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REVIEW ARTICLE

Marker-Assisted Breeding for Enhancing Stress Tolerance in Rice (*Oryza sativa* L.): A Review

Marium Khatun[1], F. M. Era[1], M. S. Raihan[1], Showkat A. Waza[2], Asma Majid[2], M. Rafiqul Islam[3] and A. K. M. Aminul Islam[1]*

[1]Department of Genetics and Plant Breeding, Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur, Bangladesh

[2]Division of Genetics and Plant Breeding, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir (SKUAST-K), Jammu & Kashmir, India

[3]International Rice Research Institute (IRRI), Los Banos, Philippines

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ABSTRACT

Rice productivity faces significant challenges from climate change and sudden outbreaks of pests and diseases. Conventional breeding alone struggles to produce stress-resistant varieties, making marker-assisted breeding (MAB) a valuable complement. MAB enhances conventional breeding by employing molecular markers tightly linked to target genes, increasing efficiency without entirely replacing traditional methods. This review evaluates gene introgression effects and the role of MAB in improving rice productivity based on secondary data sources. Notable gene targets include *Xa4*, *Xa5*, *Xa13*, *Xa21* and *Xa27* for bacterial blight; *Pi2*, *Pi5*, *Pi9* and QTLs on chromosomes 1, 2, 11 and 12 for blast resistance; *Gm1* and *Gm4* for gall midge; *Saltol* for salinity tolerance; *qDTY1.1*, *qDTY2.1* and *qDTY3.1* for drought tolerance; *Sub1A* for submergence; and *yld1.1*, *yld2.1* and *GW6* for yield enhancement. Introgressing these genes has led to the development of resilient rice lines capable of thriving under biotic and abiotic stresses, with notable increases in yield over susceptible recurrent parents. For instance, the introgression line *DHA-10* (5.68 t/ha) yields more than its parent *BPT5204* (4.97 t/ha), while the submergence-tolerant *BR9157-12-2-37-13-17* produces 3.44 t/ha, outperforming *BRRI dhan33* (1.73 t/ha). These cases illustrate the transformative impact of MAB in developing high-yielding, resilient rice varieties, underscoring its invaluable role in enhancing rice productivity under diverse stress conditions.

Keywords: Marker-assisted breeding (MAB), Rice (*Oryza sativa* L.), Stress tolerance, Gene introgression, Yield enhancement

INTRODUCTION

Rice (*Oryza sativa* L.) is a primary staple crop, vital to the food security of over half the world's population, particularly in Asia and Africa, where it is fundamental to dietary intake and economic stability (Suela *et al.,* 2019). Globally, rice supplies nearly one-fifth of caloric intake and contributes around 15% of dietary protein, underscoring its importance in global nutrition (FOA, 2004). Originating in Southeast Asia, rice cultivation has expanded worldwide, with China, India and Bangladesh currently leading in production,

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*Corresponding author mail: aminulgpb@bsmrau.edu.bd

reporting outputs of 146.73, 118.00 and 35.85 million metric tons, respectively. These countries achieve average yields of 7.06, 4.02 and 4.55 metric tons per hectare from cultivation areas spanning 29.69, 44.00 and 11.83 million hectares, respectively (USDA, 2020). However, rice production's challenges are intensifying with accelerated industrialization, urbanization and population growth. The availability of arable land is decreasing, resulting in agricultural areas being repurposed for non-agricultural use. This is particularly concerning as rice yield growth stagnates in regions like Bangladesh, where yields average only 4.5 t/ha (BRRI, 2018). Additionally, rice breeders face mounting pressures fof various biotic and abiotic stresses exacerbated by climatic variability.

Rice production is vulnerable to a multitude of stress factors. Biotic stresses—including pathogens and pests endemic to tropical rice ecosystems—impose substantial yield losses. Major diseases like bacterial blight, rice blast and sheath blight, as well as insect pests such as stem borers, brown plant hopper and leaf folders, significantly compromise rice productivity (Peng, 2003; Khush & Virk, 2005; Jiang *et al.,* 2012). On the other hand, abiotic stresses, such as drought, flooding, salinity and extreme temperatures, are equally detrimental to rice yield, particularly under rainfed conditions where farmers have limited control over water availability (Wang *et al.,* 2003; Das and Rao, 2015; Dar *et al.,* 2017; Dar *et al.,* 2020). For instance, Bailey-Serres *et al.* (2012) reported that drought and submergence collectively caused a 70% harvest failure rate in 2011, underscoring the severity of these challenges.

The increasing prevalence of biotic and abiotic stresses, compounded by the impacts of climate change, necessitates the development of resilient rice varieties. Given the extended time frames (10–12 years) and costs associated with conventional breeding methods, accelerating the breeding cycle is crucial (Collard & Mackill, 2008). Conventional breeding approaches often fail to entirely eliminate undesirable alleles from breeding lines, which can be inadvertently retained across generations. Addressing these limitations, breeders now employ marker-assisted breeding (MAB) to enhance selection efficiency and precision. Marker-assisted breeding (MAB) leverages molecular markers linked to target traits, facilitating the rapid and precise introgression of desirable genes while reducing the number of backcross generations needed (Hasan *et al.,* 2015). DNA markers are especially valuable in removing unwanted genes tightly linked to target loci, allowing breeders to enhance specific regions of the rice genome with greater accuracy (Kottearachchi, 2013). Compared to traditional methods, MAB is cost-effective and significantly reduces the time required to develop stress-resilient varieties, making it a more sustainable and economical approach. Through marker-assisted selection (MAS), breeders can pyramid multiple stress-resistant genes into a single genotype, thus achieving broader resilience against biotic and abiotic stresses (Das and Rao, 2015; Dar *et al.,* 2018; Chukwu *et al.,* 2019; Dar *et al.,* 2021).

This review examines the role of marker-assisted selection in enhancing rice productivity by introgressing stress-resistant genes, highlighting MAB's capacity to overcome the limitations of conventional breeding and foster the development of climate-resilient, high-yielding rice varieties.

Why Marker Assisted Breeding?

Marker-assisted breeding (MAB) serves as a complementary approach to traditional breeding, enhancing its efficiency and effectiveness rather than replacing it (Chukwu *et al.,* 2019). Introduced in the 1990s, molecular selection techniques have revolutionized rice breeding by enabling precise identification and selection of desirable traits, accelerating breeding timelines and improving productivity (Jonas and Koning, 2013). The impacts of climate change have exacerbated the prevalence and severity of both biotic and abiotic stresses, posing serious challenges like drought, salinity and temperature extremes contribute to substantial yield losses (Table 1). MAB addresses these issues by allowing breeders to incorporate stress-resistance genes more efficiently, thereby developing resilient varieties that can withstand the increasing environmental pressures brought from a changing climate.

