

REVIEW



Potential of HKT, NHX, and HAK gene transfer responsive to salt stress in rice (*Oryza sativa* L.)

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ABSTRACT

Rice (*Oryza sativa* L.) is one of the most important staple cereal crops globally, and maximizing its yield is essential for ensuring food security. However, increasing soil salinity is a major abiotic stress that significantly restricts rice cultivation, productivity, and overall yield, particularly in coastal regions such as Bangladesh. Globally, salt stress affects nearly one-third of irrigated croplands and disrupts rice physiological processes, causing substantial yield losses even under moderate stress conditions. Genetic improvement has emerged as an effective strategy to enhance salt tolerance, as demonstrated by studies involving Saltol quantitative trait loci (QTL) introgression and transgenic overexpression of key genes. This systematic review summarizes the physiological impacts of salt stress on rice and highlights the critical roles of three gene families—HKT (High-Affinity K⁺ Transporters), NHX (Na⁺/H⁺ Antiporters), and HAK (High-Affinity K⁺ Transporters)—in maintaining ionic homeostasis under saline environments through Na⁺ exclusion, vacuolar sequestration, and K⁺ uptake. In addition, the review examines gene transfer approaches, including transgenic methods, CRISPR/Cas9-mediated genome editing, and QTL introgression. Emerging strategies such as gene stacking, synthetic promoter development, and AI-assisted breeding are also discussed as future avenues to develop highly salt-tolerant rice varieties. Overall, integrating molecular innovations with advanced breeding techniques offers sustainable solutions to mitigate salinity stress and safeguard global rice production under changing climatic conditions.

KEY WORDS

Gene transfer; HAK; HKT; NHX; *Oryza sativa* L.; Salt tolerance

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Introduction

Soil salinity already hits over 20% of the world's irrigated land, and that number just keeps creeping up because of climate change, rising sea levels and seawater intrusion kind a scary, but true [1]. In Bangladesh more than a million hectares of coastal farmland places like Khulna, Satkhira, Barisal and Noakhali are seriously salted, so yields take a big hit in the dry season when salinity peaks, big losses really [2]. Salt stress brings on osmotic pressure, ionic toxicity and then secondary oxidative damage, and together they mess with water uptake, photosynthesis, enzyme activity and nutrient balance so plants grow less and produce less, simple as that [3]. Rice feeds nearly half the world, it's central to food security but annoyingly it's also extremely vulnerable to salt stress. Effective salt tolerance really hinges on keeping a steady Na⁺/K⁺ balance inside plant cells, and that balancing act is mostly handled by specialized ion transporters. Putting these stress-responsive genes into rice by genetic engineering, QTL introgression or CRISPR-based precision breeding seems like a powerful way to make high-performing, salt-tolerant varieties that we'll need for future food security in South and Southeast Asia [4]. Recent leaps in plant molecular biology show real potential in three main ion-transporter gene families HKT, NHX and HAK for improving rice salt tolerance. In coastal Bangladesh, where traditional rice varieties often just don't survive, these

molecular breeding and gene-transfer approaches could offer sustainable solutions to keep grain production stable and protect livelihoods in saline agroecosystems. Those genes help kick out excess Na⁺, boost K⁺ uptake and sequester salt into vacuoles, letting rice maintain ion homeostasis under salty conditions that's basically how it works [5].

Background

Importance of developing salt-tolerant rice varieties

Salinisation is rising faster due to global climate change, rise in sea-level, and flooding, especially in low-lying countries like Bangladesh. Researchers have introduced salt-sensitive genes, including HKT, NHX, and HAK, to preserve ionic homeostasis and improve the resilience of plants to salinity [5]. Salt-tolerant rice varieties are an important part of food security in areas affected by the increase in soil salinity. These types of varieties have the added benefit of stabilising crop production as well as protecting rural livelihoods, which rely on rice farming [4]. Salinisation is increasing faster due to global climate change, rising sea levels, and flooding, especially in low-lying coastal countries like Bangladesh. Researchers have introduced salt-sensitive genes, HKT, NHX, and HAK, to preserve ionic equilibrium and increase the resilience of plants in saline environments [5]. The salt-tolerant rice varieties are an essential ingredient to food

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security in areas affected by increasing soil salinity. The creation of these varieties not only stabilises the production of crops but also protects the existence of rural areas based on rice production [4].

Salt-affected areas in Bangladesh

The country of Bangladesh covers a total of 1.05 million hectares of salt-impacted land, most of which are located in the southern coastline area [2]. Those principally prone to salinity are (Figure 1):

- **Khulna** (Dacope, Paikgacha)
- **Satkhira** (Shyamnagar)
- **Bagerhat** (Rampal, Mongla)
- **Barisal** (Mehendiganj)
- **Patuakhali** (Kalapara)
- **Noakhali & Lakshmipur** (coastal zones)

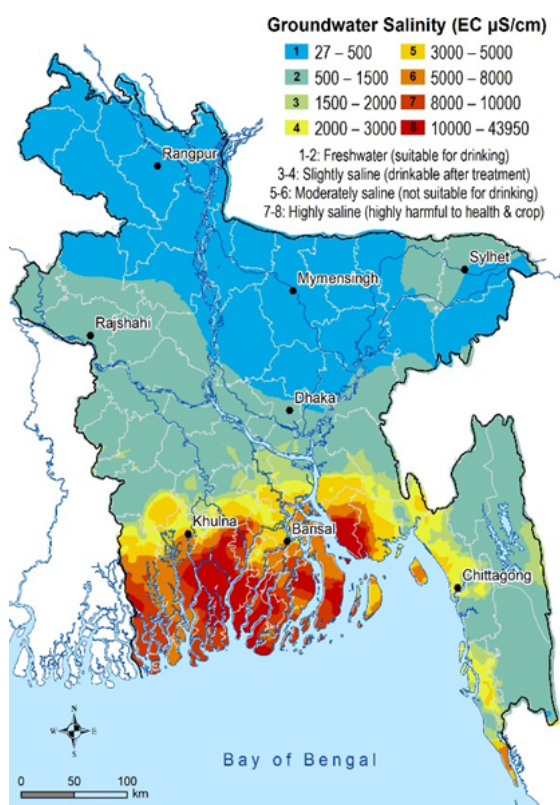


Figure 1. Global and Bangladesh salinity map.

In many farming situations, traditional types of rice varieties are not very viable in the dry season (Rabi) where salinity levels are at peak levels. Salt tolerant ones including BRRI dhan47, BRRI dhan67, BRRI dhan73, and BINA dhan10 have been developed successfully thus emphasizing the possible advantage of incorporating stress related genetic loci.

Economic perspective and benefits to farmers

Salt-tolerant rice varieties provide several economic advantages:

Higher yield in saline soils

Farmers can cultivate rice even in moderately or highly saline areas, securing 1–3 tons/ha yield where traditional varieties produce almost nothing.

Reduced production loss

In coastal Bangladesh, salinity causes annual crop losses worth millions of dollars. Salt-tolerant rice reduces these losses.

Opportunity for dry-season cultivation

Varieties like BRRI dhan47 allow farmers to grow a second crop where previously land remained fallow.

