



## Tansley review

# Elucidating the molecular mechanisms mediating plant salt-stress responses

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## Summary

Excess soluble salts in soil (saline soils) are harmful to most plants. Salt imposes osmotic, ionic, and secondary stresses on plants. Over the past two decades, many determinants of salt tolerance and their regulatory mechanisms have been identified and characterized using molecular genetics and genomics approaches. This review describes recent progress in deciphering the mechanisms controlling ion homeostasis, cell activity responses, and epigenetic regulation in plants under salt stress. Finally, we highlight research areas that require further research to reveal new determinants of salt tolerance in plants.

## I. Introduction

Saline soil is a severely adverse environmental factor that affects seed germination, crop growth, and productivity. More than 800 million hectares of land (*c.* 6% of the world's total land area) is affected by excess salt concentrations (Munns & Tester, 2008), and this problem continues to worsen. Irrigated cultivated farm land also is threatened by secondary salt, which accumulates in irrigated soils as water evaporates. In certain areas, it may be economically viable to leach these secondary salts into groundwater.

Most plant/crop species are glycophytes, which are not salt-tolerant and are adversely affected by high salt. Salt stress is commonly caused by high concentrations of sodium ( $\text{Na}^+$ ) and chloride ions in soil (Ismail *et al.*, 2014). There are three salt-induced stress pathways: osmotic stress, ionic stress, and secondary stress. Osmotic stress results from the effect of high salt

concentrations in the soil and/or water. Excess soluble salts in the soil reduce the water potential (i.e. reduce water availability to the plant) at the root surface, thereby reducing plant uptake of water (Hasegawa *et al.*, 2000), which leads to water deficit in plants. Ionic stress results from the toxic effect of salt ions inside plant cells. Salts taken up by roots undergo long-distance transport in the transpiration stream to shoots, and eventually accumulate in leaves (Munns & Tester, 2008). High concentrations of  $\text{Na}^+$  in the cytoplasm disrupt the uptake of other ions into plant cells, which has adverse effects on many metabolic pathways. For example, potassium ( $\text{K}^+$ ) is important for the catalytic activities of many enzymes (Fu & Luan, 1998; Lazof & Bernstein, 1999). Osmotic and ionic stresses can cause secondary stresses in plants, including the accumulation of toxic compounds and disruption of nutrient balances. Reactive oxygen species (ROS) such as hydroxyl radicals, hydrogen peroxide, and superoxide anions accumulate in plant cells

under salt stress (Shen *et al.*, 1997; Tsugane *et al.*, 1999; Hong *et al.*, 2000; Zhu *et al.*, 2007; Hazman *et al.*, 2015; Li *et al.*, 2015). ROS can severely damage cellular structures and macromolecules such as enzymes, DNA, and lipids (Wang *et al.*, 2009a; Arya *et al.*, 2012; Gollmack *et al.*, 2014; Genisel *et al.*, 2015).

Determining plant salt-stress response mechanisms will provide valuable information for improving crop salt tolerance by genetic engineering. Significant progress in understanding plant salt-stress responses has been achieved recently through molecular genetics and genomics analysis. Here, we will discuss recent work on salt acclimation mechanisms, ion homeostasis, and cell activity regulation under salt stress in plants.

## II. Sensing salt stress

Salt stress can induce osmotic and/or ionic stresses in plants. It is not completely understood how excess  $\text{Na}^+$  is sensed by plants, and it is not known whether plants have a  $\text{Na}^+$  sensor or receptor. Osmotic and ionic stresses lead to elevated cytosolic free calcium concentrations ( $[\text{Ca}^{2+}]_{\text{cyt}}$ ). However, salt-induced increases in  $[\text{Ca}^{2+}]_{\text{cyt}}$  in Arabidopsis roots generally occur in the cortical and endodermal cell layers (Choi *et al.*, 2014), whereas mannitol-induced increases in  $[\text{Ca}^{2+}]_{\text{cyt}}$  in roots generally occur in the epidermal cell layer (Kiegle *et al.*, 2000). These results suggest that excess salt may be perceived by  $\text{Na}^+$  and osmotic sensors in different cell types. Arabidopsis roots subjected to excess NaCl accumulate high  $\text{Na}^+$  concentrations in root tissue within the first 2 min of exposure (Essah *et al.*, 2003), whereas  $\text{Na}^+$  efflux from the root tissue starts at 10 min (Bose *et al.*, 2015). These results suggest that excess  $\text{Na}^+$  is rapidly sensed by plants, which triggers downstream sodium-stress responses.

Salt treatment activates the salt overly sensitive (SOS) pathway (exports  $\text{Na}^+$  ions out of cells and is highly conserved in plants) within 2 h, thereby activating SOS2 kinase and SOS1  $\text{Na}^+$  antiporter (increases  $\text{Na}^+$  efflux) (Lin *et al.*, 2009). Salt stress also triggers abscisic acid (ABA) pathways and osmotic stress signaling. Salt treatment increases ABA concentrations in plant cells (Duan *et al.*, 2013; Geilfus *et al.*, 2015) and activates sucrose nonfermenting 1-related protein kinase 2 (SnRK2) kinase activity (Krzywińska *et al.*, 2016), and salt treatment of a *protein phosphatase 2c (pp2c)* double mutant (*abi1-2 pp2ca-1*) leads to higher SnRK2 kinase activity (Krzywińska *et al.*, 2016). However, some evidence also indicates that salt/osmotic stress-mediated SnRK2 activation is independent of ABA signaling (Boudsocq *et al.*, 2007; Zhang H. *et al.*, 2011; Zhang *et al.*, 2016). These results suggest that salt stress-induced activation of osmotic signaling proceeds possibly through both ABA-dependent and -independent pathways and may be independent of a  $\text{Na}^+$  sensor.

The expression of many stress-responsive genes is induced by both salt and osmotic stress (e.g. by mannitol and polyethylene glycol (PEG)). This suggests that excess salt induces both ionic and osmotic stresses (Sewelam *et al.*, 2014). Transcriptome studies in Arabidopsis indicate that osmotic stress induces 1118 genes and salt stress induces 932 genes, with 435 overlapping genes; osmotic and salt stresses repress 364 and 367 genes, respectively, with 154 overlapping genes (Sewelam *et al.*, 2014). These results indicate

that salt stress is probably perceived by both osmotic and  $\text{Na}^+$  sensors, which triggers both osmotic and ionic signaling.

