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Genetic and Physiological Mechanism of Salt Tolerance in Rice: Special Reference to SKC1 and HKT Genes

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Abstract: *Salt stress poses a significant threat to rice (Oryza sativa L.) production, a staple crop essential for global food security, particularly in Asia where salinity affects vast agricultural lands due to climate change and rising sea levels. This review explores the genetic and physiological mechanisms underlying salt tolerance in rice, with special emphasis on the SKC1 (OsHKT1;5) and HKT gene families. Physiologically, rice maintains Na*$^+$*/K*$^+$ *homeostasis through mechanisms such as sodium exclusion via the SOS pathway, selective K*$^+$ *uptake, vacuolar compartmentalization, osmotic adjustment, and enhanced antioxidant defenses to mitigate reactive oxygen species (ROS)-induced damage. Genetically, key quantitative trait loci (QTLs) like Saltol on chromosome 1, along with genes such as SKC1 and OsHKT1;5, regulate ion transport and exclusion, preventing Na*$^+$ *toxicity in shoots. SKC1 encodes a Na*$^+$*-selective transporter that sustains K*$^+$*/Na*$^+$ *ratios under stress, while HKT transporters facilitate root-shoot Na*$^+$ *partitioning. Breeding strategies, including marker-assisted selection (MAS) for introgressing Saltol and HKT alleles into elite varieties, and biotechnological tools like CRISPR/Cas9 for editing genes such as OsRR22 and DST, have advanced the development of salt-tolerant cultivars. Integrating multi-omics approaches and physiological profiling offers promising avenues for future breeding. This synthesis underscores the interplay between genetics and physiology in enhancing rice resilience, supporting sustainable agriculture in saline environments.*

Keywords; *Salt tolerance, Rice, Oryza sativa, SKC1 gene, HKT genes, Ion homeostasis, Na+/K+ ratio, Saltol QTL, Marker-assisted selection, CRISPR/Cas9, Antioxidant defense, Osmotic adjustment, Sodium exclusion, Vacuolar compartmentalization, Breeding strategies*

1. Introduction

The issue of salt tolerance in rice is relevant to the global food security since rice is a leading staple crop to over 50 per cent of the total world population, and nearly 90 per cent is grown and eaten in Asia (Bandumula, 2017). As climate change continues to increase, environmental problems such as high salinity by rising sea levels- are threatening the production of rice. This is especially worrying because rice is the source of nutrition to a large number of people in the world and also serves to support economies of poor nations that rely on agriculture. When salinity constraint is acted on above a threshold level, abiotic stresses may prevent the growth and development of plants, as well as immensely decrease crop yield leading to the emergence of salt tolerant genotypes of rice a precondition of survival and sustainability in agricultural productivity (Hafeez et al., 2023). These issues are aggravated by the adverse effects of climate change including changes in precipitation and temperature patterns, which exacerbate the negative exposure that agricultural production will face and increase it with increased food security risks (Toromade et al., 2024).With its plan to tackle salt tolerance in rice, the aim is to develop a sustainable and resilient crop by introducing new breeding techniques and agricultural practices. For instance, the use of genomics-assisted breeding enables accurate and efficient generation of rice strains for brackish environments, where salt content is high, ensures the potential to maintain rice production and food security (Hafeez *et al*., 2023). Salt tolerance of rice is indeed a major concern to ensure food security in the context of climate change and environmental stress. It will allow rice to be a steady supply of food for billions of people globally, and thus a key backing in achieving global food security targets.

Rice plant can accomplish Na+ and K+ homeostasis in response to salinity amid physio-ecological and molecular plans of salt tolerance to ameliorate the toxic cycle of uptake, membrane potential depolarization, and toxicity induced by excess Na+.Sodium Exclusion and Compartmentalization Na + efflux of cells by the plasma-membrane located Na +/H + exchanger protein Salt Overly Sensitive 1 (SOS1) offers a key system to counter the toxic loop of uptake, membrane potential depolarization SOD1 loss-of-function mutations predispose the plants to salt-induced inhibition of Na + efflux and accumulation in the shoot (El Mahi et al., 2019). Moreover, the upregulation of SOS1 pathway genes following overexpression of such genes like LecRLK leads to the avoidance of excess Na + ions in the cells by the rice plants and ionic homeostasis of the plant (Passricha et al., 2019). Selective K+ Uptake: This is an important role of the HKT genes, which increase the capacity of the plant to absorb K+ as opposed to Na + and therefore a greater K+ /Na + ratio, which is crucial in cell activities in saline soil (Fathalli et al., 2025). Osmotic Adjustment and Antioxidant Defense: The use of exogenous osmo-protectants (gallic acid or Mn) can assist in retaining ionic homeostasis and improving antioxidant defense system, which in turn makes detoxification of the ROS generated during the stress period possible (Rahman et al., 2022; Rahman, Nahar, et al., 2016). This does not only inhibit Na + influx, but also causes K + buildup and salt tolerance in plants. Molecular Regulation Molecular Regulation: OsWRKY53 is an ion homeostatic regulator that regulates the expression of other genes through the regulation of Na +/K + channel. Specifically, OsWRKY53 can trans-repress HKT1;5, which is a sodium transporter and takes part in the regulation of root Na + flux and homeostasis (Yu et al., 2023).

