

## Understanding the physiological and molecular mechanism of salinity stress tolerance in plants

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### Abstract

Salinity is considered a global threat to agriculture and causes a significant reduction in crop yield. In particular, salinity stress promotes reactive oxygen species (ROS) accumulation and ionic imbalance in cells, leading to oxidative stress and even cell death. A large number of genes which are involved in defense, hormone, carbohydrate and metabolic pathways are down-regulated under salinity stress. Plants respond to salinity stress through a series of physiological and molecular mechanisms including antioxidant enzymes, hormones, defense related genes and signaling pathway activation. Plant defense systems modulate the overproduction of ROS through the activation of stress responsive-genes such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and glutamine synthetase (GS) and transcription factors such as MYBs, WRKY, and ERF. The salt overly sensitive (SOS) pathway is potentially involved in salt stress tolerance. *SOS1*, *SOS3* and *SOS2* are required for the oxidative stress tolerance by reducing the uptakes, and inter-cellular and intra-cellular distribution of  $\text{Na}^+$  and  $\text{Cl}^-$ . This review discusses the discovery of stress-responsive genes and signaling pathways, and summarizes the research progress on the regulatory mechanisms of salinity stress tolerance in plants, which will help accelerate breeding programs for salinity stress tolerance.

**Keywords:** antioxidant enzymes; hormone; miRNA; ROS; salinity stress; transcription factor

### Introduction

The global population is increasing rapidly every day and is expected to reach 9.7 billion by 2050 (Anwar and Kim, 2020). Currently, a major challenge for world agriculture is to increase crop production by 70% by 2050 to feed an additional 2.3 billion people (Anwar and Kim, 2020). Salinity is one of the major factors limiting agriculture production, especially vegetable crop production (Zhao *et al.*, 2021).

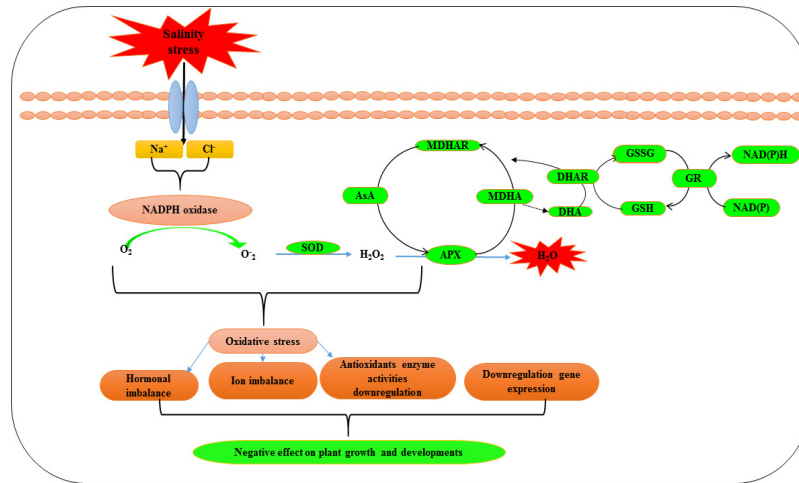
Soil salinity as an environmental factor significantly affects plant growth and development and causes many adverse problems, such as membrane disorder, irregular cell division, photosynthetic and protein synthesis, enhanced ion toxicity, and enzymatic disorders (Hussain *et al.*, 2017). According to the Food and Agriculture Organization (FAO), around 20% of the agricultural farmland is affected by salinity, which is expected to significantly increase in the oncoming years due to industrialization, overfertilization, increased use

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of low quality irrigation water, soil salinization, and natural causes such as salt intrusion in coastal zones due to rising sea levels (Anwar and Kim, 2020).

Salinity impairs plant growth and development via water stress and causes cytotoxicity due to excessive uptake of ions such as sodium ( $\text{Na}^+$ ) and chloride ( $\text{Cl}^-$ ) ions (Suzuki *et al.*, 2016). The accumulation of these ions in plant tissues may have direct toxic effects by inhibiting protein synthesis, photosynthesis, and susceptible enzymes. Plants respond to salt stress through a series of mechanisms, such as  $\text{Na}^+/\text{K}^+$  homeostasis (Suzuki *et al.*, 2016; Wang *et al.*, 2013b), hormonal biosynthesis (Xu *et al.*, 2021a), defense related gene regulation and  $\text{Na}^+$  exclusion (Galvan-Ampudia and Testerink, 2011). The excess amount of these  $\text{Na}^+$  and  $\text{Cl}^-$  ions in plant cells leads to the overproduction of ROS (reactive oxygen species), which is highly toxic and causes oxidative stress and damages proteins, lipids, carbohydrates, and DNA (Figure 1) (Sun *et al.*, 2021).



