A-5760
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REVIEW ARTICLE **Indian Journal of Agricultural Research**

Salinity Tolerance Mechanisms in Rice: A Review

O.P. Reshna, R. Beena

10.18805/IJARe.A-5760

ABSTRACT

Background: Rice (*Oryza sativa* L.) is one of the most important cereal crop globally and it is the staple food of more than half of world population. Current average yield is 10 to 15% lower than its potential yield. There are many reasons for this yield gap such as biotic and abiotic stresses, management strategies as well as nutrient deficiencies. Salinity is one of the most serious factors limiting the productivity of rice, with adverse effects on germination, plant vigor and crop yield. This salinity may be natural or induced by agricultural activities such as irrigation or the use of certain types of fertilizer.

Methods: Salinity induced ionic imbalance and osmotic stress affect water and nutrient uptake, stomatal closure, gas exchange, photosynthesis, transpiration, carbon assimilation and hence decrease in rice yield. Studying the response of rice at physiological, genetic and molecular level is the mandate to develop salt tolerant rice varieties.

Conclusion: This review described the impact of salt stress in rice, various types of salt tolerance mechanisms in rice, including the ion homeostasis, production of compatible organic solutes, antioxidative genes, salt responsive regulatory elements, role of ion transporters and channel proteins. Further, the future perspective of developing salt-tolerant varieties using landraces *via*., marker assisted breeding, genome editing tool, utilization of beneficial microorganisms.

Key words: Molecular mechanism, Physiological mechanism, Rice, Salinity, Transporters.

Department of Plant Physiology, College of Agriculture, Vellayani Kerala Agricultural University, Vellayani-695 522, Kerala, India.

Corresponding Author: R. Beena, Department of Plant Physiology, College of Agriculture, Vellayani Kerala Agricultural University, Vellayani-695 522, Kerala, India.
Email: beenaajithkumar@gmail.com

How to cite this article: Reshna, O.P. and Beena, R. (2021). Salinity Tolerance Mechanisms in Rice: A Review. Indian Journal of Agricultural Research. DOI:10.18805/IJARe.A-5760.

Submitted: 02-03-2021 **Accepted:** 05-07-2021 **Online:** 09-08-2021

Rice is one of the world's most important cereal crop which is grown over 156 mha area globally and is staple food crop of more than 50 per cent population worldwide (FAO, 2008). To maintain food security, rice production must be increased quantitatively and qualitatively to meet the requirements of the growing population in the twenty-first century (Rejeth *et al*., 2020). Although rice is adapted to a wide range of ecosystems it is susceptible to climatic changes leading to low rice productivity (Beena, 2005). Changing climate leads to periods of drought, frequent floods, sea water inundations, *etc*. which reduce the yield potential of current rice varieties. Among abiotic stresses, salinity is the second most devastating constraint in rice production after drought, affecting approximately 1 billion ha of land globally. Soil salinity affects about 800 million hectares of arable lands worldwide (Munns and Tester, 2008). Excessive use of irrigation water with improper drainage, poor quality irrigation water containing an excess level of salts, and flooding from seawater are the causes of salinity. Direct accumulation of salts disturbs metabolic processes and all major morpho-physiological and yield-related traits including tiller number, panicle length, spikelet number per panicle (Khatun *et al*., 1995), grain filling (Rao *et al*., 2013), plant biomass (Zeng *et al*., 2007) and photosynthesis (Baker 2008), leading to significantly decreased yield (Flowers and Yeo, 1981).

Salinity stress triggers a wide variety of plant responses, ranging from morphological, physiological, biochemical and molecular changes to plant system. Salt stress is first perceived by the root system and impairs plant growth both in the short term, by inducing osmotic stress caused by reduced water availability, and in the long term, by salt-induced ion toxicity due to nutrient imbalance in the cytosol. Therefore, the two main threats imposed by salinity are induced by osmotic stress and ionic toxicity associated with excessive Cl$^-$ and Na$^+$ uptake, leading to Ca^{2+} and K$^+$ deficiency and to other nutrient imbalances (Marschner, 1995). In addition, salt stress is also manifested as oxidative stress mediated by ROS. All these responses to salinity contribute to the deleterious effects on plants. However, tolerance can come with trade-offs; for example, it has long been known that stress-tolerant plants have reduced growth rates and productivity (Beena *et al*., 2018c; Nithya *et al*., 2021). Hence, understanding the basis of tolerance is also important to understand the trade-offs between tolerance and growth/productivity for potent crop improvement.