Altogether, these pathways demonstrate an intricate interconnection between genetic expression, ion transporter activation and stress response pathways that act to sustain the salinity tolerance of the rice plant by modulating a fine balance between Na^+ and K^+ ions (Prakash & Prathapasenan, 1988; V. Singh *et al*., 2018). Rice plants exhibit Na^+/K^+ homeostasis under salt stress by a variety of physiological measures that are related to the function of ion transporters, antioxidants and genetic pathways. Na + /H + Exchangers: In rice, the Salt Overly Sensitive 1 (SOS1) protein critically maintains salt tolerance through regulation of Na + homeostasis. SOS1 is a Na^+ efflux transporter, which also diminishes excessive accumulation of Na^+ in roots and shoots by catalyzing the efflux of cellular Na^+ (El Mahi *et al*., 2019). The PsLecRLK gene also compliments SOS pathway to pump-out excessive Na^+ ions under stress by up-regulating the expression in rice which resulted in salt tolerance (Passricha *et al*., 2019). Antioxidant Defense and Osmotic Regulation Salinity stress induces oxidative stress in rice for which the over activation of antioxidant defense systems act as scavengers. In the process, Root-to-shoot exudation of manganese (Mn) and gallic acid (GA) which externally applied can reduce Na^+ influx, K^+ retention, hence ionic balance. These compounds also augment the antioxidant potential inducing antioxidant enzymatic activities such as superoxide dismutase (SOD) and catalase (CAT), subsequently reducing oxidative stress (Rahman *et al*., 2022; Rahman, Nahar,*et al*., 2016).

Apoplastic barriers in the roots of rice are significant in restricting Na + uptake. Such barriers especially suberin based hinder passive transfer of Na+ into roots. These obstacles are more effective in the salt tolerant rice varieties which lead to reduced Na + accumulation and superior survival under saline environments (P. Krishnamurthy et al., 2009). Genetic Control Gene Expression and Pathways is of primary significance in salinity response in rice. Other genes that are linked to osmoresponsive and ionic regulation, such as DREB2A, LEA3 and HKT2;1 are differentially expressed to ensure the cellular ion homeostasis. RING-type E3s have been reported to mediate overexpression of stress responses in stress-tolerant rice genotypes and suppress the action of salt through an augmentation in the compatible solute accumulation towards enhanced salt stress tolerance (V. Singh et al., 2018). High cytosolic K +/Na +ratio plays a role in salt tolerance. Other transporters like SKC1 and NHX1 are entailed with efflux of Na + back into the xylem or into vacuoles, respectively, to allow the different regulation of ions in plant cells (J. Gao et al., 2007). All these molecular aberrations enable rice to endure the harmful effects of salinity by regulating ion homeostasis, osmotic balance, and antioxidant mechanisms. Hyper production of the reactive oxygen species (ROS) leading to cellular damage, ionic homeostasis disruption, and physiological dysfunction in response to salinity stress in rice. These reactive oxygen intermediates can be counteracted by the cellular antioxidant defense system, which is composed of enzymatic and non-enzymatic antioxidants, to prevent the occurrence of oxidative damages to the plant. The enzymes that are involved in this protective process are superoxide dismutase (SOD), catalase (CAT) and the ascorbate-glutathione (AsA-GSH) system, which includes enzymes glutathione reductase (GR), dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase. As an illustration, earlier studies have already indicated that the levels of SOD are greater in salt-tolerant than salt-sensitive rice genotypes and ROS detoxification is more effective (Kordrostami et al., 2017). Moreover, exogenous GA supplementation has been found to enhance ROS scavenging and consequently oxidative damage through the increase in the endogenous ascorbate, glutathione and phenolic content, the activities of these enzymes have been found to be efficient in the scavenging of ROS (Rahman et al., 2022).Ion homeostasis is also lost when plants are exposed to salinity stress, due to the accumulation of Na+ and depletion of K+, resulting in imbalanced ion concentration. The antioxidant defense system, by scavenging free radicals and recovering membrane structure stability reducing lipid peroxidation, may also help to restore ionic homeostasis, possibly through regulated gateways like calcium or manganese. Studies show that Ca supplementation improves the ion homeostasis and efficiency of antioxidant system, while Mn supplements increase anti-oxidant enzyme activity and raise glyoxalase system activities which helps to detoxify toxic substances as methylglyoxal (MG) (Rahman *et al.*, 2016; Rahman & Meah, 2017).