Higher income stability

Farmers in Satkhira and Khulna reported 25–35% higher seasonal income after switching to salt-tolerant varieties [2].

Lower input cost

Salt-tolerant varieties often require less irrigation and lower fertilizer application. Salt-induced land degradation causes significant economic losses by reducing crop productivity and increasing land management costs [6].

Nutritional value and consumer benefits

Salt-tolerant varieties, especially modern ones developed through molecular breeding, are not only stress-resilient but also nutritionally superior. For example, BRRI dhan47 contains higher protein content compared to many traditional coastal rice varieties. Salt-tolerant rice varieties often have better mineral profiles, maintaining higher levels of K^+ , Mg^{2+} , and essential micronutrients even under stress. Many new lines have been biofortified with micronutrients such as zinc and iron, improving dietary quality in malnutrition-prone rural communities.

The need to improve rice varieties via the incorporation of salt-responsive genes, including HKT, NHX, and HAK, guarantees the agronomic performance and food security of the rice varieties, hence making them the key constituents of the sustainable food system in Bangladesh and similar coastal areas around the world. There is a growing problem of global food security due to the threats of climate change, rising sea levels, coastal floods, and rising soil salinization. Novel yield can be significantly reduced even by an electrical conductivity of 34 S m⁻¹. Rice (*Oryza sativa* L.) is the staple food of about half of the globe, but it is highly susceptible to salt stress and especially in the initial seedling growth stages and reproduction. Salt stress causes negative effects to rice by causing osmotic imbalance, ionic toxicity and secondary oxidative stress. As a result of this, salt tolerance has become a necessity for sustainable salt-prone South and Southeast Asian rice production. A combination of these stressors causes the impairment of photosynthesis, disruption of nutrient uptake, and enzymatic activity, and eventually limits plant growth.

Plants have evolved complex adaptive strategies involving ion transport systems. Three key gene families, HKT (High-Affinity K^+ Transporters), NHX (Na^+/H^+ Antiporters), and HAK (High-Affinity K^+ Transporters) play critical roles in maintaining ionic balance under salt stress [7]. Advances in molecular biology and genetic engineering have enabled the transfer and modification of these genes to create salt-tolerant rice genotypes.

Impact of Salt Stress on Rice

High amounts of dissolved salts and in particular, NaCl reduce soil water potential and therefore, it introduces a scenario whereby water is in the soil matrix, but it is physiologically

unavailable to plant roots [1,5]. The osmotic stress stage is the first and the most immediate response of rice (*Oryza sativa*) to salinity, which occurs almost instantly as salts are deposited in the root zone. This is normally referred to as physiological drought whereby the plant takes in inadequate amounts of water to meet its metabolic requirements. A low turgor pressure directly interferes with cell growth resulting in root and shoot stunt growth. Whilst this kind of reduction helps in conserving water, it also has the effect of reducing uptake of CO₂, and thus reducing photosynthetic throughput. The meristematic areas and young tissues are particularly susceptible resulting in delayed leaf development, diluted tillering and impaired panicle development [3]. Such attenuation significantly reduces the pressure of cell turgor – the hydrostatic force that maintains cell morphology and supports growth. This in turn reduces photosynthetic productivity, producing less carbohydrates and restricting energy budget needed to grow and mature and eventually hinders biomass accumulation [8]. Pores in the epidermis on the leaf surface called stomata respond to osmotic stress by partially closing to reduce the rate of excessive transpiration. Salinity stress significantly reduces the growth and productivity of rice especially in coastal rice growing areas where the soil salinity increases during the dry seasons. Salinity on rice productivity depends on when the stress is experienced in the crop development cycle; salinity at the sensitive stages of crop development, especially early seedling development and reproductive development stages will lead to much greater losses of the crop production as compared to stress induced when the crop is at advanced stages of development [9].

Furthermore, hormones, including abscisic acid (ABA) which mediate stomatal closure, and coordinate gene expression related to drought and salt acclimation, are triggered by osmotic stress [10]. The production of the osmolytes such as proline, glycine betaine, and soluble sugars is increased to maintain cellular osmotic pressure. These osmolytes have the roles of maintaining cellular hydration, stabilizing proteins and membranes, and reducing oxidative damage [11]. A range of physiological and molecular responses take place across the plant also as a result of osmotic stress. Temporary osmotic stress can be overcome when the salinity level goes down, yet in the long-term, osmotic stress can debilitate the plant, distort the normative growth patterns and predispose the plant to the next stage of the toxicity caused by ions, as accumulated Na⁺ and Cl⁻ ions disrupt the enzyme processes, nutrient uptake, and photosynthetic activity [12]. The final extent of injury depends upon the magnitude and the length of the osmotic perturbation.

In salinity prone areas like coastal Bangladesh, the phase of osmotic stress gains additional significance in periods of dryness viz. the Rabi season when salinity is at its highest point. At this stage, juvenile seedlings are particularly susceptible, and the establishment of these seedlings is often suboptimal or even fatal unless tolerant varieties are used [2]. This step can therefore not be fully understood without the breeding and development of salt-tolerant rice since specific interventions like increasing root water-absorption capacity or increasing osmolyte production can significantly increase the levels of survival and productivity in saline conditions.

Ion toxicity phase

High Na⁺ levels mess with basic cell processes, they basically crowd out potassium (K⁺) and calcium (Ca²⁺) at the spots

where enzymes should bind, so enzyme activity and overall metabolic regulation go off Munns & Tester, Zhu said as much, and yeah it checks out [1,3]. After that first osmotic shock, rice moves into this ionic toxicity phase, driven by Na⁺ and Cl⁻ building up in tissues, leaves take the worst of it. Osmotic stress is mostly about water uptake being limited, ion toxicity is different it shows up when the plant can't compartmentalize or exclude the ions anymore. The end result is less protein being made, membranes get shaky, and metabolism just loses efficiency. Calcium being pushed out does more than one thing it destabilizes membranes and cuts down signaling, so stress just piles on itself. Potassium is needed for enzyme activation, stomatal control and photosynthesis, so when Na⁺ takes K⁺'s place, the plant physiology suffers pretty widely. And when Na⁺ and Cl⁻ build up you get nutrient imbalances too Na⁺ competes with K⁺ uptake and Cl⁻ can mess with nitrate assimilation, great, just what a plant needed. In severe cases whole seedlings can die if ion concentrations pass the tolerance threshold not pretty [11]. Over time ion toxicity piles up into stunted growth, fewer tillers, messed up reproductive development and then, yeah, big yield losses. You'll see leaf tip necrosis, chlorosis (yellowing) and tissue dying off progressively, which cuts photosynthetic area and limits carbs [12]. Usually, the older leaves show it first, they act like sinks for the extra salts obvious in hindsight, but still rough for the plant.