Impacts of salinity stress on rice growth and development

Salt stress severely influences the morphology of rice plants which comprise of stunted plant growth, chlorosis, leaf burning, leaf rolling, poor root growth, wilting and senescence (Zhang *et al*., 2012). Salinity bring down the photosynthetic rate and associated parameters such as transpiration, stomatal conductance and intercellular CO_2, concentration (Munns, 2002). Salinity affects the pollination, fertilization and causes spikelet sterility in rice (Pearson and Bernstein,1959); delays heading and affect yield components (Grattan *et al*., 2002).

The biochemical impacts typically comprise of oxidative stress and ionic stress. Salt stress increases ROS production which can elevate oxygen–induced cellular damage. With the rise in salinity level, indices of oxidative stress *viz*., superoxide radical and H_2O_2, content increased in leaves of all the cultivars and this increase was more notable in salt-sensitive varieties and non-significant in resistant cultivars. There was 10 fold increase in Na^+ concentration in salt sensitive "IR29" compared to salt tolerant rice variety "Pokkali" (Golldack *et al*. 2003). Elevated concentration of cytoplasmic Na^+ and reduction of K^+ result in changes of membrane potential, osmotic pressure, turgor pressure, calcium signaling, reactive oxygen species signaling, transcriptional regulation, alteration of gene expression, modification of protein expression pattern and spectra of *siRNA*s, signaling molecules, phytohormones and metabolites. NaCl at a concentration as low as 50 mM is lethal at the seedling stage (Yeo *et al*.1990). High sodium concentrations over 100 mM often have inhibiting effect on protein synthesis at least in salt-sensitive glycophytes like rice (Flowers and Yeo, 1981).

Na^+ is the principal poisonous ion in salinized soil and low Na^+/K^+ ratio in the cytoplasm is essential to maintain a number of enzymatic reactions. Plants under salt stress normally absorb Na^+ and simultaneously inhibit K^+ absorption. High salt domains can shatter the ion homeostasis of plant cells, knock down the ionic balance and affect the distributions of ion at whole plant levels under salinity, increased osmotic pressure of the soil solution which restricts the water absorption and entry of water into the seeds, interruption of nutrient uptake, induces stomatal closure (Almansouri *et al*., 2001).

Salinity alters a wide array of metabolic processes in growing plants and induces changes in contents and activities of many enzymes. Sugar metabolism is critically affected when the plant grown under salinity condition. Under salinity, the starch content in roots declined more in salt sensitive *cvs*. Ratna and Jaya than in salt tolerant *cvs*. CSR-1 and CSR-3. The content of reducing and non-reducing sugars, and the activity of sucrose phosphate synthase was increased more in the sensitive than in the tolerant cultivars. Acid invertase activity decreased in shoots of the salt tolerant cultivars, whereas increased in salt sensitive cultivars. Starch phosphorylase activity decreased in all cultivars (Dubey and Singh, 1999). To better understand the impacts of salinity on plant growth, it is necessary to study the changes in metabolites involved in respiratory metabolism. A considerable reduction in saccharide abundance, including glucose, fructose, xylose, and sucrose has been reported in rice exposed to salinity (Sanchez *et al*., 2008). These saccharides are required as sources of glucose for glycolysis and may also contribute to osmotic adjustment in plants.

Mechanisms for salinity tolerance in rice

It is essential to know the basic molecular mechanisms of salt tolerance for the crop improvement programs to develop high yielding salt tolerant varieties. Salt tolerance is regarded as a complex quantitative trait which is controlled by multiple genes. Many adaptive responses at molecular, cellular and physiological level results in tolerance or resistance of rice plant to salt stress. There are mainly three mechanisms observed in rice.

