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REVIEW ARTICLE

Adaptation of plants to salt stress: the role of the ion transporters

Paheli Malakar[1] · **Debasis Chattopadhyay**[1]

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Abstract

Adaptation to high salinity is achieved by cellular ion homeostasis which involves regulation of toxic sodium ion (Na^+) and Chloride ion (Cl^-) uptake, preventing the transport of these ions to the aerial parts of the plants and vacuolar sequestration of these toxic ions. Ion transporters have long been known to play roles in maintaining ion homeostasis. Na^+ enters the cell through various voltage dependent selective and non-selective ion channels. High Na^+ concentration in the plasma membrane is balanced either by uptake of potassium ion (K^+) by various potassium importing channels, by salt exclusion mechanism or by sequestration of Na^+ in the vacuoles. Therefore, the role of high-affinity potassium transporter, the salt overly sensitive pathway, the most well-defined Na^+ exclusion pathway that exports Na^+ from cell into xylem and tonoplast localized cation transporters that compartmentalizes Na^+ in vacuoles need to be studied in detail and applied to make the plant adaptable to saline soil. Knowledge on the regulation of expression of these transporters by the hormones, microRNAs and other non-coding RNAs can be utilized to manipulate the ion transport. Here, we reviewed paradigm of the ion transporters in salt stress signalling pathways from the recent and past studies aiding transformation of basic knowledge into biotechnological applications to generate engineered salt stress tolerant crops.

Keywords Salt stress · Ion transporters · Ion homeostasis · SOS pathway

Introduction

As a consequence of global climate change and irrigational malpractices, one of the environmental constraints in agriculture is soil salinity, which reduces crop yield. According to the FAO (Food and Agriculture organization) study, saline soil is defined as soil having electrical conductivity of 4 dS m^{-1} or higher in the saturation extract (Munns 2005). High salinity affects about 20% of the world's agricultural land and half of irrigated lands (Pitman and Läuchli 2002). Plants or crops are classified into two groups on the basis of the acclimatization of salt stress, i.e., glycophytes which are salt sensitive and halophytes, called as salt tolerant.

Two major salt stress induced effects are osmotic stress and ionic stress (Munns et al. 2020; Van Zelm et al. 2020). Osmotic stress occurs due to reduced level of water potential in plants (Hasegawa et al. 2000b). Ionic stress occurs when toxic ions have a detrimental effect on plants and imbalance of homeostasis of ions causing disruption of uptake of other ions. These two stresses result in oxidative stress in plants, i.e., generation of ROS (hydroxyl radicle, hydrogen peroxide, superoxide anions) (Shen et al. 1997; Tsugane et al. 1999). High ROS concentration can damage carbohydrate, protein, lipid and DNA in plant cells. Upon generation of ROS, compatible osmolytes like mannitol, proline, sorbitol, glycine betaine etc. are accumulated in plant cells to protect the plants from the adverse effect of ROS. Under salt stress osmolytes were produced to cope up with the stress by scavenging ROS, maintenance of cell turgor and helps in sequestration of Na^+ from cytosol to vacuole (Ismail and Horie 2017). Along with osmolytes, antioxidant enzymes are also produced for ROS removal. Enzymatic scavengers include glutathione peroxidase (GPX), catalase (CAT), superoxide dismutase (SOD), glutathione reductase (GR), guaiacol peroxidase (GPOX), ascorbate peroxidase (APX) (Yang and Guo 2018).

Phytohormones also play important role in plant growth and development in salt stress (Ali et al. 2020). ABA has a multifaceted role in stress tolerance in plants by delaying

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✉ Debasis Chattopadhyay
debasis@nipgr.ac.in

[1] National Institute of Plant Genome Research, Aruna Asaf Ali Marg, New Delhi 110067, India

senescence, delaying transpiration and regulating various metabolic processes. ABA promotes Dehydrin gene expression which was shown to confer salt stress tolerance (Martínez-Andújar et al. 2020). Auxin also plays role in plant growth and development. Expression of various auxin-responsive genes like auxin/indoleacetic acid (Aux/IAA), small auxin-up RNA (SAUR) and GH3 family of genes are upregulated to confer salt tolerance (Sun et al. 2018). Brassinosteroids were reported to play essential role in pollen tube growth, germination, photosynthesis and reproduction in salt stress. Expression of Brassinoisteroid insensitive 1-aasociated receptor kinases (BAK1) family of genes is upregulated causing tolerance in plants (Siddiqui et al. 2019).

Salt stress for prolonged period can cause ion toxicity in plants disrupting ion homeostasis maintenance, generating oxidative stress and ultimately suppressing plant growth and development (Basu et al. 2021). Ion exclusion is one of the main approaches to confer salt resistance in plants. Na^+ ion is considered cytotoxic at cytosolic concentrations of 100 mM or above (Serrano et al. 1998). The competition between Na^+ and K^+ ions is the main critical factor determining Na^+ ion toxicity in plants (Maathuis and Amtmann 1999; Zhu 2001). Low Na^+:K^+ in cytosol is achieved by excluding Na^+ from cytosol to apoplast and by vacuole sequestration of Na^+ ions. K^+ is a necessary macronutrient for a number of physiological and biochemical activities in plants (Hasanuzzaman et al. 2018). Plants adopt a very sophisticated ion transport network to cope up with salt stress (Tang et al. 2020). A variety of membrane proteins regulate the absorption and efflux of inorganic ions including Na^+, K^+, Ca^{2+} and so on (Amin et al. 2021). Hence, a thorough understanding of ion homeostasis maintenance under salt stress and the function of related transporters is very much required for making strategies to achieve salt tolerance. The various mechanisms involving salt uptake and exclusion along with ion homeostasis maintenance are discussed in this article. In addition to this, transgenic approaches to modify the expression of ion transporters for improving salt tolerance are also addressed here.

