TOPICAL REVIEW

Membrane Proteins in Plant Salinity Stress Perception, Sensing, and Response

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Abstract

Plants have several mechanisms to endure salinity stress. The degree of salt tolerance varies significantly among different terrestrial crops. Proteins at the plant's cell wall and membrane mediate different physiological roles owing to their critical positioning between two distinct environments. A specific membrane protein is responsible for a single type of activity, such as a specific group of ion transport or a similar group of small molecule binding to exert multiple cellular effects. During salinity stress in plants, membrane protein functions: ion homeostasis, signal transduction, redox homeostasis, and solute transport are essential for stress perception, signaling, and recovery. Therefore, comprehensive knowledge about plant membrane proteins is essential to modulate crop salinity tolerance. This review gives a detailed overview of the membrane proteins involved in plant salinity stress highlighting the recent findings. Also, it discusses the role of solute transporters, accessory polypeptides, and proteins in salinity tolerance. Finally, some aspects of membrane proteins are discussed with potential applications to developing salt tolerance in crops.

Graphical Abstract
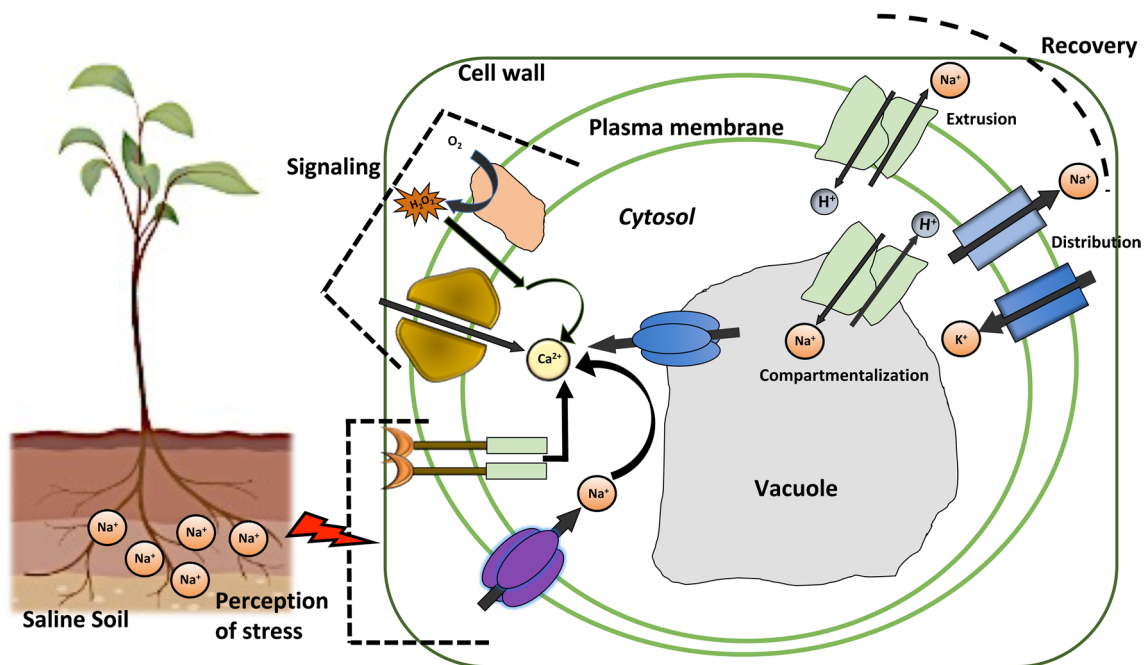
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Introduction

Soil salinity is a severe challenge affecting agricultural productivity globally. Declining cultivable lands due to soil salinization and the increase in food demand due to the population surge further worsen the situation (Kumar and Sharma 2020). Hence, there is an urgent need to deal with the soil salinity problem in the agricultural sector. Cultivation of salt-tolerant crop varieties in saline lands could be a potential solution to recover the soil quality and sustainable agricultural production (Kumar and Sharma 2020). Na^+ is one of the predominant ions responsible for salinity. Because excess Na^+ interferes with the regular metabolic activity in plants, the Na^+ level is maintained lower than the K^+ level in plant cytoplasm.

A simplified scheme of salinity stress in the plant is presented in Fig. 1. The entire processes of perception, signaling, and response to the salinity stress can be outlined as follows. The osmosensory and ion-sensory proteins in the cell wall and the plasma membrane perceive salinity in the form of osmotic and ionic stress, respectively. Osmotic and ionic stress results in the intracellular Ca^{2+} spike, acting as a signal, initiating several downstream

processes such as plasma membrane enzyme-dependent Reactive Oxygen Species (ROS) production. ROS production causes oxidative stress. In response to the signaling and oxidative stress, membrane transporters and pumps get involved in reducing the salinity stress. The recovery from salinity stress is caused by Na^+ extrusion, Na^+ compartmentalization, and partitioning of Na^+ across the plant organs (Van Zelm et al. 2020). Further, the small molecule transporters also transport the phytohormones and compatible solutes during the recovery phase. Hence membrane proteins (Table 1.) can be regarded as a checkpoint of the pathways that requires connecting external stimuli to the intracellular repercussion.

Recent genomic data of different plant species suggested that many membrane proteins in the plant genome are involved in abiotic stress tolerance (Tang et al. 2020). Despite a large number of membrane proteins in plant salinity stress, they can be categorized into a few basic types based on their primary function: ion homeostasis, osmosensing or ion sensing, signaling, redox homeostasis, solute transport, and accessory membrane polypeptides and proteins. In this work, a comprehensive review of plant membrane proteins in salinity stress is done. The review also discusses the role of solute transporters and accessory
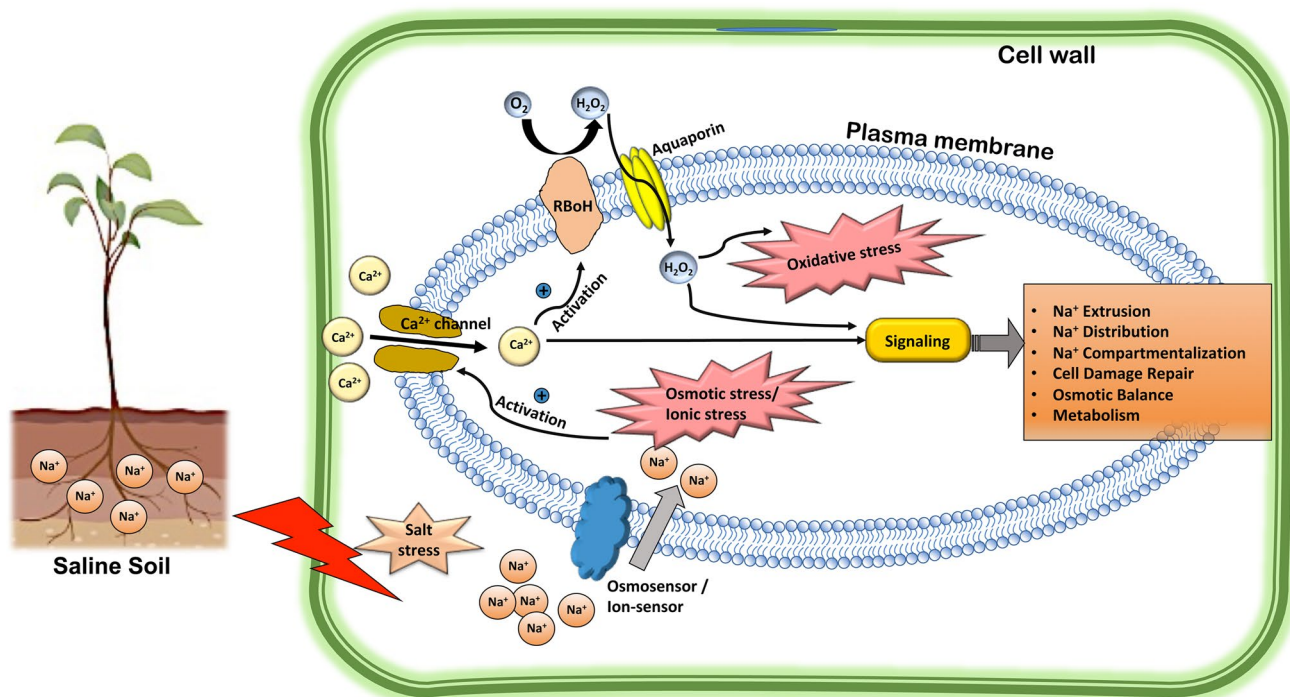

Fig. 1 Simplified scheme of salinity stress in plants: plants perceive salinity as osmotic and ionic stress and is consequently converted into Ca^{2+} signaling. Ca^{2+} also activates apoplastic ROS production through plasma membrane RBoH enzyme. Plant aquaporin transports ROS into the cytosol, facilitating oxidative stress. Ca^{2+} and ROS act as long-distance stress signal that activates many pathways to mitigate salinity stress. The main job of the signaling is to activate proteins and different transcription factor-mediated gene expressions primarily involved in Na^+ extrusion, Na^+ compartmentalization, Na^+ distribution, cell damage repair, osmotic balance, and metabolism

Table 1 Membrane proteins involved in plant salinity stress

Protein name	Function in salt tolerance	References
Ion channel (ion homeostasis)		
HKT	*High Affinity K^+ Transporters* group of channel/transporter are subdivided into two groups: HKT1 and HKT2. The established primary role of HKT1 is Na^+ retrieval from Xylem, i.e., Na^+ partitioning. Overexpression increases salt tolerance HKT2 is involved in Na^+ adsorption during K^+ deficient condition; suppression of expression increase salt tolerance	Hamamoto et al. (2015) and Riedelsberger et al.(2021)
CNGC	*Cyclic nucleotide gated channel* group are possible member of the non-specific cation channels (NSCC); Inactivation of CNGC10 shows tolerance to salt	Jin et al. (2015) and Jarratt-Barnham et al.(2021)
iGluR	*Ionotropic glutamate receptors* are possible member of the non-specific cation channels (NSCC); can transport Na^+, K^+, and Ca^{2+}	Demidchik et al. (2004) and Wang et al. (2019b)
AKT1, KAT1	*Inward-rectifying K^+ channel*; K^+ acquisition; heterologous expression shows salt tolerance	Obata et al. (2007) and Ahmad et al. (2016b)
AKT2, AKT3	*Weakly voltage regulated K^+ transport*; K^+ transport across plasma membrane; K^+ acquisition	Shabala and Cuin (2008)
SKOR	*Staler K^+ Outward Rectifying K^+ Channel* participates in K^+ distribution; overexpression increases salt tolerance	Long-Tang et al. (2018)
GORK	*Gated Outward rectifying K^+ channel* activated in response to the membrane depolarization; K^+ acquisition during salt stress condition	Adem et al. (2020)
TPC	*Intracellular two-pore channels* employ Ca^{2+} release into the cytosol; Ca^{2+} signaling; overexpression enhances salt tolerance	Wang et al. (2013), Ahmad et al. (2016a) and Guo et al. (2017)
OSCA	*Mechanosensitive Ca^{2+} channel* initiate Ca^{2+} signaling in response to the membrane tension	Hou et al. (2014) and Yuan et al. (2014)
CLC	*Intracellular Chloride Channels* reduces shoot Cl^- load; Cl^- compartmentalization; contribute to the salinity tolerance	Nguyen et al. (2016) and Wei et al. (2019)
SLAH	*Slow-type anion channels* distribute root-to-shoot Cl^-	Cubero-Font et al. (2016) and Qiu et al. (2016)
Secondary active transporter (ion homeostasis)		
SOS1	*Plasma membrane Na^+/H^+ antiporter*; Na^+ extrusion and long distance Na^+ distance transport; overexpression increase salt tolerance	Wu et al. (1996) and Shi et al. (2002)
NHX	*Intracellular Na^+/H^+ antiporter*; Na^+ compartmentalization; overexpression increase salt tolerance	Apse et al. (1999) and Bassil et al. (2019)
CHX/CAX	*Intracellular cation/H^+ exchanger*; Various function including maintenance of cytosolic K^+/Na^+ ratio; Ca^{2+} compartmentalization	Chanroj et al. (2012), Isayenkov et al. (2020) and Tsujii et al. (2020)
KAE	K^+ *exchange antiporter* possibly responsible for indirect intracellular Ca^{2+} influx in response to the initial hyperosmotic shock	Stephan et al. (2016), Chanroj et al. (2012), Isayenkov et al. (2020) and Tsujii et al. (2020)
HAK/KU	*High affinity K^+ transporters* mainly transport K^+; but can also transport Na^+, depending on the localization responsible for K^+ distribution and accumulation and maintaining K^+/Na^+ ratio	Nieves-Cordones et al. (2010), Shen et al. (2015) and Zhang et al. (2019)
NRT	*Nitrate transporter 1 and 2* (NRT1 and NRT2) are plasma membrane H^+/NO_3^- symporters; upregulate during salinity stress;	Wang et al. (2012a) and Liu et al. (2021)