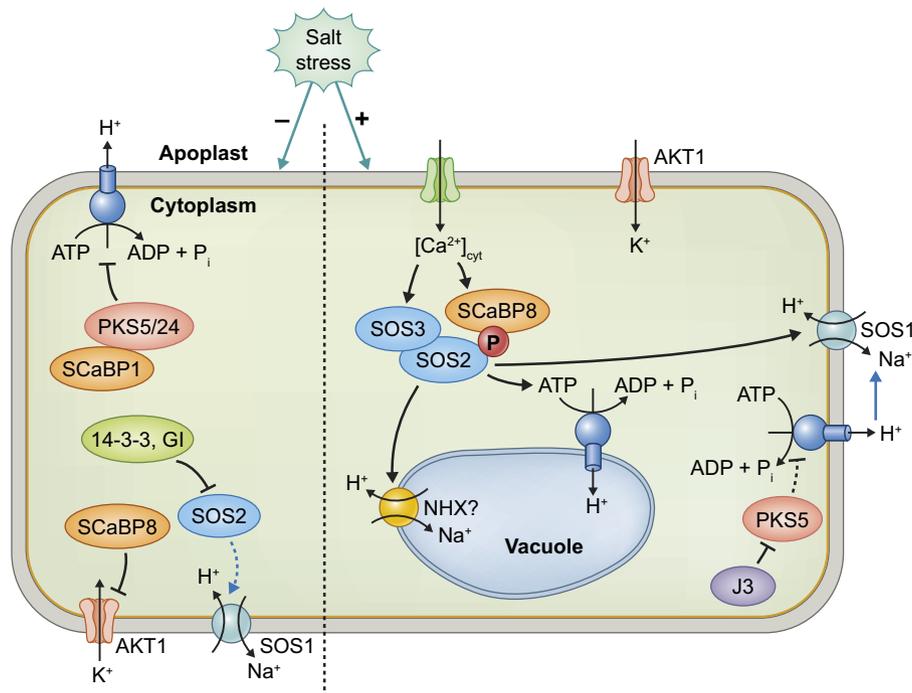
Evidence is emerging that the plant cell wall is involved in sensing of and response to salt stress (Li *et al.*, 2013; Van der Does *et al.*, 2017). The plant cell wall not only protects the cell from biotic and abiotic stresses but also is the organelle that first perceives and responds to environmental challenges (Parrotta *et al.*, 2015). Maintenance and sensing of active cell wall integrity (CWI) are critical for both stress protection and response. Three plasma membrane-located Arabidopsis leucine-rich repeat receptor kinases (LRR-RKs), LRR-RK MALE DISCOVERER 1-INTERACTING RECEPTOR LIKE KINASE 2/LEUCINE-RICH REPEAT KINASE FAMILY PROTEIN INDUCED BY SALT STRESS (MIK2), FEI1 and FEI2 (named after the Chinese word for fat), are key regulators in CWI sensing and the salt stress response (Xu *et al.*, 2008; Van der Does *et al.*, 2017). In addition to the CWI status perception, modulation of cell wall-related processes is also involved in the response to salt stress. Lignin content and composition are changed upon exposure to abiotic and biotic stresses (Moura *et al.*, 2010). A bi-functional protein, short root in salt medium (RSA3)/MURUS3 (MUR3)/KATAMARI1 (KAM1)-encoded xyloglucan galactosyltransferase, which is involved in cell wall biosynthesis and maintenance of endomembrane organization, minimizes cellular damage by limiting the ROS concentration in the cell and regulates stress-related gene expression under salt stress (Li *et al.*, 2013). Therefore, a possible salt-sensing mechanism would be that cell wall damage and component change upon salt stress trigger the machinery of cell wall maintenance and CWI sensing, which would further activate the plant salt response and avoidance mechanism and regulate root growth and architecture.

## III. Ion homeostasis regulation

Maintaining cellular ion homeostasis is an important adaptive trait of salt-tolerant plants during the response to excess ions. A suitable  $\text{K}^+:\text{Na}^+$  ratio in the cytoplasm can be obtained by reducing cytoplasmic  $\text{Na}^+$  and increasing cytoplasmic  $\text{K}^+$ , which prevents cellular damage and nutrient deficiency (Niu *et al.*, 1995; Serrano *et al.*, 1999). Mechanisms to reduce cytoplasmic  $\text{Na}^+$  include restricting  $\text{Na}^+$  uptake, increasing  $\text{Na}^+$  efflux, and compartmentalizing  $\text{Na}^+$  in the vacuole (Fig. 1).

Specific transport systems for  $\text{Na}^+$  uptake have not been identified in plant cells.  $\text{Na}^+$  influx across the plasma membrane probably occurs via the high-affinity  $\text{K}^+$  channel (HKT), the weakly voltage-dependent nonselective cation channel (NSCC), the low-affinity  $\text{K}^+$  channel (e.g. Arabidopsis  $\text{K}^+$  Transporter1 (AKT1)), the nonselective outward-rectifying conductance (NORC), and/or the voltage-independent channel (VIC) (Blumwald *et al.*, 2000; Tuteja, 2007). All of these channels can mediate  $\text{Na}^+$  and  $\text{K}^+$  influx into plant cells, although some channels display more selectivity for  $\text{K}^+$  than  $\text{Na}^+$  (Blumwald *et al.*, 2000; Tuteja, 2007).

HKT1 is considered a key determinant of plant salinity tolerance in response to salt stress (Platten *et al.*, 2006). HKT1 may improve salt tolerance by reducing  $\text{Na}^+$  accumulation in shoot tissue, which



**Fig. 1** Maintaining ionic homeostasis in the plant cell. Under normal conditions (without salt stress), 14-3-3 and GIGANTEA (GI) proteins negatively regulate the salt overly sensitive (SOS) pathway by interacting with and repressing SOS2 kinase activity, and the activity of plasma membrane (PM) H<sup>+</sup>-ATPase is inhibited by SOS3-like calcium-binding protein1 (ScaBP1)/calcineurin B-like protein2 (CBL2) (calcium-binding protein) and SOS2-like protein5 (PKS5)/SOS2-like protein24 (PKS24) (serine/threonine protein kinases). Arabidopsis K<sup>+</sup> transporter1 (AKT1) activity is repressed by ScaBP8. Under salt stress, the SOS pathway is activated by a calcium signal, and ScaBP8 is phosphorylated by SOS2, which might dissociate from AKT1, a potassium channel. SOS1 sodium transport requires a proton gradient created by PM H<sup>+</sup>-ATPases whose activity is activated by DnaJ homolog 3 (J3; heat shock protein 40-like) through inhibition of PKS5 kinase activity. Vacuolar partitioning of Na<sup>+</sup> is mediated by the vacuolar Na<sup>+</sup>/H<sup>+</sup> exchanger (NHX) (a vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter) driven by the proton gradient created by vacuolar H<sup>+</sup>-ATPases and H<sup>+</sup>-pyrophosphatases. The activity of the vacuolar H<sup>+</sup>-ATPase and Na<sup>+</sup>/H<sup>+</sup> exchanger can be activated by SOS2.

protects leaves from Na<sup>+</sup> toxicity (Ren *et al.*, 2005; Sunarpi *et al.*, 2005; Horie *et al.*, 2009; Møller *et al.*, 2009). Arabidopsis *HKT1* is strongly expressed in root stelar cells and leaf vascular tissues (Mäser *et al.*, 2002). The *bkt1* mutants are sensitive to salt stress, and accumulate more Na<sup>+</sup> in shoots and less Na<sup>+</sup> in roots, suggesting that HKT1 functions in the distribution of Na<sup>+</sup> between root and shoot by retrieving Na<sup>+</sup> from the root-to-shoot xylem sap (Rus *et al.*, 2004; Davenport *et al.*, 2007). Tissue-specific *HKT1* expression, such as in the pericycle or vascular bundle, enhances salt tolerance in the whole plant (Møller *et al.*, 2009). *HKT1* mutations suppress the salt-hypersensitive phenotypes in both *sos2* and *sos3* mutants, suggesting that HKT1 coordinates with the SOS pathway to modulate Na<sup>+</sup>/K<sup>+</sup> homeostasis in plant cells (Rus *et al.*, 2001, 2004). Genome-wide association studies (GWASs) and quantitative trait locus (QTL) analyses to determine genetic variations in plant salt tolerance have enabled the cloning of many *HKT* loci in different plant species, indicating that selection of HKT proteins for plant salt resistance has occurred during evolution and in plant breeding programs (Ren *et al.*, 2005; Asins *et al.*, 2013; Ariyaratna *et al.*, 2016).

Although little is known about the regulatory mechanisms that restrict Na<sup>+</sup> uptake, the mechanisms mediating Na<sup>+</sup> efflux are well known in Arabidopsis. A Ca<sup>2+</sup>-dependent Na<sup>+</sup> efflux pathway was established from genetic screens of *sos* mutants subjected to salt stress. In this pathway, the helix E-loop-helix F (EF-hand) calcium-

binding proteins SOS3 and SOS3-LIKE CALCIUM BINDING PROTEIN8/CALCINEURIN B-LIKE PROTEIN10 (ScaBP8/CBL10) sense and decode the cytosolic calcium signal elicited by high salt concentrations (Liu & Zhu, 1998; Ishitani *et al.*, 2000; Quan *et al.*, 2007; Zhu, 2016). SOS3/ScaBP8 then interacts with and activates the serine/threonine protein kinase SOS2 in the plasma membrane (Halfter *et al.*, 2000; Quan *et al.*, 2007; Lin *et al.*, 2009). SOS3 functions primarily in roots, whereas ScaBP8 functions primarily in shoots (Quan *et al.*, 2007; Zhu, 2016). ScaBP8 activity is important during vegetative development under salt stress, and this protein functions independently of the SOS pathway for reproductive development (Monihan *et al.*, 2016). Activated SOS2 phosphorylates and activates the plasma membrane Na<sup>+</sup>/H<sup>+</sup> antiporter SOS1 (Shi *et al.*, 2000; Qiu *et al.*, 2002; Lin *et al.*, 2009). SOS1 is a key determinant of Na<sup>+</sup> transport from the cytoplasm to the apoplast, which is driven by the proton gradient created by the plasma membrane H<sup>+</sup>-ATPase (PM H<sup>+</sup>-ATPase) (Schachtman & Liu, 1999; Shi *et al.*, 2000). SOS1 transport activity is autoinhibited by an intermolecular interaction between its transmembrane and cytosolic domains (Núñez-Ramírez *et al.*, 2012). SOS2 phosphorylates SOS1 at serine 1044 in the C-terminal auto-inhibitory domain (Quintero *et al.*, 2011), which relieves SOS1 autoinhibition and results in SOS1 activation (Quintero *et al.*, 2011; Jarvis *et al.*, 2014). SOS1 also is activated by Mitogen-activated protein kinase (MAPK6/MPK6)

phosphorylation, which occurs via phosphatidic acid (PA)-mediated salt-stress signaling (Yu *et al.*, 2010).