Salt uptake mechanism

Voltage-dependent non-selective cation channels (NSCC)

At high NaCl levels in the soil, this is the main route of Na^+ entry into the roots (TESTER 2003; Horie 2004). There are two types of nonselective cation channels (NSCC), i.e. CNGC (cyclic nucleotide gated channels) and GLR (glutamate activated channel) (Leng et al. 2002; Demidchik et al. 2004). CNGC channels have been found in all domains of life, including plants (Duszyn et al. 2019). These channels belong to non-selective cation channels which uptake Na^+, K^+ and Ca^{2+} (Demidchik and Maathuis 2007; Mian et al. 2011; Hanin et al. 2016). Four amino acid residues (WRTW) in the calmodulin-binding domain of CNGC are responsible for its interaction with calmodulin (Duszyn et al. 2019). Although the downregulation of this channel can avert the toxic Na^+ influx, it can cause harm to the plants as uptake of other beneficial ions can be inhibited. For an example, in rice the downregulation of OsCNGC1 contributes to confer salt stress tolerance whereas in *Arabidopsis*, *Atcngc10* mutant was found to exhibit enhanced growth in salt stress and *Atcngc3* mutant showed increased tolerance after being exposed to high level of NaCl and KCl in comparison with wild type (Jin et al. 2015). There are twenty members of CNGC family in *Arabidopsis* (Talke et al. 2003). Among them many CNGC channels have been characterized in *Arabidopsis* like AtCNGC1, 2, 3, 4 and 10 etc. (Leng et al. 2002; Balagué et al. 2003; Li et al. 2005; Gobert et al. 2006). AtCNGC1 and 4 are equally permeable to Na^+ and K^+ (Leng et al. 2002; Balagué et al. 2003). AtCNGC2 only permits the entry of K^+, not Na^+ entry (Leng et al. 2002). AtCNGC3 is primarily expressed in cortical and epidermal root cell (Gobert et al. 2006). Na^+ uptake in root by non-selective cation channels has been shown to be inhibited by increased level of Ca^{2+} ions.

Potassium channels

Na^+ interferes with K^+ uptake by binding to the transporters present in root plasma membrane. The non-voltage-gated and voltage-gated K + channels are the two types of high-affinity K^+ transporters found in plants (Ragel et al. 2019). In *Arabidopsis*, the Shaker-like family of voltage-gated channels consists of nine members that are all found at the plasma membrane (Ragel et al. 2019). Potassium channel in Arabidopsis thaliana 1 (KAT1) and AKT1 are the most common shaker type inward K^+ channels (Jegla et al. 2018). They have a high selectivity for K^+ than Na^+ and do not have much impact in Na^+ uptake (Amtmann and Sanders 1998). There may be electrophysiological variations regarding the uptake of these two ions. In the halophyte *Suaeda maritima,* low affinity Na^+ uptake pathway is similar to the mechanism of K^+ ion uptake by AKT1 channel (Wang et al. 2007). It has been shown that K^+ channels also have a substantial role in Na^+ influx in the susceptible rice cultivar but not in the tolerant one. Such findings suggest that K^+ channels are one of the pathways for Na^+ entry in root cells.

Carrier type transporters

High affinity K^+ transporters (HKT) mediate the transport of both Na^+ and K^+ ions. The HKT family is K^+ transporter superfamily HKT/Trk/Ktr-type present in microorganisms and plant (Yamaguchi et al. 2013). These transporters either selectively transport Na^+ ions or carries out Na^+ and K^+ symport. Two types of HKT transporters have been discovered in plants. Na^+ selective transport is mediated by Class I HKT transporters while Na^+/K^+ transport is generally mediated by class II HKT transporters (Uozumi et al. 2000; Mäser et al. 2002). It is determined by the presence of highly conserved residue present in the first pore loop forming motif in the polypeptide or the extracellular Na^+ and K^+ concentration (Yao et al. 2010). If the conserved residue is serine (subfamily 1) the transporter prefers higher Na^+/K^+ uptake and if it is glycine HKT has a lower affinity for Na^+/K^+ influx. Monocots have several HKT isoforms, whereas *Arabidopsis* only has one class I HKT member (Ali et al. 2019). Although AtHKT1;1 has been shown to play role in root development increased expression of AtHKT1;1 causes harm to the plants (Julkowska et al. 2017). When *AtHKT1;1* is expressed in yeast strains lacking the Na^+ efflux mechanism, it makes them more sensitive to Na^+ (Locascio et al. 2019).The hypersensitivity of *sos3* mutants is suppressed by mutations in the AtHKT1 gene, indicating that wild type SOS3 and other components of the SOS regulatory pathway can limit AtHKT1 activity as Na^+ uptake transporter.

If the ratio of Na^+/K^+ is high, some members of the HAK/KUP/KT family of high affinity K^+ uptake transporters have been reported to transport Na^+ with low affinity (Pardo and Quintero 2002). In yeast expression studies, K^+ uptake by HAK/KUP/KT (high affinity K^+ uptake) was shown to be competitively inhibited by Na^+ as these two monovalent cations share the common transport pathway (Santa-María et al. 1997; Fu and Luan 1998). Salt stress has been shown to cause significant transcriptional regulation of different isoforms of HAK/KUP/KT (Chao et al. 2005; Walia 2005; Walia et al. 2007). AtHAK5, PhaHAK2 and PhaHAK5 have been reported to be permeable to Na^+ also and their expression is increased by low K^+ and decreased by salt stress (Takahashi et al. 2007a, b; Alemán et al. 2009; Nieves-Cordones et al. 2010; Wang et al. 2015). Reduced expression of HAK was proposed to be one of the key mechanisms to minimise harmful Na^+ absorption by these transporters.

Salt exclusion mechanism

It is essential for plants to have a functional efflux system in order to remove potentially harmful ions from the cytosol, such as Na^+. In salt stress thermodynamically active transport is required for exclusion of Na^+ from the cytosol. The mechanisms of exclusion of Na^+ into the apoplast or vacuole is an energized process which is coupled with H^+-ATPases activity that establishes a H^+ electrochemical potential gradient (Blumwald et al. 2000; Zhu 2001). Early studies showed that pumping capacity of tonoplast antiporters is upregulated after exposure to salt stress. The evidences of presence of Na^+/H^+ antiporters in plasma membrane too suggest the relevance of such systems in salt tolerance in plants (Katz et al. 1986).