Table 1.1 Physiological Mechanisms of Salt Tolerance in Rice

Mechanism	Key Genes/Proteins Involved	Functional Role	Supporting References
Na^+ Exclusion via SOS Pathway	SOS1, LecRLK	Na^+ efflux from roots and shoots; prevents toxic accumulation	El Mahi *et al.*, 2019; Passricha *et al.*, 2019
Selective K^+ Uptake	HKT1;5, HKT2;1	Maintains high K^+/Na^+ ratio crucial for enzyme activity	Fathalli *et al.*, 2025; Yu *et al.*, 2023
Compartmentalization in Vacuoles	NHX1, V-ATPase	Sequesters Na^+ into vacuoles to protect cytoplasm	Mansour, 2022
Antioxidant Defense	SOD, CAT, GR, AsA-GSH cycle	Detoxifies ROS, stabilizes membranes under salt stress	Kordrostami *et al.*, 2017; Rahman *et al.*, 2022
Osmotic Adjustment	Gallic Acid, Mn	Reduces Na^+ influx, enhances K^+ retention	Rahman *et al.*, 2016; Rahman, Nahar *et al.*, 2016

Finally, the antioxidant network of rice plays a key role in counteracting the detrimental effects of salinity-induced oxidative stress through maintaining redox homeostasis, strengthening ROS scavenging and recovery of osmotic/ionic balance, thereby contributing to salt tolerance of different Rice varieties (Kordrostami *et al*., 2017; Sarkar *et al*., 2013; Tuteja *et al*., 2013).

Factors Involved in Seedling Salt Tolerance of Rice The genetic studies on salt tolerance in rice identified major quantitative trait loci (QTLs) and genes that are crucial for the improvement of salt tolerance at different stages of crop development. For seedling-stage salt tolerance, one QTL meta-analysis resulted in the detection of 11 meta-QTLs on chromosomes 1 and 2. These QTLs have been found promising for use in marker-isted selection (MAS) and/or pyramiding for salt tolerance improvement (Islam *et al*., 2019). Sixteen QTLs for salt-stress seed germination were found in the recombinant inbred lines (17 IRXDJ), including four major ones that could explain large part of phenotypic variance. This implies some japonica rice cultivars are a precious reservoir of salt tolerance germplasm (Wang *et al*., 2010). As a result of the GWAS for rice seedlings, a number of candidate genes and novel loci were detected that are associated with salt tolerance, and could be priority targets in future breeding programs. Interestingly, the detected loci deviate from previously reported regions such as Saltol, indicating different underlying genetic basis for salt tolerance (Puram *et al*., 2018; Rohila *et al*., 2019).

2. Multiple Genetic Strategies and Genetic Architecture of Salt Tolerance in Rice)

A combination of linkage maps and transcriptome profiling provided stable QTLs and a number of possible candidate genes such as OsRCI2-8 (Os06g0184800) which is linked to the salt stress resistance. The outcomes of the current research might be used to enhance breeding strategies of salt-tolerant rice varieties (Geng et al., 2023). Some of the introgression line populations that they used identified several QTLs that are useful in increasing salt tolerance at one or multiple growth stages. OsSDIR1, SERF (Chapagain et al., 204) and WRKY55 were interesting candidate genes of seedlings and to a lesser degree also of reproductive stages. At the single gene level, OsHKT1;5 has received extensive reporting due to its core role in ion homeostasis which is engaged in salt resistance. It is important as demonstrated by the fact that it, together with other genes such as OsHKT1;1, SKC1 and OsSTL1, has been a fundamental gene in breeding to come up with more salt tolerant rice lineages (Raghuvanshi et al., 2021). The findings of these studies indicate the genetic complexity of the interactions that regulate salt tolerance in rice and confirm the need to combine a variety of breeding strategies to take advantage of these resources.

The Saltol QTL is commonly recognized to be important in the breeding programmes of rice since it imparts the salt tolerance at seedling level that is highly susceptible to the salinity stress. One of the primary limitations to the production of rice globally and salinuous soil, in particular, is salt stress (Q. Gao et al., 2023). The significance of Saltol is explained by the fact that it helps in the absorption and distribution of Na+, the isolation of the plant against the toxic salt ions, which is also a significant faculty

(Krishnamurthy et al., 2015). The ability to readily introgress these Saltol QTL in sensitive rice by molecular markers is one of the reasons why these QTL has such significance in rices breeding. An example is the high yielding salt sensitive rice which have been introgressed successfully with Saltol and were shown to give high yielding salt tolerant progenies (Geetha et al.). The approach has facilitated the creation of salinization resistant varieties of rice that do not lose yield and/or quality (Geetha et al., 2017). Saltol QTL in itself lies in chromosome 1 and coincides in an area of 5 Mb with seedling stage tolerance. Markers on this area have been reported to be linked with salinity tolerance and help in the selection of the trait at the seedling stage (S. L. Krishnamurthy et al., 2015; Rohila et al., 2019). The Saltol QTL controls the movement of sodium ion (Na +) symporters and Na + /K + homeostasis, maintains cell membrane stability, alleviates ion toxicity, and is also crucial to rice plant defense against salt stress (Chen et al., 2020; Yuan et al., 2022). Moreover, Saltol marker-assisted backcrossing also has been implemented in breeding programs to introgress salt tolerance in commercial cultivars without affecting desirable agronomic characteristics (Geetha et al., 2017). Its use in the framework of rice improvement has grown over the years as well as the ability of the genomic tools and finer mapping and tuning of salt tolerance as compared to earlier approximations therefore making it possible to design new stronger genotypes. Generally, Saltol QTL forms a pillar in breeding rice with salt tolerance and salt tolerant high yield and corresponding quality. This goes in line with the overall objective of improving food security on salinity affected agro-ecosystem (Islam et al., 2019).