Under normal conditions (without salt stress), the SOS pathway is inhibited by 14-3-3 and GIGANTEA (GI) proteins, which interact with SOS2 and repress its kinase activity (Kim *et al.*, 2013; Zhou *et al.*, 2014b). The ABA-INSENSITIVE 2 (ABI2) protein phosphatase 2C interacts with SOS2, and may have a role in inhibiting SOS2 kinase activity (Ohta *et al.*, 2003). The PM H<sup>+</sup>-ATPase activity is repressed by SCABP1/CBL2–SOS2-LIKE PROTEIN KINASE5 (PKS5) (Fuglsang *et al.*, 2007; Yang *et al.*, 2010). Under salt stress, both 14-3-3 and GI are degraded by the 26S proteasomal pathway (Kim *et al.*, 2013; Tan *et al.*, 2016), and PKS5 activity is repressed to release PM H<sup>+</sup>-ATPase activity (Yang *et al.*, 2010). Under salt stress, free unsaturated fatty acids activate the PM H<sup>+</sup>-ATPase by directly binding its C-terminus in Arabidopsis root cells (Han *et al.*, 2017), and the accumulation of fatty acids is required for plant salt resistance (Zhang *et al.*, 2012).

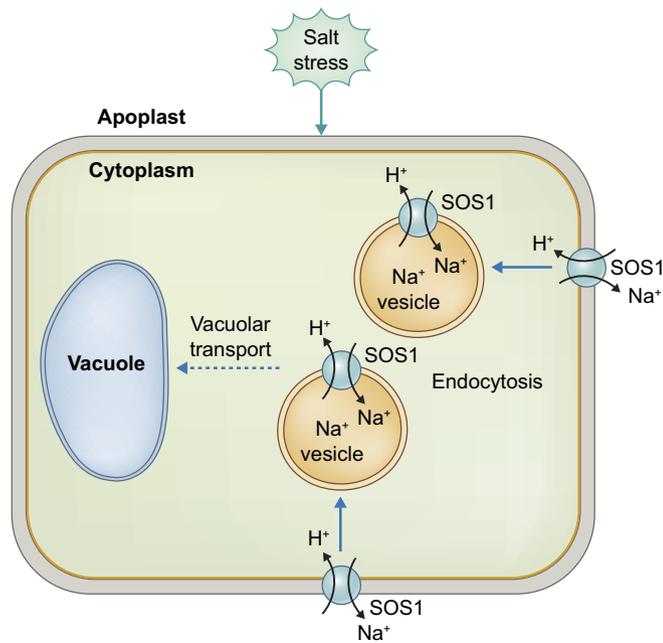
SOS2 has a central role in the SOS pathway. In Arabidopsis, SOS2 kinase is activated by NaCl, but not by KCl or mannitol (Lin *et al.*, 2009). Structural analysis of SOS2 indicates that its kinase activity requires the coordinated release of the self-inhibitory FISL motif (a 21-amino acid SOS3 binding sequence in SOS2, sequence analyses indicates that residues A, F, I, S, L and F are conserved, hence the name FISL motif) and the activation loop (Guo *et al.*, 2001; Chaves-Sanjuan *et al.*, 2014). However, it is not completely understood how SOS2 kinase activity is regulated with and without salt stress. The SOS pathway can be regulated by ROS signals (Zhou *et al.*, 2012), as the stability of SOS1 mRNA is regulated by ROS stress (Chung *et al.*, 2008). SOS2 interacts with CATALASE 2 (CAT2) and CAT3, suggesting that SOS2 is a key node connecting H<sub>2</sub>O<sub>2</sub> signaling and salt-stress responses (Verslues *et al.*, 2007). SOS2 phosphorylates ethylene-insensitive3 (EIN3) to enhance target gene expression; therefore, SOS2 might link ethylene signaling with salt-stress responses (Quan *et al.*, 2017).

The SOS pathway is crucial for the regulation of plant Na<sup>+</sup>/K<sup>+</sup> homeostasis (Zhu, 2016). SCABP8 inhibits the activity of the K<sup>+</sup> channel AKT1 by direct interaction with the AKT1 C-terminus (Ren *et al.*, 2013). SOS2 phosphorylates SCABP8, which stabilizes the association of SOS2 with the plasma membrane under salt stress (Lin *et al.*, 2009; Du *et al.*, 2011). It is unknown whether SOS2 phosphorylation of SCABP8 reduces the interaction between SCABP8 and AKT1 and relieves AKT1 activity in response to salt stress, which in turn enhances K<sup>+</sup> uptake. In this case, SOS2-mediated phosphorylation of SOS1 and SCABP8 activates both SOS1 and AKT1, thereby maintaining the Na<sup>+</sup>/K<sup>+</sup> homeostasis in the cytosol.

Overexpression of genes in the SOS pathway slightly increases plant salt tolerance (Yang *et al.*, 2009; Ma *et al.*, 2014). One possible explanation is that SOS2 and SOS3 cannot function optimally with SOS1 in shoots because SOS3 functions primarily in roots. It is also possible that previously unidentified factors interact with SOS genes during the salt-stress acclimation responses in plants. Optimum co-expression of SOS genes and unidentified factors in specific cell types/tissues may effectively improve salt tolerance.

Vacuolar partitioning of Na<sup>+</sup> is a primary adaptive mechanism for reducing cytoplasmic ion toxicity in plants grown under high salt concentrations; this mechanism is conserved in halophytes and glycophytes (Blumwald *et al.*, 2000; Hasegawa *et al.*, 2000). Vacuolar Na<sup>+</sup> compartmentalization is mediated by the vacuolar Na<sup>+</sup>/H<sup>+</sup> exchanger (NHX), which is driven by the proton gradient created by vacuolar H<sup>+</sup>-ATPase and H<sup>+</sup>-pyrophosphatase (Drozdowicz & Rea, 2001; Brini & Masmoudi, 2012). SOS2 positively regulates vacuolar H<sup>+</sup>-ATPase and Na<sup>+</sup>/H<sup>+</sup> exchanger activity in response to Na<sup>+</sup> detoxification in the cytosol (Qiu *et al.*, 2004; Batelli *et al.*, 2007). SCABP8/CBL10 interacts with SOS2 on the vacuolar membrane (Kim *et al.*, 2007), suggesting that SCABP8 is involved in the vacuolar partitioning of Na<sup>+</sup>. However, there is debate in the literature regarding which vacuolar NHX transports Na<sup>+</sup>. An early study reported that NHX1 is involved in vacuolar Na<sup>+</sup> compartmentalization and plant salt tolerance (Apse *et al.*, 2003). Recent studies report that NHX1 and NHX2 mediate K<sup>+</sup> uptake into vacuoles; Arabidopsis *nhx1* and *nhx2* null mutants display no changes in salt sensitivity and Na<sup>+</sup> sequestration in the vacuoles (Basil *et al.*, 2011; Barragán *et al.*, 2012). It would be interesting to determine whether the potassium transport activity of NHX1 and NHX2 is mediated by Na<sup>+</sup> concentration changes in the cytosol or whether NHX1 and NHX2 exchangers may primarily mediate K<sup>+</sup>/H<sup>+</sup> exchange; however, at certain Na<sup>+</sup> concentrations they may have Na<sup>+</sup>/H<sup>+</sup> exchanger activity.