Keeping a high cytosolic K⁺/Na⁺ ratio, helped by HAK transporters, is one-way enzymes and metabolism stay stable under salt stress [8]. Other tricks are limiting Na⁺ entry at the roots, pulling Na⁺ back from the xylem so it doesn't pile up in shoots via HKT transporters, and shoving Na⁺ into vacuoles through NHX antiporters [5]. Breeding gave us salt-tolerant lines like BRRI dhan47 that maintain ion homeostasis in salty conditions practical proof this matters [2]. Still, rice is naturally salt-sensitive and how well these mechanisms work depends on the variety plants have evolved a few adaptive tactics to cut ionic toxicity, but none are perfect. Maintaining adequate potassium nutrition is crucial under salt stress, as high sodium levels interfere with K⁺ uptake and disrupt cellular ionic balance [13]. Physiological responses such as osmotic adjustment, stomatal regulation, and ion homeostasis serve as indicators of plant tolerance to salinity stress [14].

That all translates to better survival, higher photosynthetic efficiency and improved grain yield in salty places, especially around the coasts of Bangladesh, where ion toxicity is a big headache during the Rabi season. If breeders and biotechnologists can find and tweak the genes for Na⁺ exclusion, vacuolar sequestration and K⁺ retention, tolerance can be boosted at tissue and whole-plant levels, simple idea, tricky in practice. So yeah, understanding the ion toxicity phase is crucial if we want to make rice more resistant to salinity.

Nutrient imbalance

Too much sodium, Na⁺, basically fights with potassium, K⁺, for the same transporters and binding spots so the plant ends up absorbing and moving less K⁺ around it's annoying. People call that nutrient imbalance, and it's a major reason rice growth and yields tank under salt stress, you know, like Munns & Tester pointed out [1]. Because potassium's needed for enzyme action, making proteins, stomata control, and keeping cellular water balance, when K is low photosynthesis falters, water-use drops and metabolism gets shaky, messy, wobble even [8]. High external sodium (Na⁺) in saline soils doesn't just

cause osmotic stress and ion toxicity. it also messes up uptake of other essentials, especially K^+ , Ca^{2+} and Mg^{2+} , big time. Potassium transporters play a crucial role in plant adaptation to saline environments by maintaining intracellular K^+ levels and a favorable Na^+/K^+ ratio. Under salt stress, the regulation of high-affinity K^+ transporters are essential for sustaining enzymatic activity, membrane stability, and overall growth in rice and other crops [15].

Calcium, weirdly, is sort of the glue for membranes and the go-to for cell signaling. When Na^+ piles up it kicks Ca^{2+} off membrane binding sites, so membranes get leakier, stuff spills out, and signals stop working properly it's not subtle. That destabilization hits organelles too, especially chloroplasts, mitochondria and vacuoles, which then drags down metabolism and energy production, as Roy, Negrao & Tester noted [8].

If K^+ , Ca^{2+} and Mg^{2+} all drop, the plant shows the classic signs: yellowing leaves, dead spots, stunted growth, and poor tillering. Magnesium is right at the heart of chlorophyll, so when Mg^{2+} uptake falls in salty soils chlorophyll breaks down, photosynthesis drops and fewer carbs are made, yeah [11]. So nutrient imbalance doesn't just tweak some processes, it lowers the plant's ability to cope with prolonged salt, plain and simple. Even with some adaptive tricks, sensitive varieties often can't keep nutrient levels where they need to be, which is why breeding salt-tolerant rice is a big priority in salty places like coastal Bangladesh [2].

Those tricks include selective ion transport, shifting Na^+ into vacuoles via NHX antiporters, and keeping a high K^+/Na^+ ratio with HAK and HKT transporters [5]. Also roots help by exuding compounds and increasing surface area they can grab more nutrients under saline conditions, not a miracle but it helps. Rice plants try to counteract nutrient imbalance through a mix of adaptive mechanisms, some effective, some barely, kind of a patchwork. So yeah, understanding nutrient imbalance is crucial if we're going to develop breeding or genetic engineering approaches that keep nutrient homeostasis under salt stress. By boosting K^+ uptake, keeping Ca^{2+} signaling working right and making Mg^{2+} more available, scientists can improve plant vigor, photosynthesis and grain yield in salty soils probably, hopefully, if everything else falls into place.

Physiological and biochemical effects

Too much salt messes with making chlorophyll and pretty much damages photosystem II, so plants can't absorb light or convert it properly [1]. Less chlorophyll not only slows photosynthesis, it also cuts down the total carbs the plant needs to grow and fill grains, yeah [3]. Salt stress hits a lot of the physiological and biochemical stuff in rice, and that shows up as smaller plants and lower yields. One of the quickest things you notice is photosynthetic efficiency dropping. Stomatal conductivity gets messed up by salt too. That means less carbon assimilation and a poorer supply of sugars for energy and building materials [8]. To avoid losing water under osmotic stress the stomata close, partially or fully, which limits CO_2 uptake for the Calvin cycle (Figure 2).

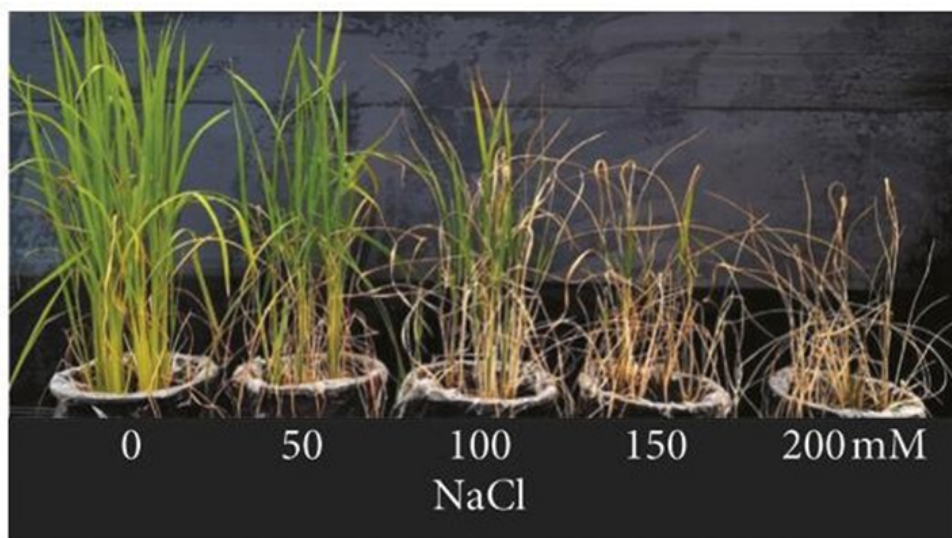


Figure 2. Diagram of salt stress effects in rice.

The result is stunted growth, delayed tillering and fewer panicles simple as that. Salt stress also spikes production of reactive oxygen species (ROS), like hydrogen peroxide (H_2O_2), superoxide (O_2^-), and those hydroxyl radicals ($\bullet OH$). ROS are normal byproducts, but when they pile up under salinity, they cause oxidative stress and damage DNA, proteins and lipids. Lipid peroxidation weakens membranes, leads to electrolyte leakage and screws up cellular metabolism [8]. Antioxidant systems SOD, CAT, POD and the rest often get overwhelmed during bad stress, so cell damage just gets worse [11]. Panicle formation is harmed, so there are fewer flowers and spikelet per plant. Tillering capacity drops because there aren't enough resources to start and elongate new shoots. Also,

grain filling suffers when carbs aren't transported well from the source leaves to developing grains, which lowers yield and makes grain quality poor [5]. All those things poor photosynthesis, stomatal closure, oxidative stress cascade into broader developmental problems.

