International Journal of Agriculture, Environment and Biotechnology
Citation: *IJAEB*: **19**(03): 139-152, September 2026
DOI: 10.30954/0974-1712.03.2026.5

ASSOCIATION FOR AGRICULTURE ENVIRONMENT AND BIOTECHNOLOGY

REVIEW PAPER

Marker-Assisted Breeding and Gene Editing for Rice Improvement: Advances and Future Directions

Tapash Dasgupta*, Payabrata Roy and Satyaki Nandan Maity

Division of Genetics and Plant Breeding, Integrated Rural Development and Management, Ramakrishna Mission Vivekananda Educational and Research Institute, Narendrapur Campus, Kolkata, India

*Corresponding author: tapashdg.cu@gmail.com (**ORCID ID:** 0000-0003-1918-915X)

Paper No. 1247 **Received:** 12-06-2026 **Revised:** 22-08-2026 **Accepted:** 05-09-2026

ABSTRACT

Modern plant breeding programs have established technologies to increase rice productivity by pyramiding essential genes and QTLs associated, to enhance yield and quality, and response to stress tolerance (both biotic and abiotic). The development of molecular markers linked to various stress tolerance mechanisms along with new genome editing technologies, has further made molecular breeding more sustainable. This progress has also helped to diminish linkage drag issues. To address stresses related to climate change, several linked markers have been discovered and widely used in plant breeding programs. But some areas where MAS has been found to be of limited use, genome editing technologies have shown success. Here we have reviewed some important examples of modern technologies in rice breeding and rice varieties that have been successfully developed from them in both comprehensive and objective approach.

HIGHLIGHTS

- New varieties of rice tolerant to multiple stresses.
- Molecular Markers linked with quantitative and major traits.
- Biochemical and Genetic Pathways of Stress Tolerance.

Keywords: Molecular Markers, Marker Assisted Selection, Gene/QTL Mapping, Biotic and Abiotic Stress Tolerance

Rice *(Oryza sativa L.)* is one of the most important staple crops and more than half of the global population especially in Asia and Africa is dependent on rice for food. Rice is the backbone of global food security. It is predominantly produced in South and East Asia, with China and India being the leading producers. It requires warm climate and a large quantity of water for higher production. According to FAO, average rice consumption was about 85 kg in Asia. In 2022, India earns more than USD 20 billion from rice export (http://www.knowledgebank.irri.org/) Rice is labour intensive crop and its cultivation provides employment for millions of people in Asia. Rice production and availability are crucial to prevent hunger in the world. Rice is adaptable to different environments from mountains to coastal areas. Although plant breeding techniques have produced high-yielding varieties, overcoming all production barriers, but at the same time, it is increasingly felt that the present-day bottleneck limitations to progress further are long breeding cycles and sensitivity of genotypes to environmental variability. The more recent genomics and molecular techniques have improved breeding efficiency through marker-assisted selection and gene editing technique.

No longer developing varieties against various diseases, abiotic stresses or improving yield

How to cite this article: Dasgupta, T., Roy, P. and Maity, S.N. (2026). Marker-Assisted Breeding and Gene Editing for Rice Improvement: Advances and Future Directions. *Int. J. Ag. Env. Biotech.*, **19**(03): 139-152.

Source of Support: None; **Conflict of Interest:** None

components are major challenges to molecular plant breeders as different techniques are now available to combat the problems. The molecular marker-assisted selection technique helps the conventional breeders a unique opportunity to develop new varieties at the shortest possible time with confidence while, gene editing further strengthens the modifications by targeting the complex traits and allows target-oriented modifications for rice improvement. This review highlights the significant research done in different approaches, focusing on key genes, quantitative traits, and integrated methods for wider adaptability in rice cultivation.

Evolution of Molecular Breeding Technologies in Rice

The plant breeding programs have upgraded due to the use of molecular markers linked to phenotypic markers as a routine technology and have made a significant impact on molecular breeding. The evolution of molecular breeding technologies has activated rice improvement, changing from phenotype-based selection to a molecular marker-based improvement program.

Rice was one of the first cereal crops to advance through molecular breeding due to its small genome, high genetic diversity, and initial global investments in genetic mapping and genomics (Khush, 2005; McCouch *et al.* 2010). Starting from hybridization-based markers to genome-based markers has aided in evolving new advanced varieties of rice, overcoming all the stresses for rice production.

Early Marker Systems

Rice was focused on as a model crop during the 1990s because of the development of a dense linkage map and the availability and use of molecular markers in the early era (McCouch *et al.* 1988). The first marker system developed in rice was restriction fragment length polymorphism (RFLP) markers, which provided the concept of genes and the framework of QTLs linked with yield and different stresses (biotic and abiotic) (McCouch and Doerge, 1995). Initially, huge success was obtained in the identification of genes by RFLP markers, but the method requires more labor, high quality of DNA, and radioactive isotopes, which limit and hinder the application of this method on a regular basis in breeding programs.

The invention of polymerase chain reaction-based markers resulted in different PCR-based markers like RAPD, SCAR, SSR, ISSR, etc. Among the different markers developed after the invention of PCR technology, simple sequence repeat (SSR) is more popular and widely used in plant breeding programs. SSR markers are more polymorphic in nature, co-dominant, reproducible, and distributed genome-wise. Moreover, the method of genotyping is very simple, which makes it popular to use in plant breeding programs (Temnykh *et al.* 2000). High-resolution genetic mapping of 12 chromosomes of rice tagged with different SSRs facilitated wide-scale use of MAS in rice. Around 2000, SSR-based linkage maps replaced RFLP, and SSR has been used in mapping and molecular breeding on a large scale (Ni *et al.* 2002). Soon SSR is widely used in rice improvement programs across Asia, including India.

Marker-Assisted Selection and Backcrossing

SSR markers that are tightly linked with phenotypic markers and quantitative trait loci can be used in early selection, like the seedling stage, without taking into account environmental variation and phenotypic expression, once those markers are found to be tightly linked with the trait of interest (Collard and Mackill, 2008). Molecular markers, especially those that are tightly linked with the major genes and have a stable effect in different environments, have been used extensively in rice improvement programs. Further, a backcrossing program using markers assisted selection that are linked with the desired genes (foreground selection), is not only unique in achieving the desired goal of incorporating the target traits in the adapted genetic background, but also in the recombinants, linkage drags can be decreased by the technique (Hospital, 2005). Because of all of these advantages, the technique is widely used by the breeders to insert stress and disease tolerance traits into widely adapted rice varieties.

In a similar manner, marker-assisted selection (MAS) has enabled the integration of several important genes like, Saltol QTL to enhance seedling-stage salinity tolerance (Bonilla *et al.* 2002), the stacking of bacterial leaf blight resistance

genes for long-lasting resistance (Sundaram *et al.* 2008), and the effective use of blast resistance (Pi) genes within high-yielding genetic frameworks (Jia *et al.* 2004) and many others. MAS has been effectively utilized to enhance drought tolerance through the incorporation of significant-effect QTLs, such as the qDTY loci, which boost yield during drought conditions (Vikram *et al.* 2011). Furthermore, marker-assisted selection has led to substantial enhancements in grain quality traits like aroma (BADH2), amylose content (Wx), and cooking quality, thus simultaneously advancing both productivity and consumer appeal (Bradbury *et al.* 2005; Bao *et al.* 2014). The development of newer varieties in the recent past over 20 years has resulted in a remarkable boosting in yield due to all of these genetic manipulations in inserting crucial genes into the widely adapted genetic background.

