

Chapter 8

Ion Transporter Genes from Wild Relatives of Cereals Hold the Key for the Development of Salinity Tolerance



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Abstract Crop productivity is often threatened by salinity in arid and semi-arid regions where irrigation is indispensable for agriculture. Excess salt in soil and water causes ion toxicity that can hamper the growth and yield of crop plants affecting various metabolic pathways. Almost all the cereal crops are sensitive to increasing salinity levels, and therefore there is a requirement for the development of salt-tolerant varieties. Though conventional breeding and interspecific hybridization offer some sort of solution to overcome this problem, genetic engineering for the development of novel salt-tolerant variety is more desirable. Salt tolerance is mediated through ion exclusion, compartmentalization of Na^+ within vacuole or restricting Na^+ transport especially to the aerial parts, in which ion transporters play a crucial role in excluding Na^+ from the cell and thus reduce ion toxicity. Most recently, the identification and functional characterization of transporter genes have received greater attention in the development of salt-tolerant crops for sustainable food production. Many wild grasses like *Sporobolus airoides*, *Spartina alterniflora*, *Distichlis palmeri*, *Pennisetum glaucum*, *Porteresia coarctata*, *Puccinellia tenuiflora*, etc. growing mostly in coastal areas or in saline environment show higher salinity tolerance as compared to glycophytes. These wild grasses can adapt to increasing salinity because of the presence of some unique strategies like the exclusion of excess salts by salt glands and maintenance of K^+/Na^+ ratio in leaves mainly due to the presence of highly efficient ion transporters. Targeting the genes responsible for ion transport in these grasses can thus be a useful aid for improving the salinity tolerance of cereal crops. This chapter covers a wide range of salt-related ion transporter genes from the wild relatives of cereal crops to assess the scope of these genes in the production of elite varieties of cereal crops that can survive in highly saline environment.

Keywords Ion exclusion · Salt-tolerant · Salinity · Ion transporters · Cereal crops

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1 Introduction

Salinity is one of the severe abiotic stresses that limits plant growth and causes a significant loss to crop yield. It is estimated that more than 800 million hectares of land is globally affected by salt stress, in which about 20% of irrigated land is included that accounts for one-third of world's food production (Rozema and Flowers 2008; Shrivastava and Kumar 2015). Increased soil salinization can rapidly transform a fertile land into barren land due to the deposition of salt in soil and can thus directly impact on the vegetation of that area. Plant growth is retarded by soil salinity, which induces osmotic stress firstly and is followed by ion toxicity. When plants are exposed to high salinity, cell metabolism is immediately affected because of the ion-specific toxicity (Blumwald et al. 2000). Under NaCl stress, plants generally face hyperionic stress due to the accumulation of toxic Na^+ and Cl^- in cells that impart ionic imbalance. The increase in Na^+ concentration within the cell can, in turn, inhibit K^+ uptake and can retard the biological activity of many enzymes resulting in less productivity and growth of the plant (James et al. 2011). Salt stress in plants is also characterized by the overproduction of ROS such as superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH^-), which imparts a negative effect on various cellular metabolisms and exerts oxidative damage of different cellular structures like proteins, lipid, DNA, etc. (Bartels and Sunkar 2005; Roychowdhury et al. 2018, 2019).

For the maintenance of normal physiology and metabolism under salt stress, plants strategize to increase their tolerance level through the accumulation of osmolytes, overexpression of antioxidative enzymes and sequestration and removal of toxic ions (Munns and Tester 2008; Roy and Chakraborty 2014). Among these, removal of toxic ion is the most determining factor as excess accumulation of Na^+ imposes serious imbalances in plant metabolism (Flowers and Lauchli 1983; Tsunekawa et al. 2009). In salt-tolerant plants, the accumulation of Na^+ in the cell is regulated by the rate of net uptake of Na^+ by root, the net translocation from root to shoot and lastly the transportation of Na^+ from shoot to root through the phloem (Tester and Davenport 2003). The presence of specialized glandular structures in the form of salt glands and bladders in several plants also accounts for removal of excess amount of Na^+ from the cells, thereby aiding in maintaining an optimal K^+/Na^+ ratio (Agarie et al. 2007).

On the basis of salinity tolerance, plants could be broadly classified into glycophytes and halophytes. Unfortunately, all the important cereal crops are glycophytic in nature, and their growth is retarded even at low concentrations of salt (50 mM NaCl). Among the cereals, rye is the most tolerant, followed by barley, maize and rice (Hoang et al. 2016). However, in the order Poales, approximately 8% of the species that include near and distant relatives of cereal crops are halophytic or salt-tolerant in nature and therefore offer a promising system for harbouring salt-tolerant genes for cereal crop improvement (Flowers and Colmer 2008). It has been realized that the ability of these grasses to maintain ion homeostasis in stressed environments is one of the most important mechanisms of salt tolerance. Mostly, in the

chloridoid and panicoid grasses, ion homeostasis is mainly achieved by efflux of excess Na^+ through bicellular salt glands (Marcum 1999). Several ion transporter genes like *SOS1* are involved in the transcription of plasma membrane specific Na^+/H^+ ion transporters for the secretion of Na^+ across the plasma membrane (Qiu et al. 2002). Also, the loading of excess Na^+ into the vacuoles of senescing and maturing leaves helps to maintain the turgor pressure of the cell maintaining a high K^+ in the cytosol (Storey 1995). Presence of Na^+/H^+ ion transporters like *NHX* in the tonoplast plays an important role in the uploading of toxic ions from the cytosol to vacuoles (Jeschke 1984). Many ion transporters from salt-tolerant grasses like *Agropyron elongatum*, *Aeluropus litoralis*, *Pennisetum glaucum*, *Puccinellia tenuiflora*, *Spartina alterniflora*, etc. have been deciphered in the last few decades, and their functionality in conferring salinity tolerance has been well explained (Shabala and Mackay 2011).