Ion exclusion

Selective uptake of salt by root cells is the initial strategy followed by rice plant to tackle the salinity stress. Rahman *et al*. (2001) reported that root cap cell expansion is an adaptive response to salinity in rice plants and this root cap cells may function in Na^+ exclusion under salinity stress. Once water is taken up by the root hair, it travels from cell to cell through intracellular regions across the cortex to handover the salt in xylem through apoplastic pathway. Suberin lamellae and casparian strip limit and force both water and salts to cross the plasma membrane into the cytoplasm, where they can continue on the symplast pathway, leading to decrease in Na^+ accumulation in the shoot (Cai *et al*., 2011). With increase in NaCl concentration in rhizosphere, there will be a fall off of transpiration rate which lowers water potential in roots, and the transport of ABA from root to shoot and give rise to stomatal closure and prevent dehydration (Zhang *et al*., 2006).

Osmotic stress tolerance

Osmotic tolerance is the plant's ability to tolerate the physiological drought aspect of salinity stress and to maintain leaf expansion and stomatal conductance by maintaining the tissue turgor (Rajendran *et al*., 2009). The early symptom of salinity stress on plants is osmotic stress which arise due to the accumulation of salts in the rhizosphere that affects negatively the plant growth (Munns and Tester, 2008). Compatible solutes accumulate in the cytosol, contribute to the decrease of cytoplasmic water potential and act as osmoprotectants. Rice plant under osmotic stress accumulates more carbohydrates or trehalose than proline (Nounjan and Theerakulpisut, 2012). Trehalose bring down Na^+ accumulation, growth inhibition and salt (an osmotically regulated gene) expression at low to medium concentration and at higher concentration hinder NaCl-induced loss of chlorophyll in blades, enhance rice growth and preserve root integrity (Garcia *et al*., 2012). Karthikeyan *et al.* (2011) observed high accumulation of proline in salt tolerant transgenic rice plants with expression of P5CS. *codA* introduced into transgenic rice plants promotes the synthesis of glycine betaine and enhancement of salt tolerance in plants (Su *et al*., 2006). Li *et al.* (2011) demonstrated that overexpression of *OsTPS1* in rice plants enhances salt tolerance by increasing the amount of trehalose and proline.

Tissue tolerance

Tissue tolerance is achieved by sequestration of Na$^+$ in the vacuole**,** synthesis of compatible solutes, production of enzymes catalyzing detoxification of reactive oxygen species. Reactive oxygen species (ROS) are dual functioning molecules which act both as toxic compounds as well as signal transduction molecules in response to abiotic as well as biotic stresses in plants (Miller *et al*. 2010). Under stress condition, there will be accumulation of plenty of ROS which will damage protein structure cause lipid peroxidation and mutation of DNA (Vaidyanathan *et al*., 2003). The antioxidant enzymes catalase (CAT) and ascorbate peroxidase (APX) are efficient scavengers of hydrogen peroxide (H_2O_2), and thus inhibit membrane lipid peroxidation, which is induced by high concentrations of H_2O_2. This is a key factor in reducing the effects of salinity stress (Mittler, 2007). Under saline condition, the capacity to scavenge reactive oxygen species decreased with age, and thus the apical region of the leaf blade suffered severe damage by Na$^+$ than the basal region in salt sensitive rice variety (Yamane *et al*. 2009). In salinity tolerant rice cultivar, gene expression and the activity of antioxidant enzymes (SOD, CAT, APX and GR) were increased and protected from oxidative stress. Under salinity stress, salt tolerant rice cultivar Pokkali was reported to have higher activity of ROS scavenging enzymes such as catalase (CAT), ascorbate (ASC) and glutathione (GSH), compared to the salt sensitive rice cultivar (Pusa Basmati). In rice during salinity stress, cell death advances in a well-regulated manner and causes PCD in the root tip of rice (Liu *et al*. 2007). Transgenic rice plants containting antioxidative genes *OsECS*, *OsVTE1* and *OsMSRA4.1* showed high salt tolerance (Choe *et al* 2013).

