

Marker-Assisted Breeding for Salt Tolerance in Rice: In Bangladesh Context.

Rifat Hasan Rabbi^{1*}

¹Department of Agricultural Science, Daffodil International University, Birulia, Dhaka-1216, Bangladesh.

Abstract

Salinity stress threatens rice (*Oryza sativa* L.) production across 1.056 million hectares of Bangladesh's coastal regions, with intensification projected due to climate change and sea-level rise. Marker-assisted breeding (MAB) has emerged as a transformative approach for developing salt-tolerant varieties, offering precision and efficiency over conventional methods. This review examines marker-assisted selection (MAS) and marker-assisted backcrossing (MABC) applications for salt tolerance improvement in Bangladesh's rice breeding programs. We analyze the genetic architecture of salt tolerance, particularly the major Saltol QTL harboring OsHKT1;5 on chromosome 1, and discuss molecular marker systems including SSRs, SNPs, and InDels utilized by the Bangladesh Rice Research Institute (BRRI). The review documents successful introgression of salt tolerance into elite varieties, resulting in seventeen released varieties including BRRI dhan47, BRRI dhan73, and BRRI dhan78, with yields of 4.5-8.3 t ha⁻¹ under saline conditions (8-14 dS m⁻¹). We evaluate physiological mechanisms of Na⁺ exclusion and ionic homeostasis, analyze breeding achievements using foreground and background selection strategies, and discuss future integration of genomic selection, GWAS, and CRISPR/Cas9 gene editing. Despite substantial progress, continued integration of molecular breeding with phenomics and participatory approaches remains essential for developing climate-resilient varieties addressing Bangladesh's intensifying salinity challenge.

Keywords: Marker-assisted breeding, salt tolerance, Saltol QTL, rice, Bangladesh, OsHKT1;5, molecular markers, coastal agriculture

1. Introduction

1.1 Global Context and Salinity Challenge in Bangladesh

Rice (*Oryza sativa* L.) serves as the primary staple food for more than half of the world's population, providing nutritional security for approximately 3.5 billion people globally (Ismail & Horie, 2017). Salinity stress affects approximately 20% of irrigated agricultural land globally, with figures projected to increase due to climate change, sea-level rise, and intensive irrigation practices (Thomson et al., 2010). Rice is classified as a salt-sensitive crop, with threshold salinity levels typically ranging from 3-4 dS m⁻¹ for modern high-yielding varieties, causing yield reductions of 20-50% depending on stress intensity (M. A. Haque et al., 2021a; Reddy et al., 2017). Bangladesh, the fourth-largest rice-producing country with annual production exceeding 39 million tons, faces acute salinity problems in its coastal belt (Kabir et al., 2016). The coastal zone extends approximately 710 kilometers along the Bay of Bengal, encompassing 19 districts covering

roughly 20% of total land area. Within this region, approximately 1.056 million hectares are affected by varying degrees of salinity, representing over 30% of net cultivable area (Ali et al., 2014; M. A. Haque et al., 2021a). Salt-affected areas increased by 26% over four decades, expanding from 0.833 million hectares in 1973 to 1.056 million hectares in 2009 (SRDI, 2010). In five severely affected coastal districts—Khulna, Satkhira, Bagerhat, Patuakhali, and Barguna—salinity levels now range between 8.1 and 16 dS m⁻¹, exceeding the tolerance threshold of currently available varieties that typically withstand 8-10 dS m⁻¹ (Shawkhatuzamman et al., 2023). The salinity problem results from tidal flooding, brackish water inundation, saline groundwater upward movement during dry season, reduced freshwater flow in transboundary rivers, commercial shrimp farming, and sea-level rise (Dasgupta et al., 2015). Salinity reduces rice production by 20-30% in Bangladesh, with some areas experiencing complete crop failure (Bhuyan et al., 2023). Economic analyses predict output declines of 15.6% in nine coastal subdistricts where soil salinity will exceed 4 dS m⁻¹ before 2050 (Dasgupta et al., 2019).

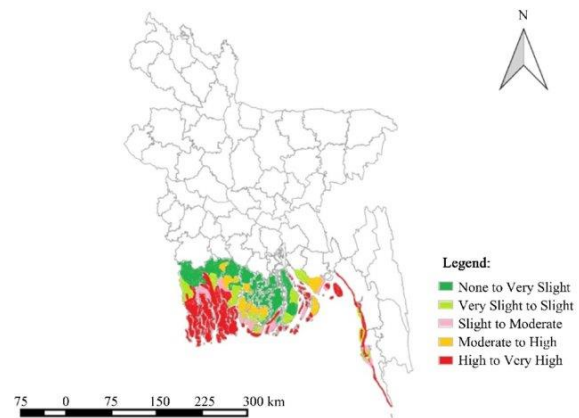


Figure 1: Salinity Status of Bangladesh.

1.2 Conventional Breeding Limitations and MAB Advantages

Traditional breeding for salinity tolerance has relied on phenotypic selection using the Standard Evaluation Score (SES) developed by IRRI, assessing salt injury on a scale of 1 (highly tolerant) to 9 (highly sensitive) (Das et al., 2016). Conventional programs have developed several salt-tolerant varieties by crossing high-yielding cultivars with tolerant landraces such as Pokkali, Nona Bokra, and Capsule (Platten et al., 2013). However, conventional breeding faces significant challenges. Salt tolerance is a complex quantitative trait controlled by multiple genes with small individual effects, exhibiting large genotype × environment interactions (Ismail & Horie, 2017). Trait expression varies substantially across developmental stages, requiring separate selection strategies (Sackey et al., 2025). Field screening is labor-intensive, time-consuming, and unreliable due to spatial heterogeneity of salt distribution (Nayak et al., 2022). Linkage drag represents a major limitation, where undesirable traits from donor parents are inadvertently introduced, resulting in inferior grain quality or reduced yield potential (Thomson et al., 2010). Conventional breeding typically requires 8-12 years to develop new varieties (Janaki Ramayya et al., 2021). Marker-assisted breeding (MAB) encompasses marker-assisted selection (MAS) and marker-assisted backcrossing (MABC), enabling breeders to select plants carrying desired alleles at early developmental stages, accelerating selection efficiency and reducing breeding cycle duration (Hasan et al., 2015). MAB allows simultaneous introgression of multiple QTLs, minimization of linkage drag through background selection, and maintenance of desirable traits from recurrent parents (Krishnamurthy et al., 2017; Yadav et al., 2020). Economic analyses estimate that MAB

saves at least 3-6 years compared to conventional breeding, with incremental benefits over 25 years ranging from \$50 to \$900 million depending on implementation (Alpuerto et al., 2009).

2. Methodology

This mini-review was conducted through a comprehensive literature search using multiple academic databases including Google Scholar, PubMed, ScienceDirect, and ResearchGate to identify relevant studies on marker-assisted breeding for salt tolerance in rice, with particular emphasis on the Bangladesh context. The search covered publications from 2000 to 2024 using keywords such as "marker-assisted breeding," "salt tolerance," "rice," "Bangladesh," "QTL," and "molecular markers" in various combinations. Peer-reviewed journal articles, research papers, and conference proceedings were included based on their relevance to marker-assisted selection techniques, salt tolerance mechanisms, QTL mapping, and breeding strategies applicable to Bangladesh's agro-climatic conditions. Studies focusing solely on conventional breeding without molecular marker applications, research on crops other than rice, and publications with insufficient data or unclear methodology were excluded from the review. Data were systematically extracted from selected literature sources focusing on key aspects including types of molecular markers (SSR, SNP, INDEL), major QTLs associated with salt tolerance, marker-assisted selection strategies, physiological and biochemical mechanisms of salt tolerance, and Bangladesh-specific challenges and breeding programs. The collected information was thematically categorized and synthesized to provide a comprehensive overview of current knowledge and practices in the field. Comparative analysis was performed to evaluate the effectiveness of different MAS approaches and marker systems in developing salt-tolerant rice varieties. Special attention was given to integrating global research findings with Bangladesh's specific requirements, including salinity-affected areas, local rice varieties, and ongoing breeding initiatives. All sources were properly cited following standard academic citation practices to ensure academic integrity throughout the review process.

