

# Molecular Breeding for Enhanced Rice Yield: The Role of Key Yield-Related Genes

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**Abstract** Rice (*Oryza sativa*) is one of the important global food crops, and the increase in its yield is of great significance for ensuring food security and alleviating the food crisis. This study analyzes the research progress and application of molecular breeding in improving rice yield. By revealing the potential role of key yield related genes in improving rice yield and quality, molecular breeding technologies such as marker assisted selection (MAS), genome selection (GS), genetic engineering, and CRISPR/Cas9 are introduced. The principles, applications, and successful cases of these technologies in rice breeding are discussed. In addition, this study also delves into the functional characteristics, gene expression research, functional genomics methods, and strategies and challenges of integrating yield related genes into breeding plans. By summarizing the successful experience, lessons learned, and best practices of molecular breeding in improving rice yield, the aim is to provide valuable reference and inspiration for future rice breeding work, and promote innovation and development in rice breeding work.

**Keywords** Rice (*Oryza sativa*); Molecular breeding; Key genes; Mark assisted selection; CRISPR/Cas9

## 1 Introduction

Rice (*Oryza sativa*) is a staple food for more than half of the world's population, making it a critical crop for global food security. The continuous increase in the global population necessitates the enhancement of rice yield to meet the growing food demand. Traditional breeding methods have significantly contributed to yield improvements; however, the advent of molecular breeding offers new avenues to further enhance rice productivity by targeting specific yield-related genes.

The importance of improving rice yield cannot be overstated. Rice production has seen a steady increase during the Green Revolution, but the rate of yield growth has slowed in recent decades. This slowdown poses a significant challenge as the population in major rice-consuming countries continues to grow at a rate of more than 1.5% per year (Jeon et al., 2011). Enhancing rice yield is essential not only to meet the food demands of a burgeoning population but also to ensure food security in the face of global climate change and other environmental stresses (Nutan et al., 2020). High-yielding rice varieties are crucial for sustaining the world's food supply and addressing the challenges posed by limited arable land and water resources (Sakamoto and Matsuoka, 2008; Xu et al., 2016; Singh et al., 2022).

Molecular breeding involves the use of genetic and genomic tools to identify and manipulate genes associated with desirable traits, such as yield, in crop plants. This approach has revolutionized rice breeding by enabling the precise selection and combination of beneficial alleles (Ikeda et al., 2013). Techniques such as marker-assisted selection (MAS), quantitative trait locus (QTL) mapping, and genome editing (e.g., CRISPR/Cas9) have been employed to enhance rice yield by targeting key genes involved in grain number, grain size, and plant architecture (Singh et al., 2022). For instance, the identification and manipulation of genes like OsSPL16/qGW8 have shown significant potential in increasing grain size and overall yield (Usman et al., 2020). Additionally, the integration of omic data, such as transcriptomics and metabolomics, has further improved the predictability and efficiency of hybrid yield prediction (Xu et al., 2016).

This study comprehensively reveals the key yield related genes of rice and their roles in molecular breeding, summarizes the current understanding of the genetic and molecular mechanisms of yield related traits in rice, focuses on the latest progress of molecular breeding technology and its application in rice yield increase, and discusses the potential challenges and future directions in the field of rice molecular breeding. Molecular breeding provides a promising approach for achieving a significant increase in rice yield. By utilizing knowledge of key yield related genes and advanced breeding techniques, we hope to develop high-yield rice varieties that can meet future food needs and contribute to global food security, making significant contributions to global food security.

## 1 Key Yield-Related Genes in Rice

### 1.1 Grain number and size genes

In the field of molecular breeding, the increase in rice yield is often closely related to the discovery and utilization of key yield related genes. These genes regulate the growth and development process of rice, thereby affecting its yield. The *Gn1a* gene is closely related to the number of grains in rice. Through research, it has been found that the protein encoded by *Gn1a* plays an important role in the development of rice meristem, affecting panicle branching and spikelet number. The mutation of *Gn1a* leads to higher grain count and significantly contributes to the heavy panicle phenotype of hybrid rice (Li et al., 2016; Wang et al., 2018).

The *GS3* gene is a key gene that controls rice grain type and weight. Research has shown that *GS3* encodes a transmembrane protein, and its domain variation significantly affects the grain length, width, and weight of rice. *GS3* is a major quantitative trait locus (QTL) for grain length and weight. The mutation of *GS3* leads to larger grain size and weight, making it a key gene in improving grain size in rice breeding programs (Li et al., 2016; Wang et al., 2018; Mao et al., 2021).

### 1.2 Panicle architecture genes

The *DEP1* gene is an important gene that affects the structure of rice panicles. Mutations in this gene can lead to changes in the structure of rice panicles, such as an increase in grain number and a reduction in panicle length. These changes help to increase the yield of rice. *DEP1* affects the structure of panicles by enhancing meristem activity, making them dense and upright with an increase in grain number. This gene is widely used in high-yield rice varieties (Huang et al., 2009; Li et al., 2016; Mao et al., 2021).

In molecular breeding, rice varieties with excellent panicle structure can be cultivated by utilizing mutants of the *APO1* gene, thereby achieving an increase in yield. *APO1* and *APO2* regulate spike size and grain number by regulating meristem activity. The *LARGE2-APO1/APO2* regulatory module is crucial for controlling these traits, making it a promising target for improving rice yield (Figure 1) (Huang et al., 2021).

Huang et al. (2021) revealed a genetic interaction between the *LARGE2* gene and the panicle structure genes *APO1* and *APO2*, which affect the size of rice panicles. Through mutations in the *APO1* gene (*APO1 cri*) and *LARGE2* gene (*large2-3*) (Figure 1), significant changes were observed in the primary and secondary branches of rice panicles, as well as the number of grains per panicle. This indicates a genetic interaction between *LARGE2* and *APO1*, which jointly regulate spike development. This discovery is of great significance for understanding the molecular mechanism of rice yield formation and future genetic improvement.