Role of membrane transporters for salt tolerance in rice

Transporting Na$^+$ out of the cytoplasm into apoplast or vacuole, which is driven, respectively, by Na$^+$/H$^+$ antiporters in plasma membrane or tonoplast, and exclusion of Na$^+$ from sensitive shoot tissues are the basic strategies for the salt stressed plants to alleviate the Na$^+$ toxicity (Hamamoto *et al*. 2015). Transporters could be considered as enzymes where conformational changes of a protein molecule are required for a complete transport cycle of ions (Gadsby, 2009).

Turnover rate of the transporter is the number of complete transport cycles performed per second. There are three main types of transporters involved in salt tolerance mechanism of rice; Na$^+$ transporters, such as vacuolar Na$^+$/H$^+$ antiporters (*NHX*s), salt overly sensitive 1 transporter (*SOS*1) and high-affinity potassium transporters (*HKTs*).

Vacuolar NHX transporters

The coupled exchange of K$^+$ or Na$^+$ for H$^+$ is mediated by a family of transporters known as *NHXs (NHX*1-6). The cytosolic Na$^+$ is compartmentalize Na$^+$ into the vacuoles by *NHXs* (Bassil and Blumwald, 2014). The compartmentation of Na$^+$ into vacuoles not only reduces the toxicity of Na$^+$ in the cytosol but also contributes to osmotic regulation. First evidence of *NHX* transporter in tonoplast vesicles from rice roots was reported by Fukuda *et al*. (1998). The mechanism of compartmentalization are the pH gradient generated by proton-translocating *H$^+$-ATPase* and proton translocating inorganic pyrophosphatase (*H$^+$- PPase*) on the tonoplast and that the amount of antiporter in vacuolar membranes. Later, Fukuda *et al*. (2004) investigated the function and intracellular localization of the product of the *OsNHX1* cloned from rice. Their results indicate that the *OsNHX1* gene encodes a vacuolar (Na$^+$, K$^+$)/H$^+$ antiporter. In addition, overexpression of *OsNHX1* improved the salt tolerance of transgenic rice cells and plants, suggesting that *OsNHX1* on the tonoplast plays important roles in removing accumulated Na$^+$ and K$^+$ in the cytoplasm into the vacuoles. Up to now, four vacuolar NHXs (OsNHX1-4) have been reported in rice (Kumar *et al*. 2013).

SOS transporter

SOS1 transporter was first isolated from rice (Martinez-Atienze *et al*., 2007). Based on genetic and biochemical criteria, they identified that *OsSOS*1 is a rice plasma membrane Na$^+$/H$^+$ antiporter and is functionally equivalent to the Arabidopsis *SOS1. H$^+$-ATPase* present in plasma membrane is responsible for Na$^+$ efflux from cytoplasm. The energy released from the hydrolysis of ATP is used to pump H$^+$ out of the cell, generating electrochemical H$^+$ gradient. The proton-motive-force generated by the H$^+$-ATP*ase* operates the Na$^+$/H$^+$ antiporters, which couple the movement of H$^+$ into the cell along its electrochemical gradient to the efflux of Na$^+$ against its electrochemical gradient.

In salt overly sensitive (*SOS*) pathway, salt stress elicited Ca^{2+} signals are perceived by Ca^{2+} binding protein *SOS*3 and activates *SOS*2, a serine/ threonine protein kinase (Halfter *et al*. 2000). Then the *SOS2-SOS3* complex phosphorylates *SOS1* which is a Na$^+$ /H$^+$ antiporter on cell membrane that extrudes Na$^+$ out of the cytosol (Guo *et al*. 2004). The transport level of *SOS1* is controlled by *SOS3-SOS2* kinase complex. When there is a higher accumulation of Na$^+$ in cytosol, *SOS*2 activates the tonoplast Na$^+$/H$^+$ antiporter that sequesters Na$^+$ into the vacuole (Blumwald, 2000). Elevation of salinity influences the Na$^+$ /H$^+$ antiporter activity and the activity is more significant in salt tolerant species than in salt sensitive ones.