3. Genetic Architecture of Salt Tolerance

3.1 Complexity as a Quantitative Trait

Salt tolerance in rice is a complex polygenic trait governed by multiple genes with varying effects (Ismail & Horie, 2017). Rice is particularly sensitive at seedling and reproductive stages, although seedling stage tolerance is crucial for crop establishment (M. Islam et al., 2011). The genetic control involves QTLs distributed across all 12 chromosomes, with individual QTLs explaining phenotypic variance from less than 5% to more than 40% (Thomson et al., 2010). Complexity manifests through ontogeny-specific expression, where tolerance mechanisms at seedling stage differ substantially from reproductive stage (Moradi & Ismail, 2007). Seedling stage tolerance primarily involves ion homeostasis, particularly Na⁺ exclusion and K⁺ maintenance, while reproductive stage tolerance additionally requires protection of floral organs and prevention of spikelet sterility (Reshna & Beena, 2021).

3.2 The Saltol QTL: A Major Breakthrough

Saltol, a major QTL mapped on chromosome 1 in recombinant inbred line FL478 from a cross between Pokkali (tolerant) and IR29 (sensitive), is responsible for maintaining low Na⁺, high K⁺, and optimal Na⁺/K⁺ homeostasis in shoots (Ju et al., 2022). Saltol explains 43-70% of phenotypic variation for seedling stage salinity tolerance and was delimited to a 10.7-12.2 Mb region on chromosome 1 (Yadav et al., 2020). The Saltol region harbors multiple candidate genes, most notably OsHKT1;5 (also known as SKC1), encoding a xylem-expressed Na⁺-selective transporter (Kobayashi et al., 2017; Ren et al., 2005). OsHKT1;5 functions by retrieving Na⁺ from xylem sap during root-to-shoot translocation, reducing Na⁺ accumulation in photosynthetically active shoot tissues while maintaining K⁺ homeostasis (Platten et al., 2013). Analysis revealed that Saltol mainly controls shoot Na⁺/K⁺ homeostasis, although multiple QTLs are required for high tolerance levels (Thomson et al., 2010).

Table 1. Major QTLs for Salt Tolerance in Rice

QTL Name	Chromosome	Marker Interval	Trait Controlled	Variance (%)	Reference
Saltol	1	RM8094-RM493	Seedling Na ⁺ /K ⁺ ratio	40-70	(Bonilla et al., 2002)
qSKC1	1	RM10793-RM3412	Shoot K ⁺ content	35-50	(Ren et al., 2005)
qSTL3	3	RM251-RM520	Reproductive fertility	15-22	(Q. Liu et al., 2015)
qSTL4	4	RM335-RM273	Yield under stress	12-18	(Q. Liu et al., 2015)

Source: Compiled from (Bonilla et al., 2002; Q. Liu et al., 2015; Ren et al., 2005; Thomson et al., 2010).

3.3 Additional QTLs and Candidate Genes

Beyond Saltol, extensive QTL mapping identified numerous genomic regions associated with salt tolerance. Meta-analysis of 567 QTLs identified 63 meta-QTLs with 95% confidence intervals, with 11 meta-QTLs having small confidence intervals localized on chromosomes 1 and 2 (Ashraf & Foolad, 2013). Studies using Bangladeshi landrace Capsule identified 30 QTLs distributed on chromosomes 1, 2, 3, 5, 10, and 12 (Mondal et al., 2025). For reproductive stage tolerance, eighteen new QTLs with LOD scores ≥ 2.5 were identified on chromosomes 1, 2, 6, 10, 11, and 12, with phenotypic variation explained reaching 42% (Ashraf & Foolad, 2013). Among genes in the Saltol region, SalT encodes a SALT protein functioning as a mannose-binding lectin crucial for salinity tolerance (Kumar et al., 2021). Additional candidates include OsIF (intermediate filament protein) and OsHBP1b (histone binding protein), both showing differential expression and conferring improved tolerance (Soda et al., 2018; P. Zhang et al., 2023).

4. Molecular Markers for Salt Tolerance Breeding

4.1 Types of Molecular Markers

Simple Sequence Repeats (SSRs) represent the most widely used marker system due to high polymorphism, co-dominant inheritance, and ease of use (Gupta & Varshney, 2000; Tahjib-Ul-Arif et al., 2018). Key SSR markers linked to Saltol include RM3412, AP3206, RM8094, RM493, and RM10793, extensively validated across diverse genetic backgrounds (Thomson et al., 2010). RM8094 and RM3412 are particularly reliable and closely flanking (Babu et al., 2017; Singh et al., 2021).

Table 2. Key molecular markers linked to Saltol QTL and their characteristics

Marker Name	Marker Type	Chromosome	Physical Position (Mb)	Distance from Saltol Center (cM)	Polymorphism Level	Application in MAB	References
RM3412	SSR	1	11.9	0.5	High	Foreground selection	(Thomson et al., 2010)
RM8094	SSR	1	10.7	2.1	High	Foreground selection	(Babu et al., 2017)
RM493	SSR	1	9.6	4.3	Moderate	Foreground selection	(M. A. Rahman et al., 2019)
RM10793	SSR	1	12.6	1.8	High	Foreground selection	(Chowdhury et al., 2016)
AP3206	SSR	1	11.5	1.2	High	Foreground selection	(Chowdhury et al., 2016)
id_1007745	KASP (SNP)	1	10.69	2.5	High	Precise foreground selection	(Marè et al., 2023)
K_id1008539	KASP (SNP)	1	12.59	1.6	High	Precise foreground selection	(Marè et al., 2023)

Single Nucleotide Polymorphisms (SNPs) have emerged as the marker system for high-throughput genotyping. The 1K-RiCA panel consisting of 1024 genome-wide SNP markers including 92 trait-specific markers has been deployed in Bangladesh (Arbelaez et al., 2019; Biswas et al., 2023). SNPs offer advantages of genome-wide distribution, high abundance, and lower cost per data point (Thomson et al., 2010). Insertion-Deletion (InDel) markers provide alternatives to SSRs with similar advantages while offering higher stability (M. A. Rahman et al., 2019). Kompetitive Allele Specific PCR (KASP) markers represent an advanced SNP genotyping platform for precise foreground selection (Marè et al., 2023).

5. Marker-Assisted Breeding Strategies

5.1 Marker-Assisted Backcrossing (MABC)

MABC combines foreground selection for target QTL, recombinant selection to minimize linkage drag, and background selection to maximize recurrent parent genome recovery, accelerating near-isogenic line (NIL) development (Hospital & Charcosset, 1997). A typical MABC program involves: (1) crossing recurrent parent (elite variety) with donor parent (FL478 or derivative); (2) foreground selection in BC₁F₁ and subsequent generations using flanking markers; (3) background selection using genome-wide polymorphic markers; (4) recurrent selection to minimize donor segment size; and (5) selfing selected BC₃F₁ or BC₄F₁ plants followed by foreground selection for homozygous lines (Mackill & Khush, 2018). Three backcrosses (BC₃) followed by selfing successfully led to Saltol introgression, with foreground selection using RM3412 and AP3206 (Gupta et al., 2008). Background selection typically uses 60-105 genome-wide polymorphic SSR markers at approximately 15-20 cM intervals (Hospital & Charcosset, 1997). Advanced programs employ high-density SNP genotyping for precise background selection, with 15,580 polymorphic SNP markers enabling selection of lines with up to 98.97% recurrent parent genome recovery (Marè et al., 2023).

5.2 Gene Pyramiding for Multiple Stress Tolerance

Combining multiple QTLs through gene pyramiding offers opportunities for broader tolerance across diverse environments (M. A. Haque et al., 2021b). Successful pyramiding of genes conferring resistance to blast (Pi2, Pi9), gall midge (Gm1, Gm4), submergence (Sub1), and salinity (Saltol) has been demonstrated in Improved Lalat (Pradhan et al., 2015). For Bangladesh's coastal ecosystem, combining salt tolerance with submergence tolerance is particularly relevant. IRRI developed multiple stress tolerance lines (IR84649-81-4-B-B and IR84645-311-22-1-B) through introgressing Saltol from Pokkali and Sub1 from Swarna-Sub1, with BRRI dhan 78 in Bangladesh and Salinas 22 in the Philippines released for commercial cultivation (GREGORIO et al., 2013).