The understanding of salt-tolerance attributes of ion transporter genes from wild grasses has encouraged the evaluation of these genes in conferring salinity tolerance in cereal crops (Bhatnagar-Mathur et al. 2008). In the past decade, plasma membrane and vacuolar Na^+/H^+ antiporters have been the centre of attention in transgenic studies for the alleviation of Na^+ -induced toxicity in plants (Zhang and Blumwald 2001; Vera-Estrella et al. 2005; Liu et al. 2008). This review, therefore, attempts to provide an in-depth status of the ion transporter genes from wild grasses and their potentiality to confer salinity tolerance in crop plants and also to assess the present status of salt-tolerant transgenic cereal crops.

2 Ion Transporters and Their Mechanism of Action in Salinity Tolerance

Several ion transporters, pumps and channel proteins located on the plasma membrane or vacuolar membrane are involved in ionic homeostasis and thus confer salinity tolerance in plants. These ion transporters include high-affinity potassium transporters (HKTs), salt overly sensitive (SOS) and non-selective cation channels (NSCCs) present on the plasma membrane. These are the carrier-type transporter that is involved in Na^+ transportation at the cellular level. Other transporters such as Na^+/H^+ antiporters (NHXs), cation transporter (CAX) and H^+ pumps are present on the vacuolar membrane that facilitates compartmentalization of Na^+ toxic ions into the vacuoles (Hasanuzzaman et al. 2015; Volkov 2015; Shabala et al. 2015; Anumalla et al. 2016).

A number of plants like rice, wheat and *Arabidopsis* show the presence of HKTs in their plasma membrane that acts either as a Na^+/K^+ symporter or Na^+ uniporter (Waters et al. 2013). HKT protein family can be divided into two groups: the first group is HKT1 that transports only Na^+ , and the other group is HKT2 that is involved in the transportation of both Na^+ and K^+ (Corratge-Faillie et al. 2010). In *Arabidopsis*, HKT1 was shown to be involved in recirculation of Na^+ from shoot to root by

loading the excess ion into the phloem and by releasing it into the roots (Berthomieu et al. 2003). It was also reported that HKT1 was involved in Na^+ unloading from xylem vessels to xylem parenchyma cells that contribute to salt tolerance in *Arabidopsis* (Sunarpi et al. 2005).

To date, SOS1, a Na^+/H^+ antiporter, is the best-known ion transporter, which is involved in Na^+ efflux from the cytosol to the apoplast of the cortical cell. It was reported by Shi et al. (2000) that SOS1 found in the root apex of *Arabidopsis* is the only transporter involved in the Na^+ exclusion from the cytosol to the apoplast, functioning as Na^+/H^+ antiporter. In transgenic plants with SOS1 gene, salt tolerance was found to be enhanced by the overexpression of SOS1 (Yang et al. 2009; Yue et al. 2012; Hasanuzzaman et al. 2015; Anumalla et al. 2016), whereas the loss in function of SOS1 showed hypersensitivity to salt even in the salt-tolerant wild relative of *Arabidopsis* – i.e. *Thellungiella salsuginea* (Oh et al. 2009). Similarly, the SOS1 gene isolated from *Salicornia brachiata*, when overexpressed in tobacco plant, showed better performance under saline environment due to extracellular Na^+ effluxing (Yadav et al. 2012). It was reported from *Arabidopsis* that the activity of SOS1 was regulated by two other proteins, viz. SOS2 and SOS3 (Shi et al. 2000). SOS3 is a calcium-binding protein which in turn induces SOS2, a serine/threonine protein kinase to activate phosphorylation in SOS1, thereby increasing Na^+/H^+ exchange activity of the SOS1 transporter (Halfter et al. 2000; Liu et al. 2000; Luan et al. 2009).

Non-selective cation channels (NSCCs) play a major role in the regulation of Na^+ transportation when the salt concentration is high in the soil. It has been demonstrated in several studies that NSCCs catalyse primary Na^+ fluxes under salinity stress (Kronzucker and Britto 2011). According to Tester and Davenport (2003), there are two classes of NSCCs, viz. cyclic nucleotide-gated channels (CNGCs) and glutamate-activated channels (GLRs). Inhibition of cation channels is associated with the amelioration of Na^+ toxicity in plants, and external Ca^{2+} plays an important role in this. Ca^{2+} and intracellular and extracellular Na^+ can all have regulatory roles by blocking the K^+ -selective outwardly rectifying channel (KOR) and thus preventing excessive Na^+ influx and cellular K^+ loss (Demidchik and Maathuis 2007). The rice CNGC1 was reported to decline Na^+/K^+ ratio by decreasing Na^+ influx and was observed to be more downregulated in salt-tolerant rice variety than the salt-sensitive variety under salinity stress (Senadheera et al. 2009). NSCC members of glutamate-activated channels from *Arabidopsis thaliana*, *AtGLR3;7*, *AtGLR1;1* and *AtGLR1;4* when expressed in *Xenopus* oocytes, were shown to exhibit Na^+ permeability, and it was also revealed that these channel proteins could function in the transportation of Na^+ , K^+ and Ca^{2+} (Roy et al. 2008; Tapken and Hollmann 2008).

Halophytes and salt-tolerant plants can tolerate salinity by lowering net Na^+ influx and resist salt stress by the accumulation of excess Na^+ inside its vacuole and efflux of excess Na^+ outside the cell (Hanana et al. 2007; Munns and Tester 2008). In saline conditions, vacuolar Na^+ sequestration reduces the toxicity of cytoplasm and lowers the osmotic potential to maintain turgor pressure. Various transporters such as Na^+/H^+ antiporters (NHXs), cation antiporters (CAXs) and auto-inhibited Ca^{2+} ATPase (ACA) are present in the vacuolar membrane for the storage and