By excluding excess Na^+ , sequestering it in vacuoles, and retaining K^+ , these genes help keep photosynthesis going, cut ROS buildup, and preserve stomatal function so they mitigate salt damage [8,2]. Understanding these physiological and biochemical responses is important for developing salt-tolerant rice that can actually survive in salt-prone areas, especially the coastal belts of Bangladesh. Rice varieties that

keep ion homeostasis through HKT, NHX and HAK transporters tend to show better resilience, both physiologically and biochemically kind of neat, and useful. Developing salt-tolerant crops requires coordinated physiological and genetic strategies that improve ion homeostasis and stress adaptation. Advances in understanding salt stress signaling and ion transport have enabled targeted approaches for enhancing crop performance under saline conditions [16]. Plant adaptation to salinity includes complicated physiological and biochemical alterations that are similar to those to other abiotic pressures like drought and high temperatures. These common stress-response mechanisms include osmotic stress response, antioxidants defense and stress-responsive gene regulation [3].

Importance of Na⁺/K⁺ Homeostasis in Salt Tolerance

A higher internal K⁺/Na⁺ ratio is basically the big physiological marker for salt tolerance in *Oryza sativa*, it's the most important one weird but true. That ionic balance gets maintained, and it protects enzymes, keeps protein structure intact, and controls those crucial metabolic processes, you know the stuff. Salt-tolerant varieties hit that balance by upregulating selected ion-transport pathways, which cut down Na⁺ buildup and keep K⁺ uptake enough sounds simple, but it's not always. If that balance is messed up, photosynthetic activity is impaired, protein synthesis falters and the cell can suffer structural damage, basically a cascade of problems. So, Na⁺/K⁺ homeostasis supports both spontaneous, natural tolerance and genetically modified salt-tolerance strategies it's the core goal, whether it happens by itself or we tinker with it.

Na⁺ exclusion

Na⁺ exclusion is the major defense mechanism utilized by plants against salinity stress to avoid excess uptake of sodium ions into the root cells at the initial stage of absorption. This process can happen by releasing Na⁺ into the immediate soil space or by limiting its diffusion into the cytoplasm via the help of specific transport proteins located on the plasma membrane, specifically the Salt Overly Sensitive (SOS1) antiporters. The delay of ion toxicity has been observed to be done at this early stage by rice cultivars, extending until cellular activities and other cellular metabolism remain active [3]. This defense mechanism becomes highly vital in the event of young seedlings where growth is highly prone to ionic imbalances. Na⁺ exclusion is an energetically challenging process, but a necessity when shielding root and shoot tissues against the harmful consequences of a high salinity background [11].

Na⁺ retrieval from xylem

Rice can sustain metabolic balance, enzymatic activity, and glucose synthesis by keeping the concentration of Na⁺ in shoots lower. Some Na⁺ unavoidably reaches the xylem and can be carried to the leaves, where it can harm photosynthetic tissues, despite exclusion mechanisms at the roots. HKT transporters like OsHKT1;5 is used by salt-tolerant rice cultivars to remove Na⁺ from xylem sap and return it to root cells or surrounding tissues [12]. Thus, under extended salt stress, Na⁺ recovery from xylem is a crucial mechanism for yield stability. By preventing salt buildup in the leaves, this procedure preserves photosynthetic activity and chloroplast function.

Vacuolar sequestration

To prevent disruption of the cytoplasmic processes, plants

store the toxic sodium ions in vacuoles. The NHX antiporters that are localized in the vacuolar membranes facilitate the process of translocation of sodium ions into the vacuoles using the proton gradients.

Rice plants find a solution to sodium poisoning by storing the ion in vacuoles by NHX antiporters. However, exclusion and retrieval processes are not entirely efficient and some amount of sodium is bound to enter the cytoplasm. Vacuolar sequestration therefore conserves osmotic pressure and allows cells to retain water in the presence of saline stress which is vital in the process of maintaining the turgor pressure, cell growth and cell metabolism. The approach also protects the key cytoplasmic enzymes and proteins against inhibition hence ensuring continuity of normal physiological processes. These transporters avoid the cytosol to attain the levels of harmful ions, by active translocation of sodium by harnessing the proton gradients across the vacuolar membranes [8]. Sodium sequestration in vacuoles is presumed to be of special importance in the case of long-term conditions of saline environments and facilitates the maintenance of growth and survival (Figure 3).

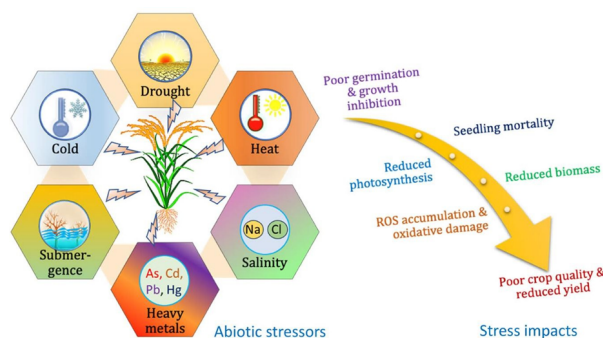


Figure 3. Ion homeostasis pathway diagram.

K⁺ retention and uptake

Potassium retention maintains the metabolic activities even in the presence of high levels of sodium. Salt stress increases the leakiness of membranes leading to the release of potassium by the cells. High salinity commonly causes the loss of potassium by increasing membrane permeability, and competing with sodium. In salt-tolerant plants, this loss is countered by the high-affinity potassium transporter (HAK) up-regulation. Highly effective potassium intake maintains cytoplasmic pH and reduces oxidative stress. In addition, energy production, carbohydrate composition, and a direct effect on vegetative growth, tillering, and grain development are based on persistent potassium retention. Saline environments cause the activation of HAKs in rice, which results in the absorption and retention of potassium. Maintaining a normal potassium level maintains the cytoplasmic pH and minimises oxidative stress as well as ensures the smooth progression of metabolic pathways [5]. Potassium is necessary in sufficient amounts because it is needed to activate enzymes, promote photosynthesis, and stimulate protein synthesis. The combination of the sodium exclusion, sodium recovery, vacuolar sequestration and potassium retention completely works in a synergetic manner to increase salt tolerance in rice and conserve the yields. Potassium is still required to activate enzymes, protein synthesis, osmotic regulation, stomatal regulation and photosynthesis [1].

HKT Gene Family and their Role in Salt Stress

Classification of HKT transporters

The amino acid composition and tissue-specific expression of these transporters vary. Under stressed circumstances, their combined function controls ion movement across great distances. Comprehending these classes offers crucial genetic targets for enhancing salt tolerance. Based on their ion selectivity, HKT transporters are classified into two major categories. Class I HKT transporters are essential for minimizing salt buildup in shoots since they primarily transfer Na^+ . When there is a food shortage or low salinity, class II HKT proteins help maintain ionic equilibrium by transporting both Na^+ and K^+ . Two primary subtypes of HKT transporters are distinguished by their ion selectivity and transport function. Under salt stress, high-affinity potassium transporter (HKT) proteins are essential membrane transporters that are vital to preserving ion homeostasis (Figure 4).