6. Salt-Tolerant Varieties in Bangladesh

6.1 BRRI's Variety Development Program

Seventeen salt-tolerant rice varieties have been developed and released in Bangladesh (Nayak et al., 2022). BRRI dhan47 represents a landmark achievement, tolerating EC 12-14 dS m⁻¹ with potential yields of 5.4-8.3 t ha⁻¹ in saline areas (Salam et al., 2009). BRRI dhan61 was developed for Boro season, exhibiting tolerance to 6-8 dS m⁻¹ with average yields of 5.5-6.0 t ha⁻¹ (M. Z. Islam et al., 2023). BRRI dhan67 tolerates 8-10 dS m⁻¹ during vegetative stage, providing average yields of 4.5-5.0 t ha⁻¹ (N. Md. F. Rahman et al., 2023). BRRI dhan73, released in 2015, was developed through MABC by introgressing Saltol from FL478 into BRRI dhan28, representing one of the first successful MAB applications in Bangladesh (N. Md. F. Rahman et al., 2023). BRRI dhan73 tolerates 10-12 dS m⁻¹ at seedling stage and yields 6.0-7.0 t ha⁻¹ under moderate stress (Hasan et al., 2015). Development involved three backcrosses with foreground selection using

RM3412, RM8094, and RM10793, and background selection with 62 polymorphic SSR markers, achieving 94-96% recurrent parent genome recovery (Babu et al., 2017). BRRI dhan78 combines tolerance to both salinity (8-10 dS m⁻¹) and submergence (12-14 days), yielding 5.5-6.5 t ha⁻¹ under moderate stress (Akter et al., 2025). BRRI dhan97, released in 2019, tolerates 8-10 dS m⁻¹ throughout all salt-sensitive stages with average yields of 4.90±0.24 t ha⁻¹ under saline conditions (Debsharma et al., 2024). Molecular characterization revealed four QTLs/genes regulating salt tolerance traits (Debsharma et al., 2024). BRRI dhan99, released in 2020 from Green Super Rice breeding line HHZ5-DT20-DT2-DT1, produces average yields of 5.45±0.32 t ha⁻¹ under saline stress, tolerating 8-10 dS m⁻¹ throughout entire growth cycle (Debsharma et al., 2024). Molecular analysis revealed eight QTLs/genes regulating salt tolerance, providing broader genetic base than BRRI dhan97 (Debsharma et al., 2024).

Table 3. Major salt-tolerant rice varieties developed and released in Bangladesh

Variety Name	Year Released	Season	Salinity Tolerance (dS m ⁻¹)	Yield Potential (t ha ⁻¹)	Plant Height (cm)	Growth Duration (days)	Special Features	Development Method	References
BRRI dhan40	2003	T. Aman	8	4.0-4.5	110-115	135-140	Lodging tolerance, shorter duration	Conventional breeding	(M. R. Islam & Gregorio, 2013)
BRRI dhan41	2003	T. Aman	8	4.0-4.5	105-110	145-150	Medium slender grain	Conventional breeding	(M. R. Islam & Gregorio, 2013)
BRRI dhan47	2007	Boro/Aus	12-14	5.4-8.3	105-110	152	High tillering, medium bold grain, premium quality	Conventional breeding + PVS	(Debsharma et al., 2024)
BRRI dhan53	2010	T. Aman	8	4.0-4.5	100-105	125-130	Photoperiod sensitive	Conventional breeding	(Rashid & Nasrin, 2014)
BRRI dhan54	2010	T. Aman	8	4.0-4.5	115-120	135-140	Lodging tolerance	Conventional breeding	(Rashid & Nasrin, 2014)
BRRI dhan61	2013	Boro	6-8	5.5-6.0	95-100	145-148	Medium bold grain, acceptable cooking quality	Conventional breeding	(M. Rahman et al., 2021)
BRRI dhan67	2014	T. Aman	8-12	4.5-5.0	110-115	125-130	Photoperiod sensitive, medium slender grain, widely adopted	Conventional breeding	(Sackey et al., 2025)
BRRI dhan73	2015	Boro	10-12	6.0-7.0	100-105	150-155	Saltol QTL introgressed,	Marker-assisted backcrossing	(M. Rahman et al., 2021)

Variety Name	Year Released	Season	Salinity Tolerance (dS m ⁻¹)	Yield Potential (t ha ⁻¹)	Plant Height (cm)	Growth Duration (days)	Special Features	Development Method	References
BRRI dhan78	2017	Boro	8-12	5.5-6.5	95-100	142	improved seedling tolerance Dual tolerance: salinity + submergence (12-14 days)	Marker-assisted backcrossing (Saltol + Sub1)	(M. Rahman et al., 2021)
BRRI dhan97	2019	Boro	8-10	4.9-6.0 (up to 7.0)	103	150	Medium bold grain, 4 QTLs/genes, comprehensive tolerance	Marker-assisted breeding	(Debsharma et al., 2024)
BRRI dhan99	2020	Boro	8-10	5.4-7.1 (up to 7.0)	94	148	Compact architecture, 8 QTLs/genes, superior tolerance	Marker-assisted breeding (GSR lineage)	(Debsharma et al., 2024)
BRRI dhan112	2023	T. Aman	10-12	4.14-6.12	104	123	Salinity tolerance and high yielding.	Marker-assisted breeding	(BRRI, 2023)
BINA dhan8	2010	Boro	10-12	4.5-5.5	100-105	140-145	Mutation breeding	Mutation + selection	(BINA, 2023)
BINA dhan10	2013	T. Aman	10-12	4.5-5.5	105-110	140	Mutation breeding	Mutation + selection	(M. Rahman et al., 2021)

Note: PVS = Participatory Variety Selection; GSR = Green Super Rice; QTLs/genes refer to molecular markers identified for salt tolerance traits.

6.2 Comparative Performance and Adoption

Multi-location trials demonstrated tangible MAB benefits. BRRI dhan73 produced average yields of 6.4 t ha⁻¹ compared to 5.1 t ha⁻¹ for BRRI dhan28 under 6-8 dS m⁻¹ stress, representing 25% yield advantage (M. Rahman et al., 2021). BRRI dhan78 yielded 5.8 t ha⁻¹ compared to 4.2 t ha⁻¹ for BRRI dhan47 in areas with combined stresses, representing 38% improvement (S. S. Islam & Hossain, 2020).

Table 4. Comparative yield performance of salt-tolerant varieties across different salinity levels in coastal Bangladesh

Location	District	Salinity Level (dS m ⁻¹)	BRRI dhan97 (t ha ⁻¹)	BRRI dhan99 (t ha ⁻¹)	BRRI dhan67 (t ha ⁻¹)	BRRI dhan28 (t ha ⁻¹)	Year
Tala	Satkhira	6-8	5.95	6.58	6.41	6.01	2019-20
Dumuria	Khulna	8-10	4.85	5.42	4.23	1.74	2019-20
Rampal	Bagerhat	10-12	4.12	4.87	3.17	0.95	2019-20
Assasuni	Satkhira	10-12	3.93	4.14	Complete damage	Complete damage	2018-19
Kaliganj	Satkhira	>12 (16-18)	Severely damaged	Severely damaged	Complete damage	Complete damage	2018-19
Koyra	Khulna	>12 (14-16)	Severely damaged	Survived	Complete damage	Complete damage	2018-19

Note: "Complete damage" indicates total crop failure; "Severely damaged" indicates <1.0 t ha⁻¹ yield.
Source: Compiled from (Debsharma et al., 2024)

Adoption studies indicate progressive uptake. Survey data from 2022 revealed salt-tolerant varieties occupied approximately 47% of total rice area in severely affected coastal districts (Illius & Azad, 2022). BRRI dhan67 cultivation expanded from 119 hectares in 2018 to 5,216 hectares in 2022 in Satkhira district (Barua et al., 2015). Farmers report that salt-tolerant varieties completely changed cultivation prospects, with 240 hectares of previously uncultivated saline land brought back under cultivation.