Changes to genome wise association studies

By employing the concept of genome-wise association studies, genome-wise mapping of complex traits such as yield flowering traits and grain quality was accomplished by analyzing a diverse gene pool, allowing for further advancement from markers-assisted selection (Zhao *et al.* (2011). At the same time, a brand-new technique called genomic selection surfaced, which produced genome-wise marker data (Meuwissen *et al.* [2001]. SNPs, genotype by sequencing (GBS), and whole genome re-sequencing are examples of more sophisticated markers that have made it easier to analyze quantitative traits. Even with all of the advancements in molecular breeding programs brought about by the rapid advancement of technology, the start of indirect selection by SSR remains essential for plant breeders to speed up the selection process more accurately, efficiently, and rapidly, resulting in the development of several improved varieties (Singh *et al.* (2016) and maximizing breeding's efficacy.

Enhancement of Important traits in the new varieties of Rice using molecular Markers

Marker-assisted selection (MAS) has been essential in improving rice genetically for significant agronomic, abiotic, and biotic stress-related traits. Well-characterized genes and QTLs have enabled precise and rapid varietal enhancement for traits like disease

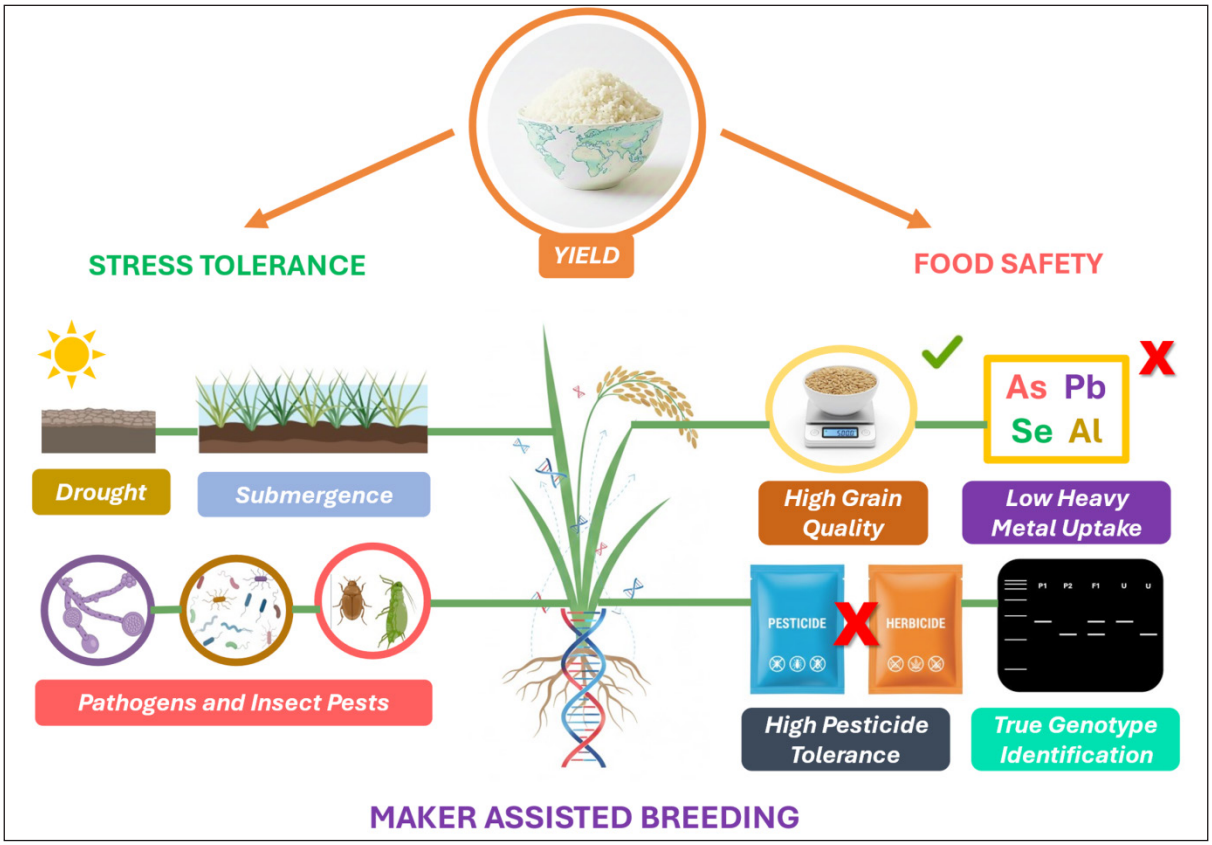


Fig. 1: Application of MAS in Crop improvement

resistance, stress-related contaminant exclusion, and submergence tolerance, which are among the first and most important accomplishments of MAS.

Marker-Assisted Improvement of Abiotic Stress Tolerance

Submergence Tolerance

Every year, flash flooding impacts over 15 million hectares of rice-growing regions in South and Southeast Asia, often leading to lowland ecosystem failure (Bailey-Serres *et al.* (2010). Two mechanisms overcoming submergence are generally noticed namely: (i) Tolerance to submergence for a brief period and (ii) Accelerated elongation ability of internode.

Tolerance for a brief period

An exceptional accomplishment in rice molecular breeding is demonstrated by the thorough examination of the SUB1 locus on chromosome 9, which identifies an ethylene-responsive factor (ERF) type of transcription factor as the primary gene that confers tolerance to submergence by reducing elongation growth and simultaneously reserving carbohydrates under submerged conditions (Xu *et al.* (2006).

From the Indian cultivar FR13A, the tolerant SUB1A-1 allele was introduced into the widely adapted high-yielding varieties Swarna, IR64, and Samba Mahsuri. This resulted in good tolerance in survival rates for roughly two weeks without compromising yield (Septiningsih *et al.* 2009). The FR13A variety is currently India's main source of submergence cultivars, and farmers like using the introgressed lines to show translation research from MAS to field level. Rice's submergence tolerance trait was found to be controlled by a major QTL (Xu and Mackill, 1996). This QTL is a very successful candidate for MAS, as evidenced by the use of simple sequence repeat markers that are closely linked to this locus to transfer this trait into different genetic backgrounds (Xu *et al.* 2004). Some other QTLs are also present in FR13A that contributes to tolerance (Nandi *et al.* 1997).

Accelerated elongation ability of internode

A major QTL near sd1 locus was found to control plant height and increase in plant height along with accelerated internode length in response to rising water level (J Dong *et al.* 2024). Toojinda *et al.* (2003) also reported alleles for shoot elongation under submergence.