To address the pressing challenges posed by climate change, emerging biotic and abiotic stresses, and the need to secure food for a growing population, rice breeders are actively engaged in targeted research efforts (Nogoy *et al.,* 2016). Using molecular markers, breeders have identified numerous stress-resistance

Table 1. Reports related to the consequences of biotic and abiotic stresses in rice cultivation

Stresses	Causes	Consequences	References
Bacterial Blight	*Xanthomonas oryzae pv.oryzae*	Partial grain filling leads to severe yield loss	Pradhan *et al.* (2015)
Blast	*Magnaporthe grisea*	70–80% yield loss during severe condition	Babujee and Gnanamanickha (2000)
Gall Midge	*Orseolia oryzae*	0.8% yield losses of total production	Biradar *et al.* (2004)
Stem borer	*Scirpophaga incestuous* (yellow), *S. innotata* (white)	Deadheart and whitehead, reduced plant vigor	Nogoy *et al.* (2016)
Submergence	Rain-fed lowland conditions	Hamper growth and average productivity	Das and Rao (2015)
Salinity	Saline containing water (Sodium), in the southern region	>50% yield losses	Molla *et al.* (2015)
Drought	Shortage of rainfall	Severe yield loss	Das *et al.* (2017)

Table 2. QTLs/genes reported to overcome the stress-related problems in rice

QTLs/genes reported	References
42 bacterial blight resistance genes, such as *Xa5, Xa13, Xa21, Xa17, Xa29(t), Xa42* etc.	Chukwu *et al.* (2019)
100 blast resistance genes but 14 genes widely used namely, *Pi1, Pi2, Pi9, Pi20 (t), Pi33, Pi39, Pi40 (t), Pi47, Pi48, Pi54rh, Pi56, Piz, Piz-t*, and *Pigm*	Hayashi *et al.* (2010); Huang *et al.* (2011); Das et *al.* (2012); Hua et *al.* (2015); Liu et *al.* (2013)
11 gall midge resistance genes	Dutta *et al.* (2014); Hasan *et al.* (2015)
Submergence1 (*Sub1*) in chromosome 9 for submergence tolerance	Septiningsih *et al.* (2013); Manivong *et al.* (2014)
Saltol for salinity tolerance	Das and Rao (2015)
Dreb1, qDTY1.1, qDTY2.1, qDTY3.1, QTLs for drought tolerance	Reddy et *al.* (2009); Lin et *al.* (2007); Das et *al.* (2017); Sandhu et *al.* (2019)

genes, facilitating the development of rice varieties that are more resilient and better suited to withstand the complex environmental pressures (Table 2).

Developing highly resistant rice varieties is a crucial strategy to combat the anticipated stresses associated with climate change. To achieve this, it is essential to compile a robust set of resistance genes within a single genotype that can perform consistently across diverse climatic conditions (Das and Rao, 2015). Marker-assisted breeding (MAB) enables breeders to efficiently incorporate target genes early in the breeding process, allowing for rapid development of varieties with strong, broad-spectrum resistance to both biotic and abiotic stresses with greater precision (Das et *al.,* 2017).

Types of Markers used in Marker Assisted Breeding

According to Chukwu *et al.* (2019), there are three primary types of markers used for identifying genes of interest in rice breeding: morphological markers, biochemical markers and molecular markers. Among these, molecular markers—also referred to as DNA-based markers—are particularly advantageous due to their ability to scan the entire rice genome and provide high-density coverage of each chromosome (Akhtar *et al.,* 2010). Molecular markers can be further categorized into two main types based on detection methods: PCR-based markers and hybridization-based markers (Yang *et al.,* 2015). Molecular markers are widely preferred in rice breeding due to their high precision and flexibility. Their number is virtually unlimited, allowing for comprehensive genome-wide scanning and enabling high-resolution mapping of traits. The genetic distance between markers should be less than 5 cM for effective phenotypic prediction in rice. Additionally, intragenic markers improve reliability by closely associating markers with phenotypic traits, making them highly effective in rice breeding programs.

Examples of commonly used DNA-based markers in rice include RG556, pTA 248, Xa13prom, RG64, P28, RM444, RM547, SUB1BC2, RM10745, Os01g0197700, RM212 and RM319. These markers are used for selecting genes linked to resistance against various biotic and abiotic stresses, ultimately improving the resilience and productivity of rice (Das *et al.,* 2017).

Conventional Breeding vs Marker-Assisted Breeding

While markers can be applied at any stage of the breeding process, their benefits are most pronounced during early-stage selection. By identifying and discarding undesirable lines in initial generations, marker-assisted breeding (MAB) allows breeders to focus resources on more promising lines compared to conventional methods (Akhtar *et al.,* 2010). Ribaut and Betrán (1999) demonstrated that MAB enables efficient early-generation selection, reducing the number of lines requiring evaluation in later stages. In conventional breeding approaches such as bulk or single seed descent, homozygous lines are typically selected at advanced generations (e.g., F_5 or F_6). However, with MAB, breeders can screen for homozygous lines as early as the F_2 generation by targeting and fixing specific alleles, thereby expediting the breeding process (Fig. 1).

Marker Assisted Gene Pyramiding

Incorporating multiple resistance or tolerance genes into a single genotype is known as gene pyramiding (Collard and Mackill, 2008). This approach is essential for enhancing the durability of resistance and minimizing the risk of resistance breakdown, especially under escalating biotic and abiotic pressures. Molecular markers enable precise selection in gene pyramiding, making it a feasible strategy within marker-assisted breeding (MAB) frameworks (Das and Rao, 2015). According to Das *et al.* (2017), marker-assisted gene pyramiding generally involves two critical steps. The first is the *accumulation step*, where all genes of interest (GOI) are sequentially introduced into a single genotype. The second is the *fixation step*, wherein the accumulated genes are converted into a homozygous state, ensuring stable inheritance.