Table 5. Breeding achievements and variety release trends for salt tolerance in Bangladesh (2003-2024)

Period	Number of Varieties Released	Key Varieties	Breeding Approach	Tolerance Level (dS m ⁻¹)	Average Yield Improvement (%)	Adoption Rate in Coastal Areas (%)
2003-2010	5	BRRI dhan40, 41, 47, 53, 54	Conventional breeding + landrace utilization	8-14	40-60	15-25
2011-2015	4	BRRI dhan61, 67, 73; BINA dhan10	Conventional + initial MAB (Saltol)	6-12	25-45	30-40
2016-2020	4	BRRI dhan78, 97, 99; BINA dhan22	Marker-assisted breeding (Saltol, Sub1, multiple QTLs)	8-12	35-55	45-60

Period	Number of Varieties Released	Key Varieties	Breeding Approach	Tolerance Level (dS m ⁻¹)	Average Yield Improvement (%)	Adoption Rate in Coastal Areas (%)
2021-2024	4 (projected)	BRRIdhan104, 106, advanced introgression lines	Genomic selection + MAB, SNP-based selection	8-14	40-65 (projected)	50-70 (projected)
Total (2003-2024)	17+	Multiple stress-tolerant varieties	Evolution from conventional to genomic approaches	6-14	25-65	15-70 (progressive)

Note: Adoption rates represent percentage of rice area in severely salt-affected coastal districts. Source: Compiled from (Debsharma et al., 2024; M. R. Islam & Gregorio, 2013; M. Z. Islam et al., 2023; M. Rahman et al., 2021; Rashid & Nasrin, 2014).

7. Physiological and Molecular Mechanisms

7.1 Ion Homeostasis and Na⁺ Exclusion

Maintenance of ion homeostasis, particularly Na⁺ and K⁺ regulation, represents the primary tolerance mechanism (Ismail & Horie, 2017). Excessive Na⁺ uptake disrupts cellular K⁺ homeostasis and causes metabolic dysfunction (Ismail & Horie, 2017). Salt-tolerant genotypes maintain significantly lower shoot Na⁺ and higher K⁺, resulting in favorable Na⁺/K⁺ ratios (Thomson et al., 2010). Saltol confers tolerance through enhanced Na⁺ exclusion mediated by OsHKT1;5, which retrieves Na⁺ from ascending xylem sap, reducing delivery to leaf blades (Kobayashi et al., 2017; Ren et al., 2005). OsHKT1;5 knockout mutants exhibited significantly higher shoot Na⁺ and increased sensitivity, confirming its critical role (Ren et al., 2005). Near-isogenic lines with Saltol maintained shoot Na⁺ concentrations approximately 40% lower than non-Saltol lines under 12 dS m⁻¹ stress, with Na⁺/K⁺ ratios of 0.3-0.4 compared to 0.8-1.2 in sensitive genotypes (Thomson et al., 2010).

Table 6. Physiological parameters distinguishing salt-tolerant and salt-sensitive rice genotypes

Parameter	Salt-Tolerant Genotypes (with Saltol)	Salt-Sensitive Genotypes (without Saltol)	Difference (%)	Measurement Conditions	References
Shoot Na ⁺ concentration (mg g ⁻¹ DW)	15-25	35-55	-40 to -55%	12 dS m ⁻¹ , 21 days	(Thomson et al., 2010)
Shoot K ⁺ concentration (mg g ⁻¹ DW)	45-60	30-45	+33 to +50%	12 dS m ⁻¹ , 21 days	(Thomson et al., 2010)

Parameter	Salt-Tolerant Genotypes (with Saltol)	Salt-Sensitive Genotypes (without Saltol)	Difference (%)	Measurement Conditions	References
Na ⁺ /K ⁺ ratio	0.3-0.4	0.8-1.2	-63 to -67%	12 dS m ⁻¹ , 21 days	(Singh et al., 2021)
Proline content (μmol g ⁻¹ FW)	45-65	20-30	+125 to +167%	12 dS m ⁻¹ , 14 days	(M. Z. Islam et al., 2023)
SOD activity (units mg ⁻¹ protein)	110-135	65-85	+58 to +69%	10 dS m ⁻¹ , 14 days	(Reddy et al., 2017)
Survival rate (%)	70-80	20-30	+150 to +267%	12 dS m ⁻¹ , 21 days	(Marè et al., 2023)
Visual salt injury score (SES)	3-5	7-9	-44 to -56%	12 dS m ⁻¹ , 21 days	(Thomson et al., 2010)

Note: SES = Standard Evaluation Score (1 = highly tolerant, 9 = highly sensitive); DW = dry weight; FW = fresh weight

7.2 Osmotic Adjustment and Antioxidant Defense

Salt-tolerant genotypes accumulate compatible solutes to lower cellular osmotic potential and maintain turgor (Ismail & Horie, 2017). Proline concentrations in tolerant varieties are 2-5-fold higher than sensitive varieties, functioning in osmotic adjustment and as antioxidant (Reddy et al., 2023). BRRI dhan73 accumulated 45-65 μmol g⁻¹ proline under 12 dS m⁻¹ stress compared to 20-30 μmol g⁻¹ in non-tolerant genotypes (Islam et al., 2020). Salt stress triggers excessive reactive oxygen species (ROS) production causing oxidative damage (Mishra et al., 2023). Tolerant genotypes maintain 40-80% higher activities of antioxidant enzymes including superoxide dismutase, catalase, and ascorbate peroxidase under salt stress (Mishra et al., 2023). BRRI dhan73 showed significantly higher SOD activity (125 units mg⁻¹ protein) compared to BRRI dhan28 (78 units mg⁻¹ protein) under 10 dS m⁻¹ salinity (Barua et al., 2015).

7.3 Transcriptional Regulation

Salt tolerance involves coordinated regulation through complex transcriptional networks. Transcription factors from NAC, WRKY, AP2/ERF, bZIP, and MYB families play crucial roles (J. Liu et al., 2016). OsDREB family members function as master regulators activating stress-responsive genes (Dubouzet et al., 2003). NAC transcription factors OsNAC45 and SNAC1 enhance tolerance through transcriptional activation of genes involved in stomatal closure and ROS scavenging (Hu et al., 2006; A. Zhang et al., 2019).

8. Genome Editing for Precision Improvement

8.1 CRISPR/Cas9 Technology

CRISPR/Cas9 enables direct, targeted modification of specific genomic sequences to create desired alleles or knockout undesirable genes (Shan et al., 2013; A. Zhang et al., 2019). CRISPR-targeted mutagenesis of OsRR22 significantly increased salt tolerance, with transgene-free homozygous lines obtained by T1 segregation (Takagi et al., 2013). CRISPR-mediated knockout of OsbHLH024 enhanced expression of ion transporter genes OsHKT1;3, OsHAK7, and OsSOS1, thereby enhancing tolerance (Alam et al., 2022).

Table 7. Candidate genes for CRISPR-mediated salt tolerance improvement

Gene Name	Chromosome	Function	Editing Strategy	Expected Outcome	Validation Status	References
OsRR22	4	B-type response regulator, negative regulator of salt stress	Knockout	Enhanced salt tolerance	Validated in transgenic rice	(A. Zhang et al., 2019)
OsHKT1;5	1	Na ⁺ -selective transporter in xylem	Promoter editing or allele replacement	Enhanced Na ⁺ exclusion	Natural variant in Saltol, can be optimized	(Kobayashi et al., 2017)
OsDST	3	Zinc finger transcription factor, negative regulator	Knockout	Improved stomatal closure, salt tolerance	Validated in transgenic rice	(Santosh Kumar et al., 2020)
OsNAC041	11	NAC transcription factor, regulates senescence	Knockout	Delayed leaf senescence, enhanced tolerance	Validated in transgenic rice	(An et al., 2020)
OsbHLH024	12	Basic helix-loop-helix transcription factor	Knockout	Enhanced ion transporter expression	Validated in CRISPR-edited rice	(Alam et al., 2022)
OsRAV2	1	RAV family transcription factor	Knockout	Improved root development, tolerance	Validated in transgenic rice	(Santosh Kumar et al., 2020)
OsSOS1	12	Plasma membrane Na ⁺ /H ⁺ antiporter	Overexpression via promoter editing	Enhanced Na ⁺ efflux	Candidate for editing	(Kumar et al., 2021)

8.2 Genome Editing in Bangladesh Context

Dr. Zeba Islam Seraj at University of Dhaka has emphasized genome editing potential for abiotic stress tolerance, presenting ongoing work producing salt-tolerant rice by downregulating a

transporter gene in sensitive IR29 rice. This gene is downregulated in Horkuch, a salt-tolerant Bangladeshi landrace, under salt stress, demonstrating how genome editing can replicate natural tolerance mechanisms (T. Haque et al., 2020). Opportunities include leveraging extensive knowledge of salt tolerance mechanisms in Bangladeshi landraces like Horkuch, Capsule, and Matla to identify candidate genes for editing; utilizing CRISPR/Cas9 to rapidly introgress tolerance traits into popular varieties like BRRI dhan28 and BRRI dhan29; and developing transgene-free edited varieties through segregation that may face fewer regulatory hurdles. Challenges include limited genome editing infrastructure and technical expertise requiring capacity building and international collaboration; regulatory uncertainty regarding genome-edited crops; and necessity for thorough biosafety evaluation before farmer release.