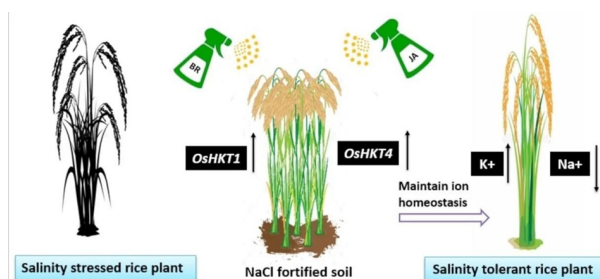


Figure 4. HKT transporter locations and functions.

- **Transporter classes:** I HKT transporters are mostly selective for sodium (Na^+) and play a key role in removing Na^+ from the xylem, preventing the accumulation of toxicity in the leaves. They are extensively expressed in the xylem parenchyma tissues and are essential in the lack of sodium in the shoot [1,12].
- **Class 2 HKT transporters** contribute to ionic homeostasis in potassium-deficient and moderately salinized environments by mediating the transmembrane mobility of Na^+ and K^+ (Na^+/K^+). The plant's dual selectivity enables it to retain a favorable K^+ to Na^+ ratio and use K^+ uptake selectivity in situations of elevated Na^+ levels [11]. Genomic studies in rice have identified key genes associated with salt tolerance, providing insights for developing improved stress-resistant varieties [18].

Understanding the functional differences and tissue-specific expression patterns of these transporters provides valuable genetic targets for breeding salt-tolerant rice varieties.

Major HKT genes in rice

OsHKT1;5(SK1)

The gene used is regularly utilized in breeding programs in Bangladesh and Asia. One of the most well studied members of the HKT family which is located in chromosome 1 in the Saltol quantitative trait locus (QTL) is OsHKT1;5. OsHKT1;5 is the most comprehensively studied HKT gene, and it is central to the process of Na^+ exclusion in *Oryza sativa*. It is very much concentrated in the cells of the xylem parenchyma thus central in acquiring sodium. Strains with strong OsHKT1;5 alleles have low leaf Na^+ concentrations, high K^+/Na^+ ratios, and high yield of grain in salty irrigation. The gene is expressed at its highest in the xylem parenchyma cells and it

plays the role of extracting Na^+ out of the xylem sap and hence it avoids its translocation to the above ground shoots [19]. The OsHKT1;5 is localised in Saltol QTL in chromosome 1, which enables elimination of Na^+ in the xylem sap and prevents its transport to the leaf tissues. Plants with an expression of strong OsHKT1;5 alleles exhibit low accumulation of Na^+ in leaves and high grain set in salty fields. The role of this transporter in the functional activity of sustaining photosynthetic efficiency and reproductive development under saline stresses is critical. Thus, OsHKT1;5 has been implemented widely in the breeding initiatives in Bangladesh, specifically in the coastal districts [2].

OsHKT2;1

OsHKT2;1 function predominantly under potassium-deficient conditions, where it mediates Na^+ -coupled K^+ uptake. This allows rice seedlings to sustain growth when soil K^+ is limiting, while also preventing Na^+ toxicity under moderate salinity. Although not the primary determinant of salt tolerance, OsHKT2;1 contributes to overall ionic homeostasis and stress adaptation during early developmental stages [1].

OsHKT1;4 and OsHKT1;1

OsHKT1;4 specifically helps to lower salt input in the early stages of stress. When combined, they aid rice's more extensive ion exclusion systems. Additionally, they aid in adjusting Na^+ transport at various salinities. When combined, these genes enhance sodium transport in rice under varying salinity, supporting the more comprehensive Na^+ exclusion mechanisms [12]. By ensuring that salt is kept out of the delicate root tissue, their spatial expression lowers cellular toxicity. Local Na^+ uptake and distribution within the roots are controlled by these transporters. These genes control the distribution and uptake of sodium in root tissue. By lowering the initial sodium input, OsHKT1;4 specifically contributes to the early stress response. In sensitive areas of the root, their targeted expression aids in preventing salt buildup.

Mechanisms of HKT-mediated salt tolerance

They aid in maintaining a greater K^+/Na^+ ratio, which is essential for enzymatic activities, by regulating Na^+ migration. Therefore, in saline soils, HKT expression is closely linked to improved yield performance. By preventing sodium from entering shoots, HKT genes shield photosynthetic tissues from ion toxicity. This defense delays the aging of leaves under stress and enhances chlorophyll synthesis. Additionally, improved Na^+ control promotes grain filling and reproductive development. Soil salinity is a major environmental constraint that degrades soil structure, limits nutrient availability, and reduces agricultural productivity worldwide. The increasing extent of salt-affected soils poses a serious challenge to sustainable crop production, particularly in irrigated and coastal regions [20].

HKT genes improve salt tolerance through several mechanisms:

1. **Shoot Na^+ exclusion:** By limiting Na^+ transport to aerial tissues, HKT transporters protect the photosynthetic apparatus from ionic toxicity.
2. **Maintaining K^+/Na^+ balance:** High K^+/Na^+ ratios ensure enzyme function, metabolic stability, and osmotic adjustment.
3. **Supporting chlorophyll synthesis and delayed senescence:** HKT activity reduces oxidative damage and preserves leaf functionality under stress.

4. **Enhancing reproductive performance:** Proper Na⁺ regulation allows for better panicle formation and grain filling, resulting in increased yield in saline soils [11,1].

NHX gene family and their role in salt tolerance

Types of NHX transporters in rice

NHX (Na⁺/H⁺ antiporters) mediate intracellular ion sequestration and pH regulation. They are classified according to their subcellular localization:

- **Vacuolar NHXs (OsNHX1, OsNHX2, OsNHX3):** Transport Na⁺ into vacuoles, crucial for cytosolic detoxification and osmotic balance.
- **Endosomal NHXs (OsNHX5, OsNHX6):** Regulate vesicular trafficking, intracellular pH, and ion distribution.
- **Plasma membrane NHXs:** Less common in rice but function in Na⁺ efflux from cells [8].

These transporters collectively maintain ionic equilibrium across cellular compartments, ensuring normal growth under saline conditions.

Major NHX genes in rice

OsNHX1

OsNHX1-expressing transgenic rice lines have improved biomass accumulation and salt tolerance. The most researched NHX gene, OsNHX1, is essential for vacuolar Na⁺ sequestration. It promotes osmotic adjustment and prevents cytosolic toxicity by storing Na⁺ in vacuoles. It stabilizes metabolic pathways, lowers cytosolic toxicity, and moves sodium ions into vacuoles. Genetic engineering programs for salt tolerance frequently use this gene. One well-known vacuolar NHX transporter is OsNHX1. OsNHX1 overexpression enhances osmotic adjustment and permits plants to sustain turgor pressure. OsNHX1 overexpression enhances biomass accumulation, turgor maintenance, and salinity survival. To increase salt tolerance, this gene has been included into transgenic rice [21].