An example of successful gene pyramiding is provided by Luo *et al.* (2016), who introduced the resistance genes *Xa4* and *Xa21* into the variety Mianhui 725, creating a new line, Wanhui 421, with 96.9% genetic similarity to Mianhui 725 through marker-assisted backcrossing. Wanhui 421 (*Xa4, Xa21*) was then crossed with IRBB27 (*Xa27*) and other

Fig. 1. Conventional breedingassisted marker-assisted breeding

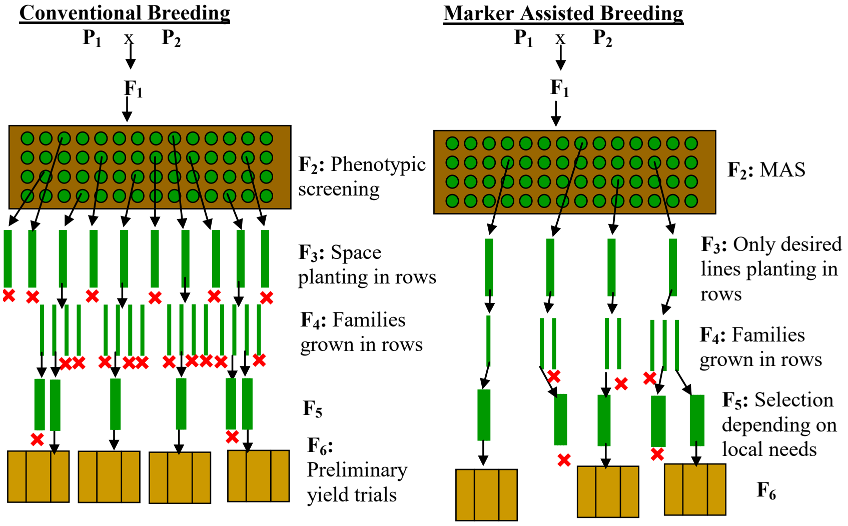
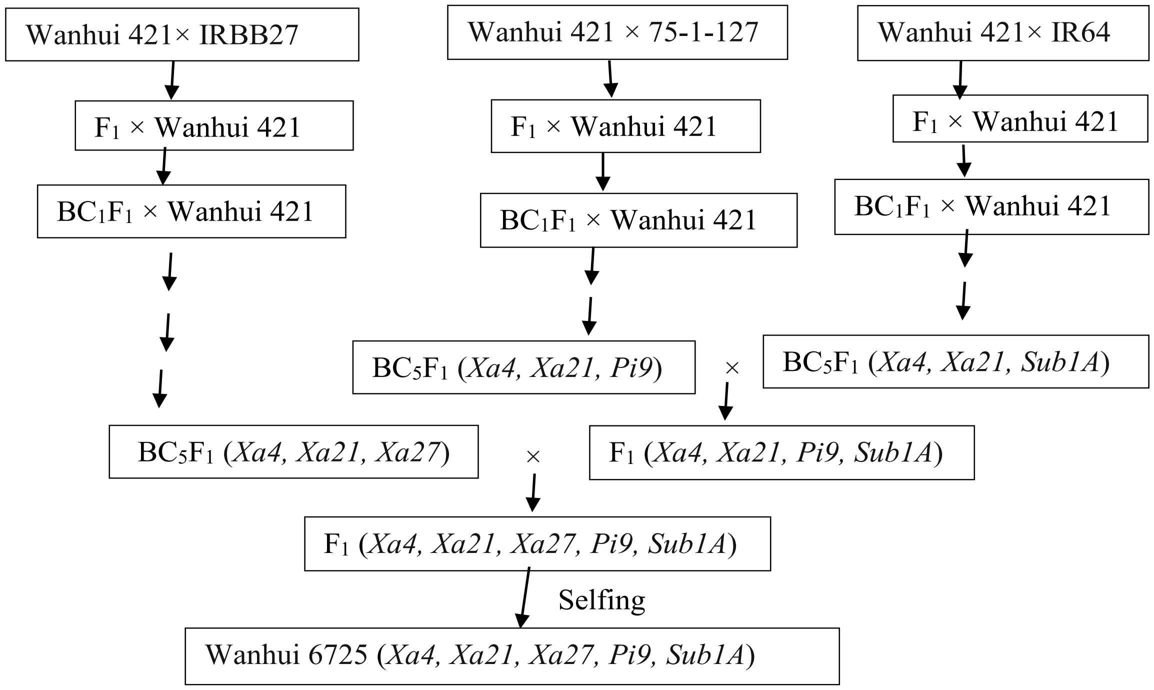


Fig. 2. Marker-assisted backcrossing for accumulating different resistance genes in one genotype.



lines, resulting in various F1 generations containing combinations of resistance genes: (*Xa4, Xa21, Xa27*), (*Xa4, Xa21, Pi9*), and (*Xa4, Xa21, Sub1A*). A high genetic similarity was achieved through multiple backcrosses (five generations) with the recurrent parent Wanhui 421, while maintaining the desired resistance genes. Further crossings and selfing of F1 generations led to F2 progeny carrying a pyramided set of genes (*Xa4, Xa21, Xa27, Pi9, Sub1A*), enhancing resistance and stabilizing the genotype for field deployment. This strategy exemplifies the precision and efficiency of MAB in developing resilient rice varieties through gene pyramiding (Fig. 2).

Marker Assisted Gene Introgression: Case Studies

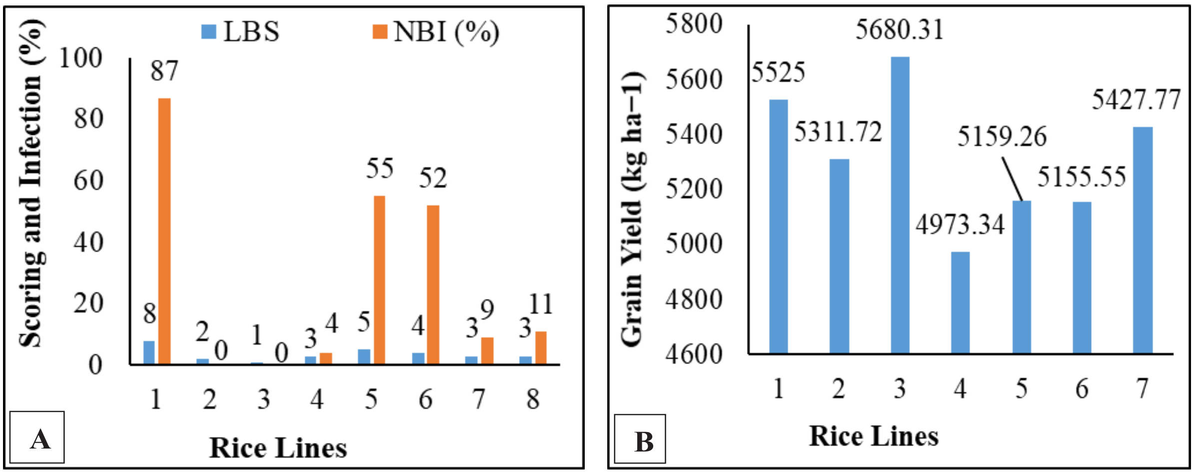
Bacterial Blight (BB) Resistance Genes Introgression

According to Luo *et al.* (2016), the introgression line Wanhui 6725 (*Xa4, Xa21, Xa27, Pi9, Sub1A*) and its hybrid, II-32A/WH6725, exhibit resistance to 27 *Xanthomonas oryzae* pv. *oryzae* (Xoo) strains originating from 10 countries. In contrast, the recurrent parent Mianhui 725, its hybrid II-32A/MH725 and the CMS line II-32A show susceptibility to 26, 23 and 24 Xoo strains, respectively. Wanhui 421 (*Xa4, Xa21*) and IRBB27 (*Xa27*) displayed moderate resistance to 22

Table 3. Resistance score of 7 lines against 5 *Xanthomonas oryzae pv. Oryzae* strains originated from China and India

Rice Lines	Strain from China			Strain from India	
	HB17	HB21	JS49-6	A3842	A3857
Mianhui 725	Susceptible	Susceptible	Susceptible	Susceptible	Susceptible
II-32A/MH725	Susceptible	Susceptible	Susceptible	Susceptible	Susceptible
Wanhui 421	Moderately Resistant	Moderately Resistant	Resistant	Susceptible	Moderately Resistant
Wanhui 6725	Resistant	Resistant	Resistant	Resistant	Resistant
II-32A/WH6725	Resistant	Resistant	Resistant	Resistant	Resistant
II-32A	Susceptible	Susceptible	Susceptible	Susceptible	Susceptible
IRBB27	Resistant	Resistant	Resistant	Resistant	Resistant

Fig. 3. Evaluation of rice lines against blast.