### 1.3 Grain weight and quality genes

*GW2* is a key gene that determines the grain weight of rice, and its regulation has a significant impact on rice yield. The protein encoded by the *GW2* gene plays an important role in cell division and growth. By regulating the expression of this gene, it can effectively change the grain weight of rice. The role of this gene in grain weight makes it a key goal of breeding programs aimed at improving rice yield (Singh et al., 2022).

The *Wx* gene is related to the quality of rice, especially the content of amylose. Although the *Wx* gene is mainly related to the starch quality and glutinosity of rice, it also indirectly affects the yield of rice. The protein encoded by the *Wx* gene is a key enzyme in the starch synthesis process, and its mutation can cause changes in the starch

composition of rice, thereby affecting the quality and yield of rice, making it an important factor in improving quality in rice breeding (Singh et al., 2022).

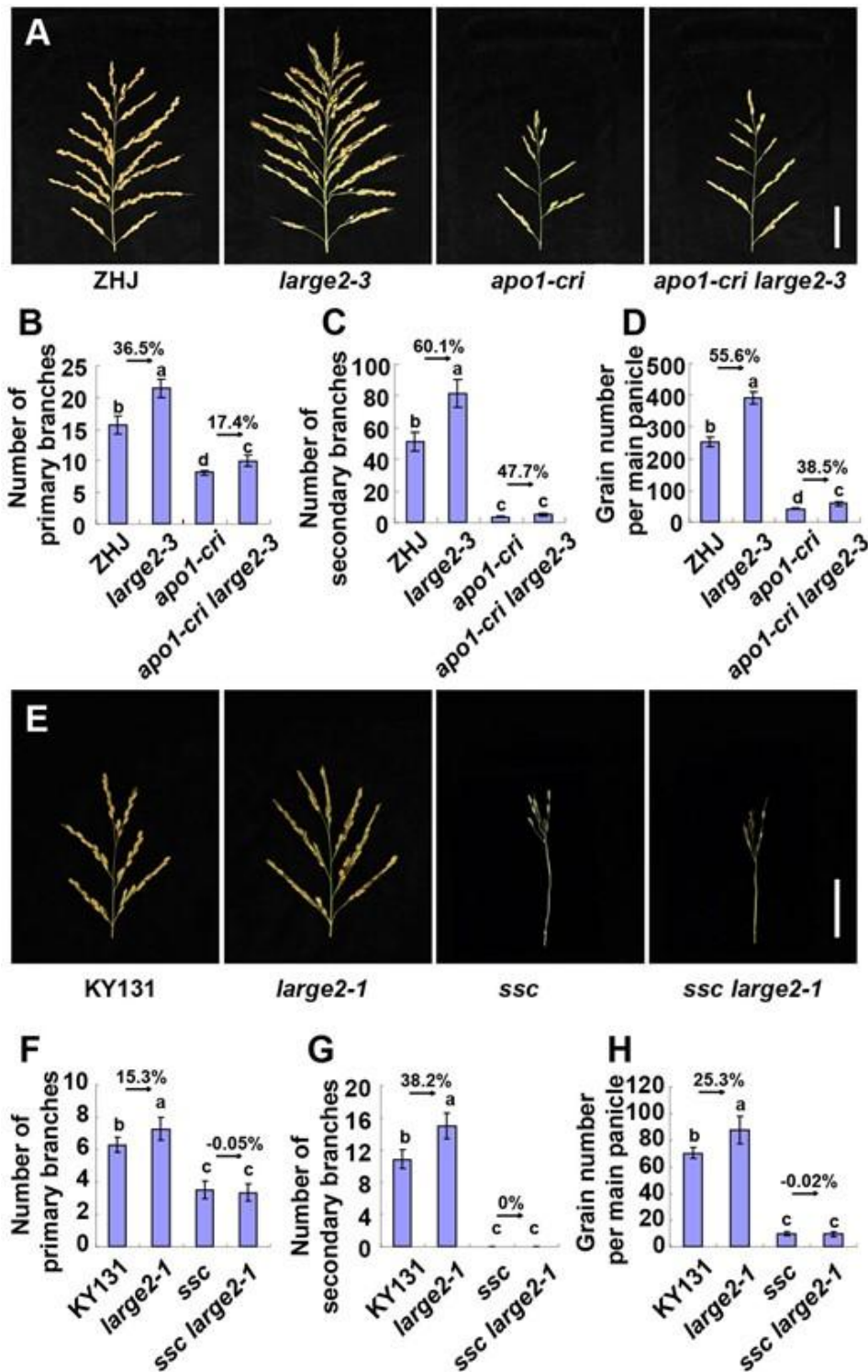


Figure 1 *LARGE2* genetically interacts with *APO1* and *APO2* to control panicle size (Adopted from Huang et al., 2021)

Image caption: A: Panicles of ZHJ, large2-3, APO1-cri, and APO1-cri large2-3 at the mature stage; B-D: Number of primary branches; B: Number of secondary branches; C: and grain number per panicle; D: of ZHJ, large2-3, APO1-cri, and APO1-cri large2-3 panicles (n≥16). E: Panicles of KY131, large2-1, ssc, and ssc large2-1 at the mature stage; F-H: Number of primary branches; F: Number of secondary branches; G: Grain number per panicle (H) of KY131, large2-1, ssc, and ssc large2-1 panicles (n≥16). Values (B-D, F-H) are given as mean±SD (Adopted from Huang et al., 2021)

## 2 Molecular Breeding Techniques

### 2.1 Marker-assisted selection (MAS)

Marker-Assisted Selection (MAS) is a molecular breeding technique that utilizes DNA markers linked to specific genes or quantitative trait loci (QTLs) to select desirable traits in breeding populations. This method allows for the precise identification and incorporation of genes associated with resistance to biotic and abiotic stresses, as well as improved agronomic traits. MAS can be combined with conventional breeding approaches to enhance the efficiency and accuracy of developing high-yielding, stress-resistant rice cultivars (Jena and Mackill, 2008; Ludwików et al., 2015; Das et al., 2017).