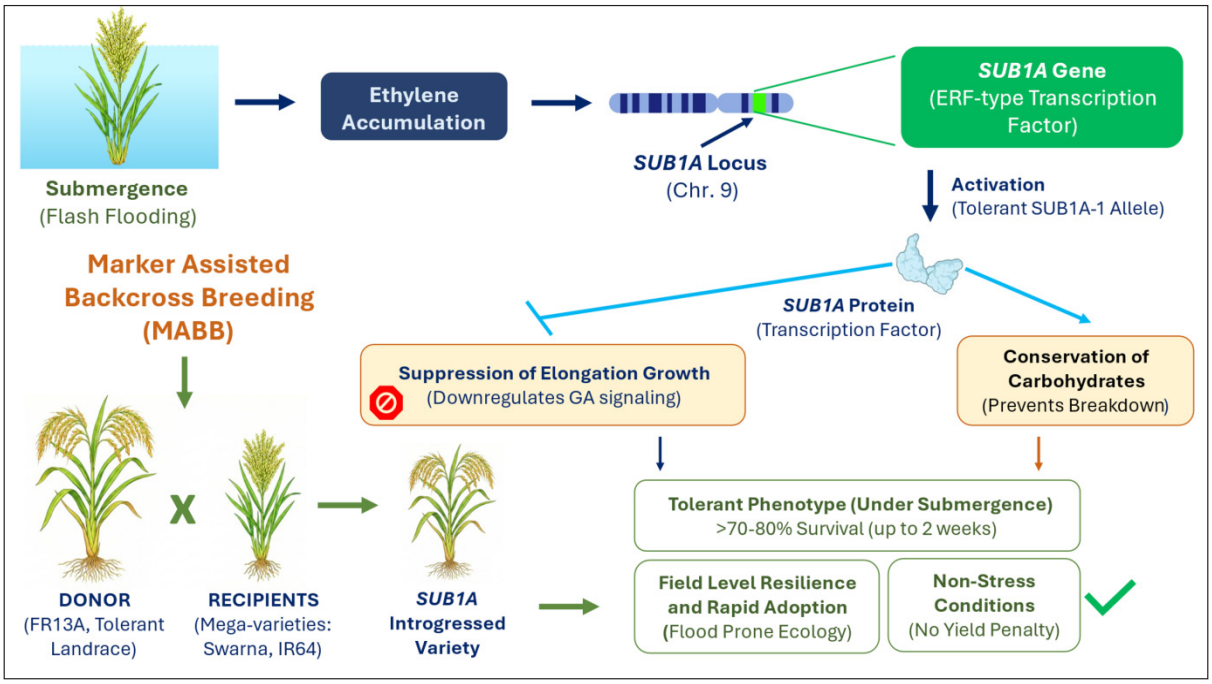


Fig. 2: Molecular Pathway and Breeding Scheme for Submergence Tolerance in Rice

Drought, Salinity, and Heat Tolerance

Tolerance to Low Temperature

The ability to withstand low temperatures has been found to be crucial in regions of the tropics that are temperate, subtropical, and high elevation. The tolerance of Indica cultivars is lower than that of Japonica cultivars. Shirasawa *et al.* (2012) discovered two QTLs that were backcrossed into a Japanese temperate rice from a tropical japonica cultivar. Andaya and Mackill (2003) discovered a small QTL effect at the booting stage of a cross between an indica IR50 and a temperate japonica M202. In general, these QTLs at the booting stage had a small effect. In contrast to the booting stage, cold tolerance at the vegetative stage is dominated by both major and minor QTLs. The cross M202/IR50 showed that the main QTLs regulated cold-induced wilting and necrosis tolerance. Certain QTLs allow *indica* cultivars to withstand cold, particularly in tropical climates.

QTL at germination stage

QTLs for low temperature at germination stage were identified by Misawa *et al.* (2000) in a cross between japonica and indica.

Salinity tolerance

Koyama *et al.* (2001) mapped QTLs for tolerance to salinity in rice and they carried out the work from the cross between IR4630-22-2-5-1-3 (tolerant) and IR15324-117-3-2-2 (susceptible). They also found several QTLs for many traits under saline condition but all have very low contribution towards control of traits. On the otherhand, Saltol QTL was identified as a major contributor towads control of salnity tolerance. The QTL is located on chromosome 1. The work (Gregario, 1997) was carried out from the cross between Pokkali (tolerant) and IR29 (susceptible). During seedling stage, these cultivars keep Na+/K+ homeostasis (Singh *et al.* 2018) acceptable that created a significant outcome in transferring salt tolerant character to other adapted variety. Soon after several BRRI Dhan lines of Bangladesh and Pusa Basmati 1121 in India were developed which made great success in salt affected areas.

Heat tolerance

Specially for the characteristics like spikelet fertility, pollen viability, and grain filling under high-temperature stress, heat tolerance has garnered more attention recently. GWAS and biparental mapping have identified a number of QTLs and genes, such as qHTSF4.1 and COLD1 (which has pleiotropic effects on temperature response), providing new pathways for MAS and genomics-assisted breeding (Shanmugavadivel *et al.* 2017).

Arsenic Tolerance and Grain Arsenic Accumulation

Rice is a staple food in India and many parts of South East Asia. The anaerobic cultivation of rice in this rice dominated areas, makes contamination in ground water due as arsenic is abundantly found in this situation and this creates a major challenge to food safety in this zone, as presence of inorganic arsenic is lethal to human being when such grains are consumed by people (Dasgupta *et al.* (2004); Meharg and Zhao (2012)). Apart from anaerobic cultivation, the physiological mechanism of arsenite, silicon and phosphate being the common path of uptake, make rice more susceptible to arsenic due to more uptake of arsenic than other cereal crops (Zheng *et al.* 2011). So, reduction of rice

Table 1: Major biotic and abiotic stress tolerance genes/QTLs, markers, and MAS-derived rice varieties in Asia

Stress	Gene/QTL	Chr.	Markers	MAS-derived varieties
Submergence	*SUB1A*	9	RM219, RM8300	Swarna-Sub1, IR64-Sub1
Drought	*qDTY1.1, qDTY12.1*	1, 12	RM431, RM28166	Sahbhagi Dhan, DRR Dhan 42
Salinity	*Saltol*	1	RM8094, RM3412	Pusa Basmati 1121-Saltol
Cold	*qCTS12.1, COLD1*	12	SNP-based	Himdhan, temperate lines
BLB	*Xa4, Xa21, xa13*	4, 11, 8	Gene-specific	Improved Samba Mahsuri
Blast	*Pi54, Pi2*	11, 6	RM206, Pi54MAS	Swarna-Pi54
Sheath blight	*qSB9-1, qSB11-1*	9, 11	SSR, SNP	Elite breeding lines

arsenic uptake in the grain is considered as a major challenge to the plant scientist (Norton *et al.* 2010).

Molecular Basis of Arsenic Uptake and Tolerance

Considerable progress has been made in our understanding of the molecular mechanisms by which rice absorbs, transports, and detoxifies arsenic. Arsenite uptake and xylem loading are important processes for the nodulin-26-like intrinsic proteins Lsi1 (OsNIP2;1) and Lsi2, respectively (Ma *et al.* (2008). Through phosphate transporters (OsPTs), arsenate is taken up, and in the roots, enzymes such as OsHAC1;1 and OsHAC1;2 convert it to arsenite, which limits its flow to the shoots and grains (Shi *et al.* (2016). OsABCC1, a vacuolar ABC transporter is a significant discovery that effectively lowers accumulation of As in rice grains by the sequestration of arsenic-phytochelatin complexes in nodal regions (Song *et al.* 2014). MAS has been an effective tool which utilizes natural allelic variation at these loci as well as QTLs like Astol, qAs6 and qAs8 to create rice breeding lines with significantly lower grain arsenic levels (Norton *et al.* 2010; Dasgupta and colleagues, 2004).

Marker-Assisted Improvement of biotic stress tolerance in Rice

The yielding capacity of rice is limited by several biotic stresses. Diseases like blast, bacterial leaf blight (BLB), and sheath blight cause severe yield loss in different rice growing areas and resistance caused by inherent capacity of the germplasm is considered as most eco-friendly control of the disease rather than agronomic management. QTLs and resistance genes have been incorporated into high-performing rice varieties thanks in large part to marker-assisted selection (MAS).

Sheath Blight Resistance

According to Willocquet *et al.* 2000, sheath blight caused by Rhizoctonia solani can damage rice production 10 to 30 percent or more depending upon severity of the disease. Sheath blight resistance, in contrast to many other rice diseases, is primarily quantitative and regulated by several QTLs with moderate effects, which has historically impeded breeding advancement.

Since QTL mapping and genomics have been accomplished, the idea of sheath blight resistance has significantly improved. Using a mapping population derived from Oryza nivara, (Neelam *et al.* 2024) discovered 29 QTLs for sheath blight resistance and associated multiple loci with genes encoding serine/threonine kinases and thaumatin-like proteins. Finding SBRR1-R alleles, which activate resistance without lowering yield, was a significant result in breeding for sheath blight resistance (Cao *et al.* 2022).