9. Challenges and Future Prospects

9.1 Current Challenges

Despite substantial progress, several challenges persist. The complex genetic architecture involving multiple QTLs with small to moderate effects and substantial genotype $\times$ environment interactions complicate breeding efforts (Ismail & Horie, 2017). While Saltol provides significant seedling stage tolerance, achieving robust tolerance across all developmental stages requires additional QTLs that are less well characterized (Shohan et al., 2019). Linkage drag remains problematic even with MABC. Some Saltol-containing lines did not exhibit significantly different performance compared to lines without Saltol under certain conditions, indicating that genetic background, epistatic interactions, and environmental factors substantially influence tolerance expression (Emon et al., 2015). The discrepancy between seedling stage and reproductive stage tolerance presents another challenge, as QTLs for reproductive stage tolerance map to different chromosomal regions (Shohan et al., 2019).

Table 8. Comparison of breeding approaches for salt tolerance improvement in rice

Approach	Duration (years)	Precision	Advantages	Limitations	Cost	Implementation Status in Bangladesh	References
Conventional breeding	8-12	Low	No special equipment needed, utilizes natural variation	Long duration, linkage drag, unreliable phenotyping	Low	Established, multiple varieties released	(Singh et al., 2021)
Marker-assisted backcrossing (MABC)	5-7	High	Reduced linkage drag, foreground and background selection	Requires molecular lab infrastructure	Moderate	Successfully implemented, BRRI dhan73, BRRI dhan78 released	(Hasan et al., 2015)

Approach	Duration (years)	Precision	Advantages	Limitations	Cost	Implementation Status in Bangladesh	References
Genomic selection (GS)	3-5	High	Genome-wide prediction, captures small-effect QTLs	High genotyping costs, requires bioinformatics	Moderate-High	Pilot implementation at BRRI, 1.5 year cycle reduction	(Biswas et al., 2023)
CRISPR/Cas9 genome editing	2-4	Very High	Precise gene editing, no linkage drags, transgene-free options	Regulatory uncertainty, requires transformation	High	Research stage, pilot studies ongoing	(A. Zhang et al., 2019)
MABC + GS integration	3-4	Very High	Combines major QTL selection with genome-wide prediction	Requires advanced infrastructure and expertise	High	Recently adopted at BRRI	(Biswas et al., 2023)

Technical constraints include substantial investment requirements in laboratory infrastructure, equipment, and trained personnel that can be constraining for developing countries (Alpuerto et al., 2009). The transition to SNP-based high-throughput platforms requires bioinformatics infrastructure and expertise for data management that may be limited (Spindel et al., 2015). Field phenotyping remains challenging due to spatial heterogeneity of salinity and difficulty creating uniform saline conditions (M. Rahman et al., 2021).

9.2 Adoption Constraints

Ultimate impact depends on farmer adoption and integration into cropping systems. Constraints include inadequate seed production and distribution systems in remote coastal areas; limited farmer awareness regarding new variety characteristics and appropriate management; and seed cost considerations that may deter resource-poor farmers (M. Rahman et al., 2021). Consumer preferences for specific grain quality characteristics influence adoption regardless of agronomic performance. Competition for land use from shrimp aquaculture represents a socioeconomic challenge beyond breeding program scope (Dasgupta et al., 2015).

9.3 Climate Change and Future Directions

Climate change projections indicate intensifying salinity problems due to sea-level rise, increased storm surge frequency, and altered rainfall patterns (Dasgupta et al., 2015). Current varieties typically withstand 8-12 dS m⁻¹, but some areas already experience salinity exceeding 16 dS m⁻¹, necessitating varieties with even higher tolerance (M. Rahman et al., 2021). The interaction of

salinity with other abiotic stresses including heat, drought, and submergence requires varieties with multiple stress tolerance traits (Singh et al., 2021).

10. Conclusion

Soil salinity poses a critical threat to rice production in Bangladesh's coastal regions, but marker-assisted breeding has proven transformative, enabling development of seventeen improved salt-tolerant varieties including BRRI dhan73 and BRRI dhan78 through successful Saltol QTL introgression. The integration of advanced genomic tools—genomic selection, GWAS, and CRISPR/Cas9—promises accelerated progress, with genomic selection at BRRI already achieving seven-fold improvement in genetic gain and reducing breeding cycles by 1.5 years. Despite this progress, intensifying climate-driven salinity demands varieties with even higher tolerance and multiple stress resilience. Key challenges include technical and resource constraints requiring continued investment in infrastructure, genotyping platforms, and human capacity, alongside strengthening seed systems and farmer adoption mechanisms. The underexploited genetic diversity in Bangladeshi landraces, systematic genomic characterization, and regional collaboration offer significant opportunities for further advancement.

Marker-assisted breeding exemplifies how molecular genomics can address pressing agricultural challenges. As technologies become more accessible, the prospects for developing climate-resilient rice varieties grow increasingly promising. For Bangladesh and similar nations facing rising food demand amid intensifying abiotic stresses, continued investment in stress breeding is essential for ensuring food security and sustaining rural livelihoods.

References:

- Akter, S., Begum, R., Dipti, S. S., Alim, Md. A., Shuchy, S. I., Shozib, H. B., & Hasan, Md. R. (2025). Effect of Degree of Milling (DOM) on Physicochemical and Nutritional Quality of Selected Rice Variety (BRRI dhan78). *International Journal of Food Science*, 2025(1), 6034633. <https://doi.org/10.1155/ijfo/6034633>
- Alam, M. S., Kong, J., Tao, R., Ahmed, T., Alamin, Md., Alotaibi, S. S., Abdelsalam, N. R., & Xu, J.-H. (2022). CRISPR/Cas9 Mediated Knockout of the OsBHLH024 Transcription Factor Improves Salt Stress Resistance in Rice (*Oryza sativa* L.). *Plants*, 11(9), 1184. <https://doi.org/10.3390/plants11091184>
- Ali, M. N., Yeasmin, L., Gantait, S., Goswami, R., & Chakraborty, S. (2014). Screening of rice landraces for salinity tolerance at seedling stage through morphological and molecular markers. *Physiology and Molecular Biology of Plants: An International Journal of Functional Plant Biology*, 20(4), 411–423. <https://doi.org/10.1007/s12298-014-0250-6>
- Alpuerto, V.-L. E. B., Norton, G. W., Alwang, J., & Ismail, A. M. (2009). Economic Impact Analysis of Marker-Assisted Breeding for Tolerance to Salinity and Phosphorous Deficiency in Rice. *Review of Agricultural Economics*, 31(4), 779–792. <https://doi.org/10.1111/j.1467-9353.2009.01466.x>
- An, H., Liu, K., Wang, B., Tian, Y., Ge, Y., Zhang, Y., Tang, W., Chen, G., Yu, J., Wu, W., Liu, X., Zhao, Y., Li, J., Zhang, H., Yang, B., Jiang, X., Peng, C., Zhou, C., Zhu, C., ... Wan, J. (2020). Genome-wide association study identifies QTLs conferring salt tolerance in rice. *Plant Breeding*, 139(1), 73–82. <https://doi.org/10.1111/pbr.12750>
- Arbelaez, J. D., Dwiyantri, M. S., Tandayu, E., Llantada, K., Jarana, A., Ignacio, J. C., Platten, J. D., Cobb, J., Rutkoski, J. E., Thomson, M. J., & Kretschmar, T. (2019). 1k-RiCA (1K-Rice Custom Amplicon) a novel genotyping amplicon-based SNP assay for genetics and breeding applications in rice. *Rice (New York, N.Y.)*, 12(1), 55. <https://doi.org/10.1186/s12284-019-0311-0>