Table 1 (continued)

Protein name	Function in salt tolerance	References
H⁺ Pump (ion homeostasis)		
pm-H⁺-ATPase	*Plasma membrane H⁺-ATPase* create H⁺ gradient across the plasma membrane for different H⁺-driven ion transporters (e.g., SOS1); Overexpression responsible for salt tolerance	Silva and Gerós (2009) and Fan et al. (2019)
v-H⁺-ATPase	*Vacuolar H⁺-ATPase* create H⁺ gradient across the vacuolar membrane for different H⁺-driven ion transporters	Kluge et al. (2003) and Silva and Gerós (2009)
v-H⁺-PPase	*Vacuolar H⁺- pyrophosphatase* facilitate H⁺ gradient across the vacuolar membrane for different H⁺-driven ion transporters	Kluge et al. (2003), Silva and Gerós (2009) and Krebs et al. (2010)
Ca²⁺-ATPase	*Intracellular Ca²⁺-ATPase* does Ca²⁺ compartmentalization; controls Ca²⁺ concentration post Ca²⁺ signaling	Huda et al. (2013)
Osmosensing, ion-sensing and signaling		
MOCA1	*Monocation induced [Ca²⁺]$_{Intracellular}$ increases 1* is an ion sensing protein; possibly indirect Ca²⁺ transport through membrane microdomain formation; control of plasma membrane dynamics by glycosphingolipid synthesis	Jiang et al. (2019)
RLK	*Receptor-like kinase* involved in various signaling processes; recognizes cell wall damage followed by direct/indirect activating calcium channels (e.g., FERONIA). Others recognizes apoplastic stimuli and directly/indirectly Ca²⁺ channel opening (e.g., HPCA1)	Feng et al. (2018), Zhao et al. (2018) and Wu et al. (2020)
Redox homeostasis		
RBoH	*Plasma membrane NADPH dependent Respiratory burst oxidase homologs* generate apoplastic Reactive Oxygen Species; indirectly regulated by Ca²⁺ signaling; ROS signaling and oxidative stress during salt stress	Choi et al. (2014) and Seifikalhor et al. (2019)
Solute transporters		
PIP	*Plasmamembrane Intrinsic Proteins* or plant aquaporin does water and ROS transport; controlling osmotic stress; contribute to the salt tolerance	Dynowski et al. (2008) and Horie et al. (2011)
ProT2	*Proline transporter* transport proline as osmoticum; proline distribution during salt stressed condition	Rentsch et al. (1996)
UPS5	*Ureide permease 5* engaged in long distance transports metabolite allantoin and controls osmotium content, associated with the salinity recovery phase	Lescano et al. (2016)
STP13	*Sugar transporters*; metabolite transport during recovery phase	Yamada et al. (2011)
ABCG25, ABCG36	*ATP binding Cassette G proteins* in recovery phase transport phytohormones controlling salt stress	Kim et al. (2010) and Park et al. (2016)
PHT4;6	*Phosphate transporter* recycles phosphate from glycosylation; may be cell wall synthesis	Cubero et al. (2009)

Table 1 (continued)

Protein name	Function in salt tolerance	References
Accessory membrane polypeptide and protein		
RCI	*Rare Cold Inducible* (RCI) group of small transmembrane polypeptides involved in abiotic stress; possibly aiding stability and activity of membrane protein	Mitsuya et al. (2005) and Liu et al. (2012)
*Os*PM1	*ABA-induced wheat plasma membrane polypeptide 19* (AWPM-19) group of membrane polypeptide; possibly aiding stability and activity of membrane protein; associated with ABA signaling	Yao et al. (2018) and Wang et al. (2021)
Patellin-1, Flotillin-2	*Accessory membrane proteins* does interaction with various ion transporters and membrane trafficking; interaction with other membrane proteins; vesicular transport of Na^+	Junková et al. (2018), Zhou et al. (2018), Khalilova et al. (2020) and Flowers et al. (2019)
Remorin	Plant-specific microdomain integral membrane protein; could be responsible for membrane protein stability	Raffaele et al. (2009) and Yue et al. (2014)
ANNX	*Annexin are* peripheral membrane proteins perform Ca^{2+} transport and signaling and intricately related to the membrane protein–protein interaction	Huh et al. (2010)

proteins in plant salt tolerance. Finally, the knowledge gap in membrane proteins in plant salinity stress response and the possibilities to develop salt-tolerant crops based on the plant membrane protein are discussed.

Membrane Proteins in Ion Homeostasis

Membrane Proteins in Sodium Homeostasis

Na^+ stress in plants is primarily sensed and controlled by the roots. No Na^+ specific channels on plant root plasma membrane are identified to date. A recent proposition suggests that vesicular transport enables a large Na^+ influx into halophyte cells (Flowers et al. 2019). However, several non-selective cation channels (NSCC) are also believed to be involved in the initial Na^+ influx (Demidchik and Maathuis 2007) (Fig. 2). High Affinity K^+ Transporters (HKTs) are one group of non-selective ion channel/transporter that transport Na^+ and K^+ (Riedelsberger et al. 2021). Several HKT genes and their functions in plants are highly variable, but their primary functions are ion accumulation under starved conditions, salt tolerance by ion compartmentalization, and partitioning (Hamamoto et al. 2015). Class I HKT channels are evidenced to perform K^+ and Na^+ transport (Gassmann et al. 1996). Overexpression of HKT1 has promoted salt tolerance by locally restricting Na^+ (Wang et al. 2019a). Class II HKTs co-transport Na^+ and K^+ and are activated during K^+ deficiency. One of the members of class II, HKT2;1, is responsible for distributing the Na^+ from root to shoot, thereby enhancing the salt tolerance in barley (Mian et al. 2011). HKT2;1 is also responsible for increasing Na^+ content in plant cell. Excess Na^+ is toxic; hence repression of HKT2;1 gene is also demonstrated to improve salt tolerance in rice (Wei et al. 2021). Na^+ is also transported through the High-Affinity K^+ uptake (HAK) family of transporters. For example, a HAK family transporter *Zm*HAK24 in maize and its orthologues in rice and wheat specifically transport Na^+; confer salt tolerance by restricting Na^+ in the root (Zhang et al. 2019). HAK activity is more relevant to the K^+ acquisition; therefore will be discussed in the K^+ homeostasis section. Na^+ homeostasis is also controlled by the ligand-gated channels such as Cyclic Nucleotide Gated Channels (CNGCs) (Jarratt-Barnham et al. 2021). Expression profiles of CNGCs change with salt stress. A CNGC homolog in *Arabidopsis thaliana At*CNGC10 contributes to the increase in $[Na^+]_{cytosol}$ under saline environmental conditions hence it negatively regulates plant salt tolerance (Jin et al. 2015). Another group of ligand-gated ion channels, ionotropic glutamate receptors channels (iGluRs), are also implicated in transporting Na^+ and K^+. The precise role of iGluRs in maintaining the K^+/Na^+ ratio is not clear but it has
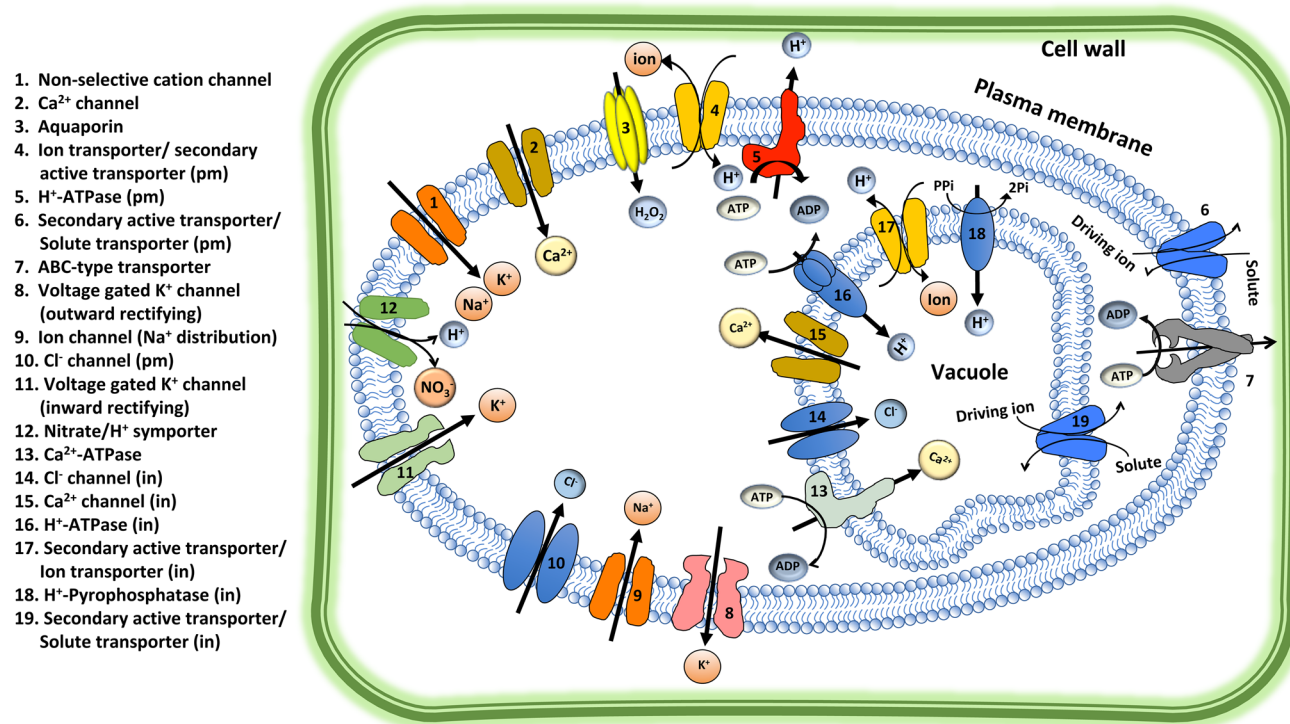
1. **Non-selective cation channel**
2. **Ca²⁺ channel**
3. **Aquaporin**
4. **Ion transporter/ secondary active transporter (pm)**
5. **H⁺-ATPase (pm)**
6. **Secondary active transporter/ Solute transporter (pm)**
7. **ABC-type transporter**
8. **Voltage gated K⁺ channel (outward rectifying)**
9. **Ion channel (Na⁺ distribution)**
10. **Cl⁻ channel (pm)**
11. **Voltage gated K⁺ channel (inward rectifying)**
12. **Nitrate/H⁺ symporter**
13. **Ca²⁺-ATPase**
14. **Cl⁻ channel (in)**
15. **Ca²⁺ channel (in)**
16. **H⁺-ATPase (in)**
17. **Secondary active transporter/ Ion transporter (in)**
18. **H⁺-Pyrophosphatase (in)**
19. **Secondary active transporter/ Solute transporter (in)**