Role of SOS (Salt Overly Sensitive) pathway in plasma membrane in maintaining ion homeostasis

The Na^+ exclusion mechanism at the root-soil interface has been well studied after the discovery of SOS pathway and the plasma membrane localized Na^+/H^+ exporter or SOS1 (Qiu et al. 2002; Shi et al. 2002). In *Arabidopsis*, SOS1 facilitates the maintenance of Na^+ homeostasis by exclusion of the ion from root epidermis to rhizosphere. SOS1 is expressed primarily in root epidermal cells, particularly at root tip and xylem parenchyma cells. SOS1 expression has been shown to be regulated by class-I histone deacetylation in salt stress and salt tolerance is improved by suppression of the histone deacetylation mediated process (Sako et al. 2016). Intracellular Ca^{2+} level is increased by sensing the high concentration of Na + ions in cytoplasm. It facilitates the binding of Ca^{2+} ions with SOS3 (myristoylated membrane bound protein), a E-loop-helix-F (EF- hand) calcium binding protein which is also known as Calcineurin B-like protein (CBL). SOS3 protein then interacts with the SOS2 protein. Interaction between SOS3 and SOS2 results in releasing regulatory domain of SOS2 from its catalytic site thereby activating SOS2 (Halfter 2000; Lin et al. 2009). In the C-terminal regulatory domain of SOS2 protein, also known as NAF domain, there is a FISL motif in which A, F, I, S, L and F residues are conserved. The motif is a 21-amino-acid sequence that acts as an interaction site for the SOS3 protein when it is coupled to calcium ions (Guo 2001; Chaves-Sanjuan et al. 2014). The SOS2 protein belongs to the serine/threonine kinase of SnRK3 or CIPK (CBL-interacting protein kinase) family. SOS3-SOS2 complex is then transported to plasma membrane and phosphorylates the SOS1 protein, known as Na^+/H^+ antiporter (Shi et al. 2000; Qiu et al. 2002; Lin et al. 2009). SOS2 activates SOS1 by phosphorylating the C terminal autoinhibitory domain of SOS1 at serine 1044 (Quintero et al. 2011). Na + ion efflux from cytoplasm to apoplast by SOS1 protein is governed by gradient of proton generated by plasma membrane associated H^+-ATPase. Mitogen activated protein kinase (MPK6) also activates SOS1 via phosphatidic acid mediated signalling pathway (Yu et al.

2010). Abscisic acid (ABA) may regulate SOS pathway through SOS2. SOS2 protein binds to ABAINSENSITIVE2 (ABI2) and *abi2* and *abi2* seedlings showed more sensitiveness to salt stress (Ohta et al. 2003).

Arabidopsis thaliana genome encodes twenty six CIPKs as well as ten CBLs (Kolukisaoglu et al. 2004). Multiple CBLs can interact and activate individual CIPKs depending on the cellular conditions (Kim et al. 2000). CBL10 (SCaBP8), like SOS3 (CBL4) can sense the calcium signal in cytosol due to high concentration of Na^+ ions. It also has a role in vacuolar Na^+ partitioning by associating with SOS2 (CIPK24) protein in the vacuole (Kim et al. 2007). CBL4 protein functions primarily in the root whereas CBL10 functions in the shoot (Quan et al. 2007; Zhu 2016). CBL10 has a key function also in vegetative growth and reproduction in salt stress. It functions independently of SOS pathway. CBL10 inhibits the Arabidopsis K^+ transporter AKT1 (Ren et al. 2013). In salt stress, the CIPK24 phosphorylates CBL10 at the C-terminus of this protein to stabilize the localization of SOS2 protein at plasma membrane (Lin et al. 2009; Du et al. 2011). It has been considered that phosphorylation of CBL10 by CIPK24 dissociates CBL10 from the AKT1 channel, thereby, promoting K^+ uptake in the cytosol. Interaction between CIPK24 and CBL10 results in the kinase complex being localized at tonoplast where it regulates Na^+ accumulation in shoot by controlling Na^+/H^+ exchange at the vacuolar membrane. In absence of CBL proteins, CIPK24 has been shown to regulate tonoplast V-ATPase. The annexin AtANN4, a putative Ca^{2+} transporter mediates elevation of Ca^{2+} in response to salt stress, whereas its subsequent phosphorylation by SOS2 repress Ca^{2+} transients, resulting in salt specific Ca^{2+} wave (Ma et al. 2019b). CIPK6 also plays role in salt stress tolerance apart from its function in auxin transport and root growth (Tripathi et al. 2009).

Under salt stress ROS molecules are generated and results in oxidative damage to plant cells (Miller et al. 2010). The expression pattern of ten Respiratory Burst Oxidase homologs (RBOH) genes, i.e., RBOHA-RBOHJ is changed in response to salt stress followed by generation of ROS molecules within a 24-h period of salt stress (Xie et al. 2011). Previous report demonstrated that under salt stress, crosstalk between ROS and Ca^{2+} signals is required in order to distribute Ca^{2+} signals between cells (Evans et al. 2016). Furthermore, AtRbohF has been shown to be phosphorylated by the Ca^{2+} signaling complex CBL1/9-CIPK26 (Drerup et al. 2013).

Orthologs of SOS1 were identified in different crops like rice, durum wheat, bread wheat and tomato and shown to function in exclusion of Na^+ in yeast complementation assay (Martínez-Atienza et al. 2007; Xu et al. 2008; OlÍas et al. 2009; Feki et al. 2011). Expression of OsSOS1 in *Arabidopsis* mutant *atsos1-1* has been shown to complement the salt hypersensitivity phenotype of the mutant (Martínez-Atienza et al. 2007). Furthermore, silencing of SlSOS1 in tomato plants showed salt hypersensitive phenotype (OlÍas et al. 2009). Inhibition of ThSOS1 has been shown to increase Na^+ accumulation in root tip and stele in *Thellungiella salsuginea,* an *Arabidopsis* relative (Oh et al. 2009). These findings indicate that SOS1 mediated Na^+ exclusion mechanism for salt stress tolerance is highly conserved among the plants.