- Ashraf, M., & Foolad, M. R. (2013). Crop breeding for salt tolerance in the era of molecular markers and marker-assisted selection. *Plant Breeding*, 132(1), 10–20. <https://doi.org/10.1111/pbr.12000>
- Babu, N. N., Krishnan, S. G., Vinod, K. K., Krishnamurthy, S. L., Singh, V. K., Singh, M. P., Singh, R., Ellur, R. K., Rai, V., Bollinedi, H., Bhowmick, P. K., Yadav, A. K., Nagarajan, M., Singh, N. K., Prabhu, K. V., & Singh, A. K. (2017). Marker Aided Incorporation of Saltol, a Major QTL Associated with Seedling Stage Salt Tolerance, into *Oryza sativa* ‘Pusa Basmati 1121.’ *Frontiers in Plant Science*, 8. <https://doi.org/10.3389/fpls.2017.00041>
- Barua, R., Biswash, M. R., & Islam, Md. M. (2015). Performance of Some Salt Tolerant Rice Genotypes in Coastal Regions of Bangladesh under Irrigated Dry Season. *Applied Science Reports*, 11(2). <https://doi.org/10.15192/PSCP.ASR.2015.11.2.7275>
- Bhuyan, M. I., Supit, I., Mia, S., Mulder, M., & Ludwig, F. (2023). Effect of soil and water salinity on dry season boro rice production in the south-central coastal area of Bangladesh. *Heliyon*, 9(8), e19180. <https://doi.org/10.1016/j.heliyon.2023.e19180>
- BINA. (2023). *Binadhan 8*. Bangladesh Institute of Nuclear Agriculture. <https://bina.gov.bd/site/page/8375e58a-0ce3-4ae5-b158-49ed055c0071/%E0%A6%AC%E0%A6%BF%E0%A6%A8%E0%A6%BE%E0%A6%A7%E0%A6%BE%E0%A6%A8-%E0%A7%AE/>
- Biswas, P. S., Ahmed, M. M. E., Afrin, W., Rahman, A., Shalahuddin, A. K. M., Islam, R., Akter, F., Syed, M. A., Sarker, M. R. A., Ifterkharuddaula, K. M., & Islam, M. R. (2023). Enhancing genetic gain through the application of genomic selection in developing irrigated rice for the favorable ecosystem in Bangladesh. *Frontiers in Genetics*, 14, 1083221. <https://doi.org/10.3389/fgene.2023.1083221>
- Bonilla, P. S., Dvorak, J., & Mackill, D. J. (2002). RFLP and SSLP mapping of salinity tolerance genes in chromosome 1 of rice (*Oryza sativa* L.) using recombinant inbred lines. *Philippine Agricultural Scientist*, 65(1), 68–76.
- BRRI. (2023). *BRRI Dhan112* (pp. 1–2). Bangladesh Rice Research Institute.
- Chowdhury, A. D., Haritha, G., Sunitha, T., Krishnamurthy, S. L., Divya, B., Padmavathi, G., Ram, T., & Sarla, N. (2016). Haplotyping of Rice Genotypes Using Simple Sequence Repeat Markers Associated with Salt Tolerance. *Rice Science*, 23(6), 317–325. <https://doi.org/10.1016/j.rsci.2016.05.003>
- Das, P., Seal, P., & Biswas, A. K. (2016). Regulation of Growth, Antioxidants and Sugar Metabolism in Rice (<i>Oryza sativa</i> L.) Seedlings by NaCl and Its Reversal by Silicon. *American Journal of Plant Sciences*, 07(03), 623–638. <https://doi.org/10.4236/ajps.2016.73055>
- Dasgupta, S., Akhter Kamal, F., Huque Khan, Z., Choudhury, S., & Nishat, A. (2015). River Salinity and Climate Change: Evidence from Coastal Bangladesh. In J. Whalley, M. Agarwal, J. Pan, & J. Whalley, *World Scientific Reference on Asia and the World Economy* (pp. 205–242). WORLD SCIENTIFIC. https://doi.org/10.1142/9789814578622_0031
- Dasgupta, S., Islam, Md. S., Huq, M., Huque Khan, Z., & Hasib, Md. R. (2019). Quantifying the protective capacity of mangroves from storm surges in coastal Bangladesh. *PLOS ONE*, 14(3), e0214079. <https://doi.org/10.1371/journal.pone.0214079>
- Debsharma, S. K., Rahman, M. A., Khatun, M., Disha, R. F., Jahan, N., Quddus, Md. R., Khatun, H., Dipti, S. S., Ibrahim, Md., Ifterkharuddaula, K. M., & Kabir, Md. S. (2024). Developing climate-resilient rice varieties (BRRI dhan97 and BRRI dhan99) suitable for salt-stress environments in Bangladesh. *PLOS ONE*, 19(1), e0294573. <https://doi.org/10.1371/journal.pone.0294573>
- Dubouzet, J. G., Sakuma, Y., Ito, Y., Kasuga, M., Dubouzet, E. G., Miura, S., Seki, M., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2003). OsDREB genes in rice, *Oryza sativa* L., encode transcription activators that function in drought-, high-salt- and cold-responsive gene expression. *The Plant Journal: For Cell and Molecular Biology*, 33(4), 751–763. <https://doi.org/10.1046/j.1365-313x.2003.01661.x>

- Emon, R. M., Islam, M. M., Halder, J., & Fan, Y. (2015). Genetic diversity and association mapping for salinity tolerance in Bangladeshi rice landraces. *The Crop Journal*, 3(5), 440–444. <https://doi.org/10.1016/j.cj.2015.04.006>
- GREGORIO, G. B., ISLAM, M. R., VERGARA, G. V., & THIRUMENI, S. (2013). RECENT ADVANCES IN RICE SCIENCE TO DESIGN SALINITY AND OTHER ABIOTIC STRESS TOLERANT RICE VARIETIES. *SABRAO Journal of Breeding and Genetics*, 45(1), 31–41.
- Gupta, P. K., Mir, R. R., Mohan, A., & Kumar, J. (2008). Wheat genomics: Present status and future prospects. *International Journal of Plant Genomics*, 2008, 896451. <https://doi.org/10.1155/2008/896451>
- Gupta, P. K., & Varshney, R. K. (2000). The development and use of microsatellite markers for genetic analysis and plant breeding with emphasis on bread wheat. *Euphytica*, 113(3), 163–185. <https://doi.org/10.1023/A:1003910819967>
- Haque, M. A., Rafii, M. Y., Yusoff, M. M., Ali, N. S., Yusuff, O., Datta, D. R., Anisuzzaman, M., & Ikbal, M. F. (2021a). Advanced Breeding Strategies and Future Perspectives of Salinity Tolerance in Rice. *Agronomy*, 11(8), 1631. <https://doi.org/10.3390/agronomy11081631>
- Haque, M. A., Rafii, M. Y., Yusoff, M. M., Ali, N. S., Yusuff, O., Datta, D. R., Anisuzzaman, M., & Ikbal, M. F. (2021b). Recent Advances in Rice Varietal Development for Durable Resistance to Biotic and Abiotic Stresses through Marker-Assisted Gene Pyramiding. *Sustainability*, 13(19), 10806. <https://doi.org/10.3390/su131910806>
- Haque, T., Elias, S. M., Razzaque, S., Biswas, S., Khan, S. F., Azad Jewel, G. M. N., Rahman, Md. S., Juenger, T. E., & Seraj, Z. I. (2020). *Natural variation in growth and physiology under salt stress in rice: QTL mapping in a Horkuch × IR29 mapping population at seedling and reproductive stages*. Plant Biology. <https://doi.org/10.1101/2020.03.01.971895>
- Hasan, M. M., Rafii, M. Y., Ismail, M. R., Mahmood, M., Rahim, H. A., Alam, M. A., Ashkani, S., Malek, M. A., & Latif, M. A. (2015). Marker-assisted backcrossing: A useful method for rice improvement. *Biotechnology, Biotechnological Equipment*, 29(2), 237–254. <https://doi.org/10.1080/13102818.2014.995920>
- Hospital, F., & Charcosset, A. (1997). Marker-assisted introgression of quantitative trait loci. *Genetics*, 147(3), 1469–1485. <https://doi.org/10.1093/genetics/147.3.1469>
- Hu, H., Dai, M., Yao, J., Xiao, B., Li, X., Zhang, Q., & Xiong, L. (2006). Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. *Proceedings of the National Academy of Sciences of the United States of America*, 103(35), 12987–12992. <https://doi.org/10.1073/pnas.0604882103>
- Illius, S., & Azad, A. (2022, April 27). Salt tolerant rice varieties bring hope to Bangladesh farmers. *The Business Standard*. <https://www.tbsnews.net/bangladesh/salt-tolerant-rice-varieties-bring-hope-bangladesh-farmers-410202>
- Islam, M. R., & Gregorio, G. B. (2013). PROGRESS OF SALINITY TOLERANT RICE VARIETY DEVELOPMENT IN BANGLADESH. *SABRAO Journal of Breeding and Genetics*, 45(1), 21–30.
- Islam, M., Salambri, M., Hassanbr, L., Collardbr, B., & Gregorio, brR. (2011). QTL mapping for salinity tolerance at seedling stage in rice. *Emirates Journal of Food and Agriculture*, 23(2), 137. <https://doi.org/10.9755/ejfa.v23i2.6348>
- Islam, M. Z., Siddique, M. A., Prince, M., Rashid, E., & Khalequzzaman, M. (2023). Molecular Diversity Analysis of Some Selected Brri Developed Rice Varieties Using Ssr Markers. *SAARC Journal of Agriculture*, 21(2), 1–14. <https://doi.org/10.3329/sja.v21i2.68567>
- Islam, S. S., & Hossain, M. Z. (2020). Morphological and yield performance of rice varieties grown in moderately and strongly saline soils of Khulna, Bangladesh. *Global Scientific Journal*, 8(3), 582–596.
- Ismail, A. M., & Horie, T. (2017). Genomics, Physiology, and Molecular Breeding Approaches for Improving Salt Tolerance. *Annual Review of Plant Biology*, 68, 405–434. <https://doi.org/10.1146/annurev-arplant-042916-040936>
- Janaki Ramayya, P., Vinukonda, V. P., Singh, U. M., Alam, S., Venkateshwarlu, C., Vipparla, A. K., Dixit, S., Yadav, S., Abbai, R., Badri, J., T. R., Phani Padmakumari, A., Singh, V. K., & Kumar, A. (2021). Marker-assisted forward