A. Blast scoring and Results of Infection (%) (resistant: 1–3, susceptible: 4-9); 1. Feng39S; 2. Hua1201S; 3. DB16206–34; 4. DB16206–38; 5. 9311; 6. Feng39S/9311; 7. DB16206–34/9311; 8. DB16206–38/9311; LBS. Leaf blast score; NBI (%). Neck blast infection (%) (Yang et al., 2019).

B. Performance for Yield; 1. DHA-1; 2. DHA-2; 3. DHA-10; 4. BPT5204; 5. DHB-19; 6. DHB-25; 7. DHB-27 (KrishnaMurthy et al., 2017)

and 24 Xoo strains, respectively (Table 3). Disease scoring for bacterial blight (BB) is based on lesion length (LL). LL ≤3.0 cm indicates resistance (R); 3.0 cm < LL ≤ 6.0 cm indicates moderate resistance (MR); 6.0 cm < LL ≤ 9.0 cm indicates moderate susceptibility (MS), and LL > 9.0 cm indicates susceptibility (S).

Blast Resistance Genes Introgression

According to Yang *et al.* (2019), the blast-resistant gene (*Pi2*) from the donor parent, Hua1201S, was introduced into the recipient line, Feng39S, through marker-assisted backcrossing, resulting in the BC_2F_5 lines DB16206–34 and DB16206–38. Markers were employed at each step to select the desirable lines. The male parent, 9311, which is susceptible to blast, was used to produce hybrids. An evaluation trial in China (2018) assessed resistance to leaf and neck blast (Fig. 3A). Hua1201S showed a leaf blast score of 2, while DB16206–34, DB16206–38 and their hybrids (DB16206–34/9311 and DB16206–38/9311) exhibited resistance with scores of 1, 3 and 3, respectively. Conversely, Feng39S, 9311 and their hybrid (Feng39S/9311) displayed susceptibility with scores of 5, 8 and 4, respectively, and high susceptibility to neck blast, with infection rates ranging from 52% to 87%. Hua1201S, DB16206–34, DB16206–38 and their hybrids showed resistance to neck blast, with little or no infection.

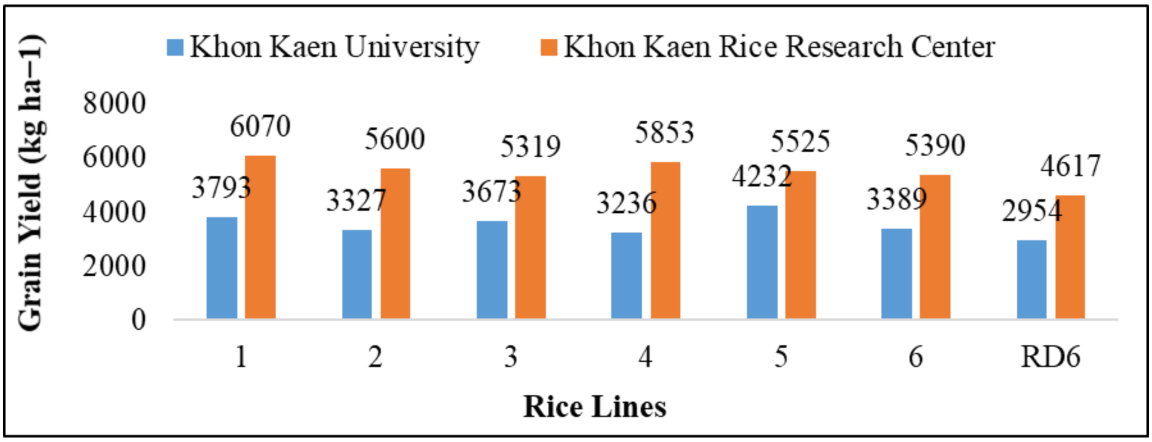
Similarly, KrishnaMurthy *et al.* (2017) reported that the popular but blast-susceptible variety Samba Mahsuri (BPT5204) was improved by introgressing *Pi2* and *Pi5* genes from C101A51 and IRBL-5M through MAB. The *Pi2* (DHA-1, DHA-2, DHA-10) and *Pi5* (DHB-19, DHB-25, DHB-27) introgressed lines demonstrated higher yields than the recurrent parent BPT5204, with DHA-10 achieving the highest yield (5,680 kg ha^{-1}) compared to BPT5204 (4,973 kg ha^{-1}) (Fig. 3B).

Nan *et al.* (2019) conducted an experiment at Khon Kaen University (KKU) and Khon Kaen Rice Research Center (KKRRC) in Thailand. They pyramided blast-resistant QTLs from Jao Hom Nin (on chromosomes 1 and 11) and P0489 (on chromosomes 2 and 12), along with the bacterial blight resistance gene *Xa*5 from IR62266, into the rice variety RD6. Using marker-assisted backcrossing, they developed introgression lines that showed higher grain yields than the recurrent parent RD6 (Fig. 4). Among these, the BC_2F_3 line 2-8-2-36 achieved the highest yield compared to other lines and the recurrent parent.