*HKT*1 function in ion transport:

Sodium concentration in shoots is affected by the regulation of sodium transport from root to shoot by the family of *HIGH-AFFINITY POTASSIUM TRANSPORTERS (HKTs*). The members of this family can be divided into two classes according to their affinity for either sodium or potassium, caused by a single amino acid substitution in the pore region of the transporter. The *HKT*1 subclass transports sodium, while the HKT2 subclass transports potassium. *OsHKT*2; 2 is present in the salt-tolerant 'Pokkali' cultivar, but absent in 'Nipponare', can mediate both Na$^+$ and K$^+$ influx. This would explain why 'Pokkali' cutivar is salt tolerant (Garciadeblas *et al*., 2003). Identified three hybrid *HKT* gene (named *OsHKT2;2/1; OsHKT2*;1/2) in 'Nona Bokra' and *OsHKT*2;2

from 'Pokkali' (Oomen *et al*., 2012). These genes may contribute to the salt tolerance by maintaining K^+ uptake under salinity conditions.

HAK/KUP family transporters

Importance of K^+ retention ability in root and leaf tissues, role of HAK/KUP family of transporters in K^+ uptake and its possible linkage with Ca^{2+} and ROS signaling, control of xylem K^+ loading control of phloem K^+ recirculation in salt stressed plants (Wu *et al*., 2018).

Role of ion channel proteins for salt tolerance in rice

Ion channels in an open state/conformation allow passage of over 106-108 ions per second via a selective pore formed within a protein molecule. The diameter of the pore is determined by the molecular structure of ion channel. The diameter of the pore and amino acids lining it essentially determine the ion selectivity of ion channel and potential number of passing ions per unit of time. Some of the important channel proteins present in rice are: *OsAKT1* (K^+ inwardrectifying channel), *OsKCO*1 (K^+ outward-rectifying channel), *OsTPC*1 (Ca^{2+} permeable channel), *OsCLC*1 (Cl^- channel) and *OsNRT1*;2 (nitrate transporter).

Role of protein kinases for salt tolerance in rice

Important protein kinases involved in salt tolerance mechanism in rice are Mitogen-activated protein kinases (*MAPKs*), sucrose non-fermenting1-related kinase 2 (*SnRK2*) family members have been designated as stressactivated protein kinases (*OsSAPK*), receptor-like cytoplasmic kinases (*RLCKs*). Over-expression of *OsMAPK*5 (encoding an abscisic acid-inducible MAPK), enhances salt tolerance in rice (Xiong and Yang, 2003). *OsMAPK*44, reduced the salt injury by maintaining ion homeostasis in transgenic rice (Jeong *et al*., 2006). *OsMAPK*33 exhibits salinity tolerance in transgenic rice by altered expression of ion transport genes such as the K^+ /H^+ antiporter or other downstream positive regulators of salt tolerance in the MAPK pathway (Lee *et al*., 2011). The expressions of all the ten *OsSAPKs* (stress activated protein kinases) are induced under salt stress conditions by osmotic stress and/or ABA dependent signaling (Cutler *et al*., 2010). Overexpression of *SAPK4* improved germination, growth and development in seedlings and mature rice plants under salinity following alteration in the expression of genes involved in ion homeostasis and oxidative stress responses (Diédhiou *et al*., 2008). Overexpression of *SAPK6* in rice up-regulates the expression of the enzymes involved in diverse salt stress-responsive metabolic pathways under salt stress conditions.

Role of transcription factors and miRNAs for salt tolerance in rice

Transcription factors (TFs) are protein that controls the rate of transcription of genetic information from DNA to messenger RNA, by binding to a specific DNA sequence. Several salt responsive TFs were identified in rice, *OsCOIN* (Liu *et al*., 2007), *OsNAC*6 (Nakashima *et al*. 2007), *OsNAC*5 (Takasaki *et al*, 2010), *OsDREB2A* (Mallikarjuna *et al*., 2011), *OsMYB*2 (Yang *et al*., 2012), *OsTZF*1 (Jan *et al*., 2013), *OsBZIP*71 (Liu *et al*., 2014) which improve salt tolerance by various mechanisms like the accumulation of osmoprotectants and antioxidants, increase transporter activity for Na^+ and K^+ ions, regulate the expression of other saltresponsive genes.