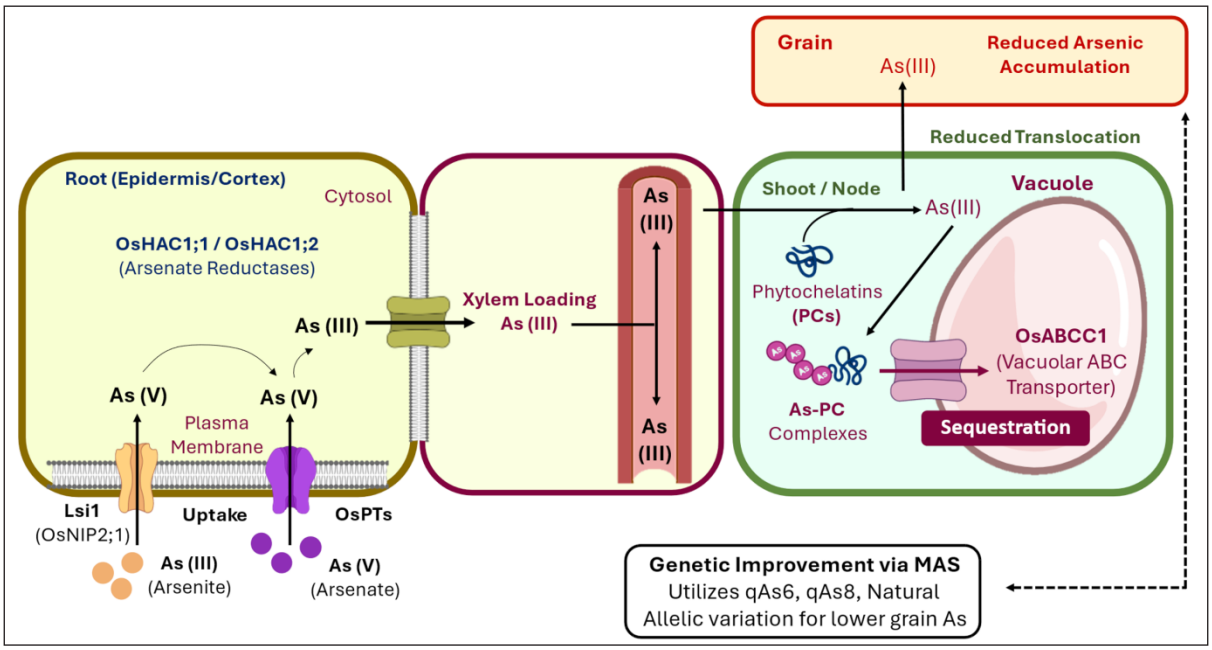


Fig. 3: Arsenic Uptake Pathway in Rice

Table 2: Genes and QTLs governing arsenic tolerance and grain arsenic accumulation in rice

Gene/QTL	Chromosome	Function / Trait	Key markers	Major references
Lsi1 (OsNIP2;1)	2	Arsenite influx transporter	Indel, CAPS	Ma *et al.* (2008); Norton *et al.* (2010)
Lsi2	3	Arsenite efflux and xylem loading	SSR-linked	Ma *et al.* (2008)
OsHAC1;1, OsHAC1;2	2, 4	Arsenate reduction	SNP-based	Shi *et al.* (2016)
OsABCC1	8	Vacuolar sequestration, low grain Arsenic.	Gene-based	Song *et al.* (2014)
qAs6, qAs8	6, 8	Grain arsenic accumulation	RM225, RM248	Norton *et al.* (2010);

Cross-talk between developmental and defense pathways has been highlighted by the involvement of transcriptional regulatory networks, such as the BZR1–NAC29/NAC31 module, which combines growth regulation, immunity, and brassinosteroid signaling (Yuan *et al.* (2018).

Bacterial Leaf Blight Resistance

The bacterium Xanthomonas oryzae pv is the cause of bacterial leaf blight (BLB). oryzae (Xoo), a vascular disease, can cause yield losses of more than 50% during severe outbreaks (Nino-Liu *et al.* (2006)). There are about 40 BLB resistance gene, discovered till now. Many of them have undergone cloning techniques and functional description. Four of the most important genes for resistance to BLB are Xa4, xa5, xa13, Xa21. They work in a variety of ways, like prevention of effector activity of the pathogen recognition of the pathogen through PRRs (Pathogen Recognition Receptors) (Song *et al.* 2023; McCouch and Iyer-Pascuzzi, 2007). A number of these genes have been introgressed into many susceptible but elite varieties through MAS-derived gene pyramiding tools, producing long-term broad-spectrum resistance. Improved Basmati cultivars such as Pusa Basmati 1718 and Pusa Basmati 1885 having introgressed with xa13 and Xa21 have shown improved resistance to BLB at field levels maintaining superior quality simultaneously (Ellur *et al.* 2016).

Blast Resistance

Rice blast, caused by *Magnaporthe oryzae* is one of the most damaging diseases in rice and it affects at every stage of rice plants. The resistance to blast is offered by NBS-LRR dominated genes which follows the model of gene for gene mechanism. In addition to the many QTLs and more than 100 blast resistance genes that have been discovered, broad-spectrum genes like Pi9, Pi54, and Pita have been extensively used in breeding programs (Sharma *et al.* 2010). In gene pyramiding strategies, several Pi genes are combined (e.g. 3. Pi54 + Pi2) through MAS have generated lines that exhibit long-lasting resistance to a variety of blast races (Singh *et al.* 2015).

Moreover, it has been found that blast resistance and developmental signal closely interact with each other. That is growth and defense mechanism pathway interacts with each other and that is why tillering capacity and yield ameliorates with blast resistance (Xie *et al.* 2019)

Integrated Disease Resistance Strategies in Rice

Due to the frequent simultaneous or sequential disease pressures that rice fields encounter, single-gene resistance strategies are susceptible to failure. As a result, integrated disease resistance which combines major resistance (R) genes with quantitative resistance loci to provide long-lasting, broad-spectrum protection, is becoming more and more important in modern rice breeding. Marker Assisted Gene Pyramiding has shown its effectiveness in stacking genes from multiple donor backgrounds which provides partial resistance to combat the severity of diseases like BLB, Blast and Sheath Blight (Collard and Mackill, 2008; Kumar *et al.* 2021). GWAS and meta-QTL analyses have further reinforced integrated stress breeding by identifying the genomic regions (Meta QTL hotspots) where factors of resistance against multiple biotic stresses colocalize (Ballini *et al.* 2008).

By allowing for the simultaneous selection of several resistance traits and reducing linkage drag, these MQTL regions simplify breeding. As an

illustration of common defense signaling pathways and regulatory networks, a number of MQTLs on chromosomes 6, 9, and 11 have been linked to resistance to blast, BLB, and sheath blight (Kumar *et al.* 2020).

Marker-Assisted Improvement of Yield and Grain Quality Traits

Both farmer adoption and consumer acceptance are significantly influenced by grain yield and quality characteristics. Although many small-effect QTLs influence yield, which is a highly polygenic trait, MAS has proven successful in introducing component traits like grain weight, panicle number, and stress-resilient yield stability (Xing and Zhang, 2010).

The availability of cloned major-effect genes has made MAS particularly successful in improving grain quality. Wx (amylose content), ALK (gelatinization temperature), BADH2 (aroma), GS3, and GW2 (grain length and weight) are important examples. Through marker-assisted gene manipulation, breeders have been able to pyramid stress tolerance and disease resistance traits while also precisely adjusting cooking and eating quality (Bradbury *et al.* 2005; Fan and associates. 2006).