OsNHX2 and OsNHX3

These NHX genes work together to produce long-term resistance to extended exposure to salt. By avoiding ionic imbalances, they also aid in maintaining the integrity of the membrane. These genes control intracellular pH and sustain cell growth in conjunction with OsNHX1. In conditions of moderate to high salinity, their expression is frequently increased. They sustain turgor-driven development under stress by maintaining the vacuolar ion content. These genes enable cell growth and expansion by controlling intracellular pH and vacuolar ion balance. During salt stress, they support the preservation of enzyme activity and membrane integrity. In addition to ensuring long-term resistance to high salinity, their coordinated activity with OsNHX1 promotes prolonged photosynthetic efficiency and successful reproduction [3].

Mechanism of NHX-mediated salt tolerance

Leaf expansion and biomass production are enhanced by improved vacuolar storage. The cell fights dehydration and preserves osmotic balance by accumulating Na⁺ in vacuoles. Additionally, K⁺ storage is made easier by NHX genes, which further stabilize metabolic processes. Organelles and cytoplasmic enzymes are shielded from salt by NHX-mediated sequestration. NHX activation is therefore essential for maintaining chloroplast function and delaying senescence under salt stress.

NHX transporters facilitate vacuolar Na⁺ storage, which:

- Reduces cytosolic ion toxicity.
- Maintains osmotic balance, enabling water retention.
- Supports K⁺ retention, stabilizing metabolic processes.
- Enhances biomass accumulation and leaf expansion.

Through these mechanisms, NHX genes protect chloroplast function, delay senescence, and maintain growth under prolonged salt exposure [8].

HAK Gene Family and their Role in Salt Stress

Functional classification

Environmental factors and hormonal signals control their expression. Even in harsh circumstances, K⁺ homeostasis is preserved because of HAK proteins. They are therefore necessary for plants to survive in saline soils. HAK transporters are categorized based on their physiological functions and potassium affinity. Group II and III transporters contribute to stress reactions such as salinity and dehydration and have more general ionic activities. When K⁺ uptake is hindered, Group I HAK members play a crucial role in salt stress and operate mainly at low external K⁺.

HAK (High-Affinity K⁺) transporters maintain potassium homeostasis under saline or low-K⁺ conditions.

- **Group I HAKs:** Function under K⁺ deficiency and high Na⁺ stress, ensuring enzyme activation and protein synthesis.
- **Group II and III HAKs:** Broad ion transporters involved in stress responses like drought and salinity.

HAK expression is regulated by hormonal and environmental signals, allowing plants to maintain K⁺ balance even under extreme conditions [5].

Major HAK genes in rice

OsHAK1

Additionally, this gene facilitates plants' exploration of deeper soil strata and is linked to improved root development. It plays an important role in rice's early growth phases. In saline environments, rice plants that overexpress OsHAK1 have better seedling vigor. High-affinity K⁺ uptake depends on OsHAK1, particularly when Na⁺ reduces potassium absorption. It promotes protein synthesis, enzyme activity, and the maintenance of ideal K⁺ levels in leaves and roots.

OsHAK5

Stress signals like low K⁺ and mild salinity cause an increase in OsHAK5 expression. Grain filling and panicle formation are two aspects of reproductive development that this transporter facilitates. It is thought to be essential to preserving the plant's overall ionic equilibrium. Long-distance potassium transport from roots to shoots is significantly influenced by OsHAK5. It guarantees that enough K⁺ reaches the growing tissue during salt stress, preventing sterility and yield loss.

OsHAK16 and OsHAK21

Stress signals like low K⁺ and mild salinity cause OsHAK5 expression to rise. Grain filling and panicle formation are two aspects of reproductive development supported by this transporter. It is thought to be essential for preserving the plant's overall ionic equilibrium. OsHAK5 is crucial for the

long-distance movement of potassium from roots to shoots. It guarantees that enough K⁺ reaches the growing tissue during salt stress, avoiding sterility and yield loss.

Mechanisms of HAK-mediated salt tolerance

Additionally, by preserving the ionic balance between membranes, these transporters increase the effectiveness of water utilization. High Na⁺ concentrations frequently result in K⁺ shortage, which is prevented by HAK proteins. Enzyme activity is stabilized and photosynthesis is stimulated by enough K⁺ availability. K⁺ control enhances plant metabolism and lessens oxidative damage. Therefore, in saline environments, HAK genes promote both growth and survival.

HAK transporters:

- Prevent K⁺ deficiency caused by Na⁺ interference.
- Maintain enzyme activity and photosynthesis.
- Improve water-use efficiency and metabolic stability.
- Reduce oxidative stress, protecting plant growth under salinity [11].

Gene Transfer and Genetic Engineering Approaches

Transgenic approaches

Important salt-tolerance genes have been overexpressed to create transgenic rice strains. Vacuolar Na⁺ storage is significantly improved by overexpressing OsNHX1, which increases survival under 150 mM NaCl by three to four times. Adding the Arabidopsis HKT gene (AtHKT1;1) to rice improves stress tolerance and lessens salt buildup in shoots. Potassium absorption efficiency is improved by overexpressing OsHAK1, particularly when there is high Na⁺ stress. Both physiological performance and yield stability are enhanced by these genetic modifications. One of the quickest methods for incorporating salt-tolerance characteristics is still transgenic technology.

Transgenic rice has been developed by overexpressing key HKT, NHX, and HAK genes:

- OsNHX1 overexpression enhances vacuolar Na⁺ sequestration, increasing survival by 3–4× under 150 mM NaCl.
- Introduction of AtHKT1;1 reduces shoot sodium accumulation, improving stress tolerance.
- Overexpression of OsHAK1 enhances K⁺ uptake efficiency under high Na⁺ stress.

These interventions improve both physiological performance

and yield stability, demonstrating the potential of transgenic approaches for rapid improvement [1,21].

CRISPR-Cas9 editing

CRISPR-Cas9 is a great tool for improving rice since it precisely modifies salt-responsive genes. For instance, OsHKT1;5's promoter regions can be edited to improve Na⁺ exclusion and increase its expression. Salt-sensitivity genes that impair tolerance can be eliminated with the aid of gene knockout techniques. Without adding foreign genes, base editing techniques can increase the effectiveness of ion-transporters. CRISPR lowers regulatory hurdles and speeds up breeding cycles. Rice research institutes throughout the world are using this technique more and more.

CRISPR-Cas9 provides precise and efficient gene editing for salt-tolerance traits:

- Promoter editing of OsHKT1;5 increases gene expression, enhancing Na⁺ exclusion.
- Knockout of salt-sensitivity genes removes negative regulatory elements.
- Base editing improves transporter efficiency without introducing foreign DNA.

CRISPR accelerates breeding cycles and allows for targeted improvement while minimizing regulatory challenges [3].

QTL introgression

Salt-tolerant genes from donor variety are introduced into high-yielding cultivars using QTL-based breeding. The crucial OsHKT1;5 gene is found in the Saltol QTL, which is derived from the Pokkali variety. It has been effectively introduced into BRRI dhan47, BRRI dhan55, and IR64 types. In Bangladeshi coastal fields, these modified lines exhibit increased Na⁺ exclusion and higher yields. QTL introgression is economical and appropriate for breeding efforts in underdeveloped nations. Because it doesn't involve transgenic alteration, this technique is still widely used.