**Figure 1.** A systematic model plant under salt stress increases the concentration of  $\text{Na}^+$  and  $\text{Cl}^-$  ions, leading to oxidative stress and other negative effects on plant growth

Salinity stress exhibits negative effects on various physiological and metabolic processes, hence inhibiting crop production (Figure 1) (Geng *et al.*, 2019; Sun *et al.*, 2021). For example, the water absorption capacity of the root system of plants is decreased by salinity stress, thus leading to nutritional deficiency and reduced plant growth (van Zelm *et al.*, 2020; Nayak *et al.*, 2020). Osmotic stress in the initial stage of salinity stress causes various physiological changes (Yang and Guo, 2018a; Zhao *et al.*, 2021), such as interruption of membrane potentials, nutrient imbalance, impairment of the ability to detoxify ROS (Choudhury *et al.*, 2017), unstable antioxidant enzyme activities, decreased photosynthetic capacity, and reduced size of stomatal apertures (Figure 1) (Wei *et al.*, 2021). Increased accumulation of  $\text{Na}^+$  and  $\text{Cl}^-$  ions in tissues of plants (Al Hassan *et al.*, 2016) causes severe ion imbalance and significant physiological disorders, and a large number of genes involved in the regulation of chlorophyll, photosynthesis, antioxidant enzymes, hormones, are upregulated in *Phoenix dactylifera* (Xu *et al.*, 2021b).

There is genetic variation in salt tolerance, depending upon the degree of salt tolerance that varies with plant species and varieties within species (Shi and Zhu, 2002). In the past two decades, studies have been conducted to understand the mechanism of salt tolerance in the model plant *Arabidopsis* and many other plant species (Chen *et al.*, 2021). Determining the mechanisms of plant salt-stress response will provide valuable information for improving salt tolerance of crops by genetic engineering (Geng *et al.*, 2019). Recently, significant progress has been made in understanding plant salt-stress responses through molecular genetics and genomics analysis (Horie *et al.*, 2009; Seifikalhor *et al.*, 2019). In this review, we discuss current models of salt stress tolerance mechanisms, ion homeostasis, and cellular stability under salt stress in plants.

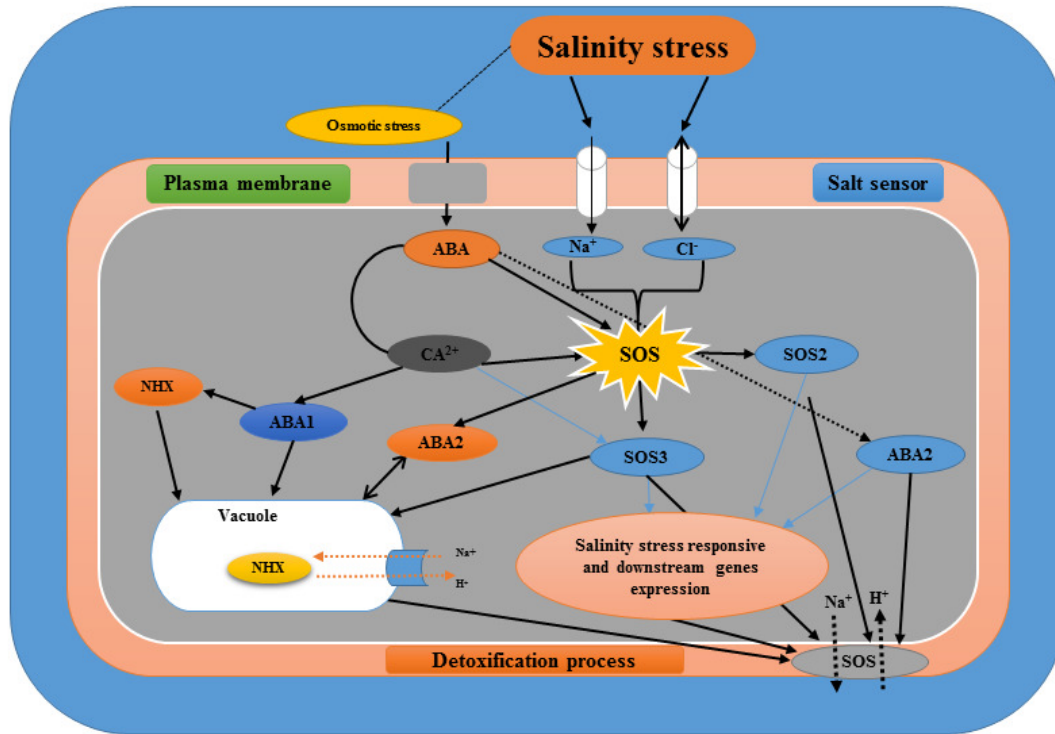
### Detrimental effects of salinity stress on plants