Table 2.1 Major QTLs and Genes Associated with Salt Tolerance in Rice

QTL/Gene	Chromosome Location	Reported Function	Reference
Saltol QTL	Chr 1 (10.6–11.5 Mb)	Controls Na^+/K^+ homeostasis at seedling stage	Krishnamurthy *et al.*, 2015; Chen *et al.*, 2020
SKC1 (OsHKT8)	Chr 1 (xylem parenchyma)	Na^+ transporter, maintains K^+/Na^+ ratio	Ren *et al.*, 2005; Song *et al.*, 2016
OsHKT1;5	Chr 1	Removes Na^+ from xylem sap, prevents shoot Na^+ toxicity	Cotsaftis *et al.*, 2012; Shohan *et al.*, 2019
OsHAK21	Chr 6	High-affinity K^+ uptake under salinity	Shen *et al.*, 2015
OsWRKY53	Regulatory gene	Regulates HKT1;5 and Na^+ transport genes	Yu *et al.*, 2023

3. Role of SKC1 Gene

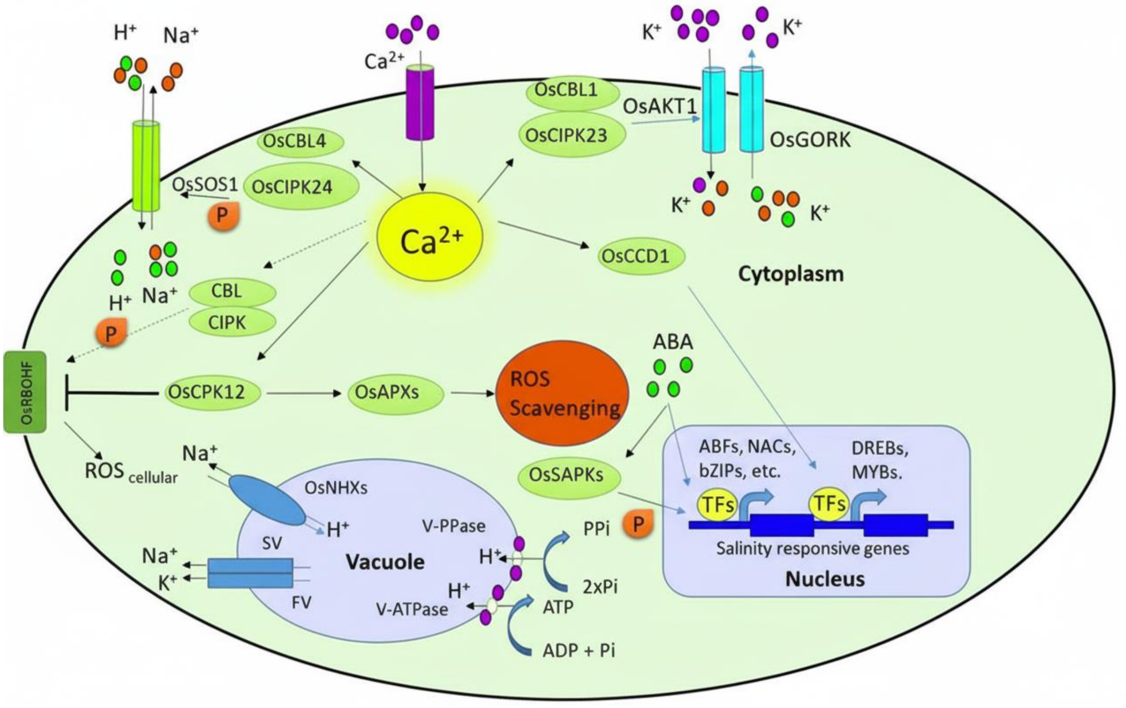
The Saltol QTL is commonly recognized to be important in the breeding programmes of rice since it imparts the salt tolerance at seedling level that is highly susceptible to the salinity stress. One of the primary limitations to the production of rice globally and salinuous soil, in particular, is salt stress (Q. Gao et al., 2023). The significance of Saltol is explained by the fact that it helps in the absorption and distribution of Na+, the isolation of the plant against the toxic salt ions, which is also a significant faculty (Krishnamurthy et al., 2015). The ability to readily introgress these Saltol QTL in sensitive rice by molecular markers is one of the reasons why these QTL has such significance in rices breeding. An example is the high yielding salt sensitive rice which have been introgressed successfully with Saltol and were shown to give high yielding salt tolerant progenies (Geetha et al.). The approach has facilitated the creation of salinization resistant varieties of rice that do not lose yield and/or quality (Geetha et al., 2017). Saltol QTL in itself lies in chromosome 1 and coincides in an area of 5 Mb with seedling stage tolerance. Markers on this area have been reported to be linked with salinity tolerance and help in the selection of the trait at the seedling stage (S. L. Krishnamurthy et al., 2015; Rohila et al., 2019). The Saltol QTL controls the movement of sodium ion (Na +) symporters and Na + /K + homeostasis, maintains cell membrane stability, alleviates ion toxicity, and is also crucial to rice plant defense against salt stress (Chen et al., 2020; Yuan et al., 2022). Moreover, Saltol marker-assisted backcrossing also has been implemented in breeding programs to introgress salt tolerance in commercial cultivars without affecting desirable agronomic characteristics (Geetha et al., 2017). Its use in the framework of rice improvement has grown over the years as well as the ability of the genomic tools and finer mapping and tuning of salt tolerance as compared to earlier approximations therefore making it possible to design new stronger genotypes. Generally, Saltol QTL forms a pillar in breeding rice with salt tolerance and salt tolerant high yield and corresponding quality. This goes in line with the overall objective of improving food security on salinity affected agro-ecosystem (Islam et al., 2019).