Gall midge Resistance Gene Introgression

Das and Rao (2015) report the development of ILGP (Improved Line for Gall Midge Resistance) lines, achieved by pyramiding resistance genes such as *Gm1* and *Gm4*, originally derived from cultivars Kavya and

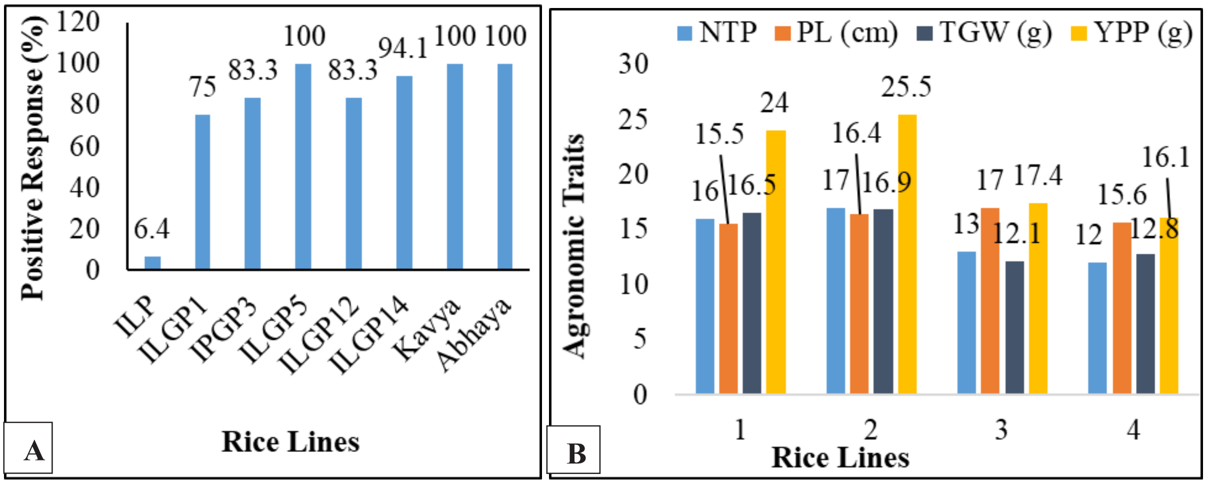
Fig. 4. Performance of 6 introgression lines including recurrent parent for yield at two locations.



1. BC2F3 2-8-2-36; 2. BC2F3 2-7-5-43; 3. BC2F3 2-8-2-19; 4. BC2F3 2-8-2-25; 5. BC2F3 9-1/15-1-28; 6. BC2F3 2-8-2-27 (Nan et al., 2019)

Abhaya, respectively. These lines exhibited a significant positive response to gall midge infestation, ranging from 75% to 100%, with Kavya (*Gm1*) and Abhaya (*Gm4*) showing close to 100% resistance. In contrast, the recurrent ILP parent line remains susceptible to gall midge, displaying only about 6.8% resistance (Fig. 5A). Kumar *et al.* (2017) further advanced a stable restorer line, RPHR-1005, used in the hybrid DRRH-3, by incorporating bacterial blight and gall midge resistance genes through marker-assisted breeding (MAB). This was accomplished by crossing Improved Samba Mahsuri (ISM), possessing the *Xa21* gene for bacterial blight resistance, with Abhaya (*Gm4*) and Aganni (*Gm8*) for gall midge resistance. Resulting lines SM1 (*Xa21, Gm4*) and SM2 (*Xa21, Gm8*) served as donors to RPHR-1005, enhancing its resilience against these stresses. Additionally, the introgression line RPIC-16-65-125 demonstrated superior performance in yield and yield-related traits over both its recurrent and donor parents (Fig. 5B). This combination of gene pyramiding and marker-assisted selection demonstrates the effectiveness of integrating multiple

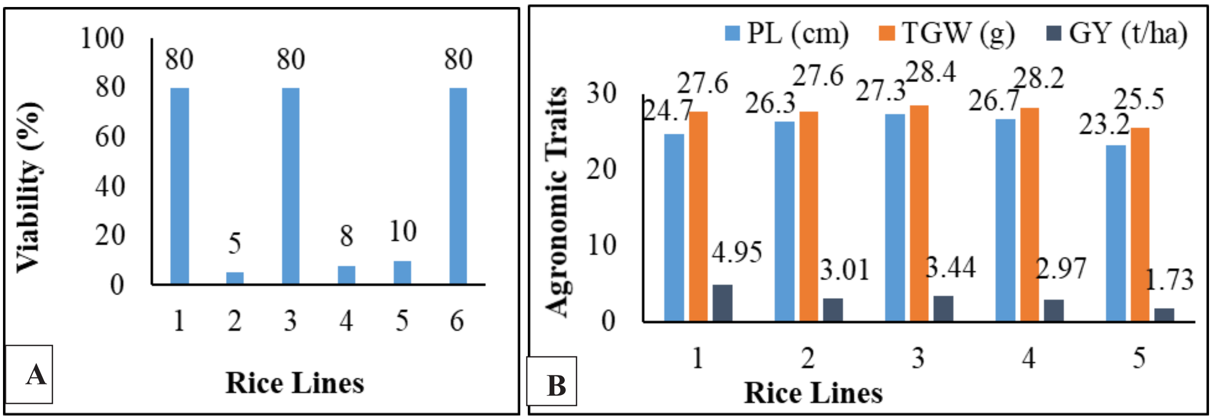
Fig. 5. Evaluation of rice lines against gall midge



A. Positive Response (%); ILP. Improved Lalat Parent; ILGP. Improved Lalat Gene Pyramid) (Das and Rao, 2015).

B. Agronomic Performance; 1. RPHR-1005; 2. RPIC-16-65-125; 3. SM1 (ISM/Abhaya); 4. SM2 (ISM/Aganni); NTP. No. of productive tillers/plant; PL. Panicle length (cm); TGW. 1000 grain weight (g); YPP. Yield per plant (g) (Kumar et al., 2017).

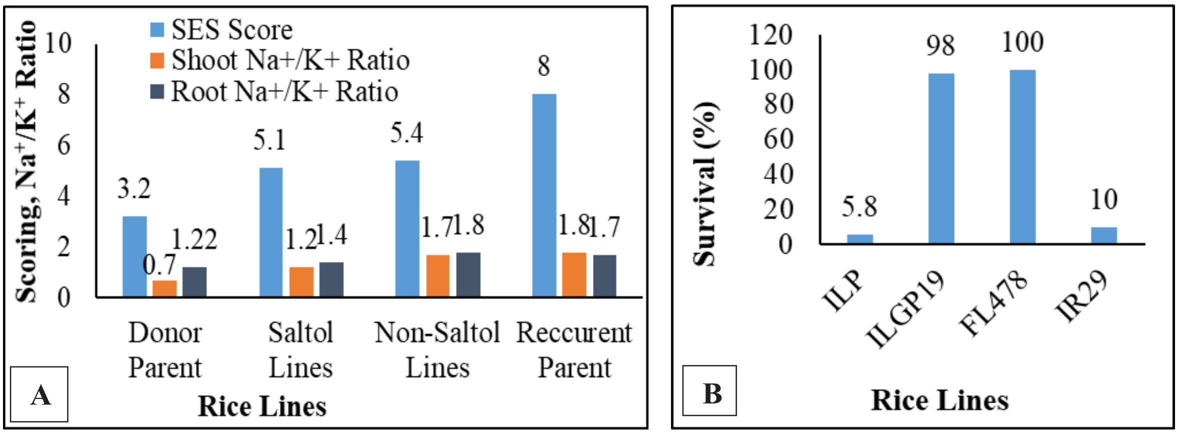
Fig. 6. Tolerance capacity of rice lines after recovery from two weeks of submergence.