- and backcross breeding for improvement of elite Indian rice variety Naveen for multiple biotic and abiotic stress tolerance. *PLOS ONE*, 16(9), e0256721. <https://doi.org/10.1371/journal.pone.0256721>
- Ju, C., Ma, X., Han, B., Zhang, W., Zhao, Z., Geng, L., Cui, D., & Han, L. (2022). Candidate gene discovery for salt tolerance in rice (*Oryza sativa* L.) at the germination stage based on genome-wide association study. *Frontiers in Plant Science*, 13, 1010654. <https://doi.org/10.3389/fpls.2022.1010654>
- Kabir, M., Salam, M., Chowdhury, A., Rahman, N., Iftekharruddaula, K., Rahman, M., Rashid, M., Dipti, S., Islam, A., Latif, M., Islam, A. S., Hossain, M., Nessa, B., Ansari, T., Ali, M., & Biswas, J. (2016). Rice Vision for Bangladesh: 2050 and Beyond. *Bangladesh Rice Journal*, 19(2), 1–18. <https://doi.org/10.3329/brj.v19i2.28160>
- Kobayashi, N. I., Yamaji, N., Yamamoto, H., Okubo, K., Ueno, H., Costa, A., Tanoi, K., Matsumura, H., Fujii-Kashino, M., Horiuchi, T., Nayef, M. A., Shabala, S., An, G., Ma, J. F., & Horie, T. (2017). OsHKT1;5 mediates Na⁺ exclusion in the vasculature to protect leaf blades and reproductive tissues from salt toxicity in rice. *The Plant Journal: For Cell and Molecular Biology*, 91(4), 657–670. <https://doi.org/10.1111/tpj.13595>
- Krishnamurthy, S. L., Sharma, P. C., Sharma, D. K., Ravikiran, K. T., Singh, Y. P., Mishra, V. K., Burman, D., Maji, B., Mandal, S., Sarangi, S. K., Gautam, R. K., Singh, P. K., Manohara, K. K., Marandi, B. C., Padmavathi, G., Vanve, P. B., Patil, K. D., Thirumeni, S., Verma, O. P., ... Singh, R. K. (2017). Identification of mega-environments and rice genotypes for general and specific adaptation to saline and alkaline stresses in India. *Scientific Reports*, 7(1), 7968. <https://doi.org/10.1038/s41598-017-08532-7>
- Kumar, S., Kaur, S., Seem, K., Kumar, S., & Mohapatra, T. (2021). Understanding 3D Genome Organization and Its Effect on Transcriptional Gene Regulation Under Environmental Stress in Plant: A Chromatin Perspective. *Frontiers in Cell and Developmental Biology*, 9, 774719. <https://doi.org/10.3389/fcell.2021.774719>
- Liu, J., Zhang, C., Wei, C., Liu, X., Wang, M., Yu, F., Xie, Q., & Tu, J. (2016). The RING Finger Ubiquitin E3 Ligase OsHTAS Enhances Heat Tolerance by Promoting H₂O₂-Induced Stomatal Closure in Rice. *Plant Physiology*, 170(1), 429–443. <https://doi.org/10.1104/pp.15.00879>
- Liu, Q., Qin, J., Li, T., Liu, E., Fan, D., Edzesi, W. M., Liu, J., Jiang, J., Liu, X., Xiao, L., Liu, L., & Hong, D. (2015). Fine Mapping and Candidate Gene Analysis of qSTL3, a Stigma Length-Conditioning Locus in Rice (*Oryza sativa* L.). *PLOS ONE*, 10(6), e0127938. <https://doi.org/10.1371/journal.pone.0127938>
- Mackill, D. J., & Khush, G. S. (2018). IR64: A high-quality and high-yielding mega variety. *Rice (New York, N.Y.)*, 11(1), 18. <https://doi.org/10.1186/s12284-018-0208-3>
- Marè, C., Zampieri, E., Cavallaro, V., Frouin, J., Grenier, C., Courtois, B., Brottier, L., Tacconi, G., Finocchiaro, F., Serrat, X., Nogués, S., Bundó, M., San Segundo, B., Negrini, N., Pesenti, M., Sacchi, G. A., Gavina, G., Bovina, R., Monaco, S., ... Valè, G. (2023). Marker-Assisted Introgression of the Salinity Tolerance Locus Saltol in Temperate Japonica Rice. *Rice*, 16(1), 2. <https://doi.org/10.1186/s12284-023-00619-2>
- Mishra, N., Jiang, C., Chen, L., Paul, A., Chatterjee, A., & Shen, G. (2023). Achieving abiotic stress tolerance in plants through antioxidative defense mechanisms. *Frontiers in Plant Science*, 14, 1110622. <https://doi.org/10.3389/fpls.2023.1110622>
- Mondal, S., Vaughn, R., Septiningsih, E. M., Singh, R. K., & Thomson, M. J. (2025). Identification of QTLs for reproductive stage salinity tolerance in rice using a cross between CSR28 and BRRI dhan28. *Crop Science*, 65(1), e70014. <https://doi.org/10.1002/csc2.70014>
- Moradi, F., & Ismail, A. M. (2007). Responses of photosynthesis, chlorophyll fluorescence and ROS-scavenging systems to salt stress during seedling and reproductive stages in rice. *Annals of Botany*, 99(6), 1161–1173. <https://doi.org/10.1093/aob/mcm052>
- Nayak, S., Habib, M. A., Das, K., Islam, S., Hossain, S. M., Karmakar, B., Fritsche Neto, R., Bhosale, S., Bhardwaj, H., Singh, S., Islam, M. R., Singh, V. K., Kohli, A., Singh, U. S., & Hassan, L. (2022). Adoption Trend of Climate-Resilient Rice Varieties in Bangladesh. *Sustainability*, 14(9), 5156. <https://doi.org/10.3390/su14095156>