MAS has been successfully employed in rice breeding to integrate multiple resistance genes into elite cultivars. For instance, the pyramiding of genes conferring resistance to blast, bacterial blight, and submergence has led to the development of rice varieties with broad-spectrum resistance and improved yield stability (Jena and Mackill, 2008; Ludwików et al., 2015; Das et al., 2017). Additionally, MAS has facilitated the stacking of multiple QTLs for stress tolerance, resulting in rice lines that exhibit enhanced resistance to salinity, drought, and other environmental stresses (Ludwików et al., 2015; Das et al., 2017).

### 2.2 Genomic selection (GS)

Genomic Selection (GS) is a breeding method that uses genome-wide markers to predict the breeding value of individuals in a population. Unlike MAS, which targets specific genes, GS incorporates all marker information into the prediction model, capturing the effects of numerous small-effect QTLs. This approach improves selection accuracy, reduces phenotyping costs, and accelerates the breeding cycle, making it particularly effective for improving complex quantitative traits such as yield (Heffner et al., 2009; Grenier et al., 2015; Spindel et al., 2015; Budhlakoti et al., 2022).

GS has shown promising results in rice breeding programs. For example, studies have demonstrated that GS models can achieve high prediction accuracies for traits such as grain yield, plant height, and flowering time. The integration of GS with genome-wide association studies (GWAS) has further enhanced the understanding of the genetic architecture of these traits, leading to more effective breeding strategies (Grenier et al., 2015; Spindel et al., 2015; Budhlakoti et al., 2022). Additionally, GS has been successfully applied in recurrent selection programs, resulting in significant genetic gains in rice populations (Grenier et al., 2015).

### 2.3 Genetic engineering and CRISPR/Cas9

Genetic engineering and CRISPR/Cas9 are powerful tools for precise gene editing in rice. CRISPR/Cas9, in particular, allows for targeted modifications of specific genes, enabling the introduction of desirable traits or the removal of deleterious alleles. This technique offers a high degree of precision and efficiency, making it a valuable tool for enhancing rice yield and stress tolerance (Jena and Mackill, 2008; Das et al., 2017).

CRISPR/Cas9 has been employed to edit key yield-related genes in rice, resulting in significant improvements in grain yield and quality. For instance, targeted modifications of genes involved in plant architecture, grain size, and stress response have led to the development of rice varieties with enhanced yield potential and resilience to environmental stresses. These advancements highlight the potential of gene editing technologies to revolutionize rice breeding and contribute to global food security (Jena and Mackill, 2008; Das et al., 2017).

Molecular breeding techniques such as MAS, GS, and CRISPR/Cas9 play a crucial role in enhancing rice yield by enabling the precise selection and modification of key yield-related genes. These approaches offer significant advantages in terms of accuracy, efficiency, and the ability to address complex traits, thereby contributing to the development of high-yielding, stress-resistant rice cultivars.

## 3 Functional Characterization of Yield-Related Genes

### 3.1 Gene expression studies

RNA-Seq and transcriptomic analyses have been pivotal in identifying and characterizing yield-related genes in rice. For instance, the study by Wei et al. (2022) utilized transcriptomic data to identify the transcription factor

OsDREB1C, which enhances photosynthetic capacity, nitrogen utilization, and flowering time, leading to significant yield increases. Similarly, the expression profiling of yield-related genes under various developmental stages and abiotic stress conditions has provided insights into the genetic reprogramming involved in yield traits (Tripathi et al., 2012). These studies highlight the importance of RNA-Seq in understanding the molecular mechanisms underlying yield improvement.

Quantitative real-time PCR (qRT-PCR) is often used to validate the expression levels of key yield-related genes identified through RNA-Seq. For example, the expression of selected yield-related genes was analyzed by qRT-PCR under abiotic stress conditions, revealing tight transcriptional regulation and stress-responsive expression patterns (Tripathi et al., 2012). This method has also been employed to confirm the overexpression of specific genes, such as *OsmiR397*, which increases grain size and promotes panicle branching, thereby enhancing overall grain yield (Wang and Ortigosa, 2013).

### 3.2 Functional genomics approaches

Mutant analysis has been instrumental in elucidating the functions of yield-related genes. Various mutants have been studied to characterize genes involved in yield traits, such as tiller number, grain number, grain size, and plant height (Sakamoto and Matsuoka, 2008). The identification and functional characterization of these mutants have provided valuable insights into the genetic basis of yield traits and have facilitated the compilation of a list of genes available for breeding high-yielding rice varieties (Ikeda et al., 2013).

Overexpression and knockdown studies are powerful tools for functional genomics. Overexpression of specific genes, such as OsDREB1C, has been shown to significantly increase grain yield (Figure 2) and improve nitrogen use efficiency (Wei et al., 2022). Similarly, the overexpression of microRNA *OsmiR397* has been reported to enhance grain size and panicle branching, leading to a 25% increase in grain yield (Wang and Ortigosa, 2013). Knockdown studies, on the other hand, help in understanding the loss-of-function effects of yield-related genes, providing a comprehensive view of their roles in yield enhancement.

