., 2018).

9.2 Recent technologies and approaches

To address the limitations of current GWS, several emerging technologies and approaches are being developed. Multi-locus GWAS methods, such as FASTmrEMMA, pLARmEB, mrMLM, and ISIS_EM-BLASSO, offer the potential to identify additional loci with major and minor effects that single-locus approaches may overlook, providing a more comprehensive understanding of the genetic basis of complex traits (Misra et al., 2018). Additionally, the integration of high-density SNP arrays and next-generation sequencing technologies has improved the resolution and accuracy of QTL mapping (Feng et al., 2016). Advanced phenotyping techniques, such as elliptic Fourier analysis for grain shape prediction, combined with kernel partial least squares (KPLS) regression, have also enhanced the precision of trait measurement and prediction (Iwata et al., 2015). Furthermore, the use of combined linkage mapping and GWAS strategies has proven effective in co-detecting QTLs and refining candidate gene identification, thereby advancing the overall understanding of genetic influences on traits (Kang et al., 2020).

9.3 Future research priorities

Future research should focus on several key areas to further advance our understanding of the genetic basis of rice grain shape and palatability. First, there is a need for functional validation of the identified QTLs and candidate genes through techniques such as CRISPR/Cas9-mediated gene editing and transgenic approaches (Niu et al., 2020; Meng et al., 2022). This will help elucidate the molecular mechanisms underlying these traits and facilitate the development of rice varieties with improved grain quality. Second, expanding the genetic diversity of the populations used in GWAS by including more diverse rice accessions from different geographical regions can enhance the discovery of novel QTLs and alleles (Lv et al., 2019; Niu et al., 2021). Third, integrating multi-omics data, including transcriptomics, proteomics, and metabolomics, with GWAS can provide a more comprehensive understanding of the genetic regulation of grain traits (Huang et al., 2013). Finally, the implementation of MAS and GS strategies in breeding programs will accelerate the translation of genetic discoveries into practical

applications for rice improvement (Feng et al., 2016; Misra et al., 2018). By addressing these priorities and leveraging emerging technologies, future research can significantly enhance our understanding of the genetic basis of rice grain shape and palatability, ultimately contributing to the development of high-yielding and high-quality rice varieties.

10 Concluding Remarks

The genetic basis of rice grain shape and palatability has been extensively studied, revealing numerous QTLs and candidate genes that influence these traits. Over 400 QTLs associated with rice grain traits have been identified, with several key genes such as *GS3*, *qSW5*, and *GW2* playing significant roles in determining grain size and shape. Advanced genotyping platforms, like the RICE6K array and high-density SNP markers, have facilitated the identification of major QTL clusters on chromosomes 7 and 12, which significantly affect grain length and width. The textural qualities of cooked rice, including adhesiveness, hardness, springiness, and cohesiveness, are influenced by genetic factors. A significant hotspot on chromosome 6 was identified for amylose content and adhesiveness, which are crucial for rice texture and palatability. The genetic diversity in grain size genes such as *GW2*, *GS5*, and *qSW5* has been shaped by both natural variation and artificial selection, providing a rich resource for breeding programs. GWAS have been instrumental in discovering new candidate genes and QTLs for grain shape and weight, with several studies emphasizing the importance of allele combinations in determining these traits.

Future research should focus on the functional validation of the identified QTLs and candidate genes, particularly at the biochemical and molecular level. This will involve in-depth studies on gene expression, protein function, and interaction networks to elucidate how these genes contribute to grain development and quality. Combining genomics, transcriptomics, proteomics, and metabolomics data will provide a comprehensive understanding of the molecular mechanisms underlying grain shape and palatability. Breeding programs should incorporate consumer preferences for rice texture and palatability by utilizing MAS and GS techniques. These approaches will enhance the precision and efficiency of breeding efforts, ensuring the development of rice varieties that meet both market demands and quality standards. Wild rice species and landraces harbor valuable genetic diversity that can be tapped into for improving grain shape and palatability. Resequencing and phenotyping of these resources will be crucial. Understanding how genetic factors influencing grain shape and palatability interact with environmental conditions will be important for developing climate-resilient rice varieties.

The genetic basis of rice grain shape and palatability is complex and involves numerous genes and QTLs. Advances in high-throughput genotyping, GWAS, CRISPR/Cas9-mediated gene editing, and multi-omics approaches have significantly enhanced our knowledge of these traits. However, translating this knowledge into practical breeding applications remains a challenge. Future research should aim to bridge this gap by focusing on functional characterization, integrating multi-omics data, and aligning breeding goals with consumer preferences and environmental sustainability. By addressing these challenges, researchers and breeders can develop rice varieties that not only perform well but also meet the quality standards desired by consumers, ensuring both productivity and palatability.

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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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