Sodium sequestration in vacuole

Na^+/H^+ exchangers (NHXs), tonoplast localized cation/H^+ antiporters mediate compartmentation of Na^+ in vacuole to counter its accumulation in cytosol. The activity of this protein is governed by the electrochemical gradient of proton generated by H^+-ATPses and H^+-pyrophosphatases which are H^+ translocating enzymes present in vacuole. Previously, NHXs were considered to play role in sequestration of excess cytosolic Na^+ into vacuole for osmotic adjustment under salt stress. Later they were shown to function in vacuolar K^+ influx under low Na^+ concentration with no transport of Na^+. NHX mediated Na^+ transport is only occurred when Na^+ concentration is high. In salt stress excessive Na^+ influx into the cytoplasm is occurred causing membrane depolarization followed by K^+ efflux from cytosol. Two-pore K^+ 1 (TPK1) channel, localized in tonoplast mediates transport of K^+ from vacuole to cytosol to replace cytosolic K^+ that has been lost due to Na^+ influx in excess. In *Arabidopsis*, eight isoforms of NHX have been found till now. Among them AtNHX7 is known as SOS1. AtNHX1-AtNHX4 are localized in the vacuole (Li et al. 2009). NHX5 and NHX6 are located at golgi apparatus, trans-golgi network as well as prevacuolar compartment. Constitutive overexpression of AtNHX1 was shown to improve salt tolerance in yeast, *Arabidopsis*, cotton, tomato, *Brassica napus* and soybean (Zhang and Blumwald 2001; Zhang et al. 2001, 2017b; Chakraborty et al. 2016; Nguyen et al. 2019). Moreover, constitutive overexpression of NHX1 homologs in different plants has been shown to improve salt tolerance in rice, wheat and barley (Zhao et al. 2006). The cation selectivity between Na^+ and K^+ is determined by hydrophilic C-terminus of NHX1 and binding of calmodulin-like protein (Yamaguchi et al. 2003, 2005). The function of AtNHX1 and AtNHX2 is redundant whereas the Na^+/K^+ selectivities of AtNHX3 and 4 are different. (Bassil et al. 2011b, 2019; Barragán et al. 2012). In *nhx1 nhx2* double mutant, significant reduction in both Na^+/ H^+ and K^+/ H^+ activity, decreased ability to retain K^+ in vacuole have been demonstrated. Furthermore, the *nhx1 nhx2* double mutant exhibited severe defects in growth and development in both vegetative and

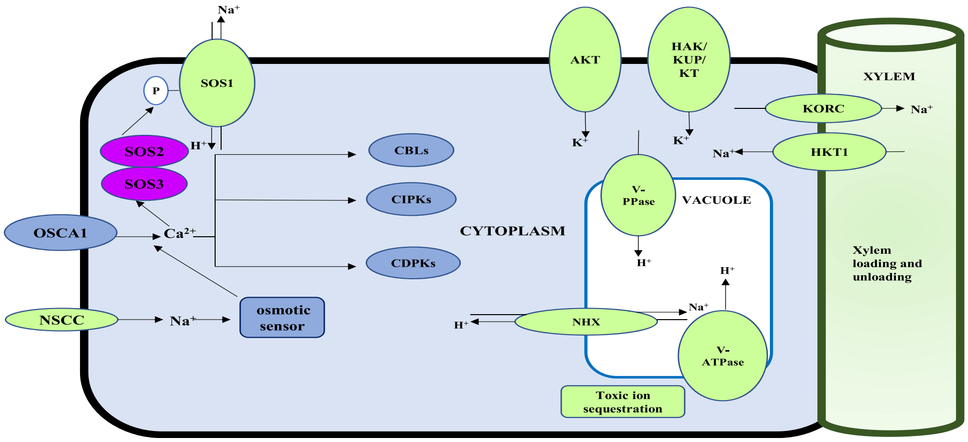

Fig. 1 Schematic overview of ion transport mechanism in salt stress signalling pathway. Na^+ ions enter the cell through NSCCs under salt stress followed by increased cytosolic Ca^{2+} concentration which activates SOS pathway. The proteins involved in SOS pathway are CBL and CIPK. Calcium signalling activates CDPKs also. NHX, V-ATPase and V-PPase are involved in Na^+ sequestration in vacuole. K^+ uptake in root is occurred by mainly AKT and HAK. The candidate proteins for loading Na^+ to the xylem are KORC and retrieval of Na^+ from xylem are occurred by HKT. Abbreviations: nonselective cation channels (NSCCs), SALT OVERLY SENSITIVE (SOS), Calcineurin B-like protein (CBL), CBL-interacting protein kinase (CIPK), Na^+/H^+ exchangers (NHX), vacuolar H^+-ATPase (V-ATPase) and vacuolar H^+-PPase (V-PPase), Inward-rectifying K^+ channel (AKT) and High-affinity K^+ transporter (HAK), Outward-rectifying K^+ channels (KORC), High affinity K^+ transporters (HKT)

reproductive stages. NHX1 and NHX2 were found to be more abundant in leaf guard cells than in leaf epidermis as well as in mesophyll cells, to help K^+ compartmentation in the vacuole for stomata regulation and thereby increasing transpiration rates (Andrés et al. 2014). Altogether, these studies suggest that NHX1 and NHX2 confer salt stress tolerance in plants by increasing K^+ content, enhancing ratio of K^+/ Na^+ and reducing oxidative damage. In *nhx5 nhx6* double mutant, vacuolar trafficking was shown to be disturbed causing severe reduction in plant growth and development and rendering plant hypersensitive to Na^+ (Bassil et al. 2011a). It has been demonstrated that overexpression and knockout of *AtNHX1* significantly and differentially change the expression of salt stress responsive genes. These studies suggest that proteins of NHX family play role in salt stress tolerance.

H^+ pumps, located at plasma membrane and vacuolar membrane create electrochemical gradient thereby providing energy for secondary active transport of other cations (Morsomme and Boutry 2000). H^+-ATPase and H^+-PPase are such H^+ pumps located at the tonoplast (Drozdowicz and Rea 2001; Katschnig et al. 2015; Assaha et al. 2017; Dabbous et al. 2017). Salt stress increases the activity of these two H^+ pumps(Hasegawa et al. 2000a). OVP1 and OVP2 were reported to be known as H^+-PPase proteins located at vacuole in rice (Sakakibara et al. 1996). Overexpression of H^+-PPase AVP1 was shown to improve salt stress tolerance in *Arabidopsis* and increase Na^+ accumulation in vacuole (Gaxiola et al. 2001; Jisheng et al. 2005; Yang et al. 2007). These studies suggest that overexpression of *AVP1* enhances the Na^+/ H^+ activity. TNHX1, a Na^+/H^+ antiporter and TVP1, a vacuolar pyrophosphatase were functionally characterized in wheat (Brini et al. 2005). *TNHX1* or *TVP1* overexpression *Arabidopsis* transgenic lines were found to survive better in comparison with wild type plants under both salt stress and drought stress (Brini et al. 2007). In barley, expression of HVP1, H^+-PPase protein and NHX1, Na^+/H^+ antiporter localized in vacuole was shown to be upregulated in salt stress (Fukuda and Tanaka 2006). In rice it has been discovered that simultaneous expression of *NHX* and *AVP* genes increases salt tolerance more than expression of the genes separately (Zhao et al. 2006). AVP1 interacts with the auxin transporter PIN1, resulting in an increase of auxin transport which causes better survival of plants in salt stress (Li et al. 2005). A schematic overview of the ion transport mechanism has been summarised in the Fig. 1.