Salt stress induces endocytosis (Hamaji *et al.*, 2009). Recently, intracellular membrane dynamics have been shown to function in plant salt tolerance (Fig. 2). Active vesicle movement and Na<sup>+</sup> accumulation in the vacuole are observed under salt stress in Arabidopsis root tip cells and in suspension-culture cells (Hamaji *et al.*, 2009). In salt-acclimated tobacco (*Nicotiana tabacum*) cells, Na<sup>+</sup> compartmentalization in vacuoles may be mediated by vesicle trafficking (Garcia *et al.*, 2015). Overexpression of *AtRab7* (a vesicle trafficking-regulating gene, also named *AtRabG3e*), which is involved in vesicle trafficking regulation in Arabidopsis, accelerates endocytosis in protoplasts, roots, and leaves; transgenic plants accumulate vacuolar Na<sup>+</sup> and exhibit enhanced salt tolerance (Mazel *et al.*, 2004). A synaptobrevin-like vesicle soluble N-ethylmaleimide-sensitive factor attachment protein receptor (v-SNARE), vesicle-associated membrane protein 711C (VAMP711C), mediates vesicle docking at the vacuole in response to salt stress in Arabidopsis. Suppression of *VAMP711C* expression enhances salt tolerance (Leshem *et al.*, 2006). A knockout mutant of *VAM3* (a Q-SNARE located in the vacuolar and prevacuolar compartment) displays enhanced tolerance to salt stress as a result of reduced Na<sup>+</sup> transport to shoots (Hamaji *et al.*, 2009). Phosphatidylinositol (PtdIns) and its phosphorylated derivatives are involved in intracellular membrane trafficking and endocytotic regulation. Phosphatidylinositol 5-phosphatase9 (*AtSPTase9*), a PtdIns-modifying protein that hydrolyzes the 5' position of the inositol ring, is involved in regulating vesicle trafficking in response to salt stress (Golani *et al.*, 2013). It is likely that accelerating endocytosis under salt stress enhances Na<sup>+</sup> compartmentalization in the vacuole. Alternatively, the accumulation of cytosolic vesicles by accelerating endocytosis and reducing vacuole membrane fusion may increase the number of Na<sup>+</sup>/H<sup>+</sup> antiporters (such as SOS1),



**Fig. 2** Increase of vesicle accumulation in the cytosol under salt stress. Salt induces the accumulation of cytosolic vesicles by accelerating endocytosis and reducing vacuole membrane fusion, which may be a mechanism for adapting to salt stress by increasing the number of Salt Overly Sensitive1 (SOS1)  $\text{Na}^+/\text{H}^+$  antiporters in the cytosol.

thereby enhancing  $\text{Na}^+$  uptake into vesicles and reducing  $\text{Na}^+$  concentrations in the cytosol (Fig. 2).

#### IV. Metabolite and cell activity responses to salt stress

##### 1. Osmotic stress pathways and accumulation of compatible osmolytes

Activation of salt-mediated osmotic stress pathways (both short-term and long-term) induces the biosynthesis and accumulation of compatible osmolytes to reduce the cell osmotic potential and stabilize proteins and cellular structures; this is a primary adaptive strategy (Yancey *et al.*, 1982; Blumwald, 2003). These metabolic reactions are common to all osmotic stress pathways, and are not specifically induced by excess salt (Munns, 2002, 2005). Compatible osmolytes can reduce water loss under short-term osmotic stress and enhance cell turgor and cell expansion under long-term osmotic stress (continued growth under salt stress) (Apse & Blumwald, 2002).

The type of compatible osmolytes synthesized under salt stress is at least partly species and tissue specific, and many of these compounds accumulate under heat, drought, and freezing stresses (Parvanova *et al.*, 2004; Yancey, 2005; Pirzad *et al.*, 2011; Sailaja *et al.*, 2014). Several classes of compatible osmolytes accumulate under salt stress (Table 1): charged metabolites, including proline, glycine betaine,  $\beta$ -alanine betaine, choline-*O*-sulfate, hydroxyproline, dimethylsulfonium propionate (DMSP), and putrescine (Hanson *et al.*, 1994; Summers *et al.*, 1998; Bouchereau *et al.*, 1999; Hu *et al.*, 2015); polyols, including glucosylglycerol, glycerol, mannitol, *myo*-inositol, ononitol, pinitol, and sorbitol

(Nelson *et al.*, 1999; Ferjani *et al.*, 2003; Goyal, 2007; Lee *et al.*, 2008; Conde *et al.*, 2011; Gil *et al.*, 2011; Bertrand *et al.*, 2015); sugars, including sucrose and fructose (Liu & Staden, 2001; Gil *et al.*, 2011); complex sugars, including trehalose, raffinose, and fructans (Page-Sharp *et al.*, 1999; Kerepesi & Galiba, 2000; Pommerrenig *et al.*, 2007; Nedjimi, 2011; Redillas *et al.*, 2012); and ions such as  $\text{K}^+$  (Rodríguez & Drew, 1997). Some of the metabolites are commonly accumulated in many plant species in both roots and leaves upon salt stress, such as proline, glycine betaine, polyamine, mannitol, glucose, fructose, and trehalose, and sugar mainly accumulates in shoot tissue; however, some of them are probably accumulated in specific species, such as choline-*O*-sulfate,  $\beta$ -alanine betaine, and hydroxyproline in Plumbaginaceae. A few metabolites are specifically accumulated in marine algae and *Dunaliella parva*, such as dimethylsulfonium propionate, glucosylglycerol and glycerol. In addition to functions in osmotic adjustment and detoxification, these metabolites may also directly bind to and activate/inactivate enzymes to regulate salt response. However, these activities require further study.

##### 2. ROS signaling and antioxidants involved in salt-stress responses

Salt-induced secondary stresses include the generation of ROS. Low ROS concentrations can function as a signal that activates salt-stress responses. High ROS concentrations damage proteins, lipids, DNA, and carbohydrates (Miller *et al.*, 2010). Therefore, the ROS concentration must be tightly regulated in plant cells. Detoxification signaling can mediate ROS removal and damage control and repair. Salt stress induces enzymatic and nonenzymatic systems to mitigate ROS stress (Table 2) (Gill & Tuteja, 2010; Miller *et al.*, 2010). Enzymatic scavengers include superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), guaiacolperoxidase (GPX), guaiacol peroxidase (GPOX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), glutathione peroxidase (GR), and glutathione S-transferase (GST) (Sreenivasulu *et al.*, 2000; Meloni *et al.*, 2003; Amako & Ushimaru, 2009; Das & Roychoudhury, 2014; Begaramorales *et al.*, 2015; Li *et al.*, 2015; Wang *et al.*, 2017). ROS are mainly comprised of free radicals including  $\text{O}_2^{\cdot-}$  (superoxideradical),  $\text{OH}^{\cdot}$  (hydroxylradical) and nonradicals including  $^1\text{O}_2$  (singlet oxygen) and  $\text{H}_2\text{O}_2$  (hydrogenperoxide) (Das & Roychoudhury, 2014). SOD is the most effective scavenger of reactive oxygen species and it forms the first line of defense against damage caused by ROS under environmental stress (Das & Roychoudhury, 2014). SOD generates  $\text{H}_2\text{O}_2$  from  $\text{O}_2^{\cdot-}$ ;  $\text{H}_2\text{O}_2$  is further detoxified to  $\text{H}_2\text{O}$  by APX, CAT, and GPX (Das & Roychoudhury, 2014; Ismail *et al.*, 2014). Some enzymes are required to produce nonenzymatic scavengers. DHAR, MDHAR and GR are involved in the regeneration of ascorbic acid from oxidation products, including dehydroascorbate (DHA), monodehydroascorbate (MDHA) and oxidized glutathione (GSSG). GST generates glutathione (GSH) from conjugation of an electrophilic xenobiotic compound with tripeptide glutathione (Gill & Tuteja, 2010). Nonenzymatic scavengers include ascorbic acid (ASH), alkaloids, carotenoids,