Fig. 2 Ion and solute transporting membrane proteins: Plasma membrane (pm) and intracellular membrane transporters (in) are shown. The primary function of each type of transporter is numbered, and corresponding descriptions are enlisted. Plasma membrane (pm) transporters are mainly responsible for the ion extrusion and distribution across different plant organs, whereas intracellular (in) transporters do the compartmentalization and locally control the ion concentration. Non-selective ion channels do not discriminate between Na⁺ and K⁺ and can be non-gated or ligand-gated. K⁺ specific channels are mainly voltage-gated. Intracellular Ca²⁺-ATPase participates in Ca²⁺ homeostasis. Many solute transporters are driven by ions, whereas ABC transporters are driven by ATP hydrolysis

been regarded as one of the means to tackle salinity stress (Demidchik et al. 2004).

Na⁺ transport by secondary active transporters mainly occurs during the recovery phase. The primary Na⁺ extruding plant plasma membrane secondary active transporter is SOS1 (NHX7 in Arabidopsis) (Wu et al. 1996). It is a Na⁺/H⁺ antiporter that transports Na⁺ out of the cytosol in exchange for H⁺. SOS1 is also vital for the root-to-shoot distribution of Na⁺ in plants, thus conferring a long-distance salt transport (Shi et al. 2002). Plant intracellular Na⁺/H⁺ antiporters NHXs also play a significant role in salt tolerance. (Apse et al. 1999; Bassil et al. 2019). NHXs are involved in Na⁺ compartmentalization, but their activity can vary from one plant to the other depending on the level of salt tolerance (Rodríguez-Rosales et al. 2009). In Arabidopsis, NHX1 and NHX2 can transport Na⁺ and K⁺, but when the cytoplasmic Na⁺ concentration increases, the transporters participate in the sequestration of Na⁺ in the vacuole; hence contribute to the plant salt tolerance (Bassil et al. 2019). NHX5 and NHX6 reside in the endosomal membrane to confer protein sorting during salt stress (Bassil et al. 2019). The other two NHXs of Arabidopsis, NHX3, and NHX4, are more specific toward Na⁺ and K⁺,

respectively, and are mainly involved in vacuole transport and pH maintenance (Bassil et al. 2019). The functioning of Na⁺/H⁺ antiporter is driven by the proton gradient, which is established by H⁺-ATPases and H⁺-PPases (Shi et al. 2002; Silva and Gerós 2009). The fact that the deletion of plasma membrane H⁺-ATPase becomes salt sensitive and the overexpression of the same with SOS1 increases salinity tolerance in Arabidopsis endorse the importance of plasma membrane-H⁺-ATPase (Fan et al. 2019). Unlike Arabidopsis, the expression profile and the regulation of plasma membrane H⁺-ATPase activity of the salt-resistant plant is different. The comparison showed that ATPase activity increases upon salt exposure in leaves of salt-tolerant plants compared to salt-sensitive plants (Sahu and Shaw 2009). Further analysis showed that the variability of the H⁺-ATPase activity could be due to the different regulatory networks present in these plants (Gévaudant et al. 2007). Vacuolar-H⁺-ATPase (VHA) and H⁺-pyrophosphatase (H⁺-PPase) present in tonoplast energize the NHXs to compartmentalize salts in tonoplast (Kluge et al. 2003). Like plasma membrane H⁺-ATPase, VHA also shows an altered expression profile and activity level in salt-tolerant plants compared to a salt-sensitive plants (Wang et al. 2001; Jaarsma and De Boer 2018).

However, research showed that VHA is essential for nutrient storage in tonoplast, whereas H^+-PPase creates the H^+ gradient for salt accumulation (Krebs et al. 2010).

Membrane Proteins in Potassium Homeostasis

Like Na^+, K^+ absorption and distribution are essential to maintain the K^+/Na^+ ratio. K^+ channels (Fig. 2) responsible for plant salt tolerance are primarily voltage-gated channels and belong to three major groups: inward rectifying—controlling K^+ influx (AKT1, KAT1), outward rectifying—controlling K^+ efflux (SKOR and GORK), and weakly voltage regulated—direct both in and out K^+ transport (AKT2 and AKT3) (Shabala and Cuin 2008; Dreyer and Uozumi 2011). These channels are also regarded as shaker-type K^+ channels. The major inward rectifying K^+ channels found to enhance salt tolerance are KAT1 and AKT1. KAT1 is shown to increase salt tolerance in yeast. KAT1 increases the K^+ content in cells upon salinity stress (Obata et al. 2007). AKT1, on the other hand, is responsible for K^+ uptake and drought tolerance (Ahmad et al. 2016b). Outward rectifying channels such as GORK response to the salinity stress induced depolarization of the plasma membrane. Depolarization occurs due to the increasing Na^+ influx into the cell. In response to the depolarization, GORK maintain the plasma membrane potential by removal of cellular K^+. This destabilizes the cytosolic K^+/Na^+ ratio. Therefore, to prevent depolarization-mediated K^+ loss, plant reduces the expression of GORK (Adem et al. 2020). Another K^+ channel of the same group, Stelar K^+ Outward Rectifier (SKOR), passes the K^+ to the xylem for its distribution. It is demonstrated that a constitutive expression of melon SKOR in Arabidopsis improves its salinity tolerance (Long-Tang et al. 2018). Outward rectifying K^+ channels are also crucial for long-distance K^+ transport, balancing the cytosolic K^+/Na^+ ratio (Wegner and De Boer 1997). The weakly voltage-regulated K^+ channels AKT2/AKT3 demonstrated that the direction of the rectification and the voltage dependency is due to the sequence variations among different plants (Huang et al. 2021). AKT2/AKT3 control K^+ content and hence sucrose transport in phloem cells (Rubio et al. 2020). In rice, AKT2/AKT3 expression levels are reduced during salinity stress; however, its impotence may vary in plants depending on the variations in the direction of the rectification and the voltage dependency.

(Schmidt et al. 2013; Huang et al. 2021). Non-voltage gated K^+ channels in plants are two-pore channels (TPC) that are exclusively located in the tonoplast or intracellular membrane. The primary function of the K^+ specific TPC is to transport K^+ toward the cytoplasmic direction to stabilize the cytoplasm K^+/Na^+ ratio. Overexpression of K^+ specific TPC is therefore expected to resist the salt stress. Transgenic overexpression of TPCs improves plant salt tolerance (Wang

et al. 2013; Ahmad et al. 2016a). Recently a structure-based study of Arabidopsis two-pore channel *At*TPC1 shows that the channel is specific to Ca^{2+} but cannot discriminate between monovalent ions (Na^+ and K^+) (Guo et al. 2017).

Transporter and carrier protein entailing K^+ transport across plant membrane belongs to KT/HAK/KUP transporter family (Li et al. 2018). HAK transporters are comparatively well-characterized members of the KT/HAK/KUP transporter family. Although the variation of ion specificity has been reported for HAK members in plants, HAK transporters preferably transport K^+. Depending on the expression and localization, it primarily renders a K^+ accumulation in the plant during low K^+ environments and maintains the K^+/Na^+ ratio by redistributing K^+ (Nieves-Cordones et al. 2010; Shen et al. 2015).

Cation/H^+ antiporters are a large group of secondary active transporters in plants and can be subdivided into three main types: NHX, CHX, and KEA (Chanroj et al. 2012; Jia et al. 2018). Their functions and physiological roles are diverse (Isayenkov et al. 2020; Tsujii et al. 2020). While most NHXs preferentially transport Na^+, quite a few K^+ transporting CHXs are known. *At*CHX13 and *At*CHX14 are two critical Arabidopsis transporters active during K^+ deficiency in the environment. *At*CHX13 is located in the root carrying out the acquisition of K^+, whereas *At*CHX14 is expressed in the xylem parenchyma cell controlling the root to shoot movement of K^+ (Zhao et al. 2015). A cation/H^+ antiporter *Gs*CHX19.3 of *Glycine soja* shows a relatively higher expression in leaf and flower in response to the salinity stress (Jia et al. 2017). *Gs*CHX19.3 shows the highest homology with *A. thaliana* CHX19, and when overexpressed in Arabidopsis, it confers salt tolerance. The primary roles of K^+/H^+ transporters are restricting K^+ outflow from root cells and distributing K^+ from root to shoot.

Membrane Proteins in Chloride and Nitrogen Homeostasis

Chlorine and nitrogen are two elements absorbed and transported in plants as anions. Chloride homeostasis plays a significant part in plant salinity tolerance. In some plants, such as soybean and avocado, Cl^- shows a more toxic effect than Na^+ because these plants have a robust Na^+ exclusion system than Cl^- (Wu and Li 2019). Chloride transporters (Fig. 2) such as Slow Anion Channels (SLAC/SLAH) and Chloride channels (CLC) are documented to affect salt tolerance directly. In *Arabidopsis, At*SLAH is critical in Cl^- homeostasis during salinity stress. *At*SLAH1 and *At*SLAH3 heteromer has a significant contribution to the chloride distribution from root to shoot under salinity stress. During salinity stress, reduced *At*SLAH1 expression causes decline in Cl^- content in xylem sap; preventing Cl^- from reaching the shoot (Cubero-Font et al. 2016; Qiu et al. 2016).