By modulating the gene expression at the post-transcriptional level, miRNAs can regulate plant development and respond to environmental stress (Table 1).

Approaches to improve salt tolerance in rice

Conventional breeding methods such as use of *in vitro* selection, interspecific hybridization and pooling physiological *etc*. were used to enhance salinity tolerance (Flowers, 2004). Superior structured design to breeding for salinity tolerance acquired when there was a better understanding of the function regulation and function of the responsive genes and their association to QTL regions (Negrao *et al*., 2012). Fig 1 shows the different approaches used for developing salt tolerant rice varieties. In India, there were many success stories in developing and releasing the salt tolerant cultivars including CSR10, CSR13, CSR27, Narendra usar 2 and Narendra usar 3 (Singh *et al*., 2004) and those varieties have been used to reclaim saline soils in India.

Table 1: List of salt stress-related rice miRNAs and their predicted target gene.

miRNA	Up-regulation	Down-regulation	Target gene	Reference
Osa-miR393	In leaves under salt and drought stress	In roots under salt and drought stress	*OsTIR1*, *OsAFB2*	Xia *et al.* 2012
Osa-miR408	Under heat, cold and salt stress		*OsUCL30, OsIAA6*	Sun *et al.* 2018
Osa-miR319a		Under drought and salt stress	*AsPCF5*, *AsPCF6*, *AsPCF8*, *AsTCP14*, *AsNAC60*	Zhou *et al.* 2013
Osa-miR820	In leaves under salt, heat and drought stress	In roots under salt, heat and drought stress	*OsDRM2*	Sharma *et al.* 2015
Osa-miR12477	In leaves and shoots under salt stress		*L-ascorbate oxidase*	Parmer *et al.* 2020

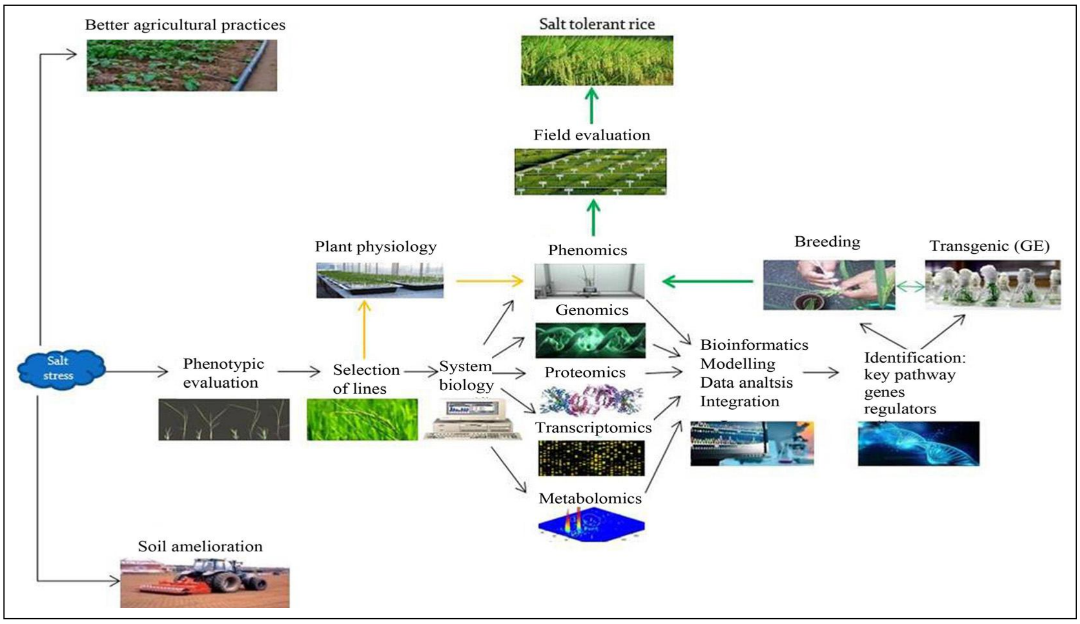

Fig 1: Approaches for developing of salt tolerant rice plants.