Long distance sodium transport regulation

After Na^+ uptake in the root, it is transported into the stele radially and then loaded Na^+ into xylem and moved to the transpirational stream to reach to the shoot. So, controlling Na^+ loading into the xylem is very much important to reduce the transfer and accumulation of Na^+ in shoot. Studies by cryo-scanning electron microscope and X-ray microanalysis revealed that radial Na^+ transport in root is occurred through the cortical cells, pericycle and xylem parenchyma cells where Na^+ concentration is very high in comparison with the other cell layers (Läuchli et al. 2008).

AtHKT1;1 mainly expresses in the vasculature and regulates the distribution of Na^+ ions between root and shoot (Essah 2003; Rus 2004; Sunarpi et al. 2005; Rus et al. 2006; Demidchik and Maathuis 2007; Horie et al.

2009; Yao et al. 2010). OsHKT2;1 was found to restrict radial transport of Na^+ at the cortex region of root preventing Na^+ reaching the xylem (Horie et al. 2007). OsHKT2;1 was also found to localize in the vascular bundle in the shoot where it facilitates Na^+ loading in the phloem for its translocation in root (Golldack et al. 2002; Laurie et al. 2002). Similarly, AtHKT1;1 has been shown to retrieve Na^+ from xylem and sequester in cortex (Plett and Møller 2010). HKT homologs in other plants have been shown to act in stele to retrieve Na^+ from xylem into xylem parenchyma cells. For an instance, OsHKT1;5 in rice has been reported to localize at xylem parenchyma cells retrieving Na^+ from xylem into xylem parenchyma cells (Cotsaftis et al. 2012).

Both HKT and SOS1 are localized in the xylem region where Na^+ loading into the xylem is occurred (Shi et al. 2000, 2002; Sunarpi et al. 2005). In high saline condition SOS1 mediates Na^+ retrieval from xylem whereas in mild salt stress it causes Na^+ loading into xylem (Shi et al. 2002; Yue et al. 2012). In contrast, HKT1 mediates retrieval of Na^+ from xylem into xylem parenchyma cells. After loading of Na^+ into the xylem it is transported to leaf via transpirational stream. One of the important salt stress tolerance mechanisms in plants is Na^+ exclusion from shoot. As most of the metabolic processes occur in the leaf blade it must be safeguarded from Na^+ damage. So, after reaching of Na^+ in the leaf it must be retranslocated to the basal part of the plant. According to the phloem recirculation model, AtHKT1 plays role in Na^+ recirculation from shoot to root. Na^+ is initially loaded into the shoot phloem cells and then transported to root by downstream phloem cells thereby reducing over accumulation of Na^+ ions in shoot (Berthomieu et al. 2003). Another pathway of Na^+ transport is retrieval of this ion from xylem sap to xylem parenchyma cells mediated by AtHKT1;1 preventing the transport of Na^+ into leaves (Berthomieu et al. 2003; Sunarpi et al. 2005; James et al. 2006; Davenport et al. 2007). These two mechanisms of Na^+ transport may be functionally coupled for the basipetal translocation of Na^+ ions in plants inhibiting Na^+ transport from root to shoot, thereby enhancing salt tolerance (Pardo 2010). In *Arabidopsis*, a loss-of-function mutation in *HKT1;1* causes Na^+ ion accumulation in leaves but not in roots with a very negligible effect of net Na^+ ion uptake in plants (Berthomieu et al. 2003; Rus 2004; Sunarpi et al. 2005).

Recent studies in wheat revealed that *Nax1* and *Nax2* loci which code for HKT1;4 and HKT1;5 respectively control in retrieval of Na^+ from xylem into xylem parenchyma cells and regulate SOS1 activity in Na^+ loading into xylem thereby reducing Na^+ transport from root to shoot. *Nax1* and *Nax2* null mutants showed reduced expression of *SOS1* and Na^+ is retrieved back to the stele from xylem thereby increasing Na^+ accumulation in root (Zhu et al. 2016). Recent studies revealed that OsHKT1;4 localizes at stem to mediate Na^+ exclusion thereby improving salt tolerance (Suzuki et al. 2016). As documented in maize, pepper and barley, after reaching to the leaf tissues Na^+ is translocated into the phloem and then it goes back to root to decrease its level in shoots (Ketehouli et al. 2019). EpHKT1;2 of extremophile *Eutrema parvula* was also shown to play role in salt tolerance (Ali et al. 2018).

Members of Cation/H^+ exchangers family (CHX) are also considered to participate in Na^+ and K^+ translocation. This group of transporters primarily exchange cations against proton motive force and controls osmotic conditons (Isayenkov et al. 2020). AtCHX13 and AtCHX17 are K^+ transporters (Cellier et al. 2004; Zhao et al. 2008). In *Arabidopsis*, *AtCHX21* is expressed primarily in root endodermis. Mutation in *AtCHX21* was shown to reduce Na^+ in xylem sap without altering concentration of Na^+ in phloem (Hall et al. 2006). *OsCHX11* expression was found to be higher in root in tolerant genotype in salt stress (Senadheera et al. 2009). The differential expression of *OsCHX11* in the rice varieties was reported to correlate with increased K^+/Na^+ ratio in salt stress tolerant genotype implying role of CHX11 in long distance Na^+ transport.