SKC1 gene plays a significant role in regulating the concentration of potassium (K +) within the shoot compartment and boosts yield stability at salty environment by preserving ion homeostasis and counteracting detrimental impact of salinity on the physiology of plants. SKC1 of high-affinity K + transporter family is also relevant in the regulation of information of intracellular K + homeostasis and is believed to make plants tolerant to salinity (Fei et al., 2003; Shabala and Cuin, 2008). Among the principal mechanisms through which SKC1 acts, it is possible to mention the enhancement of the uptake of K+ and the inhibition of Na (Na(+)) uptake in order to achieve the desired K+/Na+ ratio, which is an essential factor of salt tolerance. The salinity tolerance of plants is determined by the large potential of plants to sustain this ratio at an appropriate level. As an illustration, OsHAK21 is an ion transporter, which functions in a similar way as K + uptake and is highly involved in K +/Na + homeostasis, therefore, these transporters are highly significant to reestablishing ion balance in cases of salt stress (Shen et al., 2015). When the salt conditions are low, the genetic pathway of SKC 1 mediated is complicated and has many regulatory networks that regulate salt responsive gene or pathway expression. Genetic and proteomic responses to salt stress are also prone to influence the regulation of transporter activity, in the same manner as already shown with SKC1. These reactions comprise the imported responses to stress through a large assortment of ion transporters and vacuolar transfer systems which eventually provides key roles in the regulation of K + and Na + homeostasis in the cell. NaCl storage, as well as, maintenance of a high K ions/Na + ratio in the cytosol are highly required by salinity tolerance of plants and the vacuolar membrane transporters, especially Na +/H + antiporters are involved (Mansour, 2022; Shabala and Cuin, 2008). Further studies of the other transporters and the stress-signaling pathways resulted in the discovery of a major effect of genetic regulation of ion channels and transport proteins on salt tolerance/sensitivity of plants. As an example, the genes of stress-responsive transcription factors and transporters, such as NHX, SOS, HKT and VTPase, are thought to be involved in the increase of plant salinity tolerance through regulating ion distribution and homeostasis among other plant species (A. Mishra & Tanna, 2017; Salwan et al., 2019).In conclusion, the SKC1 gene controls shoot K^+ concentration and improves yield stability under salinity by a genetic process of maintaining ionic hemostasis. This includes the expression and regulation of ion transporters, vacuolar transport systems, and stress signaling pathways that regulate ion acquisition and distribution as a whole during plant adaptation to saline environment.

4. Role of HKT Gene Family

The HKT1;5 genes play a significant role in salt tolerance; they are necessary in the regulation of Na+ delivery and exclusion in rice. It is a member of the family of high-affinity K + transporters that regulate the homeostasis of Na + in plants. HKT1;4 is primarily involved in restricting the accumulation of Na + in the shoots through its action as a Na + removal mediator by the xylem sap and therefore preventing the salinity tolerance response due to dramatic accumulation of foliar Na + as one of the primary key determinants in tolerance response (Cotsaftis et al., 2012; Hauser & Horie, 2010). OsHKT1;5 is highly expressed in the roots when compared to the shoots and in root cells, in the parenchyma of the xylem around xylem vessels. The localization of this expression indicates the significance of this expression in regulating Na+ transport between root and shoot. The high salt tolerant rice varieties having the high OsHKT1;5 expression correlate with the low Na+ level in the shoot tissues indicating that this gene is involved in maintaining the Na +/K + ratio low in saline condition (Shohan et al., 2019). Research has indicated that salt tolerance in plants should be carried out at low Na +/K +. HKT1;5 is involved in this process, and it enables Na+ exclusion and transportation in the plant (Huang et al., 2008). Moreover, gene expression experiment and structural modeling have also revealed that the levels of OsHKT1;5 transcripts along with certain OsHKT1;5 structural limitations also play role in the Na+ regulatory process in various rice genotypes. It is also required to control this level to prevent salt mediated damage to the photosynthetic tissues (Cotsaftis et al., 2012). The salt-tolerant rice Pokkali also demonstrated efficient Na + sequestration in roots catalyzed by HKT1 transporters and the salt-sensitive variety demonstrated increased expression of Na + transporters such as HKT1:5 in developing panicles, implying that there is variation in regulation mechanism among genotypes (Chakraborty et al., 2019).