Major achievements of MAS in abiotic and biotic stress tolerance breeding

Because of their robustness, co-dominant inheritance, reproducibility, and affordability, simple sequence repeat (SSR) markers have been the cornerstone of rice marker-assisted breeding programs for almost thirty years (McCouch *et al.* (2002)). SSRs are still frequently utilized in public-sector breeding programs, particularly in developing nations, despite the popularity of SNP-based platforms. This is because they are simple to implement and require little infrastructure.

Historic accomplishments in MAS include the introgression of Saltol for seedling-stage salinity tolerance and Sub1 for submergence tolerance. In stressful situations, a number of mega-varieties, such as Swarna-Sub1 and IR64-Sub1, have shown consistent performance (Xu *et al.* 2006; Phing Lau *et al.* 2016). Afterwards, elite backgrounds were used to incorporate drought-yield QTLs (qDTY1.1, qDTY2.2, and qDTY12.1) using MAS (Kumar *et al.* in 2014).

Genes for resistance to bacterial blight (Xa21, xa13, Xa7, xa5), blast resistance (Pi2, Pi9, Pita), and resistance to brown planthoppers (Bph3, Bph14) were successfully pyramided as a result of a

Table 3: Summary of Integrated Disease Resistance Mechanisms and Breeding Strategies

Disease	Pathogen	Key genetic basis	Resistance mechanism	Breeding application
Sheath blight	*Rhizoctonia solani*	Multiple QTLs (e.g., *qSBR3.1*), *SBRR1*	Quantitative resistance, ROS homeostasis, receptor-like kinase signalling	Pyramiding of QTLs; deployment of *SBRR1*
BLB	*Xanthomonas oryzae* pv. *oryzae*	R genes (*Xa21, xa5, xa13*, etc.)	Effector recognition and defense activation	MAS-based gene pyramiding
Blast	*Magnaporthe oryzae*	R genes (*Pi54, Pi9*) and QTLs	Gene-for-gene HR and downstream signalling	Broad-spectrum resistance through pyramiding

Table 4: Widely used SSR markers in rice marker-assisted breeding

Marker	Chromosome	Associated trait
RM219	9	Submergence (*SUB1*)
RM8300	9	Submergence (*SUB1*)
RM8094	1	Salinity (*Saltol*)
RM206	11	Blast (*Pi54*)
RM225	6	Grain arsenic accumulation
RM3412	11	Salinity tolerance

Table 5: Cultivars released in India by CVRC through application of MAS

Sl. No.	Name of variety	Year of release by CVRC	Pedigree	Average productivity (t/ha)	Special traits	Released for States
1	Improved Samba Mahsuri (RP-Bio5260	2008	Samba Mahsuri background (BPT5204)	4.75 to 5	Salinity tolerance	AP, Telangana, TN, Karnataka, Odisha, Chhattisgarh, Jharkhand, Bihar, Gujarat, Maharashtra
2	Pusa Basmati 1509	2013	Pusa 1301 x PB1121	5 to 5.5 under irrigated condition	Moderate resistant to leaf and brown spot, good grain quality	Punjab, Haryana, Delhi, Western UP, Uttarakhand, J and K
3	Pusa Basmati 1718	2017	MAS derived lines of PB	4.65	Resistance to BLB, export quality, short duration	Punjab, Haryana, UP
4	Pusa Basmati 1847	2021	Improved NIL of PB1509 with introgression of xa13, Xa21,, Pi54 and Pi2	5.8	Resistance to BLB and Blast	Punjab, Haryana, Uttarakhand.
5	Pusa Basmati 1885	2021	PB1121 with xa13 + Xa21+Pi2+Pi54	4.68	Resistance to BLB and Blast	Punjab, Haryana, Delhi GI areas

molecular assisted selection program. Numerous varieties throughout Asia, including India, have developed long-lasting resistance as a result of these efforts (Sundaram *et al.* 2009; Singh *et al.* 2015).

Limitations of MAS

Notwithstanding its various achievements, molecular assisted selection is limited in its ability to restructure a number of traits, such as yield components, grain quality, and the ability to get rid of undesired linkage drag. These restrictions gave gene editing a wider range of applications when combined with MAS.

Gene Editing in Rice Breeding

Rice genomics and precise target-oriented breeding have greatly improved with the development of new technology and the CRISPR/Cas method. Using a very different transgenic technique, this new technology altered key genes without adding DNA from other plant or animal sources, leading to the creation of new varieties with the least amount of disruption to biosafety and functional genomes. There are numerous instances where the technology has proven effective, including gene knockout, promoter modification, rapid QTL candidate gene authentication, genome-wide association, and marker-assisted techniques. Research on these genes has improved phenotypes in otherwise adapted elite genotypes. The technology (gene editing) is particularly effective for many major genes or modification of regulators that work negatively to the desired effect (anonymous).

Yield and Plant Architecture

In order to boost rice productivity, this new technology restructures many genes linked to yield and plant structure components that were previously identified by QTLs. Grain length, width, and weight (GW) have all increased as a result of research on GS3 and GW2, the regulators that act negatively on grain size. Similarly, the number of spikelets per panicle has increased due to the correction of Gn1a, which is in charge of cytokinin degradation (Ashikari *et al.* 2005).

With regard to the genes DEP1 and IPA1, which are in charge of erect plant type, moderately reasonable tiller number, and ideal plant structure, this gene editing technique has also improved plant structural characteristics. By improving light interception and lodging resistance, this modification boosts yield productivity, especially for high-input agronomic practices (Yadav *et al.* 2017, Jiao *et al.* 2024).

Grain Quality Traits

Because there are many distinct major genes with definite, predictable phenotypic effects, grain quality traits are the main traits to be addressed when editing genes. Breeders can now precisely manipulate the amylose content of the Wx gene to modify the cooking and eating quality traits to suit consumer preferences thanks to this technology. The predicted deletion of BADH2 has also been done to increase aroma in otherwise non-aromatic varieties without lowering yield. Recent studies have also shown that new technology has restructured genes, particularly those related to grain chalkiness, like FLO2, illustrating the significance and implications of this method to improve milling quality, which will increase market demand while maintaining other agronomic traits (Zhou *et al.* 2021).

Improvement of Stress Tolerance through Gene Editing

Gene editing is a novel technique to increase resistance to biotic and abiotic stresses, in addition to studies on yield and quality enhancement. In this contemporary applied field, the majority of methods focus on enhancing defense pathways by addressing negative regulators of stress responses. For instance, removing OsRR22, a cytokinin signaling regulator, markedly improved tolerance to salinity without impeding unfavourable growth. The drought tolerance can also be upgraded by expediting regulation of water use, and deleting precisely OsPYL genes which are specifically involved in signaling of abscisic acid (Usman *et al.* 2020).

Integration of MAS and Gene Editing: A Unified Breeding Strategy

The combination of gene editing and marker-assisted selection (MAS) is the most promising future approach to rice improvement. When donor alleles are unavailable in elite germplasm, MAS is still very effective at introducing major resistance genes and large-effect QTLs controlling disease resistance and abiotic stress tolerance. Gene editing technology on the contrary, can edit genes in the new genetic background and helps in the restructuring of genes which is difficult to modify through conventional methods. Thus, yield, quality and regulatory genes can be further boosted up by the newer gene editing technology.