Potassium homeostasis maintenance

K^+ is the most abundant cation in plant and is a macronutrient. It accounts for upto 10% of dry mass of plant (Véry and Sentenac 2003). There is evidence that the difference in salt stress tolerance mechanism between halophytes and glycophytes is attributed to post translational modification of K^+ transporter (Himabindu et al. 2016). The concentration of cytosolic K^+ is kept constant at around 100 mM. Maintaining a steady level of intracellular K^+ concentration is critical for normal functioning of plant growth and development. Salt stress causes changes in the maintenance of cellular K^+ homeostasis, thereby affecting all of these physiological and metabolic functions. Hence increase in K^+/Na^+ ratio helps plant to achieve normal functioning of cellular metabolism, growth and productivity (Anschütz et al. 2014; Himabindu et al. 2016). Salinity tolerance is determined by the increased K^+ concentration inside the cells (Rubio et al. 2020). In salt stress high K^+/Na^+ ratio can be maintained by root K^+ absorption, K^+ loading in xylem for translocation to shoot and reduction in cytosolic K^+ efflux.

Potassium absorption in root

K^+ is absorbed primarily through two processes at the root-soil contact. The first one is low affinity K^+ uptake (LAT) occurred when the external K^+ concentration in mM range.

Shaker family of K^+ channel, i.e., AKT1 mediates low affinity K^+ uptake. CBL1/9 interacts with CBL-interacting protein kinase 23 (CIPK23), which in turn phosphorylates AKT1 and causes K^+ uptake under low K^+ condition (Xu et al. 2006). Recent findings suggest that CBL1/CIPK23 complex physically interact with AKT1 in the plasma membrane to regulate K^+ transport (Sánchez-Barrena et al. 2020). The second process is high affinity K^+ uptake when external K^+ concentration in µM range. K^+ transporters belonging to KUP/HAK/KT family, such as HAK5 and K^+ Uptake Permease 7 (KUP7) mediate high affinity uptake. A crucial factor in salt stress resistance is maintaining a higher negative potential inside the plasma membrane facilitating K^+ uptake (Pottosin and Dobrovinskaya 2014). Short-term salt stress was shown to cause the negative membrane potential of barley and pea plants to be same but in long-term stress barley maintained a higher negative potential than pea plants making barley more susceptible to salt (Bose et al. 2014). Negative membrane potential is achieved by plasma membrane localized H^+-ATPase activity. The fundamental difference in salt tolerance mechanism between halophytes and glycophytes has been considered to lie in the difference in pump activity which is regulated by phosphorylation of the protein (Himabindu et al. 2016). Pump activity was shown to be higher in halophyte than glycophyte. The members of HAK family mediate K^+ absorption at external concentration below 10 µM (Alemán et al. 2009). When salt stress is combined with low K^+ condition the transporter activity becomes reduced rendering plants very susceptible to salt stress. HAK activity is reduced when Na^+ increases the membrane potential resulting in K^+ efflux by outward rectifier K^+ channel (Pottosin and Dobrovinskaya 2014; Bacha et al. 2015). HAKs are typically K^+/H^+ symporters. Its activity is also dependent on the proton motive force produced by H^+-ATPase (Falhof et al. 2016). K^+ absorption through HAK may be increased by reducing membrane depolarization and increasing H^+-ATPase activity and thereby increasing resistance to low K^+ condition in salt stress. It is still unknown if HAK5 functions in the similar manner under salt stress as demonstrated by AKT1. A single amino acid substitution in certain HAKs, such as AtHAK5 and HvHAK has been demonstrated to increase K^+ absorption and confer resistance to salt stress (Mangano et al. 2008; Alemán et al. 2014).

The hazardous influx of Na^+ into the cytosol along with absence of strong Na^+ efflux mechanism will inhibit K^+ absorption by membrane depolarization (Qi and Spalding 2004). H^+-ATPase is activated by SOS1 to pump out protons, resulting in proton motive force that is utilized to stimulate Na^+ efflux. It has been reported that *sos1* null mutants exhibited decreased K^+ uptake (Horie et al. 2012; Mansour 2014). In comparison with the *SOS1* overexpression lines, plants lacking the SOS1 transporter have been reported to accumulate more Na^+ and had lower K^+ uptake. These findings substantiate the role of SOS pathway in K^+ uptake in salt tolerance.

Class II members of HKTs mediate K^+ absorption in salt stress (Tada and Ohnuma 2020). Only monocots have this type of transporter, implying that monocots have a higher capacity to withstand salt stress than dicots (Plett and Møller 2010). Some class I members are also K^+ selective due to additional amino acid residues SGGG in the selectivity filter that change their specificity from Na^+ to K^+ (Ali et al. 2012). These mutated HKT homologs are mostly found in halophytes, such as ThHKT1;2 in *Thellungiella*, McHKT1 in *Mesenbryanthemum* and, EcHKT1;2 in salt resistant glycophytes *Eucalyptus* (Gierth and Mäser 2007).

Potassium loading in xylem for translocation in shoot

The major route for K^+ to reach to shoot is through the transpirational stream in xylem vessel. In *Arabidopsis* xylem loading of K^+ is mediated by stelar K^+ outward rectifying (SKOR) channel and KUP7 to ensure enough K^+ supply to shoot (Véry and Sentenac 2003; Ahmad and Maathuis 2014; Han et al. 2016; Nieves-Cordones et al. 2016). The voltage sensor of SKOR has been found to have residues that are ROS-sensitive. SKOR mediated K^+ loading in xylem is attributed to change by ROS (Demidchik et al. 2014). When the residue is replaced with another amino acid, SKOR sensitivity to ROS is lost indicating the arrest of K^+ efflux which in turn affects K^+ homeostasis in salt stress. ROS generation is entirely inhibited in *Arabidopsis* mutants atrbohD1/F1 and atrbohD2/F2 under salt stress, displaying decreased K^+ and increased Na^+ levels. This condition can be partially recovered by addition of H_2O_2.