A. Viability % (1. IR64; 2. MH725; 3. WH6725; 4. II-32A; 5. II-32A/MH725; 6. II-32A/WH6725) (Luo et al., 2016).

B. Agronomic Performance under field conditions (1. BRRI dhan52; 2. BR9157-12-2-37-13-15; 3. BR9157-12-2-37-13-17; 4. BR9157-12-2-37-13-71; 5. BRRI dhan33; PL. Panicle length (cm); TGW. 1000 grain weight (g); GY. Grain yield (t/ha) (Iftekharuddaula et al., 2016).

Fig. 7. Evaluation of rice lines for salinity tolerance.



A. Comparison for SES score, shoot Na^+/K^+ ratio and root Na^+/K^+ ratio (Thomson et al., 2010).

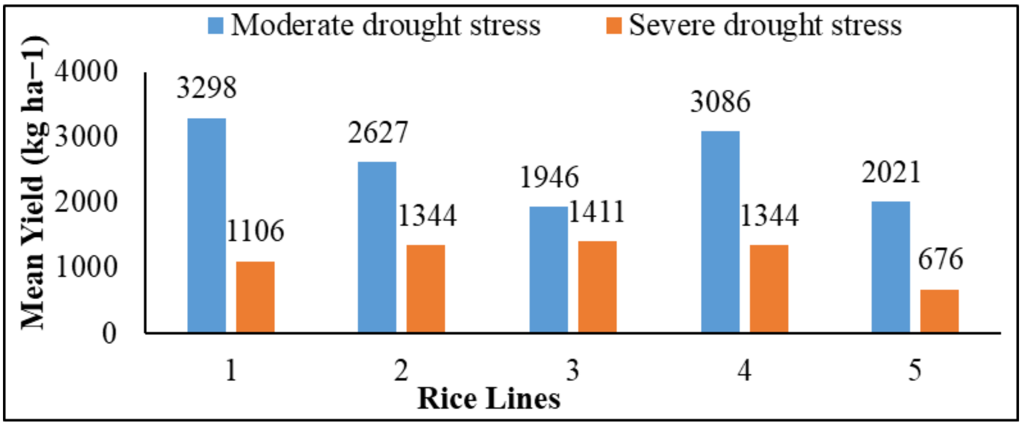
B. Survival percentage against salinity stress (ILP. Improved Lalat Parent; ILGP. Improved Lalat Gene Pyramid) (Das and Rao, 2015).

resistance genes to improve crop resilience against specific pests and diseases.

Submergence Tolerance Gene Introgression

Luo *et al.* (2016) described the introgression line Wanhui 6725, which contains multiple resistance genes (*Xa4*, *Xa21*, *Xa27*, *Pi9*, and *Sub1A*) and its hybrid II-32A/WH6725, both of which demonstrated tolerance to two weeks of submergence. This tolerance is also observed in the donor parent, IR64 (*Sub1A*), which exhibits high viability and robust recovery following submergence. In contrast, the recipient parent, Mianhui 725, its hybrid II-32A/MH725 and the CMS line II-32A are susceptible to submergence, with poor recovery and often leading to high mortality or poor plant health post-submergence (Fig. 6A). Wanhui 6725, II-32A/WH6725 and IR64 show approximately 80% survival rate post-submergence recovery, underscoring the effectiveness of the *Sub1A* gene in improving submergence tolerance.

Fig. 8. Mean yield performance of rice lines under moderate and severe drought in field conditions



(1. IR 96321-1447-651-B-1-1-2; 2. IR 96321-558-563-B-2-1-1; 3. IR 96322-34-260-B-5-1-1; 4. IR 96322-34-223-B-1-1-1 and 5. Swarna) (Sandhu et al., 2019).

Iftekharuddaula *et al.* (2016) further highlight the introgression of the *SUB1* gene into BRRI dhan33 from BRRI dhan52 using marker-assisted breeding (MAB). This enhancement led to the development of three promising introgression lines: BR9157-12-2-37-13-15, BR9157-12-2-37-13-17 and BR9157-12-2-37-13-71. These lines exhibit an increased yield advantage of 1.24–1.71 t/ha over the recurrent parent and outperform it in key agronomic traits (Fig. 6B).

Salinity Tolerance Gene Introgression

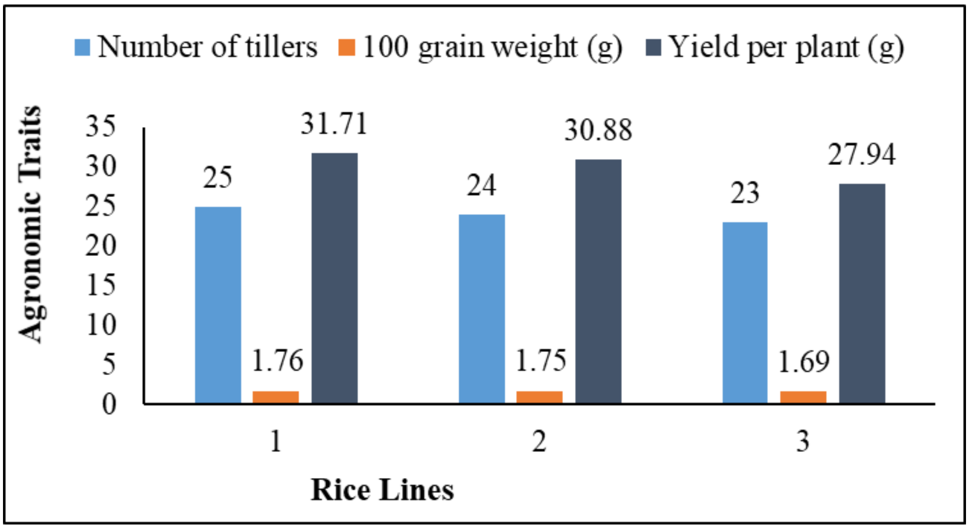
Thomson *et al.* (2010) reported significant differences in salt tolerance traits between the donor parent FL478 (*IR 66946-3R-178-1-1*) and the recurrent parent IR29. FL478, a salt-tolerant line, shows a lower SES (Standard Evaluation System) score and reduced Na+/K+ ratios in both shoots and roots compared to IR29, which is sensitive to salt stress (Fig. 7A). Consequently, salt-tolerant *Saltol* introgression lines derived from FL478 exhibit enhanced yield under salinity stress, yielding 24-33% more than IR29. These lines maintain about 20% more yield under saline conditions relative to non-stressed conditions. This study utilized SSR markers to select for salt tolerance traits, with seedlings evaluated in a hydroponic system at 12 dS m^{-1} EC. Das and Rao (2015) also highlight the robustness of *Saltol* introgression lines under severe salinity, noting survival capacities of up to 98% for lines like ILGP, compared to only 5.8% for the recurrent parent ILP, which carries bacterial blight resistance genes (*Xa4*, *Xa5*, *Xa13* and *Xa21*). FL478 achieves 100% survival under salinity stress, whereas IR29, being highly susceptible, shows minimal survival. These findings underscore the value of salt tolerance breeding through *Saltol* gene introgression for enhancing resilience in saline-prone rice cultivation areas.