translocation of Na^+ from the cytosol during salt stress. There are also some proton pumps, viz. V- H^+ -PPase and the vacuolar H^+ -ATPase in tonoplast that also aids in Na^+ compartmentalization. Na^+ loading in vacuoles is controlled by NHX proteins which are operated by electrochemical gradient of proton generated across the vacuolar membrane. NHX can function as both Na^+/H^+ and K^+/H^+ exchangers under salt conditions (Apse et al. 2003; Leidi et al. 2010). Most of the *NHX* genes are expressed under salt stress and help in maintaining K^+ homeostasis in the cytosol for the growth and development of the plant in saline environments (Pardo et al. 2006; Xu et al. 2013). Maathuis and Amtmann (1999) reported that the Na^+ sequestration helped the plants under salt stress in different aspects such as maintenance of ionic homeostasis in the cytosol, enhancing the efflux of Na^+ and controlling the osmotic potential of tonoplast. NHX1, a $\text{Na}^+,\text{K}^+/\text{H}^+$ exchanger, is the best-known transporter for vacuolar Na^+ sequestration, and most of the NHX transporter such as AtNHX1, AtNHX2, AtNHX3, AtNHX4 and OsNHX1 are located on the tonoplast, which was reported from *Arabidopsis* and rice, and the overexpression of these genes has been shown to improve salinity tolerance (Apse et al. 1999; Chen et al. 2007). The transgenic rice variety carrying the *NHX* gene exhibited overexpression of OsNHX1 under saline conditions which differentiated it from the wild-type cultivar by its ability to confer higher growth rate and salt tolerance (Fukuda et al. 2004).

Cation transporters (CAXs) are located on the vacuole and belong to a multigene family of ion transporters (Kamiya et al. 2005; Shigaki et al. 2006; Martinoia et al. 2007). During Ca^{2+} stress, the upregulation of *Arabidopsis* *CAX1* and *CAX3* was reported, and most importantly the expression of *CAX3* was upregulated and enhanced during Na^+ stress as observed in the studies with yeasts (Hirschi 1999; Shigaki and Hirschi 2000). *CAX1* and *CAX3* showed differential regulation of H^+ pumps that can affect H^+ coupled ion transport and also helped in the regulation of cellular pH. On the basis of amino acid sequences, CAX family is divided into two groups: Type IA includes *CAX1*, *CAX3* and *CAX4*, whereas Type IB includes *CAX2*, *CAX5* and *CAX6* (Manohar et al. 2011).

Apart from the ion transporters, there are proton pumps that can play an important part in conferring salinity stress tolerance. There are three types of proton pumps such as P-type ATPase, vacuolar H^+ -pyrophosphatase (V- H^+ -PPase) and vacuolar H^+ -ATPase that produces electrochemical gradients throughout the plasma membrane. The P-type ATPase pumps out the cytoplasmic H^+ into extracellular space while a pH gradient is maintained between cytoplasm and vacuole by the acidification of lumen through the V- H^+ -PPase and the vacuolar H^+ -ATPase (Sze et al. 1999).

3 Cereal Crops and Their Responses to Salinity

Plants attempt a large number of physiological and biochemical strategies to improve their salt tolerance. According to Roy and Chakraborty (2014), salt-tolerance strategies include ion exclusion, osmotic tolerance and tissue tolerance.

When exposed to saline soils, plants first experience the osmotic stress which affects plant growth. After that Na^+ accumulation causes ion toxicity which upon reaching threshold level negatively impacts ion homeostasis. Plants generally tolerate salinity through osmotic balance, ionic homeostasis or tissue tolerance (Hasanuzzaman et al. 2015; Anumalla et al. 2016). On the basis of salt sensitivity, plants can be divided into two groups: glycophytes, the salt-susceptible plants, and halophytes which tolerate more salinity and can survive in high salt concentration (Tuteja et al. 2011). Most of the cereal crops are glycophytes and are highly affected by soil salinity. Various genotypes of crop plants, however, show varying degrees of growth responses to salinity (Eynard et al. 2005). According to Munns and Tester (2008), plant growth can be affected by salinity in two phases: first is the osmotic phase where the growth of young leaves is inhibited, and second is the ionic phase which speeds up the senescence of leaves. Salinity inhibits shoot elongation by inducing stomatal closure which in turn increases the temperature of leaves (Rajendran et al. 2009; Sirault et al. 2009). The basic mechanism of the ion transporters in cereal crops under salinity stress is illustrated in Fig. 8.1.

In rice, salinity shows a negative effect on yield components and slows down the heading (Grattan et al. 2002). Salinity can interfere with the germination of the seed, seedling growth, shoot growth, dry and fresh weight of shoot, size of the leaf, numbers of tillers per plant, number of spikelet and productivity (Lauchli and Grattan 2007; Moradi and Ismail 2007; Roychowdhury et al. 2013; Gupta and Huang 2014). At the flowering stage, the pollen viability can be reduced by salt stress, thus affecting the grain yield (Singh et al. 2004). Chinnusamy et al. (2005) reported that salt tolerance is controlled by multiple genes and known as a complex quantitative trait. Rice is a salt-susceptible cereal plant, mainly at the young stage (Lutts et al. 1995), and also at the mature stage, the productivity is restricted by salinity (Todaka et al. 2012). Maize is also a salt-sensitive crop and exhibits a strong inhibition in shoot growth in the first phase of salt stress (Pitann et al. 2009; Wakeel et al. 2011). According to Omoto et al. (2012), assimilation of carbon in maize is very sensitive during salinity stress. The decrease in photosynthetic pigment and stomatal conductance and impaired activities of photosynthetic enzymes are some key factors which hamper the carbon fixation capacity of maize in the saline environment (Kaya et al. 2010; Qu et al. 2012). In maize, during the reproductive phase, salinity causes a decrease in grain weight and numbers, resulting in an overall reduction in grain yield (Kaya et al. 2013). Under high salt concentration, wheat plant shows a wide range of physiological responses such as decreased water potential in leaf, loss in turgor pressure, stomatal closure, an increase of oxidative stress and production of toxic metabolites (Kingsbury and Epstein 1984; Taiz et al. 2015). Salt stress also declined the content of chlorophyll and carotenoid pigments (Ali et al. 2008) and enhances the formation of ROS (Wahid et al. 2007). It was also reported by Kong et al. (2001) and Sairam et al. (2002) that the proline, soluble sugars, glycine-betaine and abscisic acid content increased during salt stress. Barley is the most tolerant among the cereal crops under salinity stress, but its growth and yield is also affected when it is exposed to a higher level of salt concentrations. Comparing the different genotypes of barley under salt stress indicated that salt