Potassium efflux prevention

Regulation of K^+ efflux is one of the most significant salt stress adaptation mechanisms by maintaining increased K^+/Na^+ ratios. K^+ concentration in cytosol is maintained at around 100 mM under normal conditions but in salt stress the concentration drops rapidly due to exclusion of K^+ from both root and leaf cells by K^+ outward rectifying channel (KORC) (Shabala and Pottosin 2014). To mediate K^+ efflux in guard cells OST1/SnRK2.6 interacts with and phosphorylates particular KAT1 and K^+ Uptake Permease 6 (KUP6) resulting in stomatal closure under salt and osmotic stress (Sato et al. 2009; Osakabe et al. 2013). During salt stress, the Gated Outwardly-Rectifying K^+ Channel (GORK) is shown to be responsible for potassium efflux (Shabala and Cuin 2008). K^+ concentration in leaf mesophyll cells has been found to correlate with salt stress tolerance and has been used as a marker to distinguish between salt-tolerant and salt-sensitive varieties of barley and wheat (Wu et al. 2013, 2015). The ability of root to store K^+ corresponds with salt stress tolerance and it can be considered as a marker in breeding programme of wheat (Cuin et al. 2008). The K^+ homeostasis mechanism is summarised in the Fig. 2.

Role of hormones, microRNAs and long non-coding RNAs in regulating ion transporters

Plant hormones are shown to indirectly control expression or activity of the ion transporters. Abscisic acid (ABA) signal is perceived by PYRABACTIN RESISTANCE/PYRABACTIN RESISTANCE-LIKE (PYR/PYL) (Ma et al. 2009; Park et al. 2009). Binding of PYL to ABA is enhanced by the coreceptors PP2Cs such as ABI1, ABI2, HAB1 and PP2CA. PP2Cs interact with SnRK2 kinases, such as SnRK2.2, SnRK2.3 and SnRK2.6. In absence of ABA, interaction between these two molecules results in the inactivation of kinases by blocking the catalytic domain of SnRK2 kinases and also by dephosphorylation of the activation loop of the kinase (Soon et al. 2012). Catalytic domain of SnRK2 is released from the binding and inhibition of PP2C due to ABA-PYL-PP2C complex formation. Then the kinase phosphorylates and activates the downstream ion transporters such as, SOS1 (Fujii et al. 2009). CIPK23 has been shown to regulate different ion transporters after releasing from its interaction with PP2C (Lan et al. 2011).

MicroRNAs (miRNAs) have been identified to control the expression of ion transporters and their regulatory proteins under salt stress. In chickpea novmiR2 and miR5507 has been predicted to target potassium transporter HAK5 and its regulatory kinase CIPK23, respectively to reduce their expression. Expression of these two miRNAs in chickpea root is upregulated in salt stress and that of their targets is downregulated (Khandal et al. 2017). These studies suggest the role of miRNAs in potassium transport mechanism under salt stress. Auxin response factor (ARF2) has been shown to suppress HAK5 expression by binding to its promoter. Expression of a novel miRNA which targets ARF2 is increased in rice root tissues inoculated with the symbiont *Piriformospora indica*, an endophytic root fungus implying the role of this novel miRNA in potassium uptake mechanism (Kord et al. 2019). It has been shown that in wild type alfalfa and in its mutant strain miR408 which is known to target NHX is differentially expressed under salt stress (Ma et al. 2019a). miR172 which targets CNGC channel has been shown to be upregulated in mutant strain of alfalfa as compared to the wild type (Ma et al. 2019a). Expression of miR2590 which reduces the expression of CHX14/15 has been found to be drastically reduced upon salt treatment (Jiang et al. 2014; Khandal et al. 2017).

Long non-coding RNAs (lncRNAs) play crucial role in regulating gene expression in response to stresses. In the model legume *Medicago truncatula*, 10,785 lncRNA has been identified under phosphate deficiency. Two of those, PDIL2 and PDIL3 was reported to regulate phosphate transport by regulating the transcription of *PHO2*, a ubiquitin conjugating enzyme that target phosphate transporter (Wang et al. 2017). There are a few genome-wide surveys of lncRNA expression under stress conditions and prediction of putative targets including ion transporters (Li et al. 2014; Tian et al. 2016; Zou et al. 2020). In a non-model plant *Pistacia vera* L., the coding targets of the top five salt

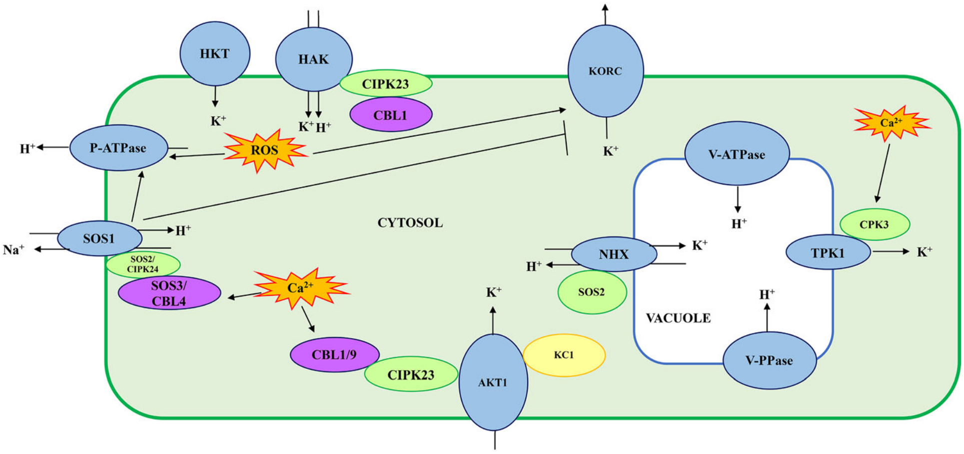

Fig. 2 Diagrammatic representation of potassium homeostasis mechanism during salt stress. Major potassium transporters as an integral part of plasma membrane are AKT1, HAK5, HKT and KORC. The potassium transporters present in tonoplast are NHX and TPK. Abbreviations: Inward-rectifying K^+ channel (AKT1), High-affinity K^+ transporter (HAK5), High affinity K^+ transporters (HKT) and K^+ outward rectifying channel (KORC), Na^+/H^+ exchangers (NHX) and Two-pore K^+ 1 (TPK)

responsive lncRNAs participate in the cation transmembrane transporter, kinase, UDP-glycosyltransferases and ATPase activity, coupled to transmembrane movement of substances (Jannesar et al. 2020).