Excessive uptake of  $\text{Na}^+$  and  $\text{Cl}^-$  ions by plants under salinity stress causes oxidative stress, which changes the overall physiological and biochemical activities in plant cells (Zhao *et al.*, 2021), resulting in impaired root growth, reduced plant height, chlorosis, irregular leaf shape and color, biomass reduction, flower induction, reduced grain size, reduced harvest index, and reduced grain yield, as presented in Fig. 1 (Wei *et al.*, 2021; Wu *et al.*, 2018). Chlorophyll accumulation is significantly reduced under salinity stress in various plant species through downregulating the expression of *glutamyl-tRNA reductase* (*HEMA1*), *Mg-chelatase* (*CHLH*) and *protochlorophyllide oxidoreductase* (Xu *et al.*, 2021b). Likewise, another study reported that salinity stress reduces chlorophyll biosynthesis through downregulation of enzymes and chlorophyll biosynthesis genes such as *HEMA1*, *CHLH* and *POR* (Wu *et al.*, 2018). Chlorophyll and photosynthesis are directly interconnected, and thus salinity is caused by a significant reduction in photosynthesis capacity through inhibiting photosynthetic enzymes, chlorophyll and carotenoids (Wu *et al.*, 2018). NaCl stress mainly affects the activities of the root, which reduces water and mineral uptake and accumulation, thus causing nutritional imbalance by negatively influencing the uptake and transport of nitrogen (N), phosphorus (P), potassium ( $\text{K}^+$ ), calcium ( $\text{Ca}^{2+}$ ), zinc ( $\text{Zn}^{2+}$ ) and other micronutrients in cabbage (Gu *et al.*, 2016). Ionic stress enhances  $\text{Na}^+$  and  $\text{Cl}^-$  ion accumulation in plant cells, which may lead to leaf senescence and cell death. A previous study reported a significant inhibitory effect of salt stress on enzymes involved in various developmental processes, which ultimately disturbs plant metabolism (Siddique *et al.*, 2011). Abiotic stress, including salinity, increases ROS accumulation which is highly toxic and severely impairs the overall metabolic activity of plants (Choudhury *et al.*, 2017), thus leading to a significant reduction in plant growth, yield and yield components.

### Regulatory mechanism under salt stress

Over the past decades, salinity stress has been intensively investigated to explore plant signaling pathways and defense regulatory mechanisms. Little is known about how plant sodium ion sensors/receptors are regulated and how  $\text{Na}^+$  is sensed under low and high salinity stresses (Horie *et al.*, 2009; Liu *et al.*, 2022). Salt stress in plants triggers an augmented level of toxic ions;  $\text{Na}^+$ ,  $\text{Ca}^{2+}$ , ROSs, which prominently affects the overall biochemical and physicochemical activities of plants (Nath *et al.*, 2019). Osmotic stress affects stretch-dependent channels ( $\text{Ca}^{2+}$ ), redox mediated channels, cytoskeleton-related mechanosensors and stretch-activated channels, and lead to deteriorated plant growth and developmental activities (Figure 1).

Salt overly sensitive (SOS) signal transduction is involved in ion homeostasis regulation, and response to  $\text{Na}^+$  accumulation in plants under salinity stress (Figure 2). The SOS pathway protects plants from accumulating excessive  $\text{Na}^+$  ions through maintaining ionic homeostasis in plant cells, thus enhancing anti-aging capabilities (Gupta *et al.*, 2021). These findings provide a fundamental basis for elucidating the sensing of  $\text{Na}^+$  cellular systems, which demonstrate that these membrane receptors or proteins may be involved in  $\text{Na}^+$  sensing inside and outside cells. Up to date, a number of salt overly sensitive genes (*SOS1*, *SOS2*, *SOS3*, *SOS4*, and *SOS5*) have been reported to be involved in  $\text{Na}^+$  sensing in Arabidopsis (Ji *et al.*, 2013; Mahajan *et al.*, 2008; Seifikalhor *et al.*, 2019).

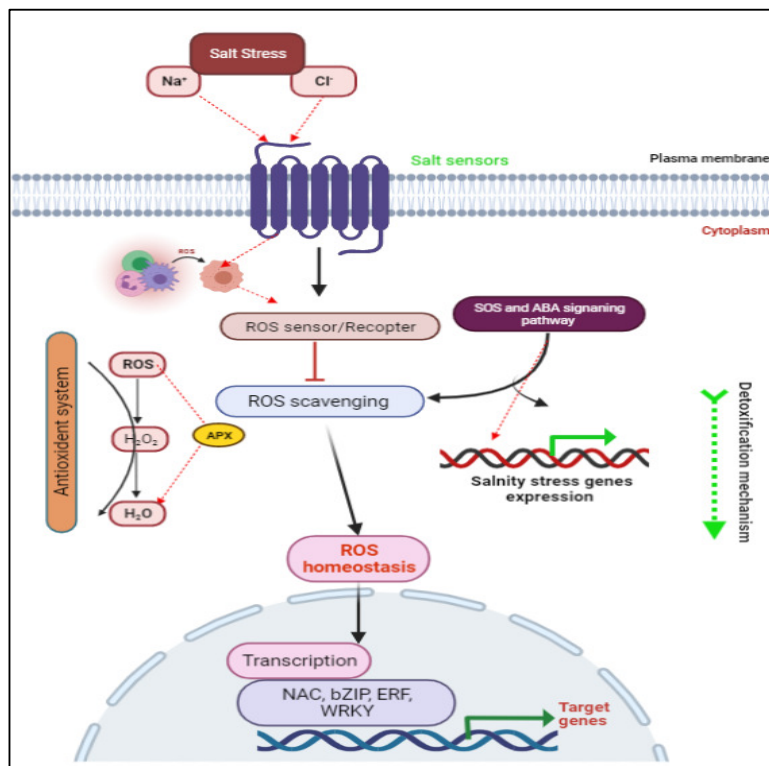


**Figure 2.** The SOS signaling pathway is involved in the detoxification process under salinity stress. *SOS1*, *SOS2*, and *SOS3* interact with the calcium signals and the ABA signals to regulate ion homeostasis by extruding excess  $\text{Na}^+$  ions out of the cell