Other chloride channels such as CLCs are intracellular and perform variable functions. *At*CLCc and *At*CLCg are two important chloride transporters responsible for salinity tolerance in Arabidopsis (Nguyen et al. 2016). The primary function of *At*CLCg is to reduce the shoot Cl⁻ content by compartmentalizing in the parenchyma cell. Cl⁻ exclusion from shoot to root has been widely studied in legume plants (Teakle and Tyerman 2010). Legume plants are unique due to their symbiotic relationship and can better manage chloride and nitrogen distribution (Vincill et al. 2005). For example, the genome-wide association study (GWAS) in soybean revealed that the chloride transporter *Gs*CLC-c2 has significant role in salinity tolerance in soybean (Wei et al. 2019; Luo et al. 2021). In principle, plant chloride channels restrict the distribution of Cl⁻ by compartmentalization.

Nitrogen in the form of NO_3^- is transported during salinity stress and is often correlated with K^+ transport (Raddatz et al. 2020). Nitrate transport is partly achieved by anion (chloride) channels SLAC/SLAH and CLC. The other two nitrate transporters, NTR1 and NTR2, are H^+-coupled NO_3^- symporters native to the plasma membrane. NTR1 and NTR2 are suggested to work due to the H^+ gradient established by plasma membrane H^+-ATPase (Liu et al. 2021). NRT1 and NRT2, both groups of nitrate transporters, are shown to be upregulated under salinity stress (Wang et al. 2012a; Liu et al. 2021). The NRT group of NO_3^- transporters mainly performs nitrogen absorption and distribution.

Membrane Protein in Calcium Homeostasis

Calcium ion transport systems can be subdivided into the Ca^{2+} influx and the Ca^{2+} efflux (Fig. 2) (Demidchik et al. 2018). Perception of salinity stress transiently induces Ca^{2+} influx into the cytosol, further amplified by ROS signaling, and is fundamentally required for propagating long-distance salinity stress signals (Choi et al. 2014). The efflux system is essential to move Ca^{2+} into the subcellular organelle, as a high concentration of Ca^{2+} in cytoplasm is toxic. The influx system consists of mechanosensitive channels (OSCA), cyclic nucleotide-gated channels (CNGC), two-pore channels (TPC), and ionotropic glutamate receptor channels (iGluRs) essential for an early stage of salinity stress perception. Mechanosensitive Ca^{2+} channels OSCA in plants sense the osmotic stress and are activated by the mechanical tension in the membrane (Hou et al. 2014; Yuan et al. 2014) (Fig. 3). Transgenic expression of rice *Os*OSCA1.4 in *A. thaliana* OSCA1.1 mutant can complement salinity and osmotic stress response (Zhai et al. 2020). Cyclic nucleotide-gated channels (CNGCs) are the ligand-gated channels with an assigned role in various stress tolerances (Demidchik et al. 2018). Most CNGCs are non-selective cation channels, but *A. thaliana* CNGC10 has been elucidated to have a role in salt tolerance. *At*CNGC10 is critical in balancing the

K^+/Na^+ ratio; nevertheless, its inactivation to increase the root K^+/Na^+ ratio corroborates that *At*CNGC10 negatively regulates salt tolerance (Guo et al. 2008; Jin et al. 2015). Since CNGCs require cyclic nucleotide for their activation, it is possible that *At*CNGC10 functions downstream to a membrane-associated osmosensory protein that produces cGMP. Similar activation has been reported for *At*CNGC2, induced by the receptor-like kinase *At*PepR1 producing cGMP (Qi et al. 2010). Two-pore channels (TPC) are responsible for propagating long-distance Ca^{2+}-dependent salinity stress signals (Choi et al. 2014). A study on the *A. thaliana* two-pore channel shows that *At*TPC1 is specific to Ca^{2+} but less specific to Na^+ and K^+ (Guo et al. 2017).

Unlike Ca^{2+} influx into the cytosol, its efflux is energy-dependent. The primary contributor to this relatively slow process is the endomembrane localized Ca^{2+}-ATPase. Arabidopsis ACA2 and ACA4 are two plant endomembrane Ca^{2+}-ATPases whose transcript levels increase during salt stress (Geisler et al. 2000; Anil et al. 2008). Expressing ACA2 in Ca^{2+}-ATPase-devoid yeast cells shows a rapid decrease in cytosolic Ca^{2+} upon salt stress (Anil et al. 2008). Plasma membrane Ca^{2+}-ATPases from other plants have been demonstrated to function in salt tolerance, as evidenced by the increased transcript levels during salinity stress (Huda et al. 2013). Other contributors to the cytoplasmic Ca^{2+} restoration are secondary active transporters such as Ca^{2+}/cation antiporters. Plant Ca^{2+}/cation exchangers are predominantly localized in the vacuole and have been examined for their function in yeasts. Ca^{2+}/H^+ exchanger CAX1 of *A. thaliana* is expressed in mesophyll cells and required for Ca^{2+} storage in the vacuole (Conn et al. 2011). Salinity stress enhances the expression level of both CAX1 and VHA, corroborating that CAX1 activity is energized by vacuolar H^+-ATPase (Han et al. 2011). Some Ca^{2+} exchangers couple Ca^{2+} transport with Na^+ transport. For instance, *A. thaliana At*NCL, a vacuolar Ca^{2+}/Na^+ exchanger sequesters Ca^{2+} into vacuole and releases Na^+ into cytosol. Therefore, unlike CAX, *At*NCL negatively influences salt tolerance (Wang et al. 2012b).

Membrane Proteins in Salinity Stress Signal Transduction

Changes in osmotic pressure and ionic concentration are two factors detected by plants to realize salinity stress (Fig. 3). Osmotic pressure causes several changes to the cellular structures of root cells, inflicting cell wall damage and an osmotic imbalance across the cell membrane. Osmosensors located in the plasma membrane can induce tension in the membrane (Haswell and Verslues 2015). Currently, the osmosensors in plants those induce membrane tension in response to salinity stress are not known (Wang et al. 2022).
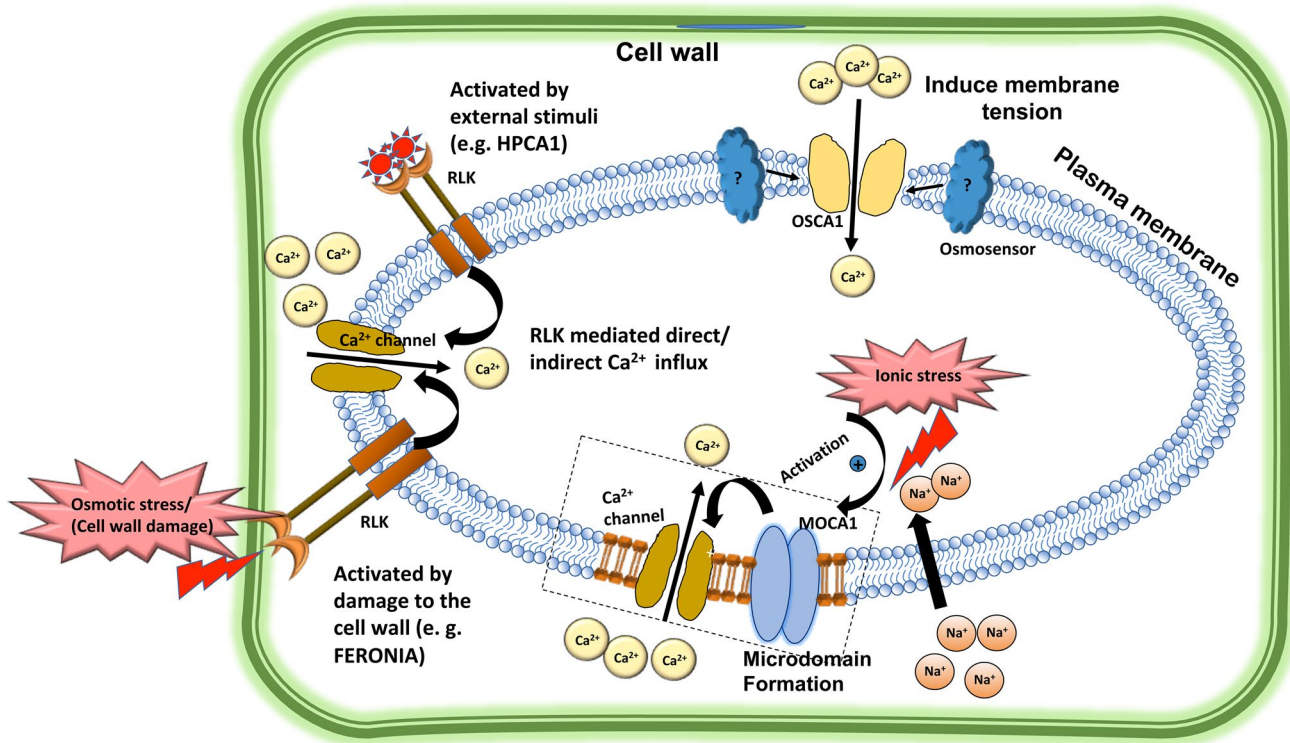
Fig. 3 Three basic modes of salinity stress perception in plants: Osmotic stress realized by putative osmosensor induces membrane tension. Membrane tension activates mechanosensitive Ca2+ channels. Another mechanism involving plasma membrane protein MOCA1 synthesizes glycosphingolipids in response to the Na^+ ion stress. MOCA1 possibly works via changing the plasma membrane dynamics to activate a putative Ca^{2+} channel. A third mechanism depends on the plasma membrane receptor-like kinases (RLKs) that detect damage to the cell wall or are activated by external stimuli such as ROS. RLKs directly or indirectly activate Ca^{2+} channels initiating the Ca^{2+} signal

However, the osmosensing could be due to multiple factors. One predominant factor is the direct distortion of the plasma membrane, inducing membrane tension. Mechanosensing Ca^{2+} channel protein families such as OSCA are activated due to the plasma membrane tension and initiate Ca^{2+} signaling (Yuan et al. 2014). Other mechanosensing membrane proteins are predicted to convert the osmotic stress into cGMP formation (Julkowska and Testerink 2015). Cyclic GMP is responsible for activating multiple non-selective ion channels including putative Ca^{2+} channels (Turek and Irving 2021). Na^+ sensors are also elucidated in plants. Monocation-Induced $[Ca^{2+}]_{intracellular}$ Increases 1 (MOCA1) is one such protein that mediates sensing of extracellular Na^+ concentration and Ca^{2+} signaling (Jiang et al. 2019). MOCA1 is a membrane protein with glucuronosyltransferase activity and is responsible for glycosphingolipid synthesis. The exact mechanism of MOCA1 is unknown, but it is thought to be responsible for nanodomain formation in plasma membrane. Nanodomain causes the activation of putative Ca^{2+} channels (Steinhorst and Kudla 2019).