Future perspectives

Generation of transgenic plants

As the basic mechanism of plant responses in salt stress is similar between the model plant *Arabidopsis* and other crop plants, identification of orthologs of ion transporter and ion-homeostasis related candidate genes for salt tolerance followed by the introduction of these genes into crop plants under control of 35S promoter or stress/tissue specific promoter can generate salt tolerant engineered plants whereas downregulation of the ion transporter genes responsible for toxic ion entry into plant cells by the approach of RNAi or gene editing can improve to mitigate salt stress in plants. Recently miRNAs have been shown to target some ion transporters in salt stress (Khandal et al. 2017; Bai et al. 2018). Although transgenic approaches have been extensively used for functional characterisation of ion transporters in salt tolerance but there is lack of reports mentioning the role of transgenic plants overexpressing miRNAs which target ion transporters in salt stress. miRNA targeting the ion transporters which help in conferring salt tolerance can be considered for genetic engineering by different approaches like target mimicry (TM) and short tandem target mimicry (STTM) to achieve salt acclimatization (Teotia et al. 2016; Zhang et al. 2017a). With the introduction of gene editing technology in several crops, this technology can be deployed to crop plants to understand the roles of the ion transporters and manipulate their functions. Recent reports of engineered salt tolerant crops for maintaining ion homeostasis under salt stress is summarized in Table 1.

Comparative gene expression analysis

Another less explored area in this study is the identification and expression analysis of novel ion transporters or their regulatory proteins under salt stress in crop species. Investigations on differential gene expression analysis can be done between stressed and unstressed plants of same species, tolerant and sensitive genotypes of same species. Expression analysis of a particular family of ion transporters or their master regulators in organisms of different but related species or such analysis between glycophytes and halophytes can unravel the key components of ion homeostasis signaling network during salt stress. Because RNA sequencing has several benefits over other existing techniques it is becoming the method of choice for differential gene expression analysis. Studying salt tolerance in plants by these tools can bridge the gap in knowledge about ion sensing, transport, signaling and homeostasis maintenance during salt stress opening the new avenues in generating salt acclimatized crop varieties. All these

Table 1 Genetic engineering of ion transporters genes to confer salt tolerance

Name of the gene	Source plant	Transgenic plant	References
HvHKT1;1	*Hordeum vulgare*	*Arabidopsis thaliana*	Han et al. (2018)
AtSOS1/AtNHX1	*Arabidopsis thaliana*	*Arabidopsis thaliana*	Pehlivan et al. (2016)
OsHKT1;1	*Oryza sativa* cv. *indica*	*Oryza sativa* cv. *japonica*	Campbell et al. (2017)
LeNHX2	*Solanum lycopersicum*	*Solanum lycopersicum*	Huertas et al. (2013)
AsNHX1	*Arachis hypogaea*	*Nicotiana tabacum*	Zhang et al. (2017c)
MdNHX1	*Malus domestica*	*Arabidopsis thaliana*	Sun et al. (2017)
AlNHX1	*Aeluropus littoralis*	Soybean	Liu et al. (2014)
OsHAK5	*Oryza sativa* cv. *Nipponbare*	*Nicotiana tabacum* cv. BY2 cells	Horie et al. (2011)
AjSOS1	*Artemisia japonica*	*Chrysanthemum morifolium*	Gao et al. (2016)
SbNHXLP	*Sorghum bicolor*	*Solanum lycopersicum*	Kumari et al. (2017)
GmNHX1	Soybean	*Arabidopsis thaliana*	Sun et al. (2019)
AtNHX1/AtAVP1	*Arabidopsis thaliana*	Soybean	Nguyen et al. (2019)
AtNHX1/AtAVP1	*Arabidopsis thaliana*	Cotton	Shen et al. (2015)
MdNHX1	*Malus domestica*	*Malus domestica*	Sun et al. (2017)
AtSOS1/AtSOS2/AtSOS3	*Arabidopsis thaliana*	*Festuca arundinacea*	Ma et al. (2014)
StNHX1	*Solanum torvum*	*Glycine max*	Chen et al. (2014)
VrNHX1	*Vigna radiata*	*Arabidopsis thaliana*	Mishra et al. (2014)

HKT, High affinity K^+ transporters; NHX, Na^+/H^+ exchangers; HAK5, High-affinity K^+ transporter; SOS, Salt Overly Sensitive; NHXLP, Na^+/H^+ antiporter-like protein; AVP1, *Arabidopsis* vacuolar H^+-pyrophosphatase strategies can improve plant growth and development as well as crop productivity against global salt crisis for food.

Conclusions

The importance of ion transporters in salt tolerance has been described in this review. The regulatory mechanism of these transporters has to be studied by different tools to gain insights into the difference in salt tolerance between glycophytes and halophytes. Change in a particular amino acid or post translational modifications (PTMs), mainly phosphorylation, fine tunes the activity of these transporters. The amino acid residues essential for transporter activity as well as PTM sites targeted by the regulatory protein of the transporters have been identified in some of the ion transporters mainly in the model plant *Arabidopsis* by site directed mutations along with mass spectrometry analysis. More studies by such tools are required to shed light on the regulatory mechanism of the other ion transporters involved in salt stress signalling pathway both in *Arabidopsis* and the crop species. To study the transporter activity, patch clamp analysis in *Xenopus* oocytes have been done for some potassium transporters but such information about other ion transporters is scarce. Rubidium ion (Rb^+)content has been determined by inductively coupled plasma (ICP) mass spectrometry to measure K^+ uptake in some *Arabidopsis* transgenic lines but there is lack of reports of such investigations in the crop plants. Studies in yeast mutant deficient in uptake of ion of interest could pave the way for functional characterisation of the ion transporters. As yeast is an easy and fast experimental system and has less members in a protein family, complementation assay in yeast for the analysis of the function of ion transporters could provide valuable information in this regard. So heterologous expression of plant genes in yeast provides platform to investigate the role of ion transporters in salt tolerance in plants. Although some reports are available in this regard for functional characterisation of ion transporters of *Arabidopsis* and rice, such experimental tools could be employed for ion transporters of other crop species too. Despite using all these tools, our understanding of ion sensors, ion transporters and the regulatory proteins of these proteins is still quite limited. The research of molecular interactions, PTMs affecting the activity of the transporters and identification of the specific residues in the transmembrane proteins is crucial for understanding the transport system involved in salt stress response and such studies should be a priority in the future.

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