Table 6: Major genes and QTLs utilized in marker-assisted breeding and gene editing in rice

Trait	Gene/QTL	Chromosome	Approach	Key Findings	Reference
Grain size	GS3	Chr 3	Gene editing	Increased grain length and TGW	Fan *et al.* 2006;
Grain width	GW2	Chr 2	MAS / Editing	Enhanced grain weight	Song *et al.* 2023
Grain number	Gn1a	Chr 1	Editing	Increased spikelet number	Ashikari *et al.* 2005
Panicle architecture	DEP1	Chr 9	Editing	Dense erect panicles	Ashikari *et al.* 2005
Yield potential	IPA1	Chr 8	Editing	Ideal plant architecture	Jiao *et al.* 2010
Submergence tolerance	Sub1	Chr 9	MAS	Flood tolerance	Xu *et al.* 2006
Salinity tolerance	Saltol	Chr 1	MAS	Seedling-stage tolerance	Thomson *et al.* 2010
Drought yield	qDTY12.1	Chr 12	MAS	Yield under drought	Kumar *et al.* 2014
Bacterial blight		Chr11	MAS	Durable resistance	Sundaram *et al.* 2009; Majumder *et al.* 2020; Bandyopadya *et al.* 2022
	Xa21, xa4;	Chr5			
	xa 5	Chr8			
	xa13				
Blast resistance	Pi9	Chr 6	MAS	Broad-spectrum resistance	Qu *et al.* 2006
Amylose content	Wx	Chr 6	Editing	Improved cooking quality	Zhou *et al.* 2021

Breeders can restructure the genetic background of newly developed varieties without disturbing the established genetic background and insert genes from distant genetic background. Hence, agronomic and quality traits of the varieties can be upgraded by utilizing near isogenic line and incorporating several genes for resistance (pyramiding) to several diseases and quality traits that offer perfect background for targeted gene editing to combine several genes simultaneously in the newer varieties. This approach of integration of gene editing and MAS increases genetic gain, reduces linkage drag, and cuts breeding cycles. A complementary and synergistic framework for creating rice varieties that are high-yielding, climate-resilient, and consumer-preferred is represented by the combination of MAS and gene editing

Future Perspectives

The combination of MAS and gene editing has brought revolutionary improvement in rice breeding program. The new superior alleles and new recombinants are being created by gene editing, while MAS displays the task of validating genes. Through GWAS and selection at the genomic level complex traits are being restructured. The newly developed varieties are more acceptable to consumers, farmers and Government as being free from transgenes. The new approaches of gene editing combined with MAS to develop high yielding, resistance to climate and diseases focuses a new breeding technology in rice improvement program.

CONCLUSION

The application of Marker-assisted breeding along with gene editing technology have provided a new way to develop modern varieties in rice through incorporation of important genes. Thus, precise and rapid addition and reconstruction of varieties are no longer a difficult task in rice breeding program enabling the way to overcome climate change and at the same time overcoming linkage drags and extending genetic resources. Thus, the strategy of MAS combined with gene editing program to develop new varieties has been proved to be essential to combat climate change and global food security in coming days.

ACKNOWLEDGEMENTS

The authors are grateful to RKMVERI for providing necessary support for writing the manuscript. The second (PR) and third author (SNM) enjoy fellowship from RKMVERI.

GENERATIVE AI DECLARATION

The author(s) confirm that there was no use of artificial intelligence (AI)-assisted technology for assisting in the writing or editing of the manuscript, and no images were manipulated using AI. The authors developed and verified all scientific content, data analysis, interpretation of results, and conclusions. The authors take full responsibility for the accuracy, integrity, and originality of the work presented, and no AI tool was listed as an author.

REFERENCES

Andaya, V. and Mackill, D. 2003. QTLs conferring cold tolerance at the booting stage of rice using recombinant inbred lines from a japonica× indica cross. *Theoretical and Applied Genetics*, **106**(6): 1084-1090.

Ashikari, M., Sakakibara, H., Lin, S., Yamamoto, T., Takashi, T., Nishimura, A., Angeles, E.R., Qian, Q., Kitano, H. and Matsuoka, M. 2005. Cytokinin oxidase regulates rice grain production. *Science*, **309**(5735): 741-745.

Bailey-Serres, J., Fukao, T., Ronald, P., Ismail, A., Heuer, S. and Mackill, D. 2010. Submergence tolerant rice: SUB1's journey from landrace to modern cultivar. *Rice*, **3**(2): 138-147.

Ballini, E., Morel, J.B., Droc, G., Price, A., Courtois, B., Notteghem, J.L. and Tharreau, D. 2008. A genome-wide meta-analysis of rice blast resistance genes and quantitative trait loci provides new insights into partial and complete resistance. *Molecular Plant-Microbe Interactions*, **21**(7): 859-868.

Bandyopadhyay, S. 2022. Screening for Bacterial Leaf Blight Resistant Genes in Some Rice Genotypes Using SSR Markers. *Current Journal of Applied Science and Technology*.

Bao, J. 2014. Genes and QTLs for rice grain quality improvement. *InTech–Open Science Open Mind*, pp. 239-278.

Bonilla, P.D., Mackell, D., Deal, K. and Gregorio, G. 2002. RFLP and SSLP mapping of salinity tolerance genes in chromosome 1 of rice (*Oryza sativa* L.) using recombinant inbred lines. *Philippine Agricultural Scientist (Philippines)*, **85**(1).

Bradbury, L.M., Henry, R.J., Jin, Q., Reinke, R.F. and Waters, D.L. 2005. A perfect marker for fragrance genotyping in rice. *Molecular Breeding*, **16**(4): 279-283.

Cao, W., Zhang, H., Zhou, Y., Zhao, J., Lu, S., Wang, X., Chen, X., Yuan, L., Guan, H., Wang, G. and Shen, W. 2022. Suppressing chlorophyll degradation by silencing

OsNYC3 improves rice resistance to Rhizoctonia solani, the causal agent of sheath blight. *Plant Biotechnology Journal*, **20**(2): 335-349.

Collard, B.C. and Mackill, D.J. 2008. Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**(1491): 557-572.

Dasgupta, T., Hossain, S.A., Meharg, A.A. and Price, A.H. 2004. An arsenate tolerance gene on chromosome 6 of rice. *New Phytologist*, pp. 45-49.

Dong, J., Ma, Y., Hu, H., Wang, J., Yang, W., Fu, H., Zhang, L., Chen, J., Zhou, L., Li, W. and Nie, S. 2024. The function of SD1 on shoot length and its pyramiding effect on shoot length and plant height in rice (*Oryza sativa* L.). *Rice*, **17**(1): 21.

Ellur, R.K., Khanna, A., Yadav, A., Pathania, S., Rajashekara, H., Singh, V.K., Krishnan, S.G., Bhowmick, P.K., Nagarajan, M., Vinod, K.K. and Prakash, G. 2016. Improvement of Basmati rice varieties for resistance to blast and bacterial blight diseases using marker assisted backcross breeding. *Plant Science*, **242**: 330-341.

Fan, C., Xing, Y., Mao, H., Lu, T., Han, B., Xu, C., Li, X. and Zhang, Q. 2006. GS3, a major QTL for grain length and weight and minor QTL for grain width and thickness in rice, encodes a putative transmembrane protein. *Theoretical and Applied Genetics*, **112**(6): 1164-1171.

Gregorio, G.B., Senadhira, D. and Mendoza, R.D. 1997. *Screening rice for salinity tolerance* (Vol. 22, No. 1, p. 30). IRRI discussion paper series.

Hospital, F. 2005. Selection in backcross programmes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**(1459): 1503-1511.

Iyer-Pascuzzi, A.S. and McCouch, S.R., 2007. Functional markers for xa5-mediated resistance in rice (Oryza sativa, L.). *Molecular Breeding*, **19**(4): 291-296.

Jia, Y., Wang, Z., Fjellstrom, R.G., Moldenhauer, K.A., Azam, M.A., Correll, J., Lee, F.N., Xia, Y. and Rutger, J.N. 2004. Rice Pi-ta gene confers resistance to the major pathotypes of the rice blast fungus in the United States. *Phytopathology*, **94**(3): 296-301.