**Table 1** Representative osmolytes involved in osmotic adjustment under salt stress in plants

Osmolytes	Probable function	Species	Tissue-specific accumulation	Reference	
Charged metabolites	Proline	Osmotic adjustment; scavenger of ROS; stabilization of protein, membrane and subcellular structure	A variety of plant species, such as <i>Arabidopsis thaliana</i> , salt <i>Distichlis spicata</i> , <i>Helianthus annuus</i> and <i>Oryza sativa</i>	Seedling, seed	Vanrensburg <i>et al.</i> (1993); reviewed by Kishor <i>et al.</i> (2005); reviewed by Mansour & Ali (2017)
	Glycine betaine	Osmotic adjustment; decrease of ROS concentration and lipid peroxidation; stabilization of membrane and macromolecule	A variety of plant species, such as <i>Beta vulgaris</i> , cyanobacterium and <i>Nicotiana tabacum</i>	Young leaf, root, suspension cell	Makela <i>et al.</i> (2000); Banu <i>et al.</i> (2009); Tsutsumi <i>et al.</i> (2015); Yamada <i>et al.</i> (2015)
	Choline-O-sulfat, $\beta$ -alanine betaine, hydroxyproline	Osmotic adjustment; sulfate detoxification	Family Plumbaginaceae	Leaf, shoot	Reviewed by Rhodes & Hanson (1993); Hanson <i>et al.</i> (1994)
	Dimethylsulfonium propionate	Osmotic adjustment	Marine algae	Marine alga cell	Giordano <i>et al.</i> (2005); Ito <i>et al.</i> (2011)
	Polyamine	Osmotic adjustment; decrease of membrane leakage; modulation of activity of ion channel; activation of antioxidant enzyme	A variety of plant species, such as <i>Arabidopsis thaliana</i> , <i>Oryza sativa</i> and <i>Spinacia oleracea</i>	Shoot, root	Reviewed by Groppa & Benavides (2008); Zapata <i>et al.</i> (2017)
Polyols	Mannitol	Osmotic adjustment; stabilization of macromolecular structure; scavenger of ROS; protection of photosynthetic apparatus	A variety of plant species, such as marine algae and <i>Arabidopsis thaliana</i>	Marine alga cell, seedling	Reviewed by Bohnert & Jensen (1996); Shen <i>et al.</i> (1997); Chan <i>et al.</i> (2011); reviewed by Slama <i>et al.</i> (2015)
	Glucosylglycerol	Osmotic adjustment; sustainability of cell division	Marine cyanobacterium	Cyanobacterium cell	Borowitzka <i>et al.</i> (1980); Ferjani <i>et al.</i> (2003)
	Glycerol	Osmotic adjustment	<i>Dunaliella parva</i> ,	<i>Dunaliella parva</i> cell	Ben-Amotz & Avron (1973)
	Sorbitol	Osmotic adjustment; stabilization of protein	<i>Plantago coronopus</i> , <i>Prunus cerasus</i>	Leaf, phloem, seedling	Ahmad <i>et al.</i> (1979); Smekens & Tienderen (2001); Pommerrenig <i>et al.</i> (2007)
Soluble sugars	Sucrose	Osmotic adjustment; affecting redox homeostasis; protection of macromolecular structure; signal molecule	<i>Plantago major</i> , <i>Solanum tuberosum</i> , etc.	Cyanobacteria cell, leaf, phloem	Reviewed by Gupta & Kaur (2005); Eggert <i>et al.</i> (2016)
	Glucose, fructose	Osmotic adjustment; carbon energy reserve; signal molecule; protecting lipid bilayer	<i>Oryza sativa</i> , <i>Solanum lycopersicum</i> , etc.	Root, leaf, fruit	Arbona <i>et al.</i> (2005); reviewed by Gupta & Kaur (2005); Yin <i>et al.</i> (2010); Boriboonkaset <i>et al.</i> (2013)
Complex sugars	Raffinose	Osmotic adjustment	<i>Coffea arabica</i>	Leaf	dos Santos <i>et al.</i> (2011)
	Trehalose	Osmotic adjustment; stabilization of membrane and protein	<i>Oryza sativa</i> , <i>Phaseolus vulgaris</i> , <i>Zea mays</i> , etc.	Leaf, root	Crowe <i>et al.</i> (1984); Fougere <i>et al.</i> (1991); Garcia <i>et al.</i> (1997); Henry <i>et al.</i> (2015)

flavonoids, GSH, phenolic compounds, and tocopherol (Hernández *et al.*, 2000; De Pascale *et al.*, 2003; Huang *et al.*, 2005; Zhang X.X. *et al.*, 2011; Borghesi *et al.*, 2011; Petridis *et al.*, 2012; Abdallah *et al.*, 2016). Overexpression of an enzyme either removing ROS or accumulating ROS scavengers may increase plant salt tolerance (Das & Roychoudhury, 2014). The enzymatic and nonenzymatic systems are not specific for salt stress. Toxic ROS accumulates in plant cells under long-term stress. Damage control and repair systems are largely conserved

across plant genera; therefore, pretreatment with one type of stress condition can enhance resistance to other stresses. Overexpression of a single gene in detoxification signaling can confer resistance or tolerance to most abiotic stresses in plants (Zhang *et al.*, 2014).

### 3. Small molecule signals

Certain small molecules function as signals that trigger downstream salt-stress responses. Proline regulates the expression of stress-

responsive genes to improve plant salt tolerance (Khedr *et al.*, 2003). Nitric oxide (NO) increases the activities of vacuolar H<sup>+</sup>-PPase and H<sup>+</sup>-ATPase in response to NaCl stress (Zhang Y. *et al.*, 2006). Carbon monoxide (CO) enhances salt tolerance in wheat (*Triticum aestivum*) by upregulating antioxidant defense pathways and maintaining ion homeostasis (Xie *et al.*, 2008). Phosphatidic acid (PA) mediates salt-stress signaling by stimulating the activity of MPK6, thereby upregulating SOS1 antiporter activity (Yu *et al.*, 2010). Hydrogen sulfide (H<sub>2</sub>S) pretreatment can enhance tolerance to salinity and osmotic stresses through coordinated regulation of the SOS and antioxidant pathways (Christou *et al.*, 2013). The small molecule  $\gamma$ -aminobutyric acid (GABA) modulates flux through carbon pathways under salt stress (Renault *et al.*, 2013; Bao *et al.*, 2015). Melatonin can mitigate the inhibitory effects of salt stress by upregulating the expression of genes that are downregulated by salt stress (Wei *et al.*, 2015). Melatonin accumulation in plant cells confers salt tolerance by reducing ROS and delaying leaf senescence (Liang *et al.*, 2015). Free unsaturated fatty acids stimulate the activity of the PM H<sup>+</sup>-ATPase under salt stress (Han *et al.*, 2017). Currently, it is not understood in detail how these small molecules enhance stress tolerance in plants. Considering the importance of small molecule signals in the control of salt response and plant development, identifying more components and unveiling the molecular regulation mechanism will enable us to better understand how plants recognize and adapt to salt stress. This is an important field for future research.

#### 4. Cytoskeletal dynamics

Salt stress affects many cell activities. Recent studies suggest that the cytoskeleton is a major player in plant responses to salt stress. The architecture of the cell's cytoskeleton is determined by microtubules (MTs), microfilaments (MFs), and MT/MF-interacting proteins. The plant cytoskeleton participates in many cellular processes such as membrane anchorage, extracellular and intracellular motility, cell division, and growth (Laporte *et al.*, 2003; Wasteneys & Yang, 2004). The cytoskeleton is highly dynamic as a consequence of rapid MT/MF polymerization and depolymerization, and can be adaptively reorganized in plant cells in response to abiotic stresses including salt stress (Shoji *et al.*, 2006; Wang *et al.*, 2007, 2011).