The plasma membrane  $\text{Na}^+/\text{H}^+$  antiporter *SOS1* is a  $\text{Na}^+$  sensor (Figure 2), which can feel  $\text{Na}^+$  before and after entering the cell. Regulating stress responsive genes (*SOS1*, *SOS3*, and *NHX1*) play a defensive role against salt stress (Gupta *et al.*, 2021; Ji *et al.*, 2013). Previous studies reported that, under salinity stress, plant activates the SOS signaling pathway to reduce the uptake of harmful ions in roots (Al Hassan *et al.*, 2016; Horie *et al.*, 2009; Miranda *et al.*, 2017). The SOS signaling pathway is the gateway for ion hemostasis, which is activated by the calcium signal ( $\text{Ca}^{2+}$ ). Calcium binding proteins (*SCaBP8*) are phosphorylated by SOS, which then activates the *SOS3/SOS2* protein kinase complex (Yang *et al.*, 2019b). The activated *SOS3/SOS2* protein induces the phosphorylation of *SOS1*. It requires a proton gradient from PM  $\text{H}^+$ -ATPase which is regulated through inhibition of the *PKS5* kinase activity by *DnaJ homolog 3* (a heat shock protein) (Yang *et al.*, 2010), and then activates the down-stream signaling pathway including hormone signaling pathway and antioxidant enzymes (Miranda *et al.*, 2017; Wei *et al.*, 2021; Wu *et al.*, 2018). Likewise, *SOS2* stimulates tonoplast  $\text{Na}^+/\text{H}^+$  antiporter, *NHX1* to mediate active  $\text{Na}^+$  uptake into vacuoles (Batelli *et al.*, 2007; Neuhaus and Trentmann, 2014). The *NHX1* gene is regulated through *ABA1* or *NHX* genes are regulated, whereas *ABI2* interacts with *SOS2* and negatively regulates ion homeostasis by inhibiting the kinase activity of *SOS2* or the activities of the targets of *SOS2* (Barragán *et al.*, 2012; Bassil *et al.*, 2011; Ji *et al.*, 2013). *CAX1* ( $\text{H}^+/\text{Ca}^+$  antiporter) is a target of *SOS2* which restores cytosolic  $\text{Ca}^{2+}$  homeostasis (Turkan and Demiral, 2009) The *SOS4* gene encodes a pyridoxal (PL) kinase involved in the biosynthesis of *PL-5-phosphate* (*PLP*), which contributes to  $\text{Na}^+$  and  $\text{K}^+$  homeostasis by regulating ion channels and transporters (Mahajan *et al.*, 2008). *SOS5* is involved in the maintenance of cell expansion (Mahajan *et al.*, 2008; Türkan and Demiral, 2009). The SOS signaling pathway is inactive under normal conditions but activated under  $\text{NaCl}$  stress to enhance stress tolerance. *GIGANTEA* and *14-3-3* proteins are involved in the deactivation of the SOS pathway through interaction with *SOS3-like*

*calcium-binding protein1 (SCaBP1)/calcineurin B-like protein2 (CBL2)* (calcium-binding protein) and *SOS2-like protein5 (PKS5)/SOS2-like protein 24 (PKS24)* (serine/threonine protein kinases), thus repressing the activities of the *SOS2* kinase and the  $H^+$ -ATPase on the plasma membrane (Yang and Guo, 2018a; Zhao *et al.*, 2021).