Receptor-like kinases (RLKs) are integral membrane or membrane-associated proteins involved in various functions, including biotic and abiotic stress perception (Dievart et al. 2020) (Fig. 3). The basic structure of these proteins is composed of a sensory domain, followed by a transmembrane domain and the cytoplasmic kinase domain (Jose et al. 2020). However, some RLKs might have an extension to the cell wall, and some RLKs are only cytoplasmic (Jose et al. 2020). The kinase domain is responsible for phosphorylating a target protein for signal transduction. RLKs directly sense the osmotic damage of the cell wall or oxidative damage of the cell membrane induced by the salinity stress (Ye et al. 2017). RLKs can be root or shoot specific, and their expressions can be up or down-regulated by the salinity stress. For instance, the LRR (Leucine-Rich Repeat)-type RLK, LP2 overexpression in rice is predominantly found in leaves, reducing salt tolerance (Wu et al. 2015). Many RLKs are induced by ROS levels and aim to control the ROS-mediated damage during salinity stress. For instance, the rice RLKs, *Os*Slk1, and *Os*STLK are induced by salt stress and reduce the ROS load and lipid oxidation (Ouyang et al. 2010; Lin et al. 2020). Some RLKs spanning the cell wall recognize peptide hormones expressed due to salinity stress. For instance, overexpression of the small hormone-like peptide

*At*Pep3 is the consequence of salinity stress. *At*Pep3 interacts through Peptide Receptor 1 (PepR1), a RLK proposed to confer salt tolerance via ion homeostasis (Nakaminami et al. 2018). Salt stress resulting in damage in the cell wall and cell–cell interaction is sensed by RLK named FERONIA, which was also proposed to work toward Ca^{2+} ion homeostasis (Feng et al. 2018). FERONIA is linked to the cell wall residing Leucine–Rich Repeat Extensions (LRX) domain that senses the cell wall damage (Zhao et al. 2018). Receptor-like kinases might have a link with the plant G-proteins. G-proteins (G_a and G_b) are also upregulated in response to the increase in salinity stress. It is an enigma if G-proteins interact with the limited number of G-protein coupled receptors present in the plant (Misra et al. 2007). However, it is proposed that the G-proteins might just work through RLK signaling (Pandey 2020).

Membrane Proteins for Reactive Oxygen Species Scavenging System

Reactive oxygen species (ROS) generated in roots play a critical role in plants sensing salinity stress. ROS travel from root to shoot results in several changes in shoot, such as the closing of the guard cells (Choi et al. 2014). A coordinated movement of ROS and Ca^{2+} from root to shoot is also responsible for stress signaling (Li et al. 2021). Salinity stress-related ROS is produced by the plant plasma membrane Respiratory Burst Oxidase Homolog (RBoH). Among the ten RBoHs in Arabidopsis, RBoHD and RBoHF are two extensively studied enzymes directly involved in salinity stress (Ma et al. 2012). Activation of RBoH is the downstream effect of the early calcium influx into the cytosol, where the Ca^{2+} binding CBL sensors (Calcineurin B-like calcium sensors) and protein kinase (CIPK) synergistically activate RBoHs (Ogasawara et al. 2008; Drerup et al. 2013). RBoHs produce ROS in the apoplastic region to minimize the negative effect of ROS in the cytosol. However, apoplastic ROS is critical for the activities of the plasma membrane pumps and voltage-gated ion channels. One known example is the regulation of the voltage-gated K^+ channel SKOR. A cysteine residue located at the apoplastic side of SKOR undergoes ROS-dependent modification to kick-start the K^+ transport (Garcia-Mata et al. 2010). Another target of apoplastic ROS is HPCA1, which is a receptor-like kinase. Apoplastic ROS oxidized an extracellular cysteine residue of HPCA1 that activates the protein and relays a putative Ca^{2+} channel opening in guard cells (Wu et al. 2020).

ROS entry to the cytosol occurs via the PLASMAMEMBRANE INTRINSIC PROTEINS (PIPs) or aquaporins (Dynowski et al. 2008) (Fig. 1). ROS molecules such as hydrogen peroxidase (H_2O_2) impose oxidative stress by damaging the membrane lipids, DNA, proteins, perturbing the

cytosolic redox potential, and positively influencing Ca^{2+} signaling (Seifikalhor et al. 2019). A common outcome of salinity stress is the change in ROS-mediated membrane permeability caused by lipid peroxidation (Mansour 2013). Another adverse effect of ROS is the activation of the IAA pathway, which leads to root growth cessation (Huang et al. 2019a). Plants discharge multiple antioxidative defense enzymes and compatible solutes to counter oxidative stress (Apel and Hirt 2004). Studying the salinity tolerance mechanisms in halophytes revealed that the better salt-tolerant plant could better manage oxidative stress (Kumar et al. 2021). Membrane proteins also take part in ROS homeostasis. Arabidopsis mitochondrial voltage-dependent anion channel (VDAC) manifests salt tolerance by ROS homeostasis (Sanyal et al. 2020). ROS positively contributes to sensing and preventing salt tolerance through Ca^{2+} signaling. Data suggests that ROS indirectly activates the intracellular K^+ channel, TPC1, for cytosolic Ca^{2+} spike and, together, they are responsible for the propagation of the salinity stress signal and prevention (Evans et al. 2016). Another instance that ROS contributes to the increase in salt tolerance could be comprehended by ROS regulation of plant annexins. Annexins are the Ca^{2+} binding membrane-associated proteins responsible for intracellular Ca^{2+} transport. Arabidopsis Annexins, *At*ANN1, and *At*ANN4 negatively regulate salt tolerance (Huh et al. 2010). *At*ANN1 is again negatively regulated by ROS, implicating that ROS has some positive affects in salt tolerance (Richards et al. 2014). Regulation of membrane protein expression by ROS is also demonstrated. Transcriptome analyses of differentially expressed genes in pumpkin reveal that ROS-producing RBoHD controls the expression of plasma membrane H^+-ATPase (AHA1) and the K^+ channel HAK5 contributing to the salt tolerance (Huang et al. 2019b). Pumpkin-grafted cucumber plants with inhibited ROS production show compromised salt tolerance and reduced plasma membrane H^+-ATPase activity (Niu et al. 2018). These results imply that ROS contributes to salt tolerance by sounding the alarm of salinity-induced damage to the cells and regulating the membrane transporters' activities.

Solute Transporters

Salinity stress induces the expression level of certain solute transporters delineating their importance in salt tolerance. Solute transporters (Fig. 2) are generally involved during the recovery phase and transport three basic groups of molecules: phytohormones, compatible solutes, and metabolites. Phytohormones are essential for signaling growth and development. ABC (ATP Binding Cassette) transporters are primarily involved in phytohormone transport (Fig. 2). For example, Abscisic acids are considered stress response

hormones transported by ABCG25, which expression level changes due to the salinity stress (Park et al. 2016). An Arabidopsis ABC transporter, *At*ABCG36, is suggested to transport phytohormones with a putative role in salt tolerance (Kim et al. 2010).

Compatible solutes or osmoticum transport is imminent during osmotic shock. Molecules such as proline, polyamines, and glycinebetaine reduce oxidative stress and provide osmoprotection under salinity stress; hence called compatible solutes or osmoticum. Only a handful of compatible solute transporters are currently attributed to the plant's salinity stress response. Proline transporter ProT2 is one such membrane protein. ProT2 expression level coincides with the proline accumulation level in the leaves. ProT2 upregulation is the consequence of salinity stress that ensures the long-distance transport of proline (Rentsch et al. 1996). Polyamine is another compatible solute that is overproduced in response to salinity stress. The recent evidence of polyamine transporter PUT3 physically interacting with Na^+/H^+ antiporter SOS1 in plasma membrane shows a possibility of PUT3 involvement in salt tolerance (Chai et al. 2020).

A significant amount of energy is invested in the recovery phase of salt-induced damage. Therefore, metabolite transporters are essential that keep up the supplies of sugars and other molecules. Numerous studies have identified the change in plant metabolite transporters' expression profiles during salinity stress (Hsu et al. 2009). Sugar transporters STP13 and UPS5 are shown differential activation pattern during salt-stressed conditions. STP13 in Arabidopsis root increases carbohydrate absorption activity of root cells during stressed conditions (Yamada et al. 2011). Ureide permease 5 (UPS5) in Arabidopsis confers salt tolerance by distributing the small molecule allantoin (Lescano et al. 2016). Additionally, UPS5 exhibits salt tolerance by root-to-shoot transport of allantoin, a metabolite pertinent to abiotic stress. Plant cell wall and cell membrane synthesis required a considerable investment of energy. A phosphate transporter PHT4;6 is essential for recycling phosphate from glycosylation toward the synthesis of cell walls and membranes (Cubero et al. 2009).

Accessory Membrane Polypeptides and Proteins

Numerous studies have identified the role of integral membrane polypeptides and proteins in plant salt tolerance. The primary roles of these proteins are yet to be identified. However, these proteins may be responsible for the stability, activity, and targeting of membrane transporters or specific ions. A group of small transmembrane polypeptides called RCI (Rare Cold Inducible) are identified in plants contributing to salt tolerance. RCI polypeptides share significant homology with the yeast PMP3 (Plasma Membrane Protein 3) peptide, which, when deleted, exhibits a salt-sensitive phenotype (Navarre and Goffeau 2000). Overexpression of RCI2A in *A. thaliana* increases salt tolerance by reducing the cellular Na^+ content (Mitsuya et al. 2005). The transgenic expression of *Musa paradisica* RCI gene in *A. thaliana* RCI2 mutant recovered Na^+ tolerance (Liu et al. 2012). It has been predicted that RCI enhances Na^+ tolerance by reducing Na^+ content in the shoot, maintaining plasma membrane fluidity, and increasing plasma membrane H^+-ATPase activity. A different group of plasma membrane polypeptide SALP1 is identified in rice that also functions to reduce Na^+ content in the shoot. In addition, SALP1 increases the proline content in rice (Yuan et al. 2016). The third group of membrane polypeptides, called ABA-induced wheat plasma membrane polypeptide 19 (AWPM-19) is also linked to the salt stress in plants. *Os*PM1, an AWPM-19, has a proven role in ABA signaling and involvement in stress tolerance (Yao et al. 2018). However, it has been recently demonstrated that *Os*PM1 has a positive role in drought tolerance but a negative role in salinity tolerance (Wang et al. 2021). Some accessory integral membrane proteins are also evidenced in interacting with the ion transporters. For example, Patellin-1, a membrane trafficking protein, interacts with SOS1 Na^+/H^+ antiporter to negatively regulate its activity (Zhou et al. 2018). Another membrane trafficking salt-responsive protein, Flotillin-2, potentially interacts with plasma membrane H^+-ATPase as detected in mass spectrometry analysis (Junková et al. 2018). Flotillins are also predicted to do intracellular trafficking of Na^+ and are associated with plant salt stress tolerance (Flowers et al. 2019; Khalilova et al. 2020). Remorins are another group of accessory membrane protein usually found in microdomains (Raffaele et al. 2009). When transiently overexpressed in Arabidopsis, the Remorin gene SiREM6 of *Setaria italic* enhances salt tolerance (Yue et al. 2014). However, the precise functions of the accessory integral membrane proteins are not known.