Wei et al. (2022) found that overexpression of the *OsDREB1C* gene significantly increased yield in transgenic rice. Key genes upregulated under nitrogen deprivation conditions were identified through RNA seq and qRT PCR analysis. The field experiment results showed that compared with the wild type, transgenic plants increased in yield, number of grains per spike, straw weight, and harvest index (Figure 2). These findings provide new strategies for improving crop yields through genetic engineering, which can help address the challenges of global food security.

The functional characterization of yield-related genes through gene expression studies and functional genomics approaches has significantly advanced our understanding of the molecular mechanisms underlying yield traits in rice. These insights are crucial for developing molecular breeding strategies aimed at enhancing rice yield.

## 4 Integrating Yield-Related Genes into Breeding Programs

### 4.1 Pyramiding multiple yield genes

Pyramiding multiple yield-related genes involves combining several beneficial alleles into a single genotype to enhance rice yield. This strategy leverages the cumulative effects of multiple quantitative trait loci (QTLs) to achieve superior performance. Marker-assisted selection (MAS) is a common approach used to facilitate the pyramiding process by identifying and selecting desirable alleles at each generation (Guo and Ye, 2014). However, challenges include the complexity of interactions between different QTLs, the need for precise phenotyping, and the potential for negative epistasis where the combined effect of multiple genes is less than their individual effects (Zong et al., 2012; Huang et al., 2016).

Several successful examples of gene pyramiding in rice breeding have been documented. For instance, the pyramiding of eight grain yield-related QTLs resulted in new rice lines with increased panicle and spikelet size, demonstrating the effectiveness of this approach (Zong et al., 2012). Another study highlighted the pyramiding of high-yielding *npt1* and *depl-1* alleles, which significantly increased rice yield potential (Wang et al., 2017).

Additionally, the integration of three *C4-specific* genes (*CA*, *PEPC*, and *PPDK*) into rice plants led to a 12% increase in grain yield, showcasing the potential of combining multiple genes to enhance photosynthetic efficiency and yield (Sen et al., 2016).

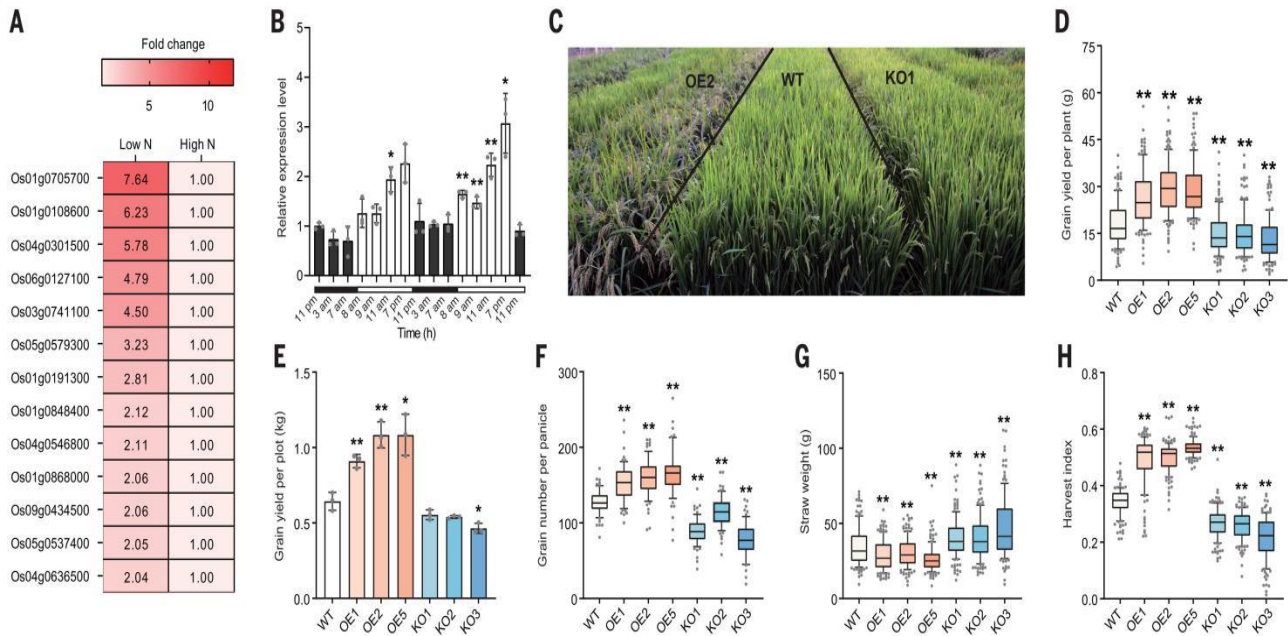


Figure 2 Overexpression of OsDREB1C in transgenic plants can increase grain yield (Adopted from Wei et al., 2022)

Image caption: A: List of the top 13 genes up-regulated in response to nitrogen deprivation (adjusted  $P < 0.05$ ). The genes represent the overlap of previously reported RNA-seq datasets (17) and an expression analysis of a subset of 118 rice transcription factors (16), and were sorted by the fold change in low versus normal nitrogen supply. The color scale represents the  $\log_2$ -fold change of the FPKM (fragments per kilobase of transcript per million mapped reads) ratio under low- versus high-nitrogen conditions, with the FPKM value of each gene under high-nitrogen conditions set to 1.00; B: qRT-PCR analysis of Os06 g0127100 expression in 10-day-old *O. sativa* cv. Nipponbare seedlings grown in soil in a growth chamber under long-day photoperiod (16 hours light/8 hours dark, 28°C, The white bar below the x-axis indicates the light period, and the black bar indicates the dark period. Data are presented as means $\pm$ SD (n = 3 biological replicates). \* $P < 0.05$ , \*\* $P < 0.01$  compared with the first time point (11:00 p.m.), Student's *t* test. C: Phenotypes of WT and transgenic rice plants grown in Beijing in 2018. (D to H) Yield-related parameters including grain yield per plant; D: grain yield per plot; E: grain number per panicle; F: straw weight; G: and harvest index; H: The data were obtained from the field experiment shown in (C). Box plots in (D) and (F) to (H) show median (horizontal lines) and 10th to 90th percentiles, and outliers are plotted as dots (n = 138 biological replicates). Data in (E) are presented as means $\pm$ SD (n=3 plots, 44 plants within a plot). \* $P < 0.05$ , \*\* $P < 0.01$  compared with WT, Student's *t* tests (Adopted from Wei et al., 2022)