Jiao, Y., Wang, Y., Xue, D., Wang, J., Yan, M., Liu, G., Dong, G., Zeng, D., Lu, Z., Zhu, X. and Qian, Q. 2010. Regulation of OsSPL14 by OsmiR156 defines ideal plant architecture in rice. *Nature Genetics*, **42**(6): 541-544.

Jiao, S., Li, Q., Zhang, F., Tao, Y., Yu, Y., Yao, F., Li, Q., Hu, F. and Huang, L. 2024. Artificial selection of the Green Revolution gene Semidwarf 1 is implicated in upland rice breeding. *Journal of Integrative Agriculture*, **23**(3): 769-780.

Khush, G.S. 2005. What it will take to feed 5.0 billion rice consumers in 2030. *Plant Molecular Biology*, **59**(1): 1-6.

Koyama, M.L., Levesley, A., Koebner, R.M., Flowers, T.J. and Yeo, A.R. 2001. Quantitative trait loci for component physiological traits determining salt tolerance in rice. *Plant Physiology*, **125**(1): 406-422.

Kumar, S., Dwivedi, S.K., Singh, S.S., Jha, S.K., Lekshmy, S., Elanchezhian, R., Singh, O.N. and Bhatt, B.P. 2014. Identification of drought tolerant rice genotypes by analysing drought tolerance indices and morpho-physiological traits. *SABRAO Journal of Breeding & Genetics*, **46**(2).

Kumar, I.S. and Nadarajah, K. 2020. A meta-analysis of quantitative trait loci associated with multiple disease resistance in rice (*Oryza sativa* L.). *Plants*, **9**(11): 1491.

Kumar, V., Jain, P., Venkadesan, S., Karkute, S.G., Bhati, J., Abdin, M.Z., Sevanthi, A.M., Mishra, D.C., Chaturvedi, K.K., Rai, A. and Sharma, T.R. 2021. Understanding rice-Magnaporthe oryzae interaction in resistant and susceptible cultivars of rice under panicle blast infection using a time-course transcriptome analysis. *Genes*, **12**(2): 301.

Ma, J.F., Yamaji, N., Mitani, N., Xu, X.Y., Su, Y.H., McGrath, S.P. and Zhao, F.J. 2008. Transporters of arsenite in rice and their role in arsenic accumulation in rice grain. *Proceedings of the National Academy of Sciences*, **105**(29): 9931-9935.

Majumder, K., Mondal, S.I., Mallick, R. and Dasgupta, T. 2020. Identification of BLB resistant genes in some rice varieties for development of high yielding bacterial leaf blight tolerant types. *Journal of Environmental Biology*, **41**(1): 85-91.

McCouch, S.R., Kochert, G., Yu, Z.H., Wang, Z.Y., Khush, G.S., Coffman, W.R. and Tanksley, S.D. 1988. Molecular mapping of rice chromosomes. *Theoretical and Applied Genetics*, **76**(6): 815-829

McCouch, S.R., Teytelman, L., Xu, Y., Lobos, K.B., Clare, K., Walton, M., Fu, B., Maghirang, R., Li, Z., Xing, Y. and Zhang, Q., 2002. Development and mapping of 2240 new SSR markers for rice (*Oryza sativa* L.). *DNA Research*, **9**(6): 199-207.

McCouch, S.R., Zhao, K., Wright, M., Tung, C.W., Ebana, K., Thomson, M., Reynolds, A., Wang, D., DeClerck, G., Ali, M.L. and McClung, A. 2010. Development of genome-wide SNP assays for rice. *Breeding Science*, **60**(5): 524-535.

McCough, S.R. and Doerge, R.W. 1995. QTL mapping in rice. *Trends in Genetics*, **11**(12): 482-487.

Meuwissen, T.H., Hayes, B.J. and Goddard, M. 2001. Prediction of total genetic value using genome-wide dense marker maps. *Genetics*, **157**(4): 1819-1829.

Misawa, S., Mori, N., Takumi, S., Yoshida, S. and Nakamura, C. 2000. Mapping of QTLs for low temperature response in seedlings of rice (*Oryza sativa* L.). *Cereal Research Communications*, **28**(1): 33-40.

Nandi, S., Subudhi, P.K., Senadhira, D., Manigbas, N.L., Sen-Mandi, S. and Huang, N. 1997. Mapping QTLs for submergence tolerance in rice by AFLP analysis and selective genotyping. *Molecular and General Genetics MGG*, **255**(1): 1-8.

Neelam, K., Aggarwal, S.K., Kumari, S., Kumar, K., Kaur, A., Babbar, A., Lore, J.S., Kaur, R., Khanna, R., Vikal, Y. and Singh, K. 2024. Molecular mapping and transfer of quantitative trait loci (QTL) for sheath blight resistance from wild rice *Oryza nivara* to cultivated rice (*Oryza sativa* L.). *Genes*, **15**(7): 919.

Ni, J., Colowit, P.M. and Mackill, D.J. 2002. Evaluation of genetic diversity in rice subspecies using microsatellite markers. *Crop Science*, **42**(2): 601-607.

NIÑO-LIU, D.O., Ronald, P.C. and Bogdanove, A.J. 2006. Xanthomonas oryzae pathovars: model pathogens of a model crop. *Molecular Plant Pathology*, **7**(5): 303-324.

Norton, G.J., Deacon, C.M., Xiong, L., Huang, S., Meharg, A.A. and Price, A.H. 2010. Genetic mapping of the rice ionome in leaves and grain: identification of QTLs for 17 elements including arsenic, cadmium, iron and selenium. *Plant and Soil*, **329**(1): 139-153.

Norton, G.J., Pinson, S.R., Alexander, J., Mckay, S., Hansen, H., Duan, G.L., Rafiqul Islam, M., Islam, S., Stroud, J.L., Zhao, F.J. and McGrath, S.P. 2012. Variation in grain arsenic assessed in a diverse panel of rice (*Oryza sativa*) grown in multiple sites. *New Phytologist*, **193**(3): 650-664.

Phing Lau, W.C., Latif, M.A., Y. Rafii, M., Ismail, M.R. and Puteh, A. 2016. Advances to improve the eating and cooking qualities of rice by marker-assisted breeding. *Critical Reviews in Biotechnology*, **36**(1): 87-98.

Qu, S., Liu, G., Zhou, B., Bellizzi, M., Zeng, L., Dai, L., Han, B. and Wang, G.L. 2006. The broad-spectrum blast resistance gene Pi9 encodes a nucleotide-binding site–leucine-rich repeat protein and is a member of a multigene family in rice. *Genetics*, **172**(3): 1901-1914.

Septiningsih, E.M., Pamplona, A.M., Sanchez, D.L., Neeraja, C.N., Vergara, G.V., Heuer, S., Ismail, A.M. and Mackill, D.J. 2009. Development of submergence-tolerant rice cultivars: the Sub1 locus and beyond. *Annals of Botany*, **103**(2): 151-160.

Shanmugavadivel, P.S., Prakash, C. and Mithra, S.A. 2019. Molecular approaches for dissecting and improving drought and heat tolerance in rice. In *Advances in rice research for abiotic stress tolerance* (pp. 839-867). Woodhead Publishing.

Sharma, T.R., Rai, A.K., Gupta, S.K. and Singh, N.K. 2010. Broad-spectrum blast resistance gene Pi-kh cloned from rice line Tetep designated as Pi54. *Journal of Plant Biochemistry and Biotechnology*, **19**(1): 87-89.