Figure 4.1. Molecular Mechanisms of Salinity Tolerance Signaling in Plant Cells



HKT (High-Affinity Potassium Transporter) transporters The physiological mechanism of regulation of root-shoot Na+ partitioning is known to be influenced by HKT transporters, especially under salinity tolerance in plants. A major role of HKT transporters is to prevent excessive accumulation of sodium (Na^+) in the shoot tissues and to exclude Na^+ efflux from xylem vessels, thereby protecting leaves from salt-induced stress (Hauser & Horie, 2010). The HKT transporter family consists of several subfamilies, each involved in distinct ion transport processes.

For example, certain HKTs transport Na^+ ions only; others are able to co-transport Na^+ and K^+. This selectivity is important for preventing other K+/Na+ homeostasis within plant tissues, that being a critical requirement for salinity tolerance (R. Gao *et al*., 2024; Su and others, 2015).

HKT_1 tissue-specific control is also critical for Na^+ homeostasis. e.g., reduced expression of HKT_1 in roots and enhanced expression in shoots under salinity stress, which can help to reduce Na^+ accumulation across the plant, resulting in greater salt tolerance (H. Zhang *et al*., 2008). Inspiringly, the expression of some HKT transporters including PeHKT1;1 in Populus were involved in the regulation of antioxidation system and improve the tolerance to salt stress, suggesting that monitoring adaption under salinity was dependent on HKTs (Xu *et al*., 2018). Collectively, HKTs play a crucial role in the regulation of Na^+transport and its distribution within plants by limiting Na^+ accumulation under salt stress, which is important for adaptation of plants to high-saline environments (Mian *et al*., 2011).

Allelic variants of HKT (High Affinity K+ Transporter) genes have important roles for increased salt tolerance that target different mechanisms in different plant species. Salt tolerance is an important trait for enhancing agricultural productivity, especially in soils affected by salinity. The HKT family of genes affects salt tolerance by controlling the Na+/K+ balance essential for plant growth under saline conditions. In addition to the QTL detected in the current study, several haplotypes of HKT were involved in high salinity tolerance on Indian wild rice (Oryza sativa), such as H5 for HKT1;5 and H1 for HKT2;3. This investigation concluded that those alleles from wild rice might be integrated into cultivated rice, improving the salt tolerance of domestic varieties (S. Mishra *et al*., 2016).

In maize (Zea mays), ZmHKT1;5 has been proved to increase salt tolerance by maintaining an appropriate Na+/K+_balance. Expression of this gene was markedly enhanced under salt stress in the salt-tolerant lines, which would help plant growth. Some single nucleotide polymorphisms (SNPs) in ZmHKT1;5 were identified to be related to the distinction of salt tolerance, and plants overexpressing the favorable allele increased transgenic tobacco's salt resistance limit (Jiang *et al*., 2018; M. Zhang *et al*., 2017). The TaHKT9-B gene has been associated with shoot K+ accumulation and salt tolerance in wheat (Triticum aestivum). One specific insertion in its promoter region was found to be associated with differential K+ contents among wheat germplasm, suggesting a mechanism for wheat tolerance towards salinity (Du *et al*., 2023). In addition, DNA methylation was identified as an epigenetic modulator of HKT gene expression and salt stress tolerance (Kumar *et al*., 2017).

In blueberry (Vaccinium corymbosum), VcHKT1;1 was found to be a Na+-selective transporter contributing to leaf Na+ exclusion and salt tolerance. An addition of the promoter due to a natural integration raised the transcription, and contributed to improved salt tolerance (Song *et al*., 2023). These genetic findings indicate that breeders could improve salt tolerance in followers species through the manipulation of allelic diversity within HKT genes. This strategy relies on the choice or design of alleles favourizing ion transport and balance to be able to cope better with saline conditions. I won't be able to crank out an entire essay, but this should illuminate how HKT allelic variation are genetically contributing to the breeding of salt tolerant crops.

5. Combination of Genetic and Physiological Information

The contribution of the SKC1 and HKT genes to physiological pathways affects ion homeostasis and transport, this being key for salt tolerance in rice. SKC1 has been reported to be implicated in the control of Na+ transport, unloading Na+ from xylem and plays an important part to ion balance under salt stress (J. Gao *et al*., 2007). Its involvement in Na+ and K+ homeostasis is critical for the plant's ability to tolerate high salinity. The HKT gene family, especially some members include HKT1;5 and HKT2;3 have been discovered to be key genes for salinity tolerance. These genes are related to Na+ transport and/or Na+-K+ co-transport activity. Certain alleles of these genes were found to be strongly associated with salt tolerance in rice (S. Mishra *et al*., 2016). In addition, rice acclimation to salinity stress is achieved through the interplay of transcription factors controlling stress-inducible gene expression. These responses contribute to ionic homeostasis, which is one of the most important factors in sustaining growth and productivity under salt stress (J. Gao *et al*., 2007). Thus, genetic variation in SKC1 and HKT genes for ion transport and their regulation of broader stress response pathways potentially would underlie the coordination of genetic and physiological mechanisms controlling salt tolerance in rice. Such information is important for breeding efforts to create rice lines that are more tolerant of salt, based upon the combination of these contributing genetic elements to modify salinity response (J. Gao *et al*., 2007; S. Mishra *et al*., 2016).