Under salt stress, MTs first undergo depolymerization followed by subsequent polymerization (Wang *et al.*, 2007). MT reorganization is important for plant salt tolerance (Wang *et al.*, 2007, 2011). Short-term salt stress in maize (*Zea mays*) roots activates MT reorientation from transverse to parallel (Blancaflor & Hasenstein, 1995). Long-term salt stress in Arabidopsis affects cortical MT organization and inhibits right-handed helical growth of roots as a result of altered microtubule arrays (Shoji *et al.*, 2006). Degradation of the MT-associated protein SPIRAL1 (SPR1) is required for rapid MT disassembly under salt stress (Wang *et al.*, 2011). MT reorganization is regulated by the ras homologous oncogenes (Rho)-related GTPase from plants (ROP2) and the ROP-interactive

**Table 2** Representative enzymatic scavengers to mitigate the effects of reactive oxygen species (ROS) under salt stress in plants

Enzymatic scavengers	Reaction catalyzed	Species	Tissue	References
SOD	$O_2^{\cdot-} + O_2^{\cdot-} + 2H^+ \rightarrow 2H_2O_2 + O_2$	<i>Vitis vinifera</i> , <i>Lactuca sativa</i> , <i>Oryza sativa</i> , <i>Helianthus annuus</i> , <i>Beta vulgaris</i> , <i>Triticum aestivum</i>	Seedling, leaf, root	Jacoby <i>et al.</i> (2010); Carassay <i>et al.</i> (2012); reviewed by Das & Roychoudhury (2014); Ikbali <i>et al.</i> (2014); Mostofa <i>et al.</i> (2015); Rahman <i>et al.</i> (2016); Hossain <i>et al.</i> (2017); Arora & Bhatla (2017)
APX	$H_2O_2 + AA \rightarrow 2H_2O + DHA$	<i>Echinochloa crusgalli</i> , <i>Lactuca sativa</i> , <i>Oryza sativa</i>	Seedling, leaf, root	Abogadallah <i>et al.</i> (2010); Carassay <i>et al.</i> (2012); reviewed by Das & Roychoudhury (2014); Mostofa <i>et al.</i> (2015)
CAT	$2H_2O_2 \rightarrow O_2 + 2H_2O$	<i>Brassica juncea</i> , <i>Brassica juncea</i> , <i>Lactuca sativa</i> , <i>Oryza sativa</i>	Seedling, leaf, root	Abogadallah <i>et al.</i> (2010); Carassay <i>et al.</i> (2012); reviewed by Das & Roychoudhury (2014); Rahman <i>et al.</i> (2016); Ranjit <i>et al.</i> (2016)
GPX	$H_2O_2 + DHA \rightarrow 2H_2O + GSSG$	<i>Brassica juncea</i> , <i>Oryza sativa</i>	Seedling, leaf, root	Reviewed by Das & Roychoudhury (2014); Mostofa <i>et al.</i> (2015); Ranjit <i>et al.</i> (2016)
DHAR	$DHA + 2GSH \rightarrow AA + GSSG$	<i>Oryza sativa</i>	Seedling	Reviewed by Das & Roychoudhury (2014); Rahman <i>et al.</i> (2016)
MDHAR	$MDHA + NADH \rightarrow 2AA + NAD$	<i>Vitis vinifera</i> , <i>Oryza sativa</i>	Seedling	Reviewed by Das & Roychoudhury (2014); Ikbali <i>et al.</i> (2014); Mostofa <i>et al.</i> (2015); Rahman <i>et al.</i> (2016)
GR	$GSSG + NADPH \rightarrow 2GSH + NADP^+$	<i>Echinochloa crusgalli</i> , <i>Brassica juncea</i> , <i>Oryza sativa</i>	Seedling, leaf, root	Abogadallah <i>et al.</i> (2010); reviewed by Das & Roychoudhury (2014); Mostofa <i>et al.</i> (2015); Ranjit <i>et al.</i> (2016)

SOD, superoxide dismutase; APX, ascorbate peroxidase; CAT, catalase; GPX, guaiacolperoxidase; DHAR, dehydroascorbate reductase; MDHAR, monodehydroascorbate reductase; GR, glutathione peroxidase; AA, ascorbic acid; DHA, reduces dehydroascorbate; GSSG, glutathione disulfide; GSH, reduced glutathione; MDHA, monodehydroascorbate; NADH, nicotinamide adenine dinucleotide; NAD, nicotinamide adenine dinucleotide; NADPH, nicotinamide adenine dinucleotide phosphate; NADP<sup>+</sup>, oxidized form of nicotinamide adenine dinucleotide phosphate.

Cdc42- and Rac-interactive binding motif (CRIB)-containing protein (RIC1) complex (Li *et al.*, 2017). Phosphatidic acid, an endogenous small molecule, regulates the activity of the MT-associated protein Microtubule-Associated Protein 65-1 (MAP65-1), thereby mediating MT stabilization in response to salt stress (Zhang *et al.*, 2012). Two proteins in the cellulose synthase complex interact with MTs through their cytoplasmic tails to mediate MT reorganization and plasma membrane localization of cellulose synthase under salt stress, which is important for plant salt tolerance (Endler *et al.*, 2015).

Long-term increases in  $[Ca^{2+}]_{\text{cyt}}$  are associated with MT dynamics, and are necessary for salt-stress responses (Wang *et al.*, 2007). The addition of calcium to salt-loaded media can increase seedling survival rates and MT dynamics (Wang *et al.*, 2007). Under salt stress, MT depolymerization enhances  $[Ca^{2+}]_{\text{cyt}}$ , and this increase is inhibited in the presence of paclitaxel (which stabilizes MTs) (Wang *et al.*, 2007). These combined results indicate that MT dynamics mediate or directly regulate  $Ca^{2+}$  influx in response to salt stress.

Salt stress induces MF assembly and bundle formation, whereas MF depolymerization is associated with cell death under long-term salt stress (Liu *et al.*, 2012). MF dynamics regulates  $[Ca^{2+}]_{\text{cyt}}$  signaling in response to salt stress; the actin-related protein2/3 (ARP2/3) complex has a role in this process by mediating mitochondrial-dependent  $[Ca^{2+}]_{\text{cyt}}$  increase under salt stress, which is essential for plant survival (Zhao *et al.*, 2013). MF dynamics are also regulated by the SOS pathway (Ye *et al.*, 2013). These combined results suggest that MF dynamics function upstream and downstream of the SOS pathway during salt-stress responses.

How cytoskeletal reorganization is regulated by salt-stress signaling remains to be elucidated. Future work will investigate the upstream regulators of MF dynamics and the functional targets of cytoskeletal reorganization under salt stress, such as ion transporters and protein trafficking.

## 5. Developmental adjustment

Plants adjust their metabolic pathways to adapt to changes in the surrounding environment under high-salt conditions. This includes developmental responses such as modulating root architecture, leaf senescence, flowering time, life cycle, growth, and biomass allocation (Munns, 2002; Munné-Bosch & Alegre, 2004; Sun *et al.*, 2008; Orsini *et al.*, 2010; Kim *et al.*, 2013; Park *et al.*, 2013).

Roots take up water and nutrients, and have a key role in plant growth, development, and survival. The root system is the first tissue that perceives salt stress. Root acclimation to changes in the soil environment can determine how plants sense and respond to stress. Salinity affects root system architecture, including primary and lateral root elongation, the number of lateral roots and root growth direction (Wang *et al.*, 2009a,b; Julkowska *et al.*, 2014). Under salt stress, lateral root initiation and organogenesis are inhibited, but lateral root growth is promoted; this is mediated by auxin redistribution in roots, which modulates root architecture plasticity (Wang *et al.*, 2009a,b). Development of the lateral root

primordium requires the establishment of an auxin gradient at the tip (De Smet *et al.*, 2007). Salt stress modulates the direction of root growth by reducing the gravity response; the altered root growth direction is correlated with both amyloplast degradation in root columella cells and PIN-FORMED2 (PIN2) localization in roots (Sun *et al.*, 2008).