Salinity tolerance is mainly controlled through a complex genetic regulatory network. High  $Na^+$  and  $Cl^-$  concentrations in plant tissues can affect the uptake and translocation capacity of water and mineral and reduce enzyme activities and plant growth (Wu *et al.*, 2018; Yañez-Yazlle *et al.*, 2021). Developmental processes of plant exposure to saline stress can be greatly affected through altering ion uptake and cellular homeostasis (El-Badri *et al.*, 2021). The SOS signaling pathway induces salinity stress tolerance through perceiving and transducing the osmotic and ion signals inside the cell to control ionic homeostasis, as presented in Figure 3 (Ji *et al.*, 2013). Recently, approaches have been used to unravel the roles of the SOS pathway and other complex regulatory networks which regulate ion homeostasis in *Arabidopsis* (Mahajan *et al.*, 2008). In *Arabidopsis*, the salt overly sensitive (SOS) pathway (Ji *et al.*, 2013) and the *calcineurin B-like (CBL)/CBL-interacting kinase (CIPK)* pathway (Hashimoto *et al.*, 2012; Mahajan *et al.*, 2008) have been reported in the regulation of salinity stress tolerance (El-Badri *et al.*, 2021). As presented in Figure 3, the cytosolic  $Ca^{2+}$  activates the *SOS2/SOS3* protein kinase complex to phosphorylate *SOS1* (Gupta *et al.*, 2021; Ji *et al.*, 2013; Shi and Zhu, 2002), which is a plasma membrane  $Na^+/H^+$  antiporter (Mahajan *et al.*, 2008; Serrano and Rodriguez-Navarro, 2001). Many homologues' genes of SOSs and CBLs have been identified, which can increase salinity stress tolerance (Figures 2) (Batelli *et al.*, 2007; Ji *et al.*, 2013). *CBL10-CIPK24* is a novel protein complex which can regulate vacuolar  $Na^+$  ions accumulation in *Arabidopsis* (Miranda *et al.*, 2017). Overexpression of *Arabidopsis thaliana CPK21* increases salinity stress tolerance by promoting the expression of *SOS1*, *NHX1*, *LEA3*, *NAC6*, *APX2*, *APX8* and *ABAs* genes, and reduces ROS accumulation in leaves (Asano *et al.*, 2011; Wen *et al.*, 2019).



**Figure 3.** The regulatory mechanism of ROS homeostasis in plants. The SOS and ABA signaling pathways activate salt stress responsive genes and antioxidant enzymes to regulate ROS production

## Physiological and molecular mechanism of salinity stress tolerance

### *Antioxidant enzymes and ROS scavenging*

Environmental stresses such as salinity, heavy metals, drought stress, etc., lead to abnormal enzymatic activities and ROS accumulation, which is produced in chloroplasts, mitochondria, peroxisomes, and several apoplastic sources, and negatively affects metabolic activities in plant cells (Gill and Tuteja, 2010; Yue *et al.*, 2022). The standard level of ROS production is required for normal activities in plants, but a slight change in ROS production may lead to detrimental effects on plant developmental processes (Gill and Tuteja, 2010).

Salinity stress enhances the production of ROS that impairs protein and DNA, carbohydrates metabolism, chlorophylls, mitochondria and lipid. Salinity stress exhibits detrimental effects on root activities, which diminishes water and nutrient uptake and accumulation, which may change many physiological traits (Yap *et al.*, 2021; Yue *et al.*, 2022). Previous studies reported that salinity increases the accumulation of toxic ions and ROS production and reduces leaf water potential and relative water contents (Arif *et al.*, 2020; Sarwar *et al.*, 2021). Plant responds to salinity stress by regulatory antioxidant enzymes (Anwar *et al.*, 2018; Sarwar *et al.*, 2021). It is reported that, under salt stress, increased enzyme activities maintain cellular homeostasis and mitigate oxidative damage in plants (Gill and Tuteja, 2010). These enzymes are associated with various plant hormones, transcription factors and signaling pathways, through which the defense system can be activated under salinity stress (Song *et al.*, 2020; Yang and Guo, 2018b).

SOD catalyzes the production of H<sub>2</sub>O<sub>2</sub> from superoxide radicals, which is converted into H<sub>2</sub>O and O<sub>2</sub> with the help of CAT enzyme, as presented in Figure 1. The APX enzymes also play a vital role in H<sub>2</sub>O<sub>2</sub> scavenging and protect plant cells. APX has a higher affinity for H<sub>2</sub>O<sub>2</sub> than CAT and POD, thus APX has more crucial role in ROS management during environmental influences (Mhamdi and Van Breusegem, 2018; Nadarajah, 2020). Many antioxidant enzyme genes have been identified which enhance salinity stress tolerance. In Arabidopsis, overexpression of *APX1*, *APX2* and *APX8* enhances salinity stress tolerance by controlling ROS production and activating antioxidant enzymes (Mhamdi *et al.*, 2018). Exposure to salinity stress alters antioxidant enzyme activities of plants. Overexpression of Mn-SOD leads to higher tolerance of salinity stress in Arabidopsis by stimulating plant defense systems and reducing the effects of ROS overproduction. The *CATA* and *CATB* genes show increased activities under salinity stress, indicating that these genes may be involved in salinity stress tolerance (Yue *et al.*, 2022). Treatment of plants with exogenous GSH results in a significant increase in GSH accumulation and antioxidant enzyme activities under salt stress, suggesting that GSH plays a crucial role in salt tolerance.