- Platten, J. D., Egdane, J. A., & Ismail, A. M. (2013). Salinity tolerance, Na⁺ exclusion and allele mining of HKT1;5 in *Oryza sativa* and *O. glaberrima*: Many sources, many genes, one mechanism? *BMC Plant Biology*, 13(1), 32. <https://doi.org/10.1186/1471-2229-13-32>
- Pradhan, S. K., Nayak, D. K., Mohanty, S., Behera, L., Barik, S. R., Pandit, E., Lenka, S., & Anandan, A. (2015). Pyramiding of three bacterial blight resistance genes for broad-spectrum resistance in deepwater rice variety, Jalmagna. *Rice (New York, N.Y.)*, 8(1), 51. <https://doi.org/10.1186/s12284-015-0051-8>
- Rahman, M. A., Thomson, M. J., De Ocampo, M., Egdane, J. A., Salam, M. A., Shah-E-Alam, M., & Ismail, A. M. (2019). Assessing trait contribution and mapping novel QTL for salinity tolerance using the Bangladeshi rice landrace Capsule. *Rice (New York, N.Y.)*, 12(1), 63. <https://doi.org/10.1186/s12284-019-0319-5>
- Rahman, M., Haque, M., Kabir, M. J., Islam, A., Sarkar, M., Mamun, M., Salam, M., & Kabir, M. (2021). Enhancing Rice Productivity in the Unfavourable Ecosystems of Bangladesh. *Bangladesh Rice Journal*, 24(2), 83–102. <https://doi.org/10.3329/brj.v24i2.53450>
- Rahman, N. Md. F., Malik, W. A., Kabir, Md. S., Baten, Md. A., Hossain, Md. I., Paul, D. N. R., Ahmed, R., Biswas, P. S., Rahman, Md. C., Rahman, Md. S., Iftekharuddaula, K. Md., Hadasch, S., Schmidt, P., Islam, Md. R., Rahman, Md. A., Atlin, G. N., & Piepho, H.-P. (2023). 50 years of rice breeding in Bangladesh: Genetic yield trends. *Theoretical and Applied Genetics*, 136(1), 18. <https://doi.org/10.1007/s00122-023-04260-x>
- Rashid, M. H., & Nasrin, S. (2014). Productivity and Preference of Salt Tolerant Boro Rice varieties in Saline Non-gher and Gher Ecosystems. *Bangladesh Rice Journal*, 18(1), 9–24.
- Reddy, I. N. B. L., Kim, B.-K., Yoon, I.-S., Kim, K.-H., & Kwon, T.-R. (2017). Salt Tolerance in Rice: Focus on Mechanisms and Approaches. *Rice Science*, 24(3), 123–144. <https://doi.org/10.1016/j.rsci.2016.09.004>
- Ren, Z.-H., Gao, J.-P., Li, L.-G., Cai, X.-L., Huang, W., Chao, D.-Y., Zhu, M.-Z., Wang, Z.-Y., Luan, S., & Lin, H.-X. (2005). A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nature Genetics*, 37(10), 1141–1146. <https://doi.org/10.1038/ng1643>
- Reshna, O. P., & Beena, R. (2021). Salinity Tolerance Mechanisms in Rice: A Review. *Indian Journal Of Agricultural Research, Of*. <https://doi.org/10.18805/IJARc.A-5760>
- Sackey, O. K., Feng, N., Mohammed, Y. Z., Dzou, C. F., Zheng, D., Zhao, L., & Shen, X. (2025). A comprehensive review on rice responses and tolerance to salt stress. *Frontiers in Plant Science*, 16, 1561280. <https://doi.org/10.3389/fpls.2025.1561280>
- Salam, M., Rahman, M., Bhuiyan, M., Uddin, K., Sarker, M., Yasmeen, R., & Rahman, M. (2009). BRRI dhan 47: A salt-tolerant variety for the boro season. *International Rice Research Notes*, 32(1), 42–43. <https://doi.org/10.3860/irrn.v32i1.1093>
- Santosh Kumar, V. V., Verma, R. K., Yadav, S. K., Yadav, P., Watts, A., Rao, M. V., & Chinnusamy, V. (2020). CRISPR-Cas9 mediated genome editing of drought and salt tolerance (OsDST) gene in indica mega rice cultivar MTU1010. *Physiology and Molecular Biology of Plants: An International Journal of Functional Plant Biology*, 26(6), 1099–1110. <https://doi.org/10.1007/s12298-020-00819-w>
- Shan, Q., Wang, Y., Li, J., Zhang, Y., Chen, K., Liang, Z., Zhang, K., Liu, J., Xi, J. J., Qiu, J.-L., & Gao, C. (2013). Targeted genome modification of crop plants using a CRISPR-Cas system. *Nature Biotechnology*, 31(8), 686–688. <https://doi.org/10.1038/nbt.2650>
- Shawkhatuzamman, M., Roy, S. R., Alam, M. Z., Majumder, P., Anka, N. J., & Hasan, A. K. (2023). Soil salinity management practices in coastal area of Bangladesh: A review. *Research in Agriculture Livestock and Fisheries*, 10(1), 1–7. <https://doi.org/10.3329/ralf.v10i1.66211>
- Shohan, M. U. S., Sinha, S., Nabila, F. H., Dastidar, S. G., & Seraj, Z. I. (2019). HKT1;5 Transporter Gene Expression and Association of Amino Acid Substitutions With Salt Tolerance Across Rice Genotypes. *Frontiers in Plant Science*, 10, 1420. <https://doi.org/10.3389/fpls.2019.01420>

- Singh, R. K., Kota, S., & Flowers, T. J. (2021). Salt tolerance in rice: Seedling and reproductive stage QTL mapping come of age. *Theoretical and Applied Genetics*, 134(11), 3495–3533. <https://doi.org/10.1007/s00122-021-03890-3>
- Soda, N., Gupta, B. K., Anwar, K., Sharan, A., Govindjee, Singla-Pareek, S. L., & Pareek, A. (2018). Rice intermediate filament, OsIF, stabilizes photosynthetic machinery and yield under salinity and heat stress. *Scientific Reports*, 8(1), 4072. <https://doi.org/10.1038/s41598-018-22131-0>
- Spindel, J., Begum, H., Akdemir, D., Virk, P., Collard, B., Redoña, E., Atlin, G., Jannink, J.-L., & McCouch, S. R. (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>
- SRDI. (2010). *Saline soils of Bangladesh*. (pp. 1–62). SRDI, Ministry of Agriculture, Dhaka, Bangladesh. <https://file-khulna.portal.gov.bd/uploads/40fbf1ba-e808-4116-b3f4-6cf0d29c7969//685/296/122/685296122c0ee038915183.pdf>
- Tahjib-Ul-Arif, Md., Sayed, M. A., Islam, M. M., Siddiqui, M. N., Begum, S. N., & Hossain, M. A. (2018). Screening of rice landraces (*Oryza sativa* L.) for seedling stage salinity tolerance using morpho-physiological and molecular markers. *Acta Physiologiae Plantarum*, 40(4), 70. <https://doi.org/10.1007/s11738-018-2645-4>
- Takagi, H., Abe, A., Yoshida, K., Kosugi, S., Natsume, S., Mitsuoka, C., Uemura, A., Utsushi, H., Tamiru, M., Takuno, S., Innan, H., Cano, L. M., Kamoun, S., & Terauchi, R. (2013). QTL-seq: Rapid mapping of quantitative trait loci in rice by whole genome resequencing of DNA from two bulked populations. *The Plant Journal: For Cell and Molecular Biology*, 74(1), 174–183. <https://doi.org/10.1111/tj.12105>
- 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., Gregorio, G. B., & Ismail, A. M. (2010). Characterizing the Saltol Quantitative Trait Locus for Salinity Tolerance in Rice. *Rice*, 3(2–3), 148–160. <https://doi.org/10.1007/s12284-010-9053-8>
- Yadav, A. K., Kumar, A., Grover, N., Ellur, R. K., Krishnan, S. G., Bollinedi, H., Bhowmick, P. K., Vinod, K. K., Nagarajan, M., Krishnamurthy, S. L., & Singh, A. K. (2020). Marker aided introgression of “Saltol”, a major QTL for seedling stage salinity tolerance into an elite Basmati rice variety “Pusa Basmati 1509.” *Scientific Reports*, 10(1), 13877. <https://doi.org/10.1038/s41598-020-70664-0>
- Zhang, A., Liu, Y., Wang, F., Li, T., Chen, Z., Kong, D., Bi, J., Zhang, F., Luo, X., Wang, J., Tang, J., Yu, X., Liu, G., & Luo, L. (2019). Enhanced rice salinity tolerance via CRISPR/Cas9-targeted mutagenesis of the OsRR22 gene. *Molecular Breeding: New Strategies in Plant Improvement*, 39, 47. <https://doi.org/10.1007/s11032-019-0954-y>
- Zhang, P., Liu, J., Jia, N., Wang, M., Lu, Y., Wang, D., Zhang, J., Zhang, H., & Wang, X. (2023). Genome-wide identification and characterization of the bZIP gene family and their function in starch accumulation in Chinese chestnut (*Castanea mollissima* Blume). *Frontiers in Plant Science*, 14, 1166717. <https://doi.org/10.3389/fpls.2023.1166717>