Future Directions

Membrane proteins play an essential role in plant salinity stress. Particularly, the ion transporters change their expression profiles and hence are suggested to be a plausible target to improve crops for increased agricultural production (Schroeder et al. 2013). Plasma membrane ion transporters primarily extrude and transport long-distance Na^+ and Cl^-. Plasma membrane transporters are also critical for K^+ acquisition during K^+ starved conditions. On the contrary, intracellular ion transporters primarily involve the sequestration of Na^+ and Cl^- and control the cytoplasmic K^+/Na^+ ratio by releasing K^+ into the cytoplasm. Despite the importance of the membrane proteins in plant salinity stress response,

some aspects of the membrane proteins are remained unexplored, such as identifying the relevant membrane protein–lipid and membrane protein–protein interactions. Lipids are critical for membrane protein function. Salinity stress induces the restructuring of the plant cell plasma membrane due to the osmotic imbalance (Mansour et al. 2015). Production of ROS due to salinity stress also affects membrane lipid compositions and structure (Mansour et al. 2015). Lipids in the membrane control the regulation and activity of membrane protein. Therefore, it is evident that alteration of the lipid composition and structure in the membrane could regulate the membrane protein distribution, function, and activity. Although plenty of work has been done on protein-lipid interaction in animal and bacterial systems, such studies are very limited in plants due to several technical difficulties. Besides, membrane protein–protein interaction is evident in salinity stress response. Such protein–protein interaction in the membrane includes the communications between the receptor-like kinase and its immediate membrane protein substrate, membrane remodeling osmo- and ion-sensors and its subsequent transporters, channels providing ion gradient for transporter function, and finally, the H$^+$-pump empowering the secondary active transporters. Identifying the critical protein–protein interaction in plants could also provide valuable information about the protein interaction network responsible for salinity stress response. The membrane protein interaction could be understood by correlating membrane proteomics and lipidomics data in differential salt treatment experiments. Another crude yet easy and direct alternative could be finding the interacting lipids and protein from the heterologous expression of plant membrane proteins (Dutta et al. 2020).

Recently, it has been suggested that adopting halophytic traits in crops could solve the salinity stress problem in agriculture (Liu et al. 2020). One significant difference between halophytes compared to salt-sensitive crops is the differential expression pattern of the membrane proteins (Assaha et al. 2017). Changes in protein expression patterns also suggest an altered protein–protein and protein-lipid interaction network in halophytes. Knowledge of such specific interactions may be essential because they can be targeted, and strategies could be developed to modulate their interactions. Additionally, membrane protein distribution in plant organs and its polarity in a cell could be changed by the distribution of the lipids. It is possible to target the specific membrane lipid synthetic pathway and their targeting to alter membrane protein distribution or polarity.

Declarations

References

Adem GD, Chen G, Shabala L, Chen Z-H, Shabala S (2020) GORK channel: a master switch of plant metabolism? Trends Plant Sci 25:434–445

Ahmad I, Devonshire J, Mohamed R, Schultze M, Maathuis FJ (2016a) Overexpression of the potassium channel TPK b in small vacuoles confers osmotic and drought tolerance to rice. New Phytol 209:1040–1048

Ahmad I, Mian A, Maathuis FJ (2016b) Overexpression of the rice AKT1 potassium channel affects potassium nutrition and rice drought tolerance. J Exp Bot 67:2689–2698

Anil VS, Rajkumar P, Kumar P, Mathew M (2008) A plant Ca2+ pump, ACA2, relieves salt hypersensitivity in yeast: modulation of cytosolic calcium signature and activation of adaptive Na+ homeostasis. J Biol Chem 283:3497–3506

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399

Apse MP, Aharon GS, Snedden WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na+/H+ antiport in Arabidopsis. Science 285:1256–1258

Assaha DV, Ueda A, Saneoka H, Al-Yahyai R, Yaish MW (2017) The role of Na+ and K+ transporters in salt stress adaptation in glycophytes. Front Physiol 8:509

Bassil E, Zhang S, Gong H, Tajima H, Blumwald E (2019) Cation specificity of vacuolar NHX-type cation/H+ antiporters. Plant Physiol 179:616–629

Chai H, Guo J, Zhong Y, Hsu CC, Zou C, Wang P, Zhu JK, Shi H (2020) The plasma-membrane polyamine transporter PUT3 is regulated by the Na+/H+ antiporter SOS1 and protein kinase SOS2. New Phytol 226:785–797

Chanroj S, Wang G, Venema K, Zhang MW, Delwiche CF, Sze H (2012) Conserved and diversified gene families of monovalent cation/H+ antiporters from algae to flowering plants. Front Plant Sci 3:25

Choi W-G, Toyota M, Kim S-H, Hilleary R, Gilroy S (2014) Salt stress-induced Ca2+ waves are associated with rapid, long-distance root-to-shoot signaling in plants. Proc Natl Acad Sci 111:6497–6502

Conn SJ, Gilliham M, Athman A, Schreiber AW, Baumann U, Moller I, Cheng N-H, Stancombe MA, Hirschi KD, Webb AA (2011) Cell-specific vacuolar calcium storage mediated by CAX1 regulates apoplastic calcium concentration, gas exchange, and plant productivity in Arabidopsis. Plant Cell 23:240–257

Cubero B, Nakagawa Y, Jiang X-Y, Miura K-J, Li F, Raghothama KG, Bressan RA, Hasegawa PM, Pardo JM (2009) The phosphate transporter PHT4; 6 is a determinant of salt tolerance that is localized to the Golgi apparatus of Arabidopsis. Mol Plant 2:535–552

Cubero-Font P, Maierhofer T, Jaslan J, Rosales MA, Espartero J, Díaz-Rueda P, Müller HM, Hürter A-L, Al-Rasheid KA, Marten I (2016) Silent S-type anion channel subunit SLAH1 gates SLAH3 open for chloride root-to-shoot translocation. Curr Biol 26:2213–2220

Demidchik V, Maathuis FJ (2007) Physiological roles of nonselective cation channels in plants: from salt stress to signalling and development. New Phytol 175:387–404

Demidchik V, Essah PA, Tester M (2004) Glutamate activates cation currents in the plasma membrane of Arabidopsis root cells. Planta 219:167–175

Demidchik V, Shabala S, Isayenkov S, Cuin TA, Pottosin I (2018) Calcium transport across plant membranes: mechanisms and functions. New Phytol 220:49–69

Dievart A, Gottin C, Périn C, Ranwez V, Chantret N (2020) Origin and diversity of plant receptor-like kinases. Annu Rev Plant Biol 71:131–156

Drerup MM, Schlücking K, Hashimoto K, Manishankar P, Steinhorst L, Kuchitsu K, Kudla J (2013) The calcineurin B-like calcium sensors CBL1 and CBL9 together with their interacting protein kinase CIPK26 regulate the Arabidopsis NADPH oxidase RBOHF. Mol Plant 6:559–569

Dreyer I, Uozumi N (2011) Potassium channels in plant cells. FEBS J 278:4293–4303

Dutta D, Esmaili M, Overduin M, Fliegel L (2020) Expression and detergent free purification and reconstitution of the plant plasma membrane Na+/H+ antiporter SOS1 overexpressed in Pichia pastoris. Biochimica Et Biophysica Acta (BBA)-Biomembranes 1862:183111

Dynowski M, Schaaf G, Loque D, Moran O, Ludewig U (2008) Plant plasma membrane water channels conduct the signalling molecule H2O2. Biochem J 414:53–61

Evans MJ, Choi W-G, Gilroy S, Morris RJ (2016) A ROS-assisted calcium wave dependent on the AtRBOHD NADPH oxidase and TPC1 cation channel propagates the systemic response to salt stress. Plant Physiol 171:1771–1784

Fan Y, Yin X, Xie Q, Xia Y, Wang Z, Song J, Zhou Y, Jiang X (2019) Co-expression of SpSOS1 and SpAHA1 in transgenic Arabidopsis plants improves salinity tolerance. BMC Plant Biol 19:1–13

Feng W, Kita D, Peaucelle A, Cartwright HN, Doan V, Duan Q, Liu M-C, Maman J, Steinhorst L, Schmitz-Thom I (2018) The FERONIA receptor kinase maintains cell-wall integrity during salt stress through Ca2+ signaling. Curr Biol 28(666–675):e665

Flowers TJ, Glenn EP, Volkov V (2019) Could vesicular transport of Na+ and Cl–be a feature of salt tolerance in halophytes? Ann Bot 123:1–18

Garcia-Mata C, Wang J, Gajdanowicz P, Gonzalez W, Hills A, Donald N, Riedelsberger J, Amtmann A, Dreyer I, Blatt MR (2010) A minimal cysteine motif required to activate the SKOR K+ channel of Arabidopsis by the reactive oxygen species H2O2*[S]. J Biol Chem 285:29286–29294

Gassmann W, Rubio F, Schroeder JI (1996) Alkali cation selectivity of the wheat root high-affinity potassium transporter HKT1. Plant J 10(5):869–882

Geisler M, Frangne N, Gomes E, Martinoia E, Palmgren MG (2000) The ACA4 gene of Arabidopsis encodes a vacuolar membrane calcium pump that improves salt tolerance in yeast. Plant Physiol 124:1814–1827

Gévaudant F, Duby G, von Stedingk E, Zhao R, Morsomme P, Boutry M (2007) Expression of a constitutively activated plasma membrane H+-ATPase alters plant development and increases salt tolerance. Plant Physiol 144:1763–1776

Guo J, Zeng W, Jiang Y (2017) Tuning the ion selectivity of two-pore channels. Proc Natl Acad Sci 114:1009–1014

Guo KM, Babourina O, Christopher DA, Borsics T, Rengel Z (2008) The cyclic nucleotide-gated channel, AtCNGC10, influences salt tolerance in Arabidopsis. Physiol Plant 134: 499–507

Hamamoto S, Horie T, Hauser F, Deinlein U, Schroeder JI, Uozumi N (2015) HKT transporters mediate salt stress resistance in plants: from structure and function to the field. Curr Opin Biotechnol 32:113–120

Han N, Shao Q, Bao H, Wang B (2011) Cloning and Characterization of a Ca 2+/H+ Antiporter from Halophyte Suaeda salsa L. Plant Mol Biol Rep 29:449–457

Haswell ES, Verslues PE (2015) The ongoing search for the molecular basis of plant osmosensing. J Gen Physiol 145:389–394

Horie T, Kaneko T, Sugimoto G, Sasano S, Panda SK, Shibasaka M, Katsuhara M (2011) Mechanisms of water transport mediated by PIP aquaporins and their regulation via phosphorylation events under salinity stress in barley roots. Plant Cell Physiol 52:663–675

Hou C, Tian W, Kleist T, He K, Garcia V, Bai F, Hao Y, Luan S, Li L (2014) DUF221 proteins are a family of osmosensitive calcium-permeable cation channels conserved across eukaryotes. Cell Res 24:632–635

Hsu J-L, Wang L-Y, Wang S-Y, Lin C-H, Ho K-C, Shi F-K, Chang F (2009) Functional phosphoproteomic profiling of phosphorylation sites in membrane fractions of salt-stressed Arabidopsis thaliana. Proteome Sci 7:1–16

Huang H, Ullah F, Zhou D-X, Yi M, Zhao Y (2019a) Mechanisms of ROS regulation of plant development and stress responses. Front Plant Sci 10:800

Huang Y, Cao H, Yang L, Chen C, Shabala L, Xiong M, Niu M, Liu J, Zheng Z, Zhou L (2019b) Tissue-specific respiratory burst oxidase homolog-dependent H2O2 signaling to the plasma membrane H+-ATPase confers potassium uptake and salinity tolerance in Cucurbitaceae. J Exp Bot 70:5879–5893