Drought Tolerance Gene Introgression

Sandhu *et al.* (2019) reported the successful development of drought-tolerant rice lines by introgressing *qDTY1.1*, *qDTY2.1* and *qDTY3.1* quantitative trait loci (QTLs) into the high-yielding but drought-sensitive variety Swarna. These introgression lines include IR 96321-1447-651-B-1-1-2 (*qDTY1.1*, *qDTY3.1*), IR 96321-558-563-B-2-1-1 (*qDTY3.1*), IR 96322-34-260-B-5-1-1 (*qDTY1.1*, *qDTY2.1*, *qDTY3.1*) and IR 96322-34-223-B-1-1-1 (*qDTY1.1*, *qDTY2.1*, *qDTY3.1*). These lines show improved yield performance under both moderate and severe drought conditions compared to the recurrent parent, Swarna (Fig. 8). In severe drought, IR 96322-34-260-B-5-1-1 achieved the highest yield of 1,411 kg/ha, while under moderate drought, IR 96321-1447-651-B-1-1-2 demonstrated the best performance with a yield of 3,298 kg/ha. In contrast, the drought-susceptible Swarna produced significantly lower yields under both the stress conditions. These results highlight the effectiveness of marker-assisted selection in pyramiding multiple drought-resistance QTLs, which can significantly enhance drought resilience and yield stability in rice varieties tailored for drought-prone regions.

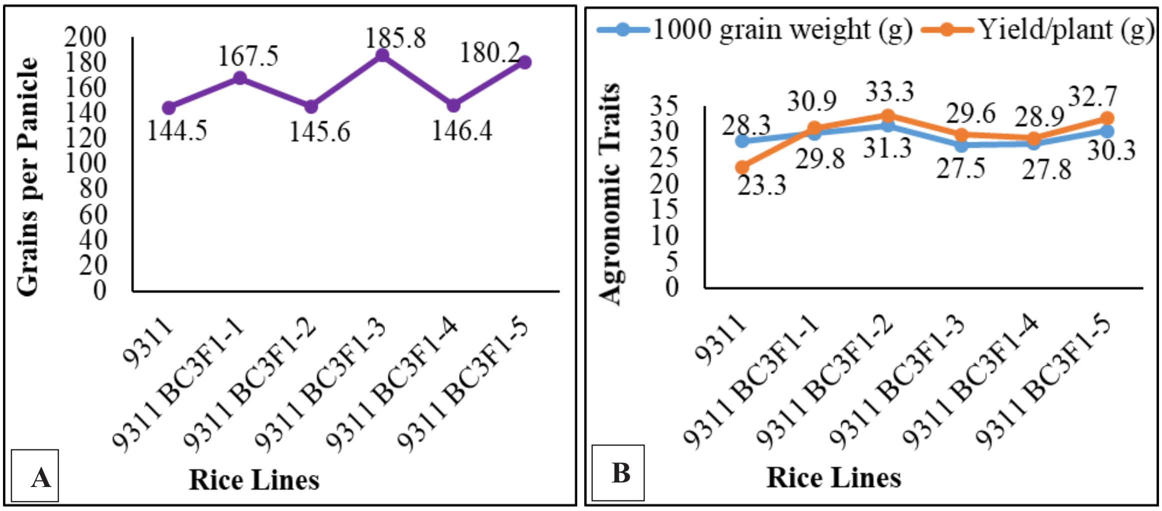
According to Muthu *et al.* (2020), a popular rice variety, Improved White Ponni (IWP) is introgressed with the abiotic stress tolerant genes for drought

Fig. 9. Performance of rice lines for yield and yield related traits under field conditions



(1. BIL 3-11-11-2; 2. BIL 3-11-9-2; 3. Improved White Ponni (IWP)) (Muthu et al., 2020).

Fig. 10. Effects of yield enhancing genes for yield and yield related traits



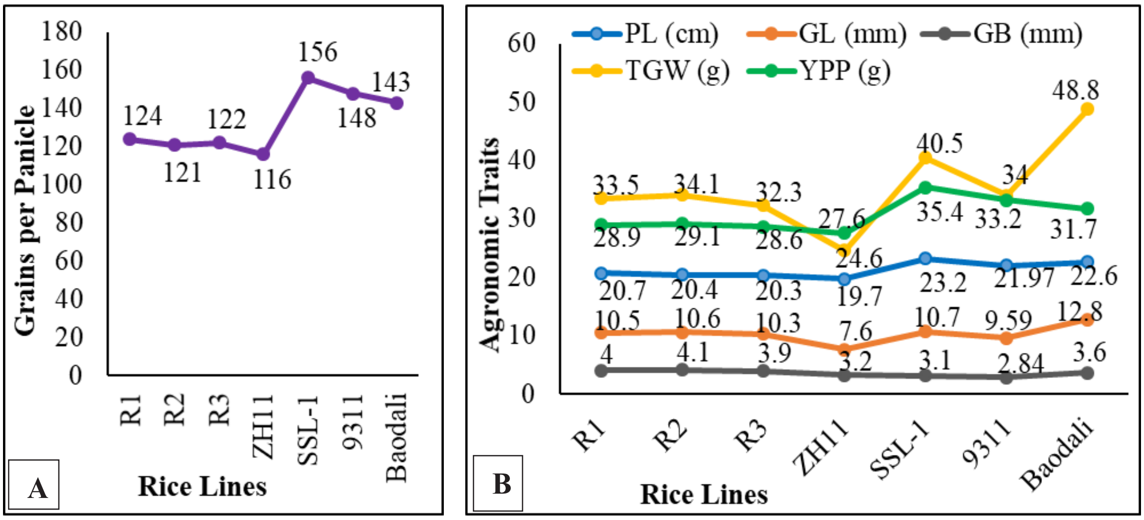
A. Grains per Panicle; B. 1000 grain weight and yield per plant (Liang et al., 2004).

(*qDTY1.1*, *qDTY2.1*), salinity (*Saltol*) and submergence (*Sub1*) through MAB from Apo, Pokkali FL478 and FR13A, respectively. Backcrossed inbred lines (BILs) (3-11-11-1, 3-11-11-2) gather all four resistant genes showing better performance for yield and yield related traits than the recipient parent IWP (Fig. 9).