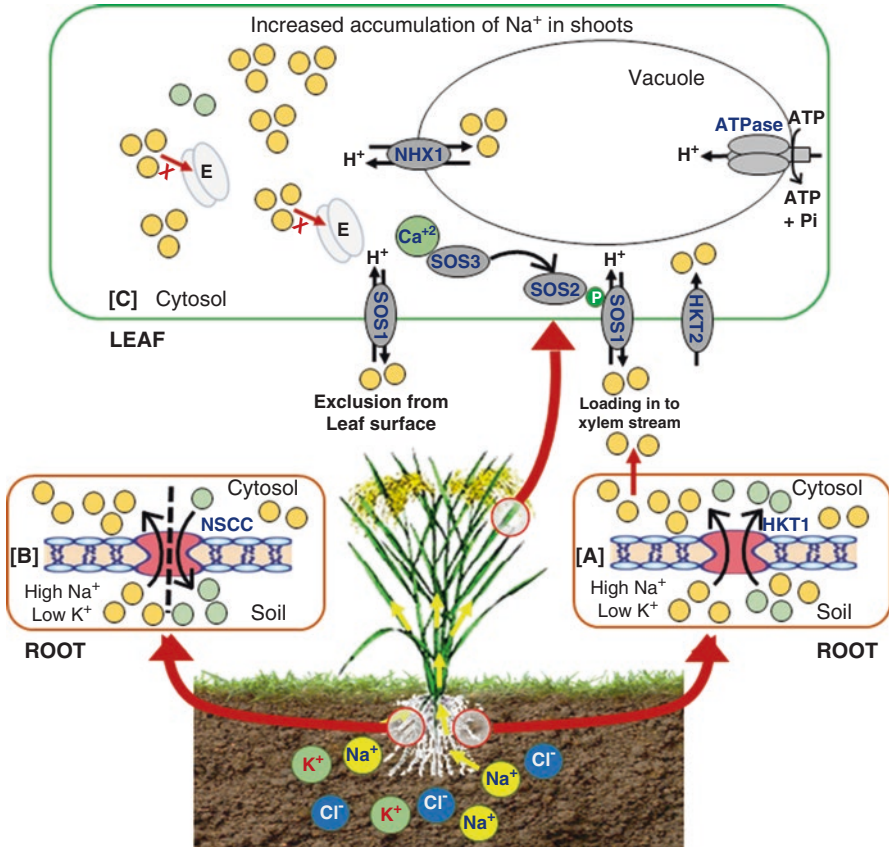


Fig. 8.1 Illustration of salinity stress responses in a typical cereal plant. The role of few ion transporters which are either upregulated or downregulated under salinity stress is shown. Owing to the susceptibility of cereals to salinity, most of the ion transporters depicted are expected to be downregulated. [A] NSCCs (nonspecific cation channels) are expected to increase the uptake of Na^+ ions through roots. [B] Also $HKT1$ (high-affinity K^+ transporters) due to high concentration of Na^+ in soil functions in Na^+ uptake rather than K^+ uptake. [C] In the leaves, SOS pathway involving $SOS3$, $SOS2$ and $SOS1$ (plasma membrane transporters) plays an important role in Na^+ ion exclusion. But in cereal crops, due to the absence of salt glands, the exclusion of Na^+ is minimal, whereas the $SOS1$ functions in recirculating the excess Na^+ ion back into the conducting tissues. As a whole Na^+ ion concentration in plant tissues increases at a high rate inhibiting the normal metabolism. Also the vacuolar proton antiporters ($NHX1$) which are dependent on $ATPases$ to function are also downregulated under salt stress; therefore the loading of excess Na^+ ions into the vacuoles is also not possible

tolerance in barley is determined by the abscisic acid pathway (Kamboj et al. 2015). Bakht et al. (2007) observed that the reduction in shoot length of barley and oats was maximum at higher concentration of $NaCl$ (150 mM). Higher level of salt stress increased ion concentration in rooting medium which resulted in the decrease of

water potential which in turn was responsible for the shortening of shoot length (Munns et al. 2002).

4 Salinity-Induced Transporters from Wild Relatives of Cereals

The native grasses growing in the coastal area face environmental conditions much different from the plants growing inland. Though there are many plants which can tolerate salt stress up to a threshold level, salt-tolerant grasses specifically are different in their distinct morphology and leaf structure allowing them to exclude excess salt from the interior. Vetiver grass (*Vetiveria zizanioides* L.) which is a salt-tolerant perennial grass found mostly in tropical and subtropical areas is different from its close relatives in having strong and extensive root system. The root system specifically provides a superior advantage to the plant in adapting and overcoming a wide range of stresses like flood, drought, high temperatures, acidity and salinity (Truong et al. 2002; Zhou and Yu 2009; Ghotbizadeh and Sepaskhah 2015). The wild vetiver grass has a high salinity threshold of about 100 mM NaCl proving its ability to tolerate high salt stress which is achieved by the plant's ability to maintain an optimum K^+/Na^+ ratio in its leaves (Liu et al. 2016). It has been observed in *Porteresia coarctata* - a wild rice variety, which is a highly salt-resistant species growing in the coastal and sub-coastal regions of India, ameliorates Na^+ toxicity by the unicellular salt hairs present on the adaxial surface of leaves (Flowers et al. 1990; Ganie et al. 2014). There is a C4 perennial halophytic grass *Aeluropus litoralis* that grows in salty areas without any toxicity symptoms owing to their ability to adjust the osmolarity of cytoplasm to match the osmolarity of sea water (Touchette 2007; Zouari et al. 2007). Also, most of the other grasses like *Sporobolus*, *Zoysia* and *Cynodon* secrete Na^+ through salt gland (Marcum 1999). Greater retention of K^+ in shoots is observed in *Puccinellia* and *Thinopyrum* by maintaining a negative membrane potential in the root cell (Teakle et al. 2013). A list of salt-tolerant grasses though not exhaustive is provided in Table 8.1, depending upon their ability to grow in high salt concentrations and presence of salt-tolerant attributes specially the salt glands.