6. Breeding and Biotechnological Approaches

Saltol and HKT alleles were also successfully introgressed in to elite rice varieties by MAS, which showed a marked increase in salt tolerance at seedling stage. MAS has been reported in several studies for this trait using different elite rice genotypes. For example, in the case of Vietnam, the Saltol QTL was adopted into elite variety AS996 of rice by MABC36. The strategy entailed screening 500 SSR markers that were earlier (79-113bp) positioned on the 12 chromosomes to identify polymorphic markers closely linked to Saltol. Plants with a high percentage of the recipient alleles and Saltol were selected in several backcrossed populations to generate a salinity-tolerant line, that is ASS996-Saltol (Huyen *et al*., 2012).

In the same way, in Tamil Nadu, the Saltol QTL was introgressed into one of the commercial popular salt sensitive variety ADT 43 through marker-assisted backcross breeding. The process resulted in the release of Saltol-introgressed lines that were not only salt-tolerant but also having greater yields and good cooking quality parameters (Geetha *et al*., 2017). In a landmark progress, elite Indian rice cv Pusa Basmati 1 (PB1) was enhanced for seedling-phase salt tolerance in the background of Saltol using MAS. Foreground selection was performed with certain Saltol-linked SSR markers, and background selection ensured the recovery of recurrent parent genome. This effort led to development of near isogenic lines (NILs) with higher salt tolerance and similar agronomic traits of PB1 (V K Singh *et al*., 2018). Lastly, the introgression approach for Saltol into IR64 a popular lowland variety is evidence of MAS efficiency in complex breeding programs. This line of approach led to introduction lines with enhanced salinity tolerance which had more than double the number of sources, compared to IR64 indicating that MAS can speed up the process in achieving stress tolerant rice varieties (Ho *et al*., 2016).

Table 6.1 Marker-Assisted Selection (MAS) for Salt Tolerance in Rice

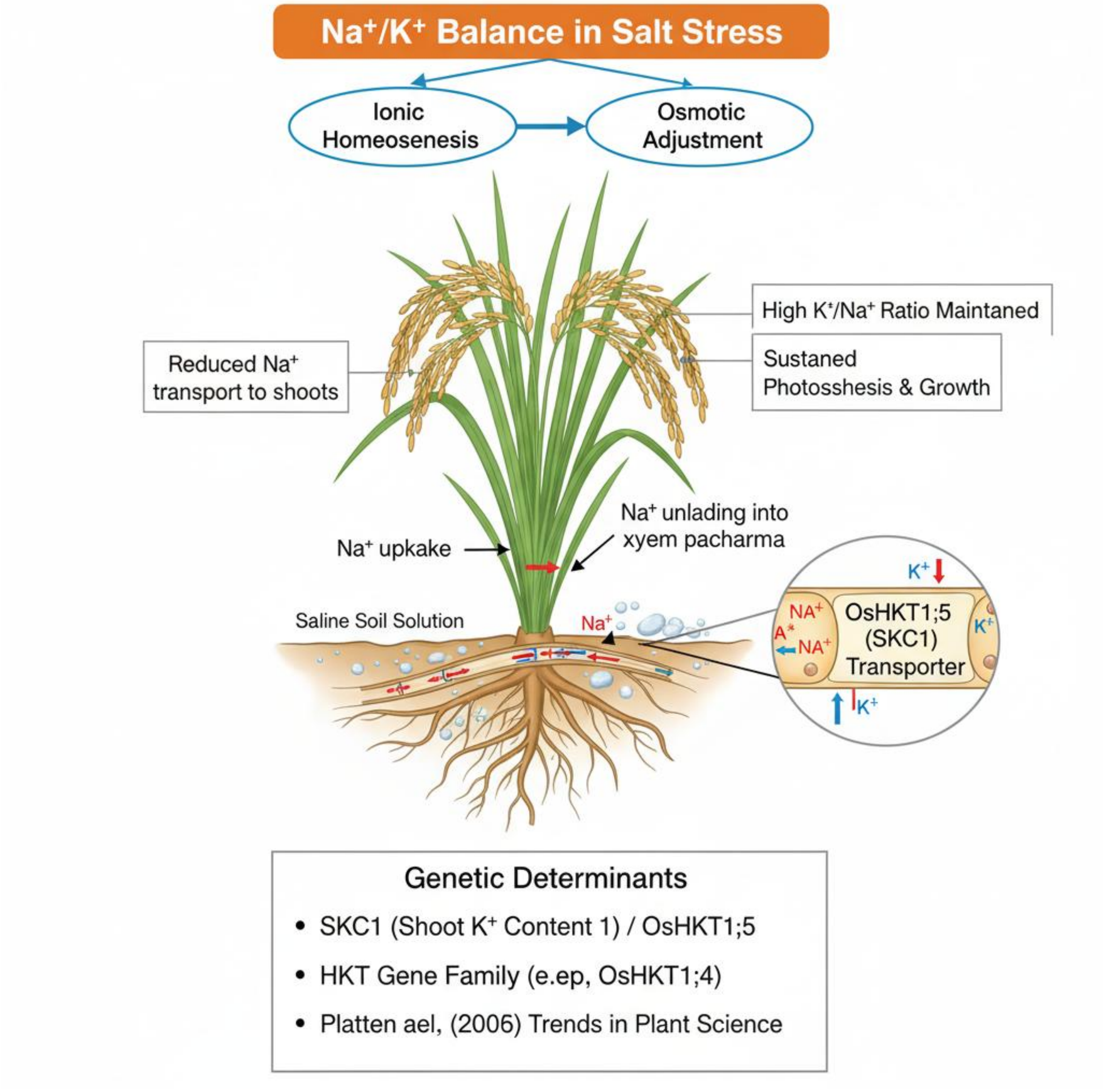
Rice Variety	**Introgressed Gene/QTL**	**Method Used**	**Outcome**	**Reference**
AS996 (Vietnam)	Saltol	MABC36 using SSR markers	Salinity-tolerant AS996-Saltol lines	Huyen *et al.*, 2012
ADT43 (Tamil Nadu)	Saltol	Backcross breeding with markers	Salt-tolerant lines with good grain quality	Geetha *et al.*, 2017
Pusa Basmati 1 (India)	Saltol	Foreground & background selection	NILs with high tolerance and quality retention	Singh *et al.*, 2018
IR64 (Philippines)	Saltol	MAS introgression	Doubled salt tolerance over parent line	Ho *et al.*, 2016