Yield Enhancing Gene Introgression

Liang *et al.* (2004) utilized *Oryza rufipogon* (IRGC 105491) as a donor parent for introducing yield-enhancing genes (*yld1.1* and *yld2.1*) into the popular hybrid rice parent line 9311 in China. The introgression lines developed showed improved yield and yield-related traits compared to 9311, which served as the recurrent parent. Marker-assisted selection (MAS) was used to screen five BC_3F_1 lines, all of which demonstrated superior performance in terms of grains per panicle, surpassing 9311 (Fig. 10A). Additionally, most BC_3F_1 lines had higher thousand-grain weight than 9311. Yield per plant was also enhanced, with the derived lines achieving more than 28 g/plant, in contrast to 9311's yield of 23 g/plant (Fig. 10B). This study emphasizes the potential of incorporating genes from wild relatives like *O. rufipogon* to boost yields in cultivated rice, demonstrating MAS as a viable method for enhancing productivity traits.

Fig. 11. Performance of *GW6* gene introgressed lines compared to donor and recipient parents for yield and yield related traits.



A. Grains per Panicle, B. Agronomic Traits (ZH11. Zhonghua 11; Near Isogenic Lines R1, R2, R3 for ZH11; SSL-1 for 9311; PL. Panicle Length (cm); GL. Grain Length (mm); GB, Grain Breadth (mm); TGW. 1000 Grain Weight (g);

Li *et al.* (2014) reported the successful transfer of the GW6 gene from Baodali into both Zhonghua 11 (japonica) and 9311 (indica) rice varieties through marker-assisted backcrossing (MAB). Three introgression lines of Zhonghua 11 and one of 9311 demonstrated enhanced agronomic traits compared to the recurrent parents (Fig. 11). In particular, the line SSL-1 achieved a significant increase in yield, producing 19% more yield per plant than 9311. This study illustrates the potential of using MAB to improve yield-related genes in both japonica and indica types, highlighting GW6 as a valuable gene for yield enhancement in rice breeding programs.

Considerations for Marker Assisted Breeding

Akhtar *et al.* (2010) outlined five key factors for successful marker-assisted backcrossing (MAB): reliability, marker assay technical procedure, polymorphism level, cost and DNA quality/quantity. Markers used in MAB should be reliable, highly polymorphic and cost-effective, with genetic distances ideally under 5 cM for effective gene transfer. The accuracy of MAB hinges on the proximity of molecular markers to the target gene, with closer markers leading to more precise selection (Nogoy *et al.,* 2016). Additionally, intragenic markers can enhance phenotype prediction reliability. The technical procedure for marker assays should be efficient, simple and fast, ensuring feasibility and minimizing procedural delays.

Recent Progress in Marker Assisted Breeding of Rice

Rice breeders have successfully developed genotypes capable of withstanding various biotic and abiotic stresses, utilizing marker-assisted breeding (MAB) techniques that rely on closely linked molecular markers (Das *et al.,* 2017). Through marker-assisted pyramiding, multiple stress-resistance genes have been introduced simultaneously, resulting in rice lines resilient to diseases/pests like bacterial blight, blast and gall midge, as well as environmental stresses such as drought, salinity and submergence. The effectiveness of these improved genotypes has significantly contributed to stable rice yields under diverse and changing climatic conditions. Table 4, as referenced, likely details specific genotypes and their associated resistance traits, highlighting the impact of the advanced breeding efforts.

CONCLUSION

Marker-assisted breeding (MAB) has significantly enhanced conventional breeding efficiency by integrating molecular markers linked to target genes. The positive impacts of gene introgression have demonstrated the advancements in developing rice lines with enhanced resistance to various biotic and abiotic stresses. For instance, Wanhui 6725 and its hybrid (II-32A/WH6725) have become resistant to 27

Table 4. List of genotypes and traits improved by marker assisted selection

Improved Genotypes	Traits	Resistant Genes	References
Pusa basmati I	Bacterial blight	*Xa13 + Xa21*	Kottapalli *et al.* (2010)
Samba Mahsuri	Bacterial blight	*Xa5 + Xa13 + Xa21*	Kottapalli *et al.* (2010)
Wanhui 6725	Bacterial blight	*Xa4+Xa21+Xa27*	Luo *et al.* (2016)
Swarna sub1	Submergence	*Sub1*	Nandi *et al.* (1997)
IR64 sub1	Submergence	*Sub1*	Reddy *et al.* (2009)
Pusa RH10	Rice blast	*Piz5 + Pi54*	Singh *et al.* (2013)
Feng39S	Rice blast	*Pi2*	Yang *et al.* (2019)
Lalat	Gal midge	*Gm1+Gm4*	Das and Rao, (2015)
Swarna	Drought	*qDTY1.1+qDTY2.1+qDTY3.1*	Sandhu *et al.* (2019)
Tapaswini	Bacterial blight	*Xa4 + Xa5 + Xa13 + Xa21*	Dokku *et al.* (2013)
Mangeumbye	Bacterial blight	*Xa4 + Xa5 + Xa21*	Suh *et al.* (2013)
IR29	Salinity	*Saltol*	Thomson *et al.* (2010)
Dongan	Anaerobic germination	*AG1 + AG2*	Kim *et al.* (2019)

Xoo strains, while the recurrent parent Mianhui 725 and related hybrids remained susceptible. Similarly, blast-resistant lines such as DB16206–34 and DB16206–38, as well as their hybrids, outperform susceptible recurrent lines like Feng39S. Against gall midge, ILGP lines (e.g., ILGP 1 and ILGP 3) exhibit improved survival, whereas the recurrent parent ILP shows minimal resistance. Submergence tolerance is also achieved, with WH6725 and its hybrid surviving two weeks of submergence while Mianhui 725 and related hybrids suffer high mortality. Similarly, yield gains are seen in blast-resistant lines such as DHA-10, which outperforms the recurrent parent BPT5204, yielding 5,680 kg/ha compared to 4,973 kg/ha. The bacterial blight-resistant line BC2F3 2-8-2-36 shows similar yield advantages. Triple-stress tolerant lines (drought, salinity and submergence) have also been developed, showing a higher per-plant yield (>31 g) than the recurrent parent IWP (28 g). Submergence-tolerant lines like BR9157-12-2-37-13-17 outperform their recurrent parent BRRI dhan33 in submerged conditions, yielding 3.44 t/ha compared to 1.73 t/ha. Introgression of the GW6 gene has also boosted yield, with lines like SSL-1 producing 19% more yield per plant than the popular hybrid parent 9311. This evidence underlines the role of MAB in increasing rice productivity and resilience, with introgression lines consistently demonstrating superior performance in yield and stress tolerance compared to recurrent parents. These results emphasize MAB as a crucial tool in sustainable rice breeding and food security initiatives.

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