## 4.2 High-throughput phenotyping

High-throughput phenotyping technologies have revolutionized the assessment of yield traits in rice breeding programs. Advances include the use of remote sensing, imaging technologies, and automated phenotyping platforms that allow for rapid and accurate measurement of plant traits under field conditions (Swamy and Kumar, 2013). These technologies enable the collection of large datasets, facilitating the identification of phenotypic variations associated with yield-related genes (Su et al., 2021).

High-throughput phenotyping has been applied to assess various yield traits, such as grain number per panicle, grain weight, and tiller number. For example, genome-wide association studies (GWAS) combined with high-throughput phenotyping have identified significant loci for yield component traits, providing valuable insights for breeding programs (Su et al., 2021). These technologies also support the evaluation of transgenic lines and QTL introgression lines, ensuring that the desired yield traits are accurately measured and selected (Guo and Ye, 2014).

### 4.3 Field trials and performance testing

Field trials are essential for evaluating the performance of new rice varieties under realistic growing conditions. The design of field trials should include randomized complete block designs (RCBD) or split-plot designs to account for environmental variability and ensure robust data collection (Swamy and Kumar, 2013). Implementing these trials involves selecting appropriate test sites, managing agronomic practices, and monitoring environmental conditions to accurately assess the performance of yield-related genes (Luan et al., 2019).

Data analysis in field trials involves statistical methods to evaluate the significance of yield differences among genotypes. Techniques such as analysis of variance (ANOVA), mixed models, and QTL mapping are commonly used to interpret the data and identify the genetic basis of yield traits (Huang et al., 2016). The integration of phenotypic and genotypic data allows for the validation of QTL effects and the identification of superior alleles for breeding programs (Guo and Ye, 2014). Additionally, Mendelian randomization analysis can be employed to understand the genetic relationships between yield and its component traits, further guiding the selection of high-yielding genotypes (Su et al., 2021). By integrating these strategies and technologies, rice breeding programs can effectively harness the potential of yield-related genes to develop high-yielding rice varieties, contributing to global food security.

## 5 Case Studies of Molecular Breeding for Yield Improvement

### 5.1 Successful varieties developed

Several high-yielding rice varieties have been developed through molecular breeding techniques. For instance, the CRISPR-Cas9 system was employed to edit three key genes, *OsPIN5b*, *GS3*, and *OsMYB30*, resulting in rice mutants with increased panicle length, enlarged grain size, and enhanced cold tolerance. These mutants demonstrated higher yields compared to wild types, showcasing the potential of gene editing in developing high-yielding rice varieties (Zeng et al., 2020). Additionally, the identification and manipulation of genes regulating agronomically important traits such as tiller number, grain number, grain size, and plant height have provided tools for tailor-made breeding programs aimed at higher grain yield (Tripathi et al., 2012).

Molecular breeding has also led to the development of rice varieties with enhanced resistance to various stresses. For example, the *RST1* gene, which regulates nitrogen metabolism and salt tolerance, was identified as a promising candidate for breeding programs aimed at developing rice cultivars with high yield and stress resistance (Deng et al., 2022). Another study successfully pyramided multiple genes/QTLs for resistance to biotic and abiotic stresses, resulting in rice lines with high degrees of resistance/tolerance to blast, gall midge, submergence, and salinity (Ludwików et al., 2015). Furthermore, introgression lines developed in high-yielding, semi-dwarf genetic backgrounds have shown improved yield under multiple abiotic stresses such as drought, flood, and temperature extremes (Kumar et al., 2020).

### 5.2 Lessons learned and best practices

The success of molecular breeding for yield improvement in rice can be attributed to several key factors. First, the use of advanced genetic tools such as CRISPR-Cas9 has enabled precise editing of target genes, leading to significant improvements in yield and stress resistance (Zeng et al., 2020). Second, the integration of molecular marker-assisted selection (MAS) has facilitated the efficient stacking of multiple resistance genes, ensuring comprehensive stress tolerance in developed varieties (Ludwików et al., 2015). Third, a thorough understanding of the molecular basis of yield-related traits and their regulation under stress conditions has been crucial for selecting the right gene combinations for breeding programs (González-Schain et al., 2016; Nutan et al., 2020).

Future breeding efforts should focus on the following recommendations to enhance rice yield and stress resistance: Continue leveraging CRISPR-Cas9 and other genome editing technologies to target multiple yield-related and stress-resistance genes simultaneously (Zeng et al., 2020; Altaf et al., 2021). Employ MAS to efficiently combine multiple resistance genes/QTLs, ensuring comprehensive stress tolerance in new varieties (Ludwików et al., 2015). Conduct detailed expression profiling of yield-related genes under various stress conditions to identify key regulatory genes and their interactions (González-Schain et al., 2016; Nutan et al., 2020). Create introgression

lines in high-yielding, semi-dwarf backgrounds to improve yield under multiple abiotic stresses without undesirable linkage drag (Kumar et al., 2020). Allocate resources effectively between traditional breeding methods and modern biotechnological tools to maximize yield improvements (Altaf et al., 2021). By following these best practices and recommendations, future molecular breeding programs can continue to develop high-yielding, stress-resistant rice varieties, ensuring food security in the face of global climate change and increasing population demands.