QTL-based breeding transfers salt-tolerance alleles from donor varieties into elite cultivars:

- The Saltol QTL from Pokkali contains OsHKT1;5.
- Introgression into IR64, BRRI dhan47, and BRRI dhan55 improves Na⁺ exclusion and yield in coastal fields.
- QTL introgression is cost-effective and suitable for resource-limited breeding programs, making it popular in developing countries (Table 1) [2,12].

Table 1. Comprehensive gene function table.

Gene Family	Gene	Chromosome	Function	Major Role Under Salt Stress	Expression Site
HKT	OsHKT1;5	Chr 1	Na ⁺ retrieval	Prevents Na ⁺ transport to shoots	Xylem parenchyma
HKT	OsHKT2;1	Chr 7	Na ⁺ /K ⁺ co-transport	Supports K ⁺ uptake under low K ⁺	Root cortex
NHX	OsNHX1	Chr 7	Na ⁺ /H ⁺ exchange	Vacuolar sequestration of Na ⁺	Tonoplast
NHX	OsNHX2	Chr 5	pH regulation	Cell expansion, osmotic balance	Tonoplast
HAK	OsHAK1	Chr 2	High-affinity K ⁺ uptake	Maintains K ⁺ /Na ⁺ balance	Plasma membrane
HAK	OsHAK5	Chr 4	K ⁺ translocation	Long-distance ion transport	Vascular bundles

Case Studies of Successful Gene Transfer

Overexpression of OsNHX1

One of the most effective gene transfer strategies for enhancing rice's salt tolerance is the overexpression of OsNHX1. Under extreme salinity, transgenic lines with the OsNHX1 gene exhibit roughly 70% better survival rates, especially above 150 mM NaCl. The gene's function in moving extra Na⁺ into vacuoles, which lowers cytosolic toxicity and preserves osmotic balance, is responsible for this improvement [21,1].

Significantly better tillering, panicle initiation, and biomass buildup have been shown in field assessments carried out in several saline-prone areas. Consequently, compared to non-transgenic controls, grain yields in paddy fields with moderate to high salinity rose by 25–30%. According to Roy, Negrao, and Tester, OsNHX1 is a promising candidate for creating high-performing salt-tolerant rice varieties that are appropriate for coastal agriculture [12].

Introgression of Saltol QTL

The essential gene OsHKT1;5, which controls sodium exclusion from shoots, is found in the Saltol QTL, which is derived from the salt-tolerant landrace Pokkali. Saltol has been effectively introduced into well-known rice varieties as BRRI dhan47, BRRI dhan55, and IR64-Saltol by marker-assisted backcrossing [19,2]. These modified lines are able to sustain development in saline coastal environments due to their markedly reduced Na⁺ accumulation in leaves and improved K⁺ retention. In places like Satkhira, Khulna, Bagerhat, and Noakhali in Bangladesh, where electrical conductivity (EC) frequently surpasses 8–12 dS/m, Saltol-introgressed types are widely used. When salinity peaks during dry seasons, farmers growing BRRI dhan47 and IR64-Saltol have reported improved plant vigor, increased grain set, and more consistent yields [2]. The effectiveness of QTL-based breeding in creating climate-resilient rice varieties is demonstrated by the success of Saltol introgression.

OsHAK1 transgenic lines

Under salty conditions, where high Na⁺ levels often inhibit K⁺ absorption, transgenic rice lines overexpressing OsHAK1 show noticeably improved potassium uptake [11, 5]. These plants grow stronger root systems, which enable better nutrient uptake and increased soil exploration. OsHAK1 overexpressing plants maintained significantly greater leaf K⁺ concentrations than wild-type plants under controlled tests with 100 mM NaCl, maintaining metabolic stability and photosynthetic efficiency. Increased development in saline environments is facilitated by improved K⁺ homeostasis, which also lowers oxidative stress and preserves cell membrane integrity. These transgenic lines show promise as candidates for upcoming breeding initiatives aimed at salinity-affected coastal and marginal regions.

Future Prospects in Developing Salt-tolerant Rice

Gene stacking (HKT + NHX + HAK)

To increase overall resistance, gene stacking combines several salt-tolerance genes into a single genotype [1,12]. Stacked types incorporate several processes at once rather than depending on a single pathway, like Na⁺ exclusion or Na⁺ sequestration. For instance, rice plants that can maintain ionic balance under high salinity may be produced by stacking HKT1;5 (Na⁺ exclusion), NHX1 (vacuolar sequestration), and HAK1 (K⁺ absorption). These plants would prevent excess Na⁺ from building up in the shoots, store it safely, and still absorb enough K⁺ for metabolic

functions. This strategy may produce cultivars that perform better than conventional single-gene transgenic lines and provide consistent yield improvements in areas under extreme salt stress. The next significant step in creating super-tolerant rice varieties is thought to be gene stacking.

CRISPR activation (CRISPRa) for native gene enhancement

A sophisticated genome-editing method called CRISPR activation (CRISPRa) boosts the expression of native plant genes without changing their DNA sequence [1,3]. Rather than introducing foreign genes, CRISPRa increases the expression of indigenous salt-tolerance genes such as OsHKT1;5, OsNHX1, and OsHAK5 by fusing an inactive Cas9 protein with transcriptional activators. By doing this, transgenic issues are eliminated, and the resulting cultivars are more likely to be approved by regulators and adopted by farmers. Additionally, CRISPRa enables precise regulation of gene expression levels, allowing for stress-specific amplification without interfering with normal growth. It offers a viable route for creating salt-tolerant rice of the future that is suitable for both domestic and foreign markets.

Synthetic promoters for stress-inducible expression

A sophisticated method of regulating gene expression is provided by synthetic promoters that are precisely made to react to osmotic stress or salt [8]. Stress-inducible promoters only activate when salinity reaches dangerous levels, as opposed to constitutive promoters, which keep genes active all the time. This reduces wasteful energy use and avoids detrimental effects on regular plant growth. For instance, only under high NaCl circumstances did a synthetic promoter connected to OsNHX1 cause substantial Na⁺ sequestration. Promoter designs that react to salinity, ROS buildup, and hormonal cues like ABA are now being investigated by researchers. Using synthetic promoters could maximize plant growth performance and significantly increase stress-specific tolerance.

Integration with phenomics and AI-driven breeding

Artificial intelligence (AI) and sophisticated phenomics platforms will be crucial to the development of salt-tolerant rice in the future [11]. Drone imaging, hyperspectral analysis, and automated root scanners are examples of high-throughput phenotyping techniques that can assess thousands of rice lines under salty circumstances with previously unheard-of accuracy. These statistics can be analyzed by machine learning algorithms to find trends in salt-tolerance characteristics and forecast how well upcoming breeding lines will fare. By identifying important genomic areas linked to Na⁺/K⁺ balance, root architecture, and stress-responsive gene networks, AI can also direct marker-based selection. Breeding cycles will be significantly accelerated by combining genomics, phenomics, and AI-driven analytics, which will result in the quick production of superior salt-tolerant cultivars appropriate for nations like Bangladesh.