### *Oxidative stress*

ROS (reactive oxygen species) plays a central role in the acclimation process of plant abiotic stress, which acts as signal molecules that regulate numerous signaling pathways in response to abiotic stresses (Gill and Tuteja, 2010). ROS is mainly produced in apoplast, chloroplast, mitochondria and peroxisomes by respiratory burst oxidase homologs, apoplast diamine oxidase, peroxidase and polyamine (Mhamdi and Van Breusegem, 2018). Under NaCl stress, plants produce excessive ROS, greatly affecting plant growth and development. *AtRbohD* and *AtRbohF* genes involved in the ROS production are upregulated under salinity stress. Previous studies have shown that *AtRbohD/AtRbohF* promotes the movement of K<sup>+</sup> in the cytosol and reduces the Na<sup>+</sup>/K<sup>+</sup> ratio in Arabidopsis. Furthermore, *AtRbohF* is involved in limiting the distribution of Na<sup>+</sup> in xylem sap and reduces the delivery of Na<sup>+</sup> ions from root to shoot through transpiration. Likewise, *AtRbohD* plays a dynamic role in salinity stress tolerance. *AtRbohD* mediates the propagation of long-distance signals triggered by salinity stress through stabilizing ROS production and triggers anti-oxidative responses to reduce oxidative damage in plant cells.

*NADPH* oxidases designated as *RBOHs* (respiratory burst oxidase homologs) are crucial signaling nodes for the ROS signaling pathway through  $\text{Ca}^{2+}$  binding EF-hand and N-terminal phosphorylation (Drerup *et al.*, 2013). The *rboha* gene mediates antioxidant enzyme activities and maintains the ROS levels under salinity stress (Suzuki *et al.*, 2011).

A large number of genes are upregulated by salt stress, such as  $\text{Ca}^{2+}$  associated *CBL/CIPK* and *CDPK* genes (Liu *et al.*, 2020). Likewise, many DEGs encoding respiratory burst *NADPH* oxidases such as *RBOHA* and *RBOHF*, *CBL/CIPK* and *CDPK* are upregulated under salinity stress (Liu *et al.*, 2020). In Arabidopsis, *Calcineurin B-like calcium*; *CBL1* and *CBL9* sensor enhance the activity of a *NADPH* oxidase, *RBOHF*, through phosphorylation, thus enhancing salinity stress tolerance (Drerup *et al.*, 2013). Oxidative stress destabilizes ionic hemostasis in cells through its toxic effect and regulation of ROS-sensitive channels (Suzuki *et al.*, 2011). Plant antioxidant enzymes cope with these toxic effects at the cellular levels for ROS-scavenging. A number of antioxidant enzyme genes have been reported to be involved in salinity stress tolerance. *APX*, *APX2* and *APX8* (Ascorbate peroxidase) (belongs to heme-peroxidase (class I) have been reported to regulate plant defense systems and function in scavenging ROS via the activation of the ABA signaling pathway and catalyzing the conversion of  $\text{H}_2\text{O}_2$  to  $\text{H}_2\text{O}$  and  $\text{O}_2$ . *GR2* and *GR3* act as a substrate for glutathione peroxidases (GPX) and glutathione S-transferase (GST) which are involved in ROS scavenging under salt stress (Yue *et al.*, 2022).

#### *Plant hormones*

Plant hormones such as BR, GA, ABA, IAA, and JA regulate the growth and development of plants and play a vital role in salinity stress tolerance (Anwar and Kim, 2020). The crosstalk of plant hormone signaling pathways and transcription factors can significantly induce salinity stress tolerance and are crucial for the growth of plants (Anwar *et al.*, 2018). Brassinosteroids (BR) are a group of plant steroid hormones that play a critical role in developmental processes including cell division, elongation, and vascular differentiation (Anwar *et al.*, 2018). BR improves plant defense systems in response to salinity stress (Yang *et al.*, 2019a). Several BR signaling pathway genes have been identified as differentially expressed genes to combat salinity. BR resistant 1/2 genes are downregulated, while the genes in the *brassinosteroid insensitive 1-associated receptor kinases* (*BAKI*) family are upregulated, leading to salt acclimation (Anwar and Kim, 2020; Anwar *et al.*, 2018). *SERK2* is a component of the BR signaling pathway that enhances salinity stress tolerance through the regulation of the BR signaling pathway, ultimately enhancing the growth and grain size of *Oryza sativa*.

Auxin is involved in plant cell elongation and growth and development (Saini *et al.*, 2013). Under salinity stress, auxin enhances the expression of a number of candidate genes that are involved in auxin biosynthesis and signaling pathways, suggesting the involvement of auxin in salinity stress tolerance. For example, the expressions of *PIN2*, *Auxin influx carrier*, *GH3*, *SAUR*, and auxin response factor genes are downregulated under salt stress (Guo *et al.*, 2020; Ribba *et al.*, 2020). IAA plays an essential role in coping with stress by producing various DEGs; transcription of genes like *gp1* and *indole-3-acetic acid-amido synthetase* helps vegetative cell elongation. The expression of various genes such as auxin-responsive genes is upregulated to reduce the toxic effect of salinity. In particular, these genes are divided into three families, namely *auxin/indoleacetic acid* (Aux/IAA), *small auxin-up RNA* (*SAUR*) and *GH3*, which induce salinity stress tolerance (Sun *et al.*, 2018). Apple *MdIAAs* express in various tissues and enhance salinity stress tolerance (Li *et al.*, 2021).