Among the multimodal strategies of salinity tolerance, management of ionic balance inside the cell seems to be of prime importance. The ion homeostasis is achieved due to the presence of several transporters in the plasma membrane and vacuolar membrane in the shoots and roots of the plants. Transcriptomic analysis in the halophytic turfgrass *Sporobolus virginicus* has revealed that several ion transporters like high-affinity potassium transporter (HKT), ABC transporters (for Cl^- transport) and H^+ -ATPase were upregulated in both the shoots and roots of the plant under salinity stress (Yamamoto et al. 2015). This indicated efficient machinery of the ion transporters in loading the excess ions into the vacuoles for maintaining an optimum concentration of ions in the cytosol. Class II HKTs which are known to

Table 8.1 List of wild grasses that could be a source of ion transporter genes for cereal crop improvement

Name of grasses species	Family	Subfamily	Attributes
<i>Aegilops triuncialis</i> L.	Poaceae	Pooideae	Presence of salt gland, mainly distributed in coastal or sub-coastal areas
<i>Aeluropus</i> spp. (<i>A. lagopoides</i> (L.) Thwaites; <i>A. littoralis</i> (Gouan) Parl.)	Poaceae	Panicoideae	Salt secreted through salt gland; increase of osmolyte like proline, soluble sugars and amino acid; habitat includes coastal, desert
<i>Agrostis</i> spp. (<i>A. pallens</i> Trin.; <i>A. stolonifera</i> L.)	Poaceae	Pooideae	Increase in concentration of proline, asparagines, glutamine, serine and glycine-betaine in response to salinity; found in seashore, open meadows, grasslands, coastal strand, woodland or forest
<i>Buchloe dactyloides</i> (Nutt.) Engelm	Poaceae	Chloridoideae	Salt gland present; a greater sodium (Na ⁺) concentration was found in the root tissue than in the shoot tissue; habitat coastal
<i>Brachiaria mutica</i> (Forssk.) Stapf	Poaceae	Panicoideae	Mainly distributed in coastal areas
<i>Cenchrus pennisetiformis</i> Steud.	Poaceae	Panicoideae	Maintain a low Na ⁺ /Ca ⁺ ratio; habitat desert and grassland
<i>Chloris</i> spp. (<i>C. virgata</i> Sw.; <i>C. gayana</i> Kunth)	Poaceae	Chloridoideae	Salt gland present to secrete Na ⁺ and K ⁺ ; found in coastal, desert and grassland area
<i>Cynodon dactylon</i> (L.) Pers.	Poaceae	Chloridoideae	Presence of salt gland, mostly glycophytic with occasional distribution in sub-coastal areas, also found in desert, grassland and forest
<i>Dactyloctenium aegyptium</i> (L.) Wild	Poaceae	Chloridoideae	Presence of salt gland; found in coastal, desert and natural grassland area
<i>Desmostachya bipinnata</i> (L.) Stapf	Poaceae	Panicoideae	Distributed in coastal, deserts, wetlands and grassland
<i>Digitaria ciliaris</i> (Retz.) Koeler	Poaceae	Panicoideae	Distributed in coastal, wetland, grassland, also abundant in roadside and wasteland
<i>Distichlis</i> spp. (<i>D. palmeri</i> (Vasey) Fassett ex I.M.Johnst.; <i>D. spicata</i> (L.) Greene)	Poaceae	Chloridoideae	Excreting salt via salt glands; found along seashore, inland and desert
<i>Eragrostis tef</i> (Zucc.) Trotter	Poaceae	Chloridoideae	Found in inland swamps
<i>Halopyrum mucronatum</i> (L.) Stapf	Poaceae	Panicoideae	Found in coastal regions
<i>Holcus lanatus</i> L.	Poaceae	Pooideae	Found in inland and sea cliff
<i>Imperata cylindrica</i>	Poaceae	Panicoideae	Presence of salt gland, invasive species with wide distribution from inland to coastal areas

(continued)

Table 8.1 (continued)

Name of grasses species	Family	Subfamily	Attributes
<i>Leptochloa fusca</i> (L.) Kunth	Poaceae	Chloridoideae	Salt gland is present; accumulate greater concentration of Na ⁺ and Cl ⁻ in shoot rather than root; habitat coastal
<i>Lolium perenne</i> L.	Poaceae	Pooideae	Found in freshwater wetlands and coastal beaches
<i>Panicum</i> spp. (<i>P. repens</i> L.; <i>P. turgidum</i> Forssk.; <i>P. virgatum</i> L.)	Poaceae	Panicoideae	Maintain low concentration of both Na ⁺ and Cl ⁻ in shoot and show Na ⁺ sequestration in root; <i>P. repens</i> found in wetlands and coastal areas; <i>P. turgidum</i> found in desert; <i>P. virgatum</i> found in plateau
<i>Paspalum</i> spp. (<i>P. distichum</i> L.; <i>P. vaginatum</i> L.)	Poaceae	Panicoideae	Accumulation of osmolytes; abundant in seashore
<i>Pennisetum</i> spp. (<i>P. divisum</i> (Forssk.ex J.F.Gmel.) Henrard; <i>P. glaucum</i> (L.) R.Br.)	Poaceae	Panicoideae	Found in coastal or large river biome
<i>Porteresia coarctata</i> (Roxb.) Tateoka	Poaceae	Oryzoideae	Presence of salt gland and found in coastal area
<i>Puccinellia</i> spp. (<i>P. distans</i> (Jacq.) Parl.; <i>P. tenuiflora</i> (Griseb.) Scribn. & Merr.)	Poaceae	Pooideae	Maintain low Na ⁺ in shoot; habitat grassland or river valley
<i>Spartina alterniflora</i> Loisel.	Poaceae	Chloridoideae	Tolerate salt stress by osmotic adjustment; dominant in saline marsh and coastal regions
<i>Sporobolus</i> spp. (<i>S. airoides</i> (Torr.) Torr.; <i>S. heterolepis</i> (Gray.) A. Gray)	Poaceae	Chloridoideae	Salt gland is present; found near the coast, foothills and desert mountains
<i>Uniola paniculata</i> L.	Poaceae	Chloridoideae	Found in coastal area
<i>Zizania aquatica</i> L.	Poaceae	Oryzoideae	Distribute from inland to coastal areas
<i>Zoysia</i> spp. (<i>Z. matrella</i> (L.) Merr.; <i>Z. tenuifolia</i> Thiele)	Poaceae	Chloridoideae	Salt glands clustered into groups of two or three; found in coastal dunes, riverbanks and grasslands