The changes of root system architecture and growth direction may be associated with plant salt avoidance. To achieve this, clathrin-mediated internalization of PIN2 at the side of the root in contact with a higher salt concentration occurs, and this requires salt-induced phospholipase D activity (Galvan-Ampudia *et al.*, 2013). Further computational modeling suggests that the change in PIN2 localization plays a dominant role in the generation of auxin asymmetry, and this asymmetry is enhanced subsequently by PIN2 itself and AUXIN-RESISTANT1 (AUX1), and is speeded up effectively by a transient upregulation of PIN1 (Van den Berg *et al.*, 2016). Salt stress affects the root meristem by altering the redox balance and auxin transport (Jiang *et al.*, 2016). An *sos3* null mutant in Arabidopsis has deficient root growth (Ishitani *et al.*, 2000). Consistent with this observation, SOS3 regulates auxin redistribution in the root tip (Zhao *et al.*, 2011). Under salt stress, the transcription factor WRKY46 and ABA antagonistically regulate root auxin concentrations and thereby affect lateral root development (Ding *et al.*, 2015). Salt stress stimulates NO accumulation; NO can repress PIN expression and reduce auxin concentrations in roots, which inhibits root elongation by reducing the size of the root meristem (Liu *et al.*, 2015).

Different Arabidopsis accessions/natural variations display distinct root system architecture (RSA) strategies under mild salt stress by modifying primary or lateral root elongation, and these RSA strategies are correlated to natural variation in ABA sensitivity and  $K^+ : Na^+$  ratio in shoot (Julkowska *et al.*, 2014). Soil salinity impairs plant nutrient uptake. Both salt stress and nutrient defect affect RSA; however, the resultant RSA responses are not exactly same (Zolla *et al.*, 2010; Kawa *et al.*, 2016). These studies indicate that salt stress-induced RSA change is modulated by multiple external and internal signals.

A plant regulates its cold stress response largely through the transcriptional network downstream of C-repeat-binding factor (CBF)/dehydration-responsive element-binding protein (DREB) and regulates ABA/water deprivation at least partly through the transcriptional network downstream of Abscisic acid responsive element binding factor (ABF) (Stockinger *et al.*, 1997; Liu *et al.*, 1998; Jia *et al.*, 2016; Zhao *et al.*, 2016). However, no such transcription factors have been determined to be involved in the salt response. Through genome-wide analysis of targets of 21 ABA-related transcription factors, a new family of transcription regulators has been identified as regulating both ABA and salt responses (Song *et al.*, 2016). It is necessary to look at transcription factors specific for salt stress. However, another possibility is that the salt stress-induced transcriptional network is mainly associated with osmotic and damage repair processes.

Cell-type-specific gene expression analysis shows that genes with similar biological functions are enriched in different root cell layers (Dinnyeny, 2010; Geng *et al.*, 2013). The expression of genes involved in cell wall biosynthesis is downregulated in epidermal and

cortical cells, the expression of microtubule-related genes is downregulated in cortical cells, and the expression of genes involved in ROS metabolism is upregulated in stele and phloem tissue, the findings of Jiang *et al.* (2012) are consistent with a previous report that ROS are involved in the regulation of xylem-sap  $\text{Na}^+$  concentrations. Salt treatment suppresses *PIN2* expression in cortical cells, suppresses auxin-response genes in columella cells, upregulates genes involved in ethylene signaling in epidermal cells, and upregulates ABA-responsive genes in every cell layer. Salt stress-induced inhibition of lateral root growth is correlated with ABA signaling in the endodermis, where ABA cross-talks with the GA pathway to regulate root growth (Duan *et al.*, 2013). Genes with specific biological functions are specifically expressed in different cell layers, suggesting that root architecture is controlled under salt stress by cell-specific signaling pathways and responses.

Leaf senescence is crucial for plant fitness and is differentially modulated under different environmental conditions (Allu *et al.*, 2014), which affects the facilitated recycling of nutrients to sink tissues and the duration of photosynthesis (Wu *et al.*, 2012; Liang *et al.*, 2014). Leaf senescence is determined by the coordinated regulation of metabolite redistribution, vegetative phase change, reproductive maturation, and programmed cell death. Leaf senescence may be modulated by endogenous factors such as phytohormone concentrations, ROS, and plant growth stage (Gan & Amasino, 1995; Woo *et al.*, 2013). Salt-induced senescence might be mediated by the same response pathways as drought-induced senescence (Pic *et al.*, 2002). Stress-induced leaf senescence is initiated by decreases in indole-3-acetic acid (IAA) and increases in ABA, and is promoted by a continuous reduction in cytokinins (CKs) (Ghanem *et al.*, 2008). Leaf senescence inhibition may be primarily mediated by CKs; exogenous application of CKs or overproduction of endogenous CKs in transgenic plants can delay leaf senescence (Rivero *et al.*, 2007; Zwack *et al.*, 2013). Leaf senescence may be initiated when leaf CK concentrations decline below specific thresholds (Noodén *et al.*, 1990; Gan & Amasino, 1995). The delay of leaf senescence enhances plant tolerance to salt stress (Liang *et al.*, 2014). Under long-term salt stress, leaf senescence protects plants from salt-stress-induced injury. Future work should determine how plants regulate conflicting pathways of leaf growth vs leaf senescence under salt stress.

## 6. Epigenetic regulation

Gene expression can be regulated by epigenetic mechanisms including DNA methylation, histone modification, and the action of small RNAs; these epigenetic mechanisms are important determinants of plant acclimation to abiotic stresses (Kinoshita & Seki, 2014). Whole-methylome sequencing of Arabidopsis indicates that stressed lineages accumulate *c.* 45% more differentially methylated cytosines at CG sites than controls, and 75% of these can be inherited (Jiang *et al.*, 2014). Similar results in rice (*Oryza sativa*) indicate that salinity-induced changes in DNA methylation can be maintained through mitotic cell divisions (Wang *et al.*, 2015). Epigenetic modification of the expression of salt-stress-responsive genes is an alternative regulatory mechanism

for rice responses to salt stress (Karan *et al.*, 2012). Changes in DNA methylation induced by somatic hybridization in a salinity-tolerant wheat line (SR3) contribute to its salt tolerance (Wang *et al.*, 2014). RDM16, a factor in the RNA-directed DNA methylation (RdDM) pathway, regulates DNA methylation by influencing DNA polymerase V (*Pol V*) transcript levels in response to salt stress in Arabidopsis (Huang *et al.*, 2013). Epigenetic modifications can mediate the memory of stress tolerance during repeated exposure to specific environmental stresses (Kinoshita & Seki, 2014; Feng *et al.*, 2015). The activation/repression of some transcription factors by DNA methylation in soybean (*Glycine max*) is related to salt tolerance (Song *et al.*, 2012). DNA methylation appears to be involved in the regulation of *HKT* expression in response to salt stress in Arabidopsis and wheat (Baek *et al.*, 2011; Kumar *et al.*, 2017).

Changes in histone modification under salt stress are involved in the regulation of plant development and growth. Changes in chromatin structure alter target gene expression. The histone deacetylases HDA6 and HD2C also alter the expression of stress-responsive genes in Arabidopsis (Chen *et al.*, 2010; Luo *et al.*, 2012). The Arabidopsis cap-binding proteins CBP20 and CBP80 modulate the splicing of genes involved in sugar and proline metabolism in response to salt stress (Kong *et al.*, 2014). Salt stress enhances FLOWERING LOCUS C (FLC) expression by reducing the association of the floral initiator Shk1 kinase binding protein1 (SKB1) with chromatin and reducing H4R3 symmetric dimethylation (H4R3sme2) levels in Arabidopsis, thereby regulating Arabidopsis flowering time under salt stress (Zhang Z. *et al.*, 2011). In maize roots, salt stress induces changes in histone acetylation in the promoter region of cell cycle genes (Zhou *et al.*, 2014a,b). Elevated acetylation levels in *H3K9* and *H3K27* sites lead to transcriptional activation of a peroxidase (POX)-encoding genes in *Beta vulgaris* and *Beta maritima* under salt-stress conditions (Yolcu *et al.*, 2016).