## 6 Future Directions and Challenges

### 6.1 Emerging technologies in molecular breeding

The future of molecular breeding in rice is poised to benefit significantly from emerging technologies. Advances in genomic tools such as CRISPR-Cas9, marker-assisted selection (MAS), and haplotype-based breeding are expected to revolutionize rice breeding programs by enabling precise genetic modifications and efficient selection of desirable traits (Singh et al., 2022). The integration of transcriptomic and metabolomic data has shown promise in enhancing the predictability of hybrid yield, with methods like LASSO and BLUP demonstrating substantial improvements in yield prediction (Xu et al., 2016). Additionally, the rational design of rice ideotypes, leveraging wide-cross compatibility and intersubspecific heterosis, is anticipated to unlock new potentials for high-yield and superior quality rice varieties (Qian et al., 2016).

### 6.2 Addressing climate change and food security

Climate change poses a significant threat to rice production, necessitating the development of rice varieties that are resilient to environmental stresses such as heat, drought, and salinity. Research has identified several quantitative trait loci (QTLs) and candidate genes associated with heat tolerance, which can be exploited through marker-assisted breeding to develop heat-tolerant rice cultivars (Raza et al., 2020). Moreover, understanding the molecular basis of plant architecture and its regulation under stress conditions is crucial for breeding high-yielding rice varieties that can sustain production under adverse environmental conditions (Nutan et al., 2020). The systematic evaluation of rice varieties has shown that improvements in yield stability and sensitivity to climate resources are critical for maintaining or increasing yields under environmental anomalies (Wang et al., 2021).

### 6.3 Ethical and regulatory considerations

The application of advanced genetic strategies in rice breeding raises important ethical and regulatory considerations. The use of genetic engineering and genome editing technologies, such as CRISPR-Cas9, necessitates careful assessment of potential risks and benefits to ensure the safety and acceptance of genetically modified organisms (GMOs) (Altaf et al., 2021). Regulatory frameworks must be established to oversee the development and deployment of genetically engineered rice varieties, ensuring that they meet safety standards and address public concerns. Additionally, ethical considerations related to the equitable distribution of benefits from these technologies must be addressed to ensure that advancements in rice breeding contribute to global food security and do not exacerbate existing inequalities (Li and Zhang, 2013).

The future of molecular breeding for enhanced rice yield lies in the integration of emerging technologies, addressing the challenges posed by climate change, and navigating the ethical and regulatory landscape. By leveraging these advancements, researchers and breeders can develop high-yielding, resilient rice varieties that contribute to global food security.

## 7 Concluding Remarks

This study discusses the key role of molecular breeding techniques in improving rice yield, with a particular focus on key yield related genes such as *Gn1a*, *GS3*, *DEP1*, *APO1*, *GW2*, and *Wx*. These genes affect yield and quality by regulating the growth and development process of rice. Molecular breeding techniques such as MAS, GS, and CRISPR/Cas9 have been widely applied in precision breeding and have achieved significant results. Gene expression and functional genomics methods contribute to a deeper understanding of gene function. In the future, it is necessary to further explore the gene network related to yield, utilize high-throughput phenotype technology and gene editing technology, and strengthen interdisciplinary cooperation to address global food security challenges.



With the continuous progress of sequencing technology and the continuous improvement of bioinformatics analysis methods, rice yield related genes and their regulatory networks can be further explored. The development of gene editing technology has provided more possibilities for precision breeding. Future research can explore how to use technologies such as CRISPR/Cas9 to accurately edit and improve key yield genes. In addition, the application of high-throughput phenotype technology and big data analysis in breeding will also become a future research hotspot.

Molecular breeding of rice is a complex and intricate process that involves precise regulation and selection of specific genes. Therefore, future research should focus more on how genes respond to different environmental pressures, in order to further reveal the adaptive mechanisms of rice. With the continuous advancement of technology and innovation in methods, it is expected to discover more new yield related genes and regulatory mechanisms, providing a more solid scientific foundation for molecular breeding of rice.

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The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

### References

- Altaf A., Gull S., Shah A., Faheem M., Saeed A., Khan I., and Zhu M., 2021, Advanced genetic strategies for improving rice yield, *Journal of Global Innovations in Agricultural Sciences*, 9(4): 167-171.  
<https://doi.org/10.22194/jgias/9.9520>
- Budhlakoti N., Kushwaha A., Rai A., Chaturvedi K., Kumar A., Pradhan A., Kumar U., Kumar R., Juliana P., Mishra D., and Kumar S., 2022, Genomic selection: a tool for accelerating the efficiency of molecular breeding for development of climate-resilient crops, *Frontiers in Genetics*, 13: 832153.  
<https://doi.org/10.3389/fgene.2022.832153>
- Das G., Patra J., and Baek K., 2017, Insight into MAS: A molecular tool for development of stress resistant and quality of rice through gene stacking, *Frontiers in Plant Science*, 8: 985.  
<https://doi.org/10.3389/fpls.2017.00985>
- Deng P., Jing W., Cao C., Sun M., Chi W., Zhao S., Dai J., Shi X., Wu Q., Zhang B., Jin Z., Guo C., Tian Q., Shen L., Yu J., Jiang L., Wang C., Chin J., Yuan J., Zhang Q., and Zhang W., 2022, Transcriptional repressor RST1 controls salt tolerance and grain yield in rice by regulating gene expression of asparagine synthetase, *Proceedings of the National Academy of Sciences of the United States of America*, 119(50): e2210338119.  
<https://doi.org/10.1073/pnas.2210338119>
- González-Schain N., Dreni L., Lawas L., Galbiati M., Colombo L., Heuer S., Jagadish K., and Kater M., 2016, Genome-wide transcriptome analysis during anthesis reveals new insights into the molecular basis of heat stress responses in tolerant and sensitive rice varieties, *Plant and Cell Physiology*, 57(1): 57-68.  
<https://doi.org/10.1093/pcp/pcv174>
- Grenier C., Cao T., Ospina Y., Quintero C., Chatel M., Tohme J., Courtois B., and Ahmadi N., 2015, Accuracy of genomic selection in a rice synthetic population developed for recurrent selection breeding, *PLoS One*, 11(5): e0154976.  
<https://doi.org/10.1371/journal.pone.0136594>
- Guo L., and Ye G., 2014, Use of major quantitative trait loci to improve grain yield of rice, *Rice Science*, 21: 65-82.  
[https://doi.org/10.1016/S1672-6308\(13\)60174-2](https://doi.org/10.1016/S1672-6308(13)60174-2)
- Heffner E., Sorrells M., and Jannink J., 2009, Genomic selection for crop improvement, *Crop Science*, 49(1): 1-12.  
<https://doi.org/10.2135/CROPSCI2008.08.0512>
- Huang L., Hua K., Xu R., Zeng D., Wang R., Dong G., Zhang G., Lu X., Fang N., Wang D., Duan P., Zhang B., Liu Z., Li N., Luo Y., Qian Q., Yao S., and Li Y., 2021, The LARGE2-APO1/APO2 regulatory module controls panicle size and grain number in rice, *The Plant Cell*, 33(4): 1212-1228.  
<https://doi.org/10.1093/plcell/koab041>