The infrastructure for targeted gene editing, such as CRISPR/ Cas9, has been successfully developed to enhance salt tolerance in rice. Luo and colleagues reported that they had obtained new type of rice germplasm with salt tolerance through editation of OsRR22 gene, a key gene regulating the salt tolerance, with CRISPR/Cas9. The new germplasm has much stronger salt tolerance compared to the non-edited line, namely suggesting the great potential of CRISPR/Cas9 in improving rice's adaptability in a saline habitat (Han *et al*., 2022).

CRISPR-Cas9 based editing of the DST gene in indica rice is another significant progress. This alteration caused a decrease in stomatal density and increase in leaf water holding capacity, which further increased the salt tolerance. The resultant mutant alleles conferred that moderate osmotic tolerance and a higher level of salt tolerance at seedling stage (Santosh Kumar *et al*., 2020). Apart from CRISPR/Cas9 system, transgenesis was also used to develop salt-tolerant rice genotypes. Expression of an Escherichia coli catalase gene (katE) in rice, for instance, rendered salt tolerance. The transgenic plants were able to grow and reproduce at much greater salt conditions relative to non-transgenic plants (Nagamiya *et al*., 2007). Vacuolar H+-Pyrophosphatase Gene: Another transgenic strategy to improve salt tolerance using the Na + /H + antiporter was through over expression of the gene encoding the vacuolar H+-pyrophosphatase (HVP10) for promoting Na+ translocation into root vacules. This genetic engineering generated new salt-tolerant and high-yielding rice lines under salt stress (Fu *et al*., 2021).

The CRISPR/Cas9-based gene editing system has also been integrated into hybrid rice breeding programs. For example, gene editing of the OsRR22 gene in a new hybrid rice platform generated novel salinity-tolerant rice varieties that retained normal agronomic characteristics, illustrating the possibility to combine gene editing with conventional breeding and improve salt resistance (Sheng *et al*., 2023). Altogether, such progress emphasizes the great promise of both CRISPR/Cas9 and transgenic technologies in the successful enhancement of salt tolerance in rice, leading to more resilient rice varieties that can thrive in saline-affected agricultural areas.

Figure 6.1. Molecular Mechanisms for Na+, K+ Balance and Salinity Tolerance in Rice



7. Conclusion and Future Perspectives

Genetics physiology integration to improve salt tolerance in rice and for meeting real alternative food demands. There are a few promising approaches for future research in this area Various omics data from genomic to transcriptomic, proteomic and metabolomics, epigenetic data to explore the system-based pathways for salt tolerance. This integration strategy will help in identification of the crucial molecular pathways and gene networks associated with salinity tolerance to be used for new breeding ideotypes (De Leon *et al*., 2015; Ullah *et al*., 2022). The search for novel alleles and

QTLs conferring salinity tolerance in rice Find out more! It can also be used to identify candidate lines for genetic improvement programs through genomic resequencing and DNA polymorphism analysis (Rasel *et al*., 2020; Subudhi *et al*., 2020). Utilizing modern technologies, marker-aided-selection transgenics, and genome editing to introgress salt tolerant traits into elite rice germplasm. Such strategies offer effective manipulation of genes and QTLs related to salt tolerance, ensuring breeding for resilient rice varieties (Dai *et al*., 2022; Haque *et al*., 2021). A detailed phenotypic study aimed at elucidating physiological responses underpinning salt tolerance. These may include the traits those associated with ion homeostasis, stress tolerance attributes like activity of antioxidant enzymes, and osmotic adjustment that are important for salinity stress management (Rasel *et al*., 2020; Yang *et al*., 2025). Interdisciplinary research with biochemistry, molecular biology and plant physiology in the context of genetic is a potential way to understand salt tolerance mechanism better. Pooling the potentials can bring to the forefront newness in rice breeding programmes considering both genetic improvements and physiological adjustability (P. Mishra *et al*., 2019; Rasel *et al*., 2020).

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