cotransport Na⁺-K⁺ in plants have been elucidated from *Sporobolus virginicus* which are known to maintain ion homeostasis in low K⁺ saline environments (Tada et al. 2014). The two transporters named as SvHKT2;1 and SvHKT2;2 were shown to be upregulated by high NaCl concentrations and low K⁺ ion, respectively, thereby regulating ion homeostasis by both outward and inward movements of K⁺ and Na⁺ ions. Similarly, transcriptomic analysis of the smooth cord grass – *Spartina alterniflora* has revealed the importance of several transporter proteins like K⁺ transporters, H⁺ transporters and Na⁺/H⁺ which played a crucial role in the ion homeostasis and adaptation of this grass in the saline environment (Bedre et al. 2016).

Wang et al. (2005) investigated the K^+ selectivity over Na^+ ion in *Puccinellia tenuiflora* in comparison to wheat and found that the accumulation of K^+ ion in the former was up to 24% higher than the latter under different NaCl treatments. This revealed the presence of high-affinity K^+ transporters in *Puccinellia tenuiflora* that was induced under NaCl stress, thereby increasing the uptake and accumulation of K^+ ion in the shoots. The gene *PtAKT1* was found to encode for these channel proteins that maintain a highly selective absorption capacity for K^+ ion under high salt stress, which was also confirmed by the presence of a high number of *PtAKT1* transcripts in roots of plants subjected to a NaCl concentration greater than 150 mM (Wang et al. 2015). A vacuolar antiporter *LfNHX1* from *Leptochloa fusca* – a halophytic forage grass was shown to be upregulated in response to different levels of salinity which played an important role in the salt tolerance of the grass (Panahi et al. 2013). Real-time PCR analysis of the *LfNHX1* gene from the plant treated with 200 and 500 mM NaCl revealed the enhancement in expression of this gene by 4–8 times in comparison to the control plants. In *Aeluropus littoralis* upregulation of ion transporter genes like *SOS1* (encoding plasma membrane antiporters), *NHX1* (encoding vacuolar transporters) and *VHA* (encoding proton pumps) located in the shoots and roots accounted for increased tolerance at high NaCl concentrations (>200 mM) by regulating the cytosolic Na^+ ion threshold (Moshaei et al. 2014). Similarly in *Aeluropus lagopoides*, differential expression of ion transporter genes, viz. *SOS1*, tonoplast *NHX1*, *HKT* and *V-ATPases*, in shoots and roots of the plants subjected to high NaCl accounted for ion homeostasis which was pivotal in conferring salinity tolerance (Sanadhya et al. 2015a, b). The expression level study of the plasma membrane (*CdSOS1*) and vacuolar (*CdNHX*) transporters from *Cynodon dactylon* and its counterparts in rice revealed the role of these transporters in salt tolerance of the former (Roy and Chakraborty 2018). *CdSOS1* expression was found to increase up to 2.5 and 5 fold in plants exposed to 100 and 200 mM NaCl concentrations, respectively. On the other hand, *CdNHX* expression increased up to 1.5 and 2 fold. In comparison, *SOS1* and *NHX* expressions in rice plants were not upregulated under NaCl treatments. The list of ion transporters that have been characterized by different wild grasses has been summarized in Table 8.2.

5 Transgenic Approaches with Wild Ion Transporter Genes

During salinity stress plant growth is positively induced by the ion transporter proteins, and thus the identification of these proteins and their related gene is essential (Maathuis 2007). The function of salt-tolerant genes and proteins can be monitored by evaluating the salt uptake at the root level, distribution pattern and the cellular influx of Na^+ and K^+ ions, long-distance transport and compartmentation at cellular as well as tissue level (Flowers and Colmer 2008). There are some useful approaches to improve salt tolerance of plants for introduction and propagation under saline conditions such as genotype screening, the introduction of salt tolerance gene and conventional breeding methods. As conventional breeding takes a long time and can

Table 8.2 List of ion transporters from wild relatives and their mechanism of action