Ethylene is involved in fruit ripening and flower induction, as well as plant responses to salinity stress. Like ACC, several precursors of ethylene participate in response to plant salinity stress. Ethylene downregulates the expression of *ETR1/ETR2/EIN4*, which delays salt tolerance. On the other hand, *EIN2* genes are upregulated and thus promote salt tolerance (Figure 4). Previous studies suggested that active ethylene signaling



is important to combat salinity (Iqbal *et al.*, 2017; Vanstraelen and Benková, 2012). The auxin signaling pathway correlates with plant antioxidant enzymes, which promote salinity stress tolerance. Abscisic Acid (ABA) is an important plant hormone in the regulation of plant growth, development and stress responses, through interacting and upregulating plant hormones and signal transduction. A previous study reported that ABA upregulates the genes involved in the synthesis of ABA, BR, GA, NAC transcription factors (*ZxNAC083* and *ZxNAC035*), chlorophyll, and other photosynthesis and defense related genes in xerophyte plants (Yin *et al.*, 2019). Likewise, many genes in the ABA signaling pathways and biosynthesis are upregulated under salt stress in the roots of *Clerodendrum inerme* (Xiong *et al.*, 2019).

A number of ABA encoding genes have been identified that induce salinity stress tolerance. *ABI5* (*ABSCISIC ACID INSENSITIVE 5*) regulates salt stress through the regulation of the ABA signaling pathway and interaction with other phytohormones to stimulate plant defense systems. *LeNCED1* encodes *9-cis-epoxycarotenoid dioxygenase*, a key enzyme in ABA biosynthesis (Arif *et al.*, 2020). These findings reflect that the ABA signaling pathways are potentially involved in salinity stress tolerance (Collin *et al.*, 2021; Skubacz *et al.*, 2016).

Cytokinins (CKs) are also important plant hormones involved in cell growth and development and biosynthesis of chloroplast (Yu *et al.*, 2021). CKs are major regulators in enhancing the defense system and protecting oxidase damage under salinity stress (Atanasova *et al.*, 1996). Plants treated with exogenous CKs (Kinetin) show a significant increase in antioxidant enzyme activities and chlorophyll content and a decrease in  $K^+$  and  $Ca^+$  accumulation under salinity stress (Ahanger *et al.*, 2018; Tounekti *et al.*, 2011). The overexpression of *PpCKX1* and *AtCKX1* enhances ABA biosynthesis, *P5CSA* gene expression and antioxidant enzyme activities under salt stress (Ahanger *et al.*, 2018). Likewise, in Arabidopsis, *MsCKX* (Cytokinin oxidase/dehydrogenase) from *Medicago sativa* improves  $K^+/Na^+$  ratio, proline accumulation and the expression levels and activities of antioxidant enzymes to enhance NaCl stress tolerance (Li *et al.*, 2019). The overexpression of *SIPT3* also improves salinity stress tolerance in *Solanum lycopersicum* (Žižková *et al.*, 2015). As an important plant hormone, gibberellins (GAs) mitigates various environmental stresses (Xue *et al.*, 2021). A previous study reported that GA interacts with *F-box*, *PIFS*, *SCLL3* and other proteins to enhance NaCl stress tolerance (Wang *et al.*, 2020). *Glycine max* treated with exogenous GA can promote GA biosynthesis and signaling genes under salts stress (Wang *et al.*, 2020; Xue *et al.*, 2021). DELLA protein positively regulates plant responses to salinity stress through interacting with ABA. Jasmonic Acid (JA) is a crucial plant hormone involved in developmental processes such as growth, chlorophyll synthesis, photosynthesis, flower and fruits, nutrients uptake and accumulation, and abiotic stress responses (Ali and Baek, 2020). Previous studies reported that JA upregulates the expression of salt responsive and metabolic pathways genes under salt stress. *Salt sensitive 3* (*RSS3*) interacts with JA signaling genes *JAZ9*, *JAZ*, and *non-R/B-like bHLHFTs* to form the *RSS3-JAZ-bHLH* complex, which is responsible for salt stress tolerance (Ali and Baek, 2020). Likewise, *Sorghum bicolor*, *PLA1* (*Phospholipase A1*) and *ACXs* (*Acyl-coenzyme A oxidase*) are expressed which activate the JA signaling pathway and biosynthesis under salinity stress (Yang *et al.*, 2017). Based on these findings, it can be concluded that plant hormones are involved directly and indirectly in salinity stress tolerance.

### *Polyamine*

Polyamines are aliphatic amines of low molecular weight, which are universally distributed in all living organisms including plants (Hussain *et al.*, 2011). In plants three main polyamines such as putrescine, spermidine, and spermine, that does not only regulate plant growth but also enhanced abiotic stress tolerance (Hussain *et al.*, 2011; Shi and Chan, 2014). Polyamine biosynthesis pathways in plants have been intensively studied, and identified number of genes *ADC* (*arginine decarboxylase*), *ODC* (*ornithine decarboxylase*) and *SAMDC* (*S-adenosylmethionine decarboxylase*), that are involved in growth. Polyamine, play a key role in



salinity stress tolerance (Alcázar *et al.*, 2020; Shi and Chan, 2014). A previous study reported that salt stress enhances the transcript level of polyamine signaling and biosynthesis gene such as *OCD*, *SPDS2A* (*Spd synthase2A*), *SPDS2B* (*Spd synthase2B*), *ADC2*, *SPMS* (*Spm synthase*), *SAMDC1* (*SAM decarboxylase1*), and *SAMDC2* (*SAM decarboxylase2*) (Gondor *et al.*, 2021).