Shi, S., Wang, T., Chen, Z., Tang, Z., Wu, Z., Salt, D.E., Chao, D.Y. and Zhao, F.J. 2016. OsHAC1; 1 and OsHAC1; 2 function as arsenate reductases and regulate arsenic accumulation. *Plant Physiology*, **172**(3): 1708-1719.

Shirasawa, S., Endo, T., Nakagomi, K., Yamaguchi, M. and Nishio, T. 2012. Delimitation of a QTL region controlling cold tolerance at booting stage of a cultivar, 'Lijiangxintuanheigu', in rice, *Oryza sativa* L. *Theoretical and Applied Genetics*, **124**(5): 937-946.

Singh, N., Choudhury, D.R., Tiwari, G., Singh, A.K., Kumar, S., Srinivasan, K., Tyagi, R.K., Sharma, A.D., Singh, N.K. and Singh, R. 2016. Genetic diversity trend in Indian rice varieties: an analysis using SSR markers. *BMC Genetics*, **17**(1): 127.

Song, W.Y., Yamaki, T., Yamaji, N., Ko, D., Jung, K.H., Fujii-Kashino, M., An, G., Martinoia, E., Lee, Y. and Ma, J.F., 2014. A rice ABC transporter, OsABCC1, reduces arsenic accumulation in the grain. *Proceedings of the National Academy of Sciences*, **111**(44): 15699-15704.

Singh, R. and Sunder, S. 2015. Identification of sources of resistance to blast and false smut of rice and their management with fungicides. *Journal of Mycology and Plant Pathology*, **45**(1): 55.

Singh, V., Singh, A.P., Bhadoria, J., Giri, J., Singh, J., Vineeth, T.V. and Sharma, P.C. 2018. Differential expression of salt-responsive genes to salinity stress in salt-tolerant and salt-sensitive rice (*Oryza sativa* L.) at seedling stage. *Protoplasma*, **255**(6): 1667-1681.

Song, Z., Zheng, J., Zhao, Y., Yin, J., Zheng, D., Hu, H., Liu, H., Sun, M., Ruan, L. and Liu, F. 2023. Population genomics and pathotypic evaluation of the bacterial leaf blight pathogen of rice reveals rapid evolutionary dynamics of a plant pathogen. *Frontiers in Cellular and Infection Microbiology*, **13**: 1183416.

Sundaram, R.M., Vishnupriya, M.R., Laha, G.S., Rani, N.S., Rao, P.S., Balachandran, S.M., Reddy, G.A., Sarma, N.P. and Sonti, R.V. 2009. Introduction of bacterial blight resistance into Triguna, a high yielding, mid-early duration rice variety. *Biotechnology Journal: Healthcare Nutrition Technology*, **4**(3): 400-407.

Sundaram, R.M., Laha, G.S., Viraktamath, B.C., Sujatha, K., Natarajkumar, P., Hari, Y., Srinivasa Rao, K., Reddy, C.S., Balachandran, S.M., Madhav, M.S. and Hajira, S.K. 2011. Marker assisted breeding for development of bacterial blight resistant rice. *Genomics and Crop Improvement: Relevance and Reservations, Institute of Biotechnology, Acharya NG Ranga Agricultural University, Hyderabad*, **500**(030): 154-182.

Temnykh, S., Park, W.D., Ayres, N., Cartinhour, S., Hauck, N., Lipovich, L., Cho, Y.G., Ishii, T. and McCOUCH, S.R. 2000. Mapping and genome organization of microsatellite sequences in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, **100**(5): 697-712.

Thomson, M.J., de Ocampo, M., Egdane, J., Rahman, M.A., Sajise, A.G., Adorada, D.L., Tumimbang-Raiz, E., Blumwald, E., Seraj, Z.I., Singh, R.K. and Gregorio, G.B. 2010. Characterizing the Saltol quantitative trait locus for salinity tolerance in rice. *Rice*, **3**(2): 148-160.

Toojinda, T., Siangliw, M., Tragoonrung, S. and Vanavichit, A. 2003. Molecular genetics of submergence tolerance in rice: QTL analysis of key traits. *Annals of Botany*, **91**(2): 243-253.

Usman, B., Nawaz, G., Zhao, N., Liao, S., Liu, Y. and Li, R. 2020. Precise editing of the OsPYL9 gene by RNA-guided Cas9 nuclease confers enhanced drought tolerance and grain yield in rice (*Oryza sativa* L.) by regulating circadian rhythm and abiotic stress responsive proteins. *International Journal of Molecular Sciences*, **21**(21): 7854.

Vikram, P., Swamy, B.M., Dixit, S., Ahmed, H.U., Teresa Sta Cruz, M., Singh, A.K. and Kumar, A. 2011. qDTY 1.1, a major QTL for rice grain yield under reproductive-stage drought stress with a consistent effect in multiple elite genetic backgrounds. *BMC Genetics*, **12**(1): 89.

Willocquet, L., Fernandez, L. and Savary, S.J.P.P. 2000. Effect of various crop establishment methods practised by Asian

farmers on epidemics of rice sheath blight caused by Rhizoctonia solani. *Plant Pathology*, **49**(3): 346-354.

Xie, P., Liu, J., Lu, R., Zhang, Y. and Sun, X. 2022. Molecular evolution of the Pi-d2 gene conferring resistance to rice blast in Oryza. *Frontiers in Genetics*, **13**: 991900.

Xing, Y. and Zhang, Q. 2010. Genetic and molecular bases of rice yield. *Annual Review of Plant Biology*, **61**(1): 421-442.

Xu, K. and Mackill, D.J. 1996. A major locus for submergence tolerance mapped on rice chromosome 9. *Molecular Breeding*, **2**(3): 219-224.

Xu, Y., Beachell, H. and McCOUCH, S.R. 2004. A marker-based approach to broadening the genetic base of rice in the USA. *Crop Science*, **44**(6): 1947-1959.

Xu, K., Xu, X., Fukao, T., Canlas, P., Maghirang-Rodriguez, R., Heuer, S., Ismail, A.M., Bailey-Serres, J., Ronald, P.C. and Mackill, D.J. 2006. Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. *Nature*, **442**(7103): 705-708.

Yadav, S., Singh, U.M., Naik, S.M., Venkateshwarlu, C., Ramayya, P.J., Raman, K.A., Sandhu, N. and Kumar, A. 2017. Molecular mapping of QTLs associated with lodging resistance in dry direct-seeded rice (*Oryza sativa* L.). *Frontiers in Plant Science*, **8**: 1431.

Yuan, D.P., Zhang, C., Wang, Z.Y., Zhu, X.F. and Xuan, Y.H. 2018. RAVL1 activates brassinosteroids and ethylene signaling to modulate response to sheath blight disease in rice. *Phytopathology*, **108**(9): 1104-1113.

Zhao, K., Tung, C.W., Eizenga, G.C., Wright, M.H., Ali, M.L., Price, A.H., Norton, G.J., Islam, M.R., Reynolds, A., Mezey, J. and McClung, A.M. 2011. Genome-wide association mapping reveals a rich genetic architecture of complex traits in *Oryza sativa*. *Nature Communications*, **2**(1): 467.

Zheng, M.Z., Cai, C., Hu, Y., Sun, G.X., Williams, P.N., Cui, H.J., Li, G., Zhao, F.J. and Zhu, Y.G. 2011. Spatial distribution of arsenic and temporal variation of its concentration in rice. *New Phytologist*, **189**(1): 200-209.

Zhou, H., Xia, D., Zhao, D., Li, Y., Li, P., Wu, B., Gao, G., Zhang, Q., Wang, G., Xiao, J. and Li, X. 2021. The origin of Wxla provides new insights into the improvement of grain quality in rice. *Journal of Integrative Plant Biology*, **63**(5): 878-888.