Ion transporters	Generic type	Source species	Mechanism of action	Reference
High-affinity potassium transporters	HKT1	<i>Puccinellia tenuiflora</i> , <i>Phragmites australis</i> , <i>Aegilops cylindrica</i>	Transports only Na ⁺ , recirculates Na ⁺ from shoot to root	Zhang et al. (2017); Takahashi et al. (2007), Arabbeigi et al. (2018)
	HKT2	<i>Aeluropus lagopoides</i>	Transports both Na ⁺ and K ⁺	Sanadhya et al. (2015a, b)
Salt overly sensitive (SOS)	SOS1	<i>Puccinellia tenuiflora</i> , <i>Cynodon dactylon</i> , <i>Leptochloa fusca</i> , <i>Aegilops cylindrica</i>	Na ⁺ /H ⁺ antiporter; efflux Na ⁺ from the cytosol to the apoplast, expressed in root parenchyma and involve in Na ⁺ loading into the xylem sap during moderate salt stress	Zhang et al. (2017); Roy and Chakraborty (2018); Taherinia et al. (2015); Arabbeigi et al. (2018)
Vacuolar antiporters (NHXs)	NHX1	<i>Puccinellia tenuiflora</i> , <i>Cynodon dactylon</i> , <i>Aeluropus lagopoides</i> , <i>Leptochloa fusca</i> , <i>Panicum virgatum</i> , <i>Lolium perenne</i> , <i>Aegilops cylindrica</i>	Involve in Na ⁺ sequestration in vacuole and maintain K ⁺ homeostasis	Zhang et al. (2017), Roy and Chakraborty (2018), Sanadhya et al. 2015a, b, Adabnejad et al. (2015), Huang et al. (2018), Tang et al. (2013), Arabbeigi et al. (2018)
H ⁺ pumps	V-H ⁺ -PPase	<i>Lolium temulentum</i>	H ⁺ transport, increase acidity in vacuole	Baldwin and Dombrowski (2006)
	Vacuolar H ⁺ -ATPase	<i>Spartina alterniflora</i> , <i>Aeluropus lagopoides</i> , <i>Lolium temulentum</i>	Involved in H ⁺ transport to vacuole and increase acidity	Baisakh et al. (2012); Sanadhya et al. (2015a, b), Baldwin and Dombrowski (2006)
	Plasma membrane H ⁺ -ATPase	<i>Aeluropus littoralis</i> , <i>Spartina patens</i> , <i>Zostera marina</i> , <i>Lolium temulentum</i>	It provides the driving force for Na ⁺ ion exclusion	Olfatmiri et al. (2014), Wu and Seliskar (1998), Muramatsu et al. (2002), Baldwin and Dombrowski (2006)

reduce plant vigour, the transgenic approach seems to be the most effective and appropriate technique for the development of salt-tolerant cultivars. Many workers have focused on the ion transporter genes as it regulates the Na⁺ inclusion and compartmentalization, plays an important role in the maintenance of cellular toxicity and helps in improving salinity tolerance. Therefore, screening the ion transporter genes in the germplasm of the cereal crops and the near and distant relatives of these

plants seems to be of great importance in designing salt-tolerant cultivars of cereal crops.

Overexpression of genes encoding vacuolar NHXs in plants treated with salt has shown that these ion transporters could improve the salt tolerance in plants including rice, wheat, tobacco, cotton and tomato up to a certain extent (Apse et al. 1999; Zhang and Blumwald 2001; Zhang et al. 2001; Agarwal et al. 2013). A number of Na^+/H^+ antiporters have been isolated and characterized by wild salt-tolerant grasses which have been used in transgenic experiments to exhibit their potentiality in increasing the salinity tolerance levels of the transgenic plants. It was observed that the *AITMP2* gene isolated from halophytic C4 grass *Aeluropus littoralis*, when expressed in transgenic tobacco, improved tolerance against salinity, osmotic, H_2O_2 , heat and freezing stresses during seed germination and seedling stage by improving ion homeostasis and membrane integrity and by regulating some genes related to salt stress (Ben Romdhane et al. 2018). Another gene *AINHX1* from *A. littoralis* exhibited improved growth in severe saline condition (150 mM NaCl) in transgenic plants which accumulated a higher level of K^+ and a lower level of Na^+ in the leaves than wild-type plants and thus helped in enhancing salt tolerance (Liu et al. 2014). Qiao et al. (2007) isolated a homolog of Na^+/H^+ antiporters, *AeNHX1* from the root of *Agropyron elongatum* which promoted salt tolerance in *Arabidopsis* and *Festuca* by improving osmotic adjustment and photosynthesis in the transgenic plants under salt stress. The *PvNHX1* gene expression in switchgrass (*Panicum virgatum* L.), when compared to the wild type or transgenic control, showed a better growth-related phenotype and also maintained K^+ homeostasis, resulting in more K^+ accumulation (Huang et al. 2017). Baisakh et al. (2012) isolated and introduced the *SaVHAc1* gene from the halophyte grass *Spartina alterniflora* in rice where it is observed that the *SaVHAc1*-expressing plants increased K^+/Na^+ ratio to protect the cytoplasm from toxic Na^+ and maintained higher chlorophyll retention. Zhang et al. (2017) analysed the expression pattern of *PtSOS1*, *PtHKT1;5* and *PtNHX1* from *Puccinellia tenuiflora* under 25 and 150 mM NaCl and observed that the expression of *PtSOS1* in roots significantly increased by 6 fold, while *PtHKT1;5* increased by 1.2-fold under 25 mM NaCl; in contrast the *PtSOS1* increased by 1.4-fold, whereas the *PtHKT1;5* increased by 2.2-fold in roots under 150 mM NaCl; on the other hand, compartmentalization of Na^+ into vacuole was mediated by *PtNHX1*. The details of the transgenic experiments are provided in Table 8.3.

6 Success Story So Far and the Way Ahead

Many transgenic cereal crops have been produced in the past two decades with enhanced salt tolerance, but the success of these plants in agricultural fields is often less talked about. Though a large amount of government and public funding has been allocated for the development of salt-tolerant designer crops, desired success till today has not been achieved. Among the cereal crops, only transgenic maize carrying the *Bt* gene for insect resistance has been known to be commercialized in

Table 8.3 List of transgenic experiments validating the wild genes in improvement of salinity stress tolerance in cereals and other plants