- Huang X., Qian Q., Liu Z., Sun H., He S., Luo D., Xia G., Chu C., Li J., and Fu X., 2009, Natural variation at the *DEP1* locus enhances grain yield in rice, *Nature Genetics*, 41: 494-497.  
<https://doi.org/10.1038/ng.352>
- Huang X., Yang S., Gong J., Zhao Q., Feng Q., Zhan Q., Zhao Y., Li W., Cheng B., Xia J., Chen N., Huang T., Zhang L., Fan D., Chen J., Zhou C., Lu Y., Weng Q., and Han B., 2016, Genomic architecture of heterosis for yield traits in rice, *Nature*, 537: 629-633.  
<https://doi.org/10.1038/nature19760>
- Ikeda M., Miura K., Aya K., Kitano H., and Matsuoka M., 2013, Genes offering the potential for designing yield-related traits in rice, *Current Opinion in Plant Biology*, 16(2): 213-220.  
<https://doi.org/10.1016/j.pbi.2013.02.002>
- Jena K., and Mackill D., 2008, Molecular markers and their use in marker-assisted selection in rice, *Crop Science*, 48: 1266-1276.  
<https://doi.org/10.2135/CROPSCI2008.02.0082>
- Jeon J., Jung K., Kim H., Suh J., and Khush G., 2011, Genetic and molecular insights into the enhancement of rice yield potential, *Journal of Plant Biology*, 54: 1-9.  
<https://doi.org/10.1007/s12374-011-9144-0>
- Kumar A., Sandhu N., Venkateswarlu C., Priyadarshi R., Yadav S., Majumder R., and Singh V., 2020, Development of introgression lines in high yielding, semi-dwarf genetic backgrounds to enable improvement of modern rice varieties for tolerance to multiple abiotic stresses free from undesirable linkage drag, *Scientific Reports*, 10: 13073.  
<https://doi.org/10.1038/s41598-020-70132-9>
- Li M., Li X., Zhou Z., Wu P., Fang M., Pan X., Lin Q., Luo W., Wu G., and Li H., 2016, Reassessment of the four yield-related genes *Gn1a*, *DEP1*, *GS3*, and *IPA1* in rice using a CRISPR/Cas9 system, *Frontiers in Plant Science*, 7: 377.  
<https://doi.org/10.3389/fpls.2016.00377>
- Li Z., and Zhang F., 2013, Rice breeding in the post-genomics era: from concept to practice, *Current Opinion in Plant Biology*, 16(2): 261-269.  
<https://doi.org/10.1016/j.pbi.2013.03.008>
- Luan X., Dai Z., Yang W., Tan Q., Lu Q., Guo J., Zhu H., Liu G., Wang S., and Zhang G., 2019, Breeding by design of CMS lines on the platform of SSSL library in rice, *Molecular Breeding*, 39: 126.  
<https://doi.org/10.1007/s11032-019-1028-x>
- Ludwików A., Cieślą A., Arora P., Das G., Rao G., and Das R., 2015, Molecular marker assisted gene stacking for biotic and abiotic stress resistance genes in an elite rice cultivar, *Frontiers in Plant Science*, 6: 698.  
<https://doi.org/10.3389/fpls.2015.00698>
- Mao T., Zhu M., Sheng Z., Shao G., Jiao G., Mawia A., Ahmad S., Xie L., Tang S., Wei X., Hu S., and Hu P., 2021, Effects of grain shape genes editing on appearance quality of erect-panicle *genjaponica* rice, *Rice*, 14(1): 74.  
<https://doi.org/10.1186/s12284-021-00517-5>
- Nutan K., Rathore R., Tripathi A., Mishra M., Pareek A., and Singla-Pareek S., 2020, Integrating dynamics of yield traits in rice responding to environmental changes, *Journal of Experimental Botany*, 2(7): 490-506.  
<https://doi.org/10.1093/jxb/erz364>
- Qian Q., Guo L., Smith S., and Li J., 2016, Breeding high-yield superior quality hybrid super rice by rational design, *National Science Review*, 3(3): 283-294.  
<https://doi.org/10.1093/NSR/NWW006>
- Raza Q., Riaz A., Bashir K., and Sabar M., 2020, Reproductive tissues-specific meta-QTLs and candidate genes for development of heat-tolerant rice cultivars, *Plant Molecular Biology*, 104: 97-112.  
<https://doi.org/10.1007/s11103-020-01027-6>
- Sakamoto T., and Matsuoka M., 2008, Identifying and exploiting grain yield genes in rice, *Current Opinion in Plant Biology*, 11(2): 209-214.  
<https://doi.org/10.1016/j.pbi.2008.01.009>
- Sen P., Ghosh S., Sarkar S., Chanda P., Mukherjee A., Datta S., and Datta K., 2016, Pyramiding of three C<sub>4</sub> specific genes towards yield enhancement in rice, *Plant Cell, Tissue and Organ Culture (PCTOC)*, 128: 145-160.  
<https://doi.org/10.1007/s11240-016-1094-2>
- Singh G., Kaur N., Khanna R., Kaur R., Gudi S., Kaur R., Sidhu N., Vikal Y., and Mangat G., 2022, 2Gs and plant architecture: breaking grain yield ceiling through breeding approaches for next wave of revolution in rice (*Oryza sativa* L.), *Critical Reviews in Biotechnology*, 44(1): 139-162.  
<https://doi.org/10.1080/07388551.2022.2112648>
- Spindel J., Begum H., Akdemir D., Virk P., Collard B., Redoña E., Atlin G., Jannink J., and McCouch S., 2015, Genomic selection and association mapping in rice (*Oryza sativa*): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding lines, *PLoS Genetics*, 11(2): e1004982.  
<https://doi.org/10.1371/journal.pgen.1004982>
- Su J., Xu K., Li Z., Hu Y., Hu Z., Zheng X., Song S., Tang Z., and Li L. 2021, Genome-wide association study and mendelian randomization analysis provide insights for improving rice yield potential, *Scientific Reports*, 11(6): e1005350.  
<https://doi.org/10.1038/s41598-021-86389-7>
- Swamy B., and Kumar A., 2013, Genomics-based precision breeding approaches to improve drought tolerance in rice, *Biotechnology Advances*, 31(8): 1308-1318.  
<https://doi.org/10.1016/j.biotechadv.2013.05.004>