Platforms such as phenomics in tandem with combination of genomics-transcriptomics-proteomics-metabolomics need to be integrated for identifying key genes/regulators which can improve salinity tolerance in rice apart from general practices like usage of better agricultural practices and soil amelioration (Reddy *et al*., 2017).

CSR 2, CSR 3, CSR 13, CSR 22, CSR 23, CSR 26, CSR 27, CSR 30, Panvel 1, Panvel 2, Panvel 3, Vyttila 1 and Vyttila 2 are the varieties developed for the coastal saline soil conventionally (Shahbaz and Ashraf, 2013). Kerala Agricultural University has released 11 Vytilla series of rice verieties.

A major QTL *saltol* was identified by Gregorio and Senadhira in salinity tolerant Pokkali responsible for maintaining Na$^+$/K$^+$ homeostasis at the seedling stage (Gregorio *et al*., 2002). Marker-assisted backcross breeding (MABB) was attempted to incorporate the *Saltol* loci from Pokkali or its derivative FL478 facilitate the development of salinity-tolerant rice varieties (Valarmathi *et al.,* 2019). *Saltol* gene introgressed Pusa Basmati 1 (PB1) showed enhanced seeding stage salt tolerance (Singh *et al*., 2018). Under salinity stress, *saltol* introgressed backcross lines showed salt tolerance by maintaining good morphological and yield traits (Banumathy *et al*., 2018).

A salt-tolerant rice mutant *rst1 was* isolated and characterized which showed significantly lower lipid peroxidation and electrolyte leakage under salinity stress but higher shoot biomass and chlorophyll content (Deng *et al.* 2015). Microarray analysis of rice mutant *RGA1* disclosed its role in regulation of multiple abiotic stresses (Jangam *et al.* 2016). One mutant variety (Shua-92) and two mutants (IR8-202 and Pokkali-M) were developed from rice varieties IR8 and Pokkali through mutation breeding, evaluated to check the yield performance for two years under salinity stress and results showed that the mutant variety Shua-92 produced 40-49 per cent more paddy yield on saline soil than the famous salinity tolerant Nona Bokra and Pokkali varieties (Baloch *et al*., 2003).

Exploiting the potential of beneficial microorganisms is an alternative strategy for ameliorating plant stress tolerance. Stress alleviation is ensured by signaling events occurring during the plant–microbe interaction and these mechanisms are regulated by a complex network of signaling events (Smith *et al*., 2017). Recent studies showed that plant growth promoting bacteria act as growth promoter as well as elicitors of salinity tolerance (Tiwari *et al*., 2016).

There are many recent developments in the understanding of the mechanisms of salt tolerance such as RNA guided CRISPR endonuclease technology including base and prime editing or targeted mutagenesis which help in gene discovery, functional analysis transferring favorable alleles into elite breeding line to accelerate the breeding of salt-tolerant rice cultivars (Ganie, 2021). As a future line of study, the advanced technologies such as, genome editing can be used as an excellent tool, for improving crop traits, with salinity stress tolerance, as a target.

CONCLUSION

Na$^+$ exclusion from the root, modulation of root–shoot transport, and cellular compartmentalization of Na$^+$, as well as maintenance of cytoplasmic osmotic balance, are crucial aspects of salt tolerance. *HKT1* plays an important role in root stellar cells, modulating sodium transport to the shoot. Tissue-specific expression of *HKT*1 at specific developmental stages can contribute to plant salt tolerance. By targeting and phosphorylating downstream components, both ABA-independent *SUCROSE NONFERMENTING1-RELATED PROTEIN KINASE2 (SnRK2s*) and ABA-dependent *SnRK2s* play pivotal roles in transcriptional regulation and posttranscriptional regulation during salt stress response.

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