Huang Y-N, Yang S-Y, Li J-L, Wang S-F, Wang J-J, Hao D-L, Su Y-H (2021) The rectification control and physiological relevance of potassium channel OsAKT2. Plant Physiol 187(4):2296–2310

Huda KM, Banu MSA, Garg B, Tula S, Tuteja R, Tuteja N (2013) Os ACA 6, a Pe rectification control and physiological relevance of potassium channel OsAKT2. Plant Physiology lasma membrane H+-ATPase confers potassium unsive genes. Plant J 76:997–1015

Huh SM, Noh EK, Kim HG, Jeon BW, Bae K, Hu H-C, Kwak JM, Park OK (2010) Arabidopsis annexins AnnAt1 and AnnAt4 interact with each other and regulate drought and salt stress responses. Plant Cell Physiol 51:1499–1514

Isayenkov SV, Dabravolski SA, Pan T, Shabala S (2020) Phylogenetic diversity and physiological roles of plant monovalent cation/H+ antiporters. Front Plant Sci 11:1451

Jaarsma R, De Boer AH (2018) Salinity tolerance of two potato cultivars (Solanum tuberosum) correlates with differences in vacuolar transport activity. Front Plant Sci 9:737

Jarratt-Barnham E, Wang L, Ning Y, Davies JM (2021) The complex story of plant cyclic nucleotide-gated channels. Int J Mol Sci 22:874

Jia B, Sun M, DuanMu H, Ding X, Liu B, Zhu Y, Sun X (2017) GsCHX19. 3, a member of cation/H+ exchanger superfamily from wild soybean contributes to high salinity and carbonate alkaline tolerance. Sci Rep 7:1–12

Jia Q, Zheng C, Sun S, Amjad H, Liang K, Lin W (2018) The role of plant cation/proton antiporter gene family in salt tolerance. Biol Plant 62:617–629

Jiang Z, Zhou X, Tao M, Yuan F, Liu L, Wu F, Wu X, Xiang Y, Niu Y, Liu F (2019) Plant cell-surface GIPC sphingolipids sense salt to trigger Ca 2+ influx. Nature 572:341–346

Jin Y, Jing W, Zhang Q, Zhang W (2015) Cyclic nucleotide gated channel 10 negatively regulates salt tolerance by mediating Na+ transport in Arabidopsis. J Plant Res 128:211–220

Jose J, Ghantasala S, Roy Choudhury S (2020) Arabidopsis transmembrane receptor-like kinases (RLKs): a bridge between extracellular signal and intracellular regulatory machinery. Int J Mol Sci 21:4000

Julkowska MM, Testerink C (2015) Tuning plant signaling and growth to survive salt. Trends Plant Sci 20:586–594

Junková P, Daněk M, Kocourková D, Brouzdová J, Kroumanová K, Zelazny E, Janda M, Hynek R, Martinec J, Valentová O (2018) Mapping of plasma membrane proteins interacting with Arabidopsis thaliana flotillin 2. Front Plant Sci 9:991

Khalilova L, Sergienko O, Orlova YV, Myasoedov N, Karpichev I, Balnokin YV (2020) Arabidopsis thaliana mutant with T-DNA Insertion in the Flot1 (At5g25250) gene promotor possesses increased resistance to NaCl. Russ J Plant Physiol 67:275–284

Kim DY, Jin JY, Alejandro S, Martinoia E, Lee Y (2010) Overexpression of AtABCG36 improves drought and salt stress resistance in Arabidopsis. Physiol Plant 139:170–180

Kluge C, Lahr J, Hanitzsch M, Bolte S, Golldack D, Dietz K-J (2003) New insight into the structure and regulation of the plant vacuolar H+-ATPase. J Bioenerg Biomembr 35:377–388

Krebs M, Beyhl D, Görlich E, Al-Rasheid KA, Marten I, Stierhof Y-D, Hedrich R, Schumacher K (2010) Arabidopsis V-ATPase activity at the tonoplast is required for efficient nutrient storage but not for sodium accumulation. Proc Natl Acad Sci 107:3251–3256

Kumar P, Sharma PK (2020) Soil salinity and food Security in India. Front Sustain Food Syst 4:174

Kumar A, Mann A, Kumar A, Kumar N, Meena BL (2021) Physiological response of diverse halophytes to high salinity through ionic accumulation and ROS scavenging. Int J Phytorem 23:1041–1051

Lescano CI, Martini C, González CA, Desimone M (2016) Allantoin accumulation mediated by allantoinase downregulation and transport by Ureide Permease 5 confers salt stress tolerance to Arabidopsis plants. Plant Mol Biol 91:581–595

Li W, Xu G, Alli A, Yu L (2018) Plant HAK/KUP/KT K+ transporters: function and regulation Seminars in cell & developmental biology. Elsevier, Amsterdam, pp 133–141

Li H, Testerink C, Zhang Y (2021) How roots and shoots communicate through stressful times. Trends Plant Sci 26:940–952

Lin F, Li S, Wang K, Tian H, Gao J, Zhao Q, Du C (2020) A leucine-rich repeat receptor-like kinase, OsSTLK, modulates salt tolerance in rice. Plant Sci 296:110465

Liu B, Feng D, Zhang B, Mu P, Zhang Y, He Y, Qi K, Wang J, Wang H (2012) Musa paradisica RCI complements AtRCI and confers Na+ tolerance and K+ sensitivity in Arabidopsis. Plant Sci 184:102–111

Liu M, Pan T, Allakhverdiev SI, Yu M, Shabala S (2020) Crop halophytism: an environmentally sustainable solution for global food security. Trends Plant Sci 25:630–634

Liu R, Cui B, Lu X, Song J (2021) The positive effect of salinity on nitrate uptake in Suaeda salsa. Plant Physiol Biochem 166:958–963

Long-Tang H, Li-Na Z, Li-Wei G, Anne-Aliénor V, Hervé S, Yi-Dong Z (2018) Constitutive expression of CmSKOR, an outward K+ channel gene from melon, in Arabidopsis thaliana involved in saline tolerance. Plant Sci 274:492–502

Luo M, Zhang Y, Li J, Zhang P, Chen K, Song W, Wang X, Yang J, Lu X, Lu B (2021) Molecular dissection of maize seedling salt tolerance using a genome-wide association analysis method. Plant Biotechnol J 19(10):1937–1951

Ma L, Zhang H, Sun L, Jiao Y, Zhang G, Miao C, Hao F (2012) NADPH oxidase AtrbohD and AtrbohF function in

ROS-dependent regulation of Na+/K+ homeostasis in Arabidopsis under salt stress. J Exp Bot 63:305–317

Mansour MMF (2013) Plasma membrane permeability as an indicator of salt tolerance in plants. Biol Plant 57:1–10

Mansour MMF, Salama KH, Allam HY (2015) Role of the plasma membrane in saline conditions: lipids and proteins. Bot Rev 81:416–451

Mian A, Oomen RJ, Isayenkov S, Sentenac H, Maathuis FJ, Véry AA (2011) Over-expression of an Na+-and K+-permeable HKT transporter in barley improves salt tolerance. Plant J 68:468–479

Misra S, Wu Y, Venkataraman G, Sopory SK, Tuteja N (2007) Heterotrimeric Gr-expression of an Na+-and K+-permeable HKT transporter in ba (*Pisum sativum*): role in salinity and heat stress and cross-talk with phospholipase C. Plant J 51:656–669

Mitsuya S, Taniguchi M, Miyake H, Takabe T (2005) Disruption of RCI2A leads to over-accumulation of Na+ and increased salt sensitivity in Arabidopsis thaliana plants. Planta 222:1001–1009

Nakaminami K, Okamoto M, Higuchi-Takeuchi M, Yoshizumi T, Yamaguchi Y, Fukao Y, Shimizu M, Ohashi C, Tanaka M, Matsui M (2018) AtPep3 is a hormone-like peptide that plays a role in the salinity stress tolerance of plants. Proc Natl Acad Sci 115:5810–5815

Navarre C, Goffeau A (2000) Membrane hyperpolarization and salt sensitivity induced by deletion of PMP3, a highly conserved small protein of yeast plasma membrane. EMBO J 19:2515–2524

Nguyen CT, Agorio A, Jossier M, Depré S, Thomine S, Filleur S (2016) Characterization of the chloride channel-like, AtCLCg, involved in chloride tolerance in Arabidopsis thaliana. Plant Cell Physiol 57:764–775

Nieves-Cordones M, Alemán F, Martínez V, Rubio F (2010) The Arabidopsis thaliana HAK5 K+ transporter is required for plant growth and K+ acquisition from low K+ solutions under saline conditions. Mol Plant 3:326–333

Niu M, Huang Y, Sun S, Sun J, Cao H, Shabala S, Bie Z (2018) Root respiratory burst oxidase homologue-dependent H2O2 production confers salt tolerance on a grafted cucumber by controlling Na+ exclusion and stomatal closure. J Exp Bot 69:3465–3476

Obata T, Kitamoto HK, Nakamura A, Fukuda A, Tanaka Y (2007) Rice shaker potassium channel OsKAT1 confers tolerance to salinity stress on yeast and rice cells. Plant Physiol 144:1978–1985

Ogasawara Y, Kaya H, Hiraoka G, Yumoto F, Kimura S, Kadota Y, Hishinuma H, Senzaki E, Yamagoe S, Nagata K (2008) Synergistic activation of the Arabidopsis NADPH oxidase AtrbohD by Ca2+ and phosphorylation. J Biol Chem 283:8885–8892

Ouyang SQ, Liu YF, Liu P, Lei G, He SJ, Ma B, Zhang WK, Zhang JS, Chen SY (2010) Receptor-like kinase OsSIK1 improves drought and salt stress tolerance in rice (*Oryza sativa*) plants. Plant J 62:316–329

Pandey S (2020) Plant receptor-like kinase signaling through heterotrimeric G-proteins. J Exp Bot 71:1742–1751

Park Y, Xu Z-Y, Kim SY, Lee J, Choi B, Lee J, Kim H, Sim H-J, Hwang I (2016) Spatial regulation of ABCG25, an ABA exporter, is an important component of the mechanism controlling cellular ABA levels. Plant Cell 28:2528–2544

Qi Z, Verma R, Gehring C, Yamaguchi Y, Zhao Y, Ryan CA, Berkowitz GA (2010) Ca2+ signaling by plant Arabidopsis thaliana Pep peptides depends on AtPepR1, a receptor with guanylyl cyclase activity, and cGMP-activated Ca2+ channels. Proc Natl Acad Sci 107:21193–21198

Qiu J, Henderson SW, Tester M, Roy SJ, Gilliham M (2016) SLAH1, a homologue of the slow type anion channel SLAC1, modulates shoot Cl− accumulation and salt tolerance in Arabidopsis thaliana. J Exp Bot 67:4495–4505

Raddatz N, de Ríos LM, Lindahl M, Quintero FJ, Pardo JM (2020) Coordinated transport of nitrate, potassium, and sodium. Front Plant Sci 11:247

Raffaele S, Bayer E, Mongrand S (2009) Up regulation of the plant protein remorin correlates with dehiscence and cell maturation; a link with the maturation of plasmodesmata? A link with the maturation of plasmodesmata? Plant Signal Behav 4:915–919