- Tripathi A., Pareek A., Sopory S., and Singla-Pareek S., 2012, Narrowing down the targets for yield improvement in rice under normal and abiotic stress conditions via expression profiling of yield-related genes, *Rice*, 5: 1-12.  
<https://doi.org/10.1186/1939-8433-5-37>
- Usman B., Nawaz G., Zhao N., Liao S., Qin B., Liu F., Liu Y., and Li R., 2020, Programmed editing of rice (*Oryza sativa* L.) *OsSPL16* gene using CRISPR/Cas9 improves grain yield by modulating the expression of pyruvate enzymes and cell cycle proteins, *International Journal of Molecular Sciences*, 22(1): 249.  
<https://doi.org/10.3390/ijms22010249>
- Xu S., Xu Y., Gong L., and Zhang Q., 2016, Metabolomic prediction of yield in hybrid rice, *The Plant Journal: for Cell and Molecular Biology*, 88(2): 219-227.  
<https://doi.org/10.1111/tpj.13242>
- Wang K., and Ortigosa S., 2013, Faculty opinions recommendation of overexpression of microRNA *OsmiR397* improves rice yield by increasing grain size and promoting panicle branching, *Nature Biotechnology*, 31(9): 848-852.  
<https://doi.org/10.3410/f.718043708.793483739>
- Wang S., Ma B., Gao Q., Jiang G., Zhou L., Tu B., Qin P., Tan X., Liu P., Kang Y., Wang Y., Chen W., Liang C., and Li S., 2018, Dissecting the genetic basis of heavy panicle hybrid rice uncovered *Gn1a* and *GS3* as key genes, *Theoretical and Applied Genetics*, 131: 1391-1403.  
<https://doi.org/10.1007/s00122-018-3085-7>
- Wang S., Wu K., Qian Q., Liu Q., Li Q., Pan Y., Ye Y., Liu X., Wang J., Zhang J., Li S., Wu Y., and Fu X., 2017, Non-canonical regulation of SPL transcription factors by a human OTUB1-like deubiquitinase defines a new plant type rice associated with higher grain yield, *Cell Research*, 27(9): 1142-1156.  
<https://doi.org/10.1038/cr.2017.98>
- Wang X., Jing Z., He C., Liu Q., Jia H., Qi J., and Zhang H., 2021, Breeding rice varieties provides an effective approach to improve productivity and yield sensitivity to climate resources, *European Journal of Agronomy*, 124: 126239.  
<https://doi.org/10.1016/J.EJA.2021.126239>
- Wei S., Li X., Lu Z., Zhang H., Ye X., Zhou Y., Li J., Yan Y., Pei H., Duan F., Wang D., Chen S., Wang P., Zhang C., Shang L., Zhou Y., Yan P., Zhao M., Huang J., Bock R., Qian Q., and Zhou W., 2022, A transcriptional regulator that boosts grain yields and shortens the growth duration of rice, *Science*, 377: 6604.  
<https://doi.org/10.1126/science.abi8455>
- Zeng Y., Wen J., Zhao W., Wang Q., and Huang W., 2020, Rational improvement of rice yield and cold tolerance by editing the three genes *OsPIN5b*, *GS3*, and *OsMYB30* with the CRISPR-Cas9 system, *Frontiers in Plant Science*, 10: 1663.  
<https://doi.org/10.3389/fpls.2019.01663>
- Zong G., Wang A., Wang L., Liang G., Gu M., Sang T., and Han B., 2012, A pyramid breeding of eight grain-yield related quantitative trait loci based on marker-assistant and phenotype selection in rice (*Oryza sativa* L.), *Journal of Genetics and Genomics*, 39(7): 335-350.  
<https://doi.org/10.1016/j.jgg.2012.06.004>



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