Source grass	Transgene	Characteristic feature	Target organism	Characters induced for salinity tolerance	Reference
<i>Aeluropus lagopoides</i>	<i>AlHKT2;1</i>	Low-affinity K ⁺ transporter	Yeast	Increased the accumulation of K ⁺ ion	Sanadhya et al. (2015a, b)
<i>Aeluropus littoralis</i>	<i>AlNHX1</i>	Na ⁺ /H ⁺ antiporter	<i>Glycine max</i>	The transgenic line exhibited improved growth by lowering the accumulation of Na ⁺ and increasing the concentration of K ⁺ in leaves under saline condition (150 mM NaCl)	Liu et al. (2014)
<i>Agropyron elongatum</i>	<i>AeNHX1</i>	Root-specific vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis, Festuca</i>	Overexpression of <i>AeNHX1</i> promoted salt tolerance improving osmotic adjustment and photosynthesis under salt stress	Qiao et al. (2007)
<i>Leptochloa fusca</i>	<i>LfNHX1</i>	Na ⁺ /H ⁺ antiporter	<i>Nicotiana tabacum</i>	Overexpression of <i>LfNHX1</i> gene conferred salinity tolerance by increasing the germination rate and root growth	Rauf et al. 2014
<i>Panicum virgatum</i>	<i>PvNHX1</i>	Na ⁺ (K ⁺)/H ⁺ antiporter	<i>Panicum virgatum</i>	Transgenic switchgrass overexpressing <i>PvNHX1</i> showed better plant height and leaf development compared to the wild-type plants	Huang et al. (2017)
<i>Pennisetum glaucum</i>	<i>PgNHX1</i>	Na ⁺ /H ⁺ antiporter	<i>Oryza sativa</i>	Overexpression of <i>PgNHX1</i> in transgenic rice plants developed a more extensive root system and promoted setting of flowers and seeds in the presence of 150 mM NaCl	Verma et al. (2007)
<i>Phragmites australis</i>	<i>PhaHAK1</i>	High-affinity K ⁺ transporter	Yeast	Enhanced uptake of K ⁺ content	Takahashi et al. (2007)
	<i>PhaNHA1</i>	Plasma membrane Na ⁺ /H ⁺ antiporter, i.e. SOS1	Yeast	Expression of this gene resulted in a lower cellular Na ⁺ content	Takahashi et al. (2009)

(continued)

Table 8.3 (continued)

Source grass	Transgene	Characteristic feature	Target organism	Characters induced for salinity tolerance	Reference
<i>Puccinellia tenuiflora</i>	<i>PutHKT2</i>	High-affinity K ⁺ transporter	Yeast, <i>Arabidopsis thaliana</i>	In yeast, <i>PutHKT2</i> increased the uptake of K ⁺ in low K ⁺ concentration medium or NaCl. In <i>Arabidopsis</i> , overexpression of this gene helped in maintaining ion homeostasis	Ardie et al. (2009)
	<i>PutAKT1</i>	K ⁺ channel protein	<i>Arabidopsis thaliana</i>	Enhanced K ⁺ under NaCl treatment and lowered the accumulation of Na ⁺ in both shoot and root	Ardie et al. (2010)
<i>Spartina alterniflora</i>	<i>SaVHAc1</i>	Vacuolar H ⁺ -ATPase subunit c1	<i>Oryza sativa</i>	Establishment of ion homeostasis by increasing K ⁺ /Na ⁺ ratio and other cations to protect the plants from toxic Na ⁺ . Higher chlorophyll retention than the wild-type plants	Baisakh et al. (2012)

many countries like the USA, Brazil, China, etc. (James 2016). This presents a gloomy picture at present when none of the cereal crops with salt-tolerant genes are in agricultural fields. This is mainly due to the failure in performance of these transgenics in field trials when compared to the laboratory results.

Molecular breeding for imparting salt tolerance in the crop germplasm could also prove to be a significantly viable option. One of the major achievements in imparting salt tolerance has been through the introgression of *saltol* quantitative trait locus (QTL), which is present in the chromosome 1 of rice and is derived from the near-isogenic lines of the salt-tolerant cultivar of rice ‘Pokkali’ (Linh et al. 2012). The genetic analysis of the *saltol* region was characterized to be containing shoot K⁺ content 1 (*SKC1*), which was eventually cloned to be identified as the gene *OsHKT1;5* which encodes for a Na⁺ transporter regulating K⁺ homeostasis (Ren et al. 2005). Recently the marker-assisted transfer of this *saltol* QTL into the aromatic rice Pusa Basmati 1 (PB1) has conferred enhanced tolerance to the cultivar at seedling stage (Singh et al. 2018). In 2013, Grain Research and Development Corporation (GRDC), Government of Australia, initiated a project for the development of salinity-tolerant wheat and barley in the light of huge losses incurred by the Australian farmers due to soil salinity (Roy et al. 2013). This initiative was started to locate the genes responsible for shoot Na⁺ exclusion and Cl⁻ accumulation for enhancing tissue tolerance to salinity and to provide molecular markers to the breeders for developing salt-tolerant cultivars. Similar target-oriented initiatives could

lead to the development of salt-tolerant cereal crops in the near future. One of the major objectives of marker-assisted breeding has been the identification of QTLs related to ion accumulation and exclusion. In this context, at least 14 QTLs from rice and 30 QTLs from barley have been reported to be involved in the regulation of ion movement (Ashraf and Foolad 2012). Some of these QTLs are *Nax1* for Na⁺ exclusion, *SKC1/OsKKT8* for K⁺/Na⁺ homeostasis, *Qkr1* for root K⁺ uptake and so on.

Therefore, it could be clearly seen that the urge for the search of novel genes and QTLs from near and distant relatives of crop plants has increased quite significantly. The future of cereal crop improvement thus undoubtedly lies in developing a good gene pool of ion transporter genes that can significantly enhance the tolerance ability of the cereal crops when introgressed into the crop genome.

7 Conclusions

Though the current status of salt-tolerant cereal crops presents a shoddy picture, however, the quest for the development of truly salt-tolerant cereal crops is highly desirable keeping in mind the challenges to enhance the crop productivity and to feed the ever-increasing world population. The complexity of salinity responses in the plants has made the picture even worse, and it has also been realized that the transfer of a single gene is not sufficient enough to make the crop plants salt-tolerant in the natural environment. However, there has been a continuous attempt to develop salt-tolerant varieties of cereal crops, and many of the successes in the in vitro conditions have the potentiality to be transformed at the larger scale. The development of modern biological tools has made the scientific community more equipped than ever, and it is high time to use the knowledge gathered during the past few decades to design the cereal crops to sustain their growth and productivity in saline environments. In this context, the ion transporter genes from the wild grasses which are near and distant relatives of cereal crops are likely to play a significant role in the near future for the development of salt-tolerant cereal crops.

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