Rentsch D, Hirner B, Schmelzer E, Frommer WB (1996) Salt stress-induced proline transporters and salt stress-repressed broad specificity amino acid permeases identified by suppression of a yeast amino acid permease-targeting mutant. Plant Cell 8:1437–1446

Richards SL, Laohavisit A, Mortimer JC, Shabala L, Swarbreck SM, Shabala S, Davies JM (2014) Annexin 1 regulates the H 2 O 2-induced calcium signature in A rabidopsis thaliana roots. Plant J 77:136–145

Riedelsberger J, Miller JK, Valdebenito-Maturana B, Piñeros MA, González W, Dreyer I (2021) Plant HKT channels: an updated view on structure, function and gene regulation. Int J Mol Sci 22:1892

Rodríguez-Rosales MP, Gálvez FJ, Huertas R, Aranda MN, Baghour M, Cagnac O, Venema K (2009) Plant NHX cation/proton antiporters. Plant Signal Behav 4:265–276

Sahu BB, Shaw BP (2009) Salt-inducible isoform of plasma membrane H+ ATPase gene in rice remains constitutively expressed in natural halophyte, *Suaeda maritima*. J Plant Physiol 166:1077–1089

Sanyal SK, Kanwar P, Fernandes JL, Mahiwal S, Yadav AK, Samtani H, Srivastava AK, Suprasanna P, Pandey GK (2020) Arabidopsis mitochondrial voltage-dependent anion channels are involved in maintaining reactive oxygen species homeostasis, oxidative and salt stress tolerance in yeast. Front Plant Sci 11:50

Schmidt R, Mieulet D, Hubberten H-M, Obata T, Hoefgen R, Fernie AR, Fisahn J, San Segundo B, Guiderdoni E, Schippers JH (2013) SALT-RESPONSIVE ERF1 regulates reactive oxygen species–dependent signaling during the initial response to salt stress in rice. Plant Cell 25:2115–2131

Schroeder JI, Delhaize E, Frommer WB, Guerinot ML, Harrison MJ, Herrera-Estrella L, Horie T, Kochian LV, Munns R, Nishizawa NK (2013) Using membrane transporters to improve crops for sustainable food production. Nature 497:60–66

Seifikalhor M, Aliniaeifard S, Shomali A, Azad N, Hassani B, Lastochkina O, Li T (2019) Calcium signaling and salt tolerance are diversely entwined in plants. Plant Signal Behav 14:1665455

Shabala S, Cuin TA (2008) Potassium transport and plant salt tolerance. Physiol Plant 133:651–669

Shen Y, Shen L, Shen Z, Jing W, Ge H, Zhao J, Zhang W (2015) The potassium transporter O s HAK 21 functions in the maintenance of ion homeostasis and tolerance to salt stress in rice. Plant, Cell Environ 38:2766–2779

Shi H, Quintero FJ, Pardo JM, Zhu J-K (2002) The putative plasma membrane Na+/H+ antiporter SOS1 controls long-distance Na+ transport in plants. Plant Cell 14:465–477

Silva P, Gerós H (2009) Regulation by salt of vacuolar H+-ATPase and H+-pyrophosphatase activities and Na+/H+ exchange. Plant Signal Behav 4:718–726

Steinhorst L, Kudla J (2019) How plants perceive salt. Nature Publishing Group, Berlin

Stephan AB, Kunz H-H, Yang E, Schroeder JI (2016) Rapid hyperosmotic-induced Ca2+ responses in Arabidopsis thaliana exhibit sensory potentiation and involvement of plastidial KEA transporters. Proc Natl Acad Sci 113:E5242–E5249

Tang R-J, Luan M, Wang C, Lhamo D, Yang Y, Zhao F-G, Lan W-Z, Fu A-G, Luan S (2020) Plant membrane transport research in the post-genomic era. Plant Commun 1:100013

Teakle NL, Tyerman SD (2010) Mechanisms of Cl(-) transport contributing to salt tolerance. Plant Cell Environ 33:566–589

Tsujii M, Tanudjaja E, Uozumi N (2020) Diverse physiological functions of cation proton antiporters across bacteria and plant cells. Int J Mol Sci 21:4566

Turek I, Irving H (2021) Moonlighting proteins shine new light on molecular signaling niches. Int J Mol Sci 22:1367

Van Zelm E, Zhang Y, Testerink C (2020) Salt tolerance mechanisms of plants. Annu Rev Plant Biol 71:403–433

Vincill ED, Szczyglowski K, Roberts DM (2005) GmN70 and LjN70. Anion transporters of the symbiosome membrane of nodules with a transport preference for nitrate. Plant Physiol 137:1435–1444

Wang B, Lüttge U, Ratajczak R (2001) Effects of salt treatment and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte Suaeda salsa. J Exp Bot 52:2355–2365

Wang H, Zhang M, Guo R, Shi D, Liu B, Lin X, Yang C (2012a) Effects of salt stress on ion balance and nitrogen metabolism of old and young leaves in rice (*Oryza sativa* L.). BMC Plant Biol 12:1–11

Wang P, Li Z, Wei J, Zhao Z, Sun D, Cui S (2012b) A Na+/Ca2+ exchanger-like protein (AtNCL) involved in salt stress in Arabidopsis. J Biol Chem 287:44062–44070

Wang F, Deng S, Ding M, Sun J, Wang M, Zhu H, Han Y, Shen Z, Jing X, Zhang F (2013) Overexpression of a poplar two-pore K+ channel enhances salinity tolerance in tobacco cells. Plant Cell Tissue Organ Cult (PCTOC) 112:19–31

Wang L, Liu Y, Li D, Feng S, Yang J, Zhang J, Zhang J, Wang D, Gan Y (2019a) Improving salt tolerance in potato through overexpression of AtHKT1 gene. BMC Plant Biol 19:1–15

Wang P-H, Lee C-E, Lin Y-S, Lee M-H, Chen P-Y, Chang H-C, Chang I-F (2019b) The glutamate receptor-like protein GLR3. 7 interacts with 14–3–3ω and participates in salt stress response in Arabidopsis thaliana. Front Plant Sci 10:1169

Wang W, Quan C, Zheng S, Wang YW, Mo Y, Ma C, Xu Z, Li L, Huang Z, Jia X (2021) OsPM1 is a positive regulator of rice tolerance to drought stress but a negative regulator of rice tolerance to salt stress. J Plant Interact 16:213–221

Wang C-F, Han G-L, Yang Z-R, Li Y-X, Wang B-S (2022) Plant salinity sensors: current understanding and future directions. Front Plant Sci 13:859224

Wegner LH, De Boer AH (1997) Properties of two outward-rectifying channels in root xylem parenchyma cells suggest a role in K+ homeostasis and long-distance signaling. Plant Physiol 115:1707–1719

Wei P, Che B, Shen L, Cui Y, Wu S, Cheng C, Liu F, Li M-W, Yu B, Lam H-M (2019) Identification and functional characterization of the chloride channel gene, GsCLC-c2 from wild soybean. BMC Plant Biol 19:1–15

Wei H, Wang X, He Y, Xu H, Wang L (2021) Clock component OsPRR73 positively regulates rice salt tolerance by modulating OsHKT2; 1-mediated sodium homeostasis. EMBO J 40:e105086

Wu H, Li Z (2019) The importance of Cl− exclusion and vacuolar Cl− sequestration: revisiting the role of Cl− transport in plant salt tolerance. Front Plant Sci 10:1418

Wu S-J, Ding L, Zhu J-K (1996) SOS1, a genetic locus essential for salt tolerance and potassium acquisition. Plant Cell 8:617–627

Wu F, Sheng P, Tan J, Chen X, Lu G, Ma W, Heng Y, Lin Q, Zhu S, Wang J (2015) Plasma membrane receptor-like kinase leaf panicle 2 acts downstream of the DROUGHT AND SALT TOLERANCE transcription factor to regulate drought sensitivity in rice. J Exp Bot 66:271–281

Wu F, Chi Y, Jiang Z, Xu Y, Xie L, Huang F, Wan D, Ni J, Yuan F, Wu X (2020) Hydrogen peroxide sensor HPCA1 is an LRR receptor kinase in Arabidopsis. Nature 578:577–581

Yamada K, Kanai M, Osakabe Y, Ohiraki H, Shinozaki K, Yamaguchi-Shinozaki K (2011) Monosaccharide absorption activity of Arabidopsis roots depends on expression profiles of transporter genes under high salinity conditions. J Biol Chem 286:43577–43586

Yao L, Cheng X, Gu Z, Huang W, Li S, Wang L, Wang Y-F, Xu P, Ma H, Ge X (2018) The AWPM-19 family protein OsPM1 mediates

abscisic acid influx and drought response in rice. Plant Cell 30:1258–1276

Ye Y, Ding Y, Jiang Q, Wang F, Sun J, Zhu C (2017) The role of receptor-like protein kinases (RLKs) in abiotic stress response in plants. Plant Cell Rep 36:235–242

Yuan F, Yang H, Xue Y, Kong D, Ye R, Li C, Zhang J, Theprungsirikul L, Shrift T, Krichilsky B (2014) OSCA1 mediates osmotic-stress-evoked Ca 2+ increases vital for osmosensing in Arabidopsis. Nature 514:367–371

Yuan X, Sun H, Tang Z, Tang H, Zhang H, Huang J (2016) A novel little membrane protein confers salt tolerance in rice (*Oryza sativa* L.). Plant Mol Biol Report 34:524–532

Yue J, Li C, Liu Y, Yu J (2014) A remorin gene SiREM6, the target gene of SiARDP, from foxtail millet (*Setaria italica*) promotes high salt tolerance in transgenic Arabidopsis. PLoS ONE 9:e100772

Zhai Y, Wen Z, Han Y, Zhuo W, Wang F, Xi C, Liu J, Gao P, Zhao H, Wang Y (2020) Heterogeneous expression of plasma-membrane-localised OsOSCA1 4 complements osmotic sensing based on hyperosmolality and salt stress in Arabidopsis osca1 mutant. Cell Calcium 91:102261

Zhang M, Liang X, Wang L, Cao Y, Song W, Shi J, Lai J, Jiang C (2019) A HAK family Na+ transporter confers natural variation of salt tolerance in maize. Nat Plants 5:1297–1308

Zhao J, Li P, Motes CM, Park S, Hirschi KD (2015) CHX 14 is a plasma membrane K-efflux transporter that regulates K+ redistribution in A rabidopsis thaliana. Plant, Cell Environ 38:2223–2238

Zhao C, Zayed O, Yu Z, Jiang W, Zhu P, Hsu C-C, Zhang L, Tao WA, Lozano-Durán R, Zhu J-K (2018) Leucine-rich repeat extensin proteins regulate plant salt tolerance in Arabidopsis. Proc Natl Acad Sci 115:13123–13128

Zhou H, Wang C, Tan T, Cai J, He J, Lin H (2018) Patellin1 negatively modulates salt tolerance by regulating PM Na+/H+ antiport activity and cellular redox homeostasis in Arabidopsis. Plant Cell Physiol 59:1630–1642

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