Limitations of the Study

Although this study provides a comprehensive synthesis of the roles of HKT, NHX, and HAK gene families in rice salt tolerance, several limitations should be acknowledged. First, the study is based on a systematic review of published literature rather than original experimental or field data; therefore, the conclusions depend on the accuracy and experimental conditions of previous studies. Variations in

genetic background, developmental stage, salinity regimes, and environmental settings across studies may limit comparability. Second, although numerous genes from these families have been identified, issues related to functional redundancy and gene-gene interactions were not experimentally validated. Moreover, complex regulatory mechanisms involving hormonal signaling, epigenetic modifications, and post-translational regulation were beyond the scope of this review. Third, most transgenic and CRISPR-based studies were conducted under controlled conditions, which may not fully reflect field-level salinity stress, particularly in heterogeneous coastal soils such as those in Bangladesh. Finally, socio-economic, regulatory, and biosafety considerations affecting farmer adoption were insufficiently explored. Addressing these gaps through integrated field trials, multi-omics approaches, and socio-economic assessments is essential for sustainable application.

Conclusion

Rice production is severely constrained by salt stress, particularly in the coastal regions of Bangladesh, where salinity affects over a million hectares of arable land. Rice plants respond to salinity through complex mechanisms such as osmotic adjustment, ion homeostasis, and activation of stress-responsive genes. The HKT, NHX, and HAK gene families play pivotal roles in maintaining cellular ionic balance by regulating Na⁺ exclusion, vacuolar sequestration, and K⁺ uptake, thereby sustaining growth and yield under saline conditions. Advances in transgenic approaches, CRISPR-based genome editing, and QTL introgression have demonstrated significant potential for enhancing salt tolerance without compromising productivity, as evidenced by the development and adoption of varieties such as BRRI dhan47 and IR64-Saltol. Beyond yield improvement, salt-tolerant rice contributes to national food security, farmer livelihood stability, and nutritional quality through improved mineral retention. Future strategies involving gene stacking, stress-inducible promoters, and AI-assisted breeding, combined with sound agronomic practices, will be critical for developing resilient rice varieties capable of withstanding increasing salinity under climate change.

Disclosure Statement

The authors do not have any conflict of interest.

References

- Munns R, Tester M. Mechanisms of salinity tolerance. *Annu Rev Plant Biol.* 2008;59(1):651-681. <https://doi.org/10.1146/annurev.arplant.59.032607.092911>
- Siddique MA, Islam MZ, Uddin Ahmed MS, Khalequzzaman M. Bangladesh Rice Research Institute (BRRI) Genebank. In *Plant Gene Banks: Genetic Resources Collections, Conservation and Sustainable Utilization 2025* (pp. 1-30). Singapore: Springer Nature Singapore. https://doi.org/10.1007/978-981-99-4236-7_32-1
- Zhu JK. Plant salt tolerance. *Trends Plant Sci.* 2001;6(2):66-71. [https://doi.org/10.1016/S1360-1385\(00\)01838-0](https://doi.org/10.1016/S1360-1385(00)01838-0)
- Majola NG, Gerrano AS, Shimelis H. Bambara groundnut (*Vigna subterranea* [L.] Verdc.) production, utilisation and genetic improvement in Sub-Saharan Africa. *Agronomy.* 2021;11(7):1345. <https://doi.org/10.3390/agronomy11071345>
- Ali B, Wang X, Saleem MH, Sumaira, Hafeez A, Afridi MS, Khan S, et al. PGPR-mediated salt tolerance in maize by modulating plant physiology, antioxidant defense, compatible solutes accumulation and bio-surfactant producing genes. *Plants.* 2022;11(3):345. <https://doi.org/10.3390/plants11030345>
- Qadir M, Quillérou E, Nangia V, Murtaza G, Singh M, Thomas RJ, et al. Economics of salt-induced land degradation and restoration. In *Natural resources forum* 2014;38(4):282-295. <https://doi.org/10.1111/1477-8947.12054>
- Venn AA, Loram JE, Douglas AE. Photosynthetic symbioses in animals. *J Exp Bot.* 2008;59(5):1069-1080. <https://doi.org/10.1093/jxb/erm328>
- Bose J, Rodrigo-Moreno A, Shabala S. ROS homeostasis in halophytes in the context of salinity stress tolerance. *J Exp Bot.* 2014;65(5):1241-1257. <https://doi.org/10.1093/jxb/ert430>
- Zeng L, Shannon MC, Lesch SM. Timing of salinity stress affects rice growth and yield components. *Agric Water Manag.* 2001;48(3):191-206. [https://doi.org/10.1016/S0378-3774\(00\)00146-3](https://doi.org/10.1016/S0378-3774(00)00146-3)
- Kader MA, Lindberg S. Cytosolic calcium and pH signaling in plants under salinity stress. *Plant Signal Behav.* 2010;5(3):233-238. <https://doi.org/10.4161/psb.5.3.10740>
- Ismail AM, Horie T. Genomics, physiology, and molecular breeding approaches for improving salt tolerance. *Annu Rev Plant Biol.* 2017;68:405-434. <https://doi.org/10.1146/annurev-arplant-042916-040936>
- Roy SJ, Negrão S, Tester M. Salt resistant crop plants. *Curr Opin Biotechnol.* 2014;26:115-124. <https://doi.org/10.1016/j.copbio.2013.12.004>
- Maathuis FJ, Amtmann AN. K⁺ nutrition and Na⁺ toxicity: the basis of cellular K⁺/Na⁺ ratios. *Ann Bot.* 1999;84(2):123-133. <https://doi.org/10.1006/anbo.1999.0912>
- Negrão S, Schmöckel SM, Tester MJ. Evaluating physiological responses of plants to salinity stress. *Ann Bot.* 2017;119(1):1-1. <https://doi.org/10.1093/aob/mcw191>
- Wang Y, Zeng FR, Wang Y, Xu S, Chen ZH. Potassium transporters and their evolution in plants under salt stress. In *Cation transporters in plants 2022* (pp. 63-83). Academic Press. <https://doi.org/10.1016/B978-0-323-85790-1.00022-1>
- Yamaguchi T, Blumwald E. Developing salt-tolerant crop plants: challenges and opportunities. *Trends Plant Sci.* 2005;10(12):615-620. <https://doi.org/10.1016/j.tplants.2005.10.002>
- Wang W, Vinocur B, Altman A. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta.* 2003;218(1):1-4. <https://doi.org/10.1007/s00425-003-1105-5>
- Kumar K, Kumar M, Kim SR, Ryu H, Cho YG. Insights into genomics of salt stress response in rice. *Rice.* 2013;6(1):27. <https://doi.org/10.1186/1939-8433-6-27>
- Ren ZH, Gao JP, Li LG, Cai XL, Huang W, Chao DY, et al. A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nat Genet.* 2005;37(10):1141-1146. <https://doi.org/10.1038/ng1643>
- Shrivastava P, Kumar R. Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi J Biol Sci.* 2015;22(2):123-131. <https://doi.org/10.1016/j.jecoenv.2014.12.024>
- Apse MP, Aharon GS, Snedden WA, Blumwald E. Salt tolerance conferred by overexpression of a vacuolar Na⁺/H⁺ antiport in *Arabidopsis*. *Science.* 1999;285(5431):1256-1258. <https://doi.org/10.1126/science.285.5431.1256>