Small RNAs (20–30 nucleotides (nt)) modulate target gene expression at the transcriptional and posttranscriptional levels (Zhang B. *et al.*, 2006; Zhang Y. *et al.*, 2006). Small RNAs are classified based on their biogenesis and precursor structures into small interfering RNAs (siRNAs) and microRNAs (miRNAs) (Ramachandran & Chen, 2008). The siRNAs are generated from double-stranded RNA precursors, and are grouped into *trans*-acting siRNAs (ta-siRNAs), heterochromatic siRNAs (hc-siRNAs), natural antisense transcript-derived siRNAs (nat-siRNAs), and long siRNAs (lsiRNAs) (Barrera-Figueroa *et al.*, 2012). Studies indicate that siRNAs and miRNAs have roles in salt-stress responses (Borsani *et al.*, 2005; Shen *et al.*, 2010; Carnavale Bottino *et al.*, 2013; Si *et al.*, 2014; Tian *et al.*, 2014; Feng *et al.*, 2015; Jian *et al.*, 2016; Srivastava *et al.*, 2017). In mangroves, ta-siRNAs may be involved in regulating chromatin structural stability and/or gene expression, and balancing the conflicting demands between plant growth and stress resistance under high-salt conditions (Wen *et al.*, 2016). Two types of siRNAs (21 and 24 nt) are derived from a pair of natural *cis*-antisense  $\Delta^1$ -pyrroline-5-carboxylate dehydrogenase (*P5CDH*) and SIMILAR TO RADICAL-INDUCED CELL DEATH (RCD)-ONE5 (SRO5) transcripts; these siRNAs control ROS

production in response to salt stress (Borsani *et al.*, 2005). The 24-nt siRNA level regulates the Arabidopsis v-myb avian myeloblastosis viral oncogene homolog 7 (AtMYB7) transcription factor, which is a member of the *R2R3-MYB* gene family, via the RdDM pathway in response to salt stress (Xu *et al.*, 2015). The miRNAs miR393, miR397b, and miR402 are induced by salt stress in Arabidopsis (Sunkar & Zhu, 2004). Under salt stress, members of the miR169 family are induced and selectively inhibit the Nuclear transcription factor Y subunit alpha (NF-YA) transcription factor (Zhao *et al.*, 2009). In rice, miR164e, miR408, and miR414 regulate the expression of ATP-binding protein (OsABP), DEAD-box helicase (OsDBH), and Dependent on eukaryotic translation initiation factor 4B (eIF4B) (DOB1)/SHAGGY-LIKE SERINE/THREONINE KINASE12 (SK12)-like DEAD-box helicase (OsDSHCT), respectively, under salt stress (Macovei & Tuteja, 2012). In Arabidopsis, miR394 regulates LEAF CURLING RESPONSIVENESS (LCR) abundance in response to salt stress (Song *et al.*, 2013).

Further work is required to completely elucidate the epigenetic regulation of plant stress responses, including the mechanisms controlling DNA methylation and histone modification at specific loci during stress responses, and how siRNAs are generated and delivered to specific loci to regulate stress-responsive gene expression.

## V. Conclusions and perspectives

It is important to identify and characterize the determinants and regulatory mechanisms of salt tolerance, in order to enhance salt-stress tolerance in important crop plants. In the last two decades, many genetic loci have been identified and cloned that have critical roles in plant salt tolerance. Studies of the SOS pathway provide relatively clear information about Na<sup>+</sup> efflux regulation. However, many determinants have not been studied in sufficient detail, and other areas require further elucidation, such as Na<sup>+</sup> signal perception, salt-triggered developmental regulation, and the molecular markers for breeding salt-resistance crops. We discuss three areas that require more extensive efforts in the future to achieve substantial progress in plant salt-stress signaling research.

### 1. Identification of the sodium sensor or receptor

Currently, the most important goal in plant salt-stress signaling research is to identify Na<sup>+</sup> sensors or receptors. Plants are likely to have a Na<sup>+</sup> sensor/receptor because Na<sup>+</sup> specifically induces many plant responses including Ca<sup>2+</sup> signaling, SOS pathway activation, and salt-responsive gene expression. In animal cells, membrane transporters with a long tail in the cytoplasm probably function as sensors or receptors of the solutes they transport (Ozcan *et al.*, 1998; Zhu, 2002; Miki & Seino, 2005). In Arabidopsis, the plasma membrane Na<sup>+</sup>/H<sup>+</sup> antiporter SOS1 has a long cytoplasmic tail (>700 amino acids) and might be a Na<sup>+</sup> sensor or receptor (Zhu, 2002). However, separating the SOS1 Na<sup>+</sup>/H<sup>+</sup> antiporter activity from the Na<sup>+</sup> sensor activity is technically challenging. Genetic screening analyses indicate that all amino acid substitutions in different *SOS1* domains generate *sos1* mutants that are

hypersensitive to salt treatment (Shi *et al.*, 2000), suggesting that SOS1 may contain other activities in addition to the Na<sup>+</sup>/H<sup>+</sup> antiporter activity. Plants lacking the hypothetical Na<sup>+</sup> sensor should be more insensitive to salt stress during early stress stages and more sensitive to salt stress during later stages; the lack or reduction in salt-stress responses in a Na<sup>+</sup> sensor mutant would reduce salt-induced growth repression during early stages of stress, whereas Na<sup>+</sup> and secondary stresses would accumulate to higher levels in a Na<sup>+</sup> sensor mutant than in wild-type plants.

Salt stress induces osmotic stress in plants. Recently, mechanosensitive ion channels in the plasma membrane (mechanosensitive channel of small conductance (MscS)-like 8 (MSL8); Hamilton *et al.*, 2015) and plastids (MSL2 and 3; Wilson *et al.*, 2014) have been reported to play a role in osmosensing in Arabidopsis, and a plasma membrane-located hyperosmolality-gated calcium-permeable channel (reduced hyperosmolality-induced [Ca<sup>2+</sup>]<sub>i</sub> increase 1 (OSCA1) Yuan *et al.*, 2014) and plastidial K<sup>+</sup> exchange antiporter (KEA) 1/2 and the KEA3 transporter (Stephan *et al.*, 2016) are also involved in this activity by evoking cytoplasmic Ca<sup>2+</sup> increases. However, it is required to determine whether these channels are involved in salt sensing and how they activate the downstream osmotic/salt response.

### 2. Identification of salt-induced signaling at different developmental and growth stages

Studies on plant salt-stress responses have examined changes in biomass, growth, and survival. The molecular mechanisms mediating salt-responsive regulation of plant developmental processes, nutrient uptake and recycling, and energy metabolism are largely unknown. All other abiotic stresses also affect these physiological processes. It remains to be determined whether these processes are specifically regulated by different stress signals and which molecules regulate these processes under salt stress. For example, SOS2, a protein kinase specifically activated by salt stress, interacts with GI and CAT2 and regulates red-light-dependent seed germination and seedling deetiolation (Verslues *et al.*, 2007; Kim *et al.*, 2013; Trupkin *et al.*, 2017). In this example, we must determine whether salt-stress signaling specifically regulates flowering time and photoperiod, and whether SOS2 has a role in this regulation.

### 3. Identification of salt-tolerance markers for crop breeding

Forward and reverse genetic analyses have enabled significant advances in our understanding of the mechanisms mediating plant acclimation to salt stress. However, mutation of a single gene rarely produces a significant enhancement in crop salt tolerance (Yang *et al.*, 2015). Many genes are important or essential for plant salt tolerance and plants lacking these genes are hypersensitive to salt stress, such as genes in the SOS pathway. Overexpression or ectopic expression of these genes only slightly improves crop salt resistance. Plant salt tolerance is a complex trait controlled by quantitative trait loci (QTLs). Next-generation sequencing and high-throughput phenotyping analysis will enable identification of QTLs or molecular markers that can be used for breeding salt tolerance in crop plants. GWASs using crop varieties with different degrees of

salt resistance also can be used for these studies, as these loci have been selected by the breeder or naturally through evolution. In future work, high-density mapping populations should be generated by crossing salt-resistant and salt-sensitive varieties; these populations can then be used for high-throughput phenotyping analysis and sequencing-based cloning.

In conclusion, although significant research advances have been made to our understanding of plant salt-tolerance mechanisms in recent years, more work is required to expand our basic knowledge, such as the elucidation of salt stress perception, the dissection of the interaction between salt stress and plant development, and, importantly, identification of key components of the salt stress response and development of efficient strategies to improve crop salt tolerance.

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