The previous study reported that exogenous polyamine application enhanced salt stress tolerance through increasing photosynthesis capacity and reduced the accumulation of Na<sup>+</sup> ions in root and shoot tissues (Alet *et al.*, 2012). Polyamine reduced the harmful effects of salt stress by protecting photosynthetic machinery and controlling ROS scavenging activity hence reducing the MDA and ROS contents in *Camellia sinensis* and *Citrus limon* (Scholey *et al.*, 2014; Xiong *et al.*, 2018). Several polyamine genes have been identified that are involved in salt stress tolerance. *Oryza sativa*, ADC gene increased the activity of ADC and polyamine contents, as well as enhanced plant growth and biomass production under salt stress (Todorova *et al.*, 2013). In Arabidopsis, *adc2* mutant affect the contents of polyamine and was more sensitive to salt stress (Fu *et al.*, 2017). These findings are suggested that ADC genes are potentially involved in salt stress. The overexpression of SAMDC enhanced salinity stress tolerance and increase plant growth in *Oryza sativa*, *Nicotiana tabacum*, and Arabidopsis (Alcázar *et al.*, 2020). Under salt stress, mutants; *acl5-1*, *spms-1*, and *double acl5-1/spms-1* (synthesis of spermine and thermospermine genes) enhanced the accumulating Na<sup>+</sup>, hence causing oxidative stress, and suggesting that polyamines enhanced salt stress tolerance (Alet *et al.*, 2012). The overexpression of *SPDS1* in apples increased the activities of antioxidant enzymes and reduce the MDA accumulation when exposed to salt stress (Neily *et al.*, 2011). *Polyamine oxidase 5* (*PAO5*) is the key gene of polyamine biosynthesis. The loss of function mutants *atpao5-2* and *5-3*, enhance the accumulation of polyamine and increase salt stress tolerance. In Arabidopsis, *spe1-1* and *spe2-1* reduced the activity of ADC and reduced polyamine accumulation and salt stress tolerance (Zarza *et al.*, 2017). Based on these findings, it can be concluded that polyamine played an important role in salinity stress tolerance, and more studies are required to explore to improve crop production.

### **The role of transcription factors in salinity stress**

#### *MYB transcription factor*

Plant MYB transcription factor is one of the largest families involved in almost all physiological and developmental processes (Wang *et al.*, 2021). MYB is named after its conserved DNA binding region, namely the MYB domain (Wang *et al.*, 2021). MYB proteins are involved in the regulatory networks of abiotic stresses (S. Table 1) (Hoang *et al.*, 2012). A number of MYB genes have been characterized that regulate salinity stress. Overexpression of *MYB49* regulates the expression of *MYB41*, *ASFT*, *FACT* and *CTP86B1* genes under salinity stress. *MYB20* negatively regulates the expression of the *PP2Cs* gene, which is the key facilitator of ABA biosynthesis under salinity stress (Cui *et al.*, 2013).

A recent study reported that *MYB7* and *MYB44* induce salinity stress tolerance through *PP2Cs* and *NAC*, and reduce the expression of *ABI1*, *ABI2*, *PP2CA*, *HAB1*, and *HAB2* (Persak and Pitzschke, 2014; Wei *et al.*, 2020). *MYB7* regulates *ABI5* to enhance salinity stress tolerance and seed germination (Kim *et al.*, 2015). ABA and proline biosynthesis genes are activated in the *MYB12* overexpression lines during salinity stress, thus leading to enhanced tolerance (Wang *et al.*, 2021). MYB transcription factor regulates salt overly sensitive pathways during salt stress (Wang *et al.*, 2021). *MYB42* overexpression induces salt tolerance through activating the *SOS2* gene by direct binding to the *SOS2* promoter, while the *myb42* mutant is sensitive to salt stress compared with the wild type (Sun *et al.*, 2020). *MYB30* modulates salinity stress tolerance by maintaining cellular redox homeostasis via *AOX1a*. The overexpression of *MYB47*, *MYB15*, and *MYB52* enhances the tolerance to salinity stress by regulating the defense system and reducing the overproduction of ROSs (Wang

*et al.*, 2021). In *Arabidopsis*, *AtMYB2* and *AtMYB44* regulate salinity stress at the mRNA level, thus the overexpression lines are more tolerant to salt stress (Abe *et al.*, 2003; Jaradat *et al.*, 2013; Jung *et al.*, 2008). A comprehensive wide analysis of the peanut genome suggests that the expression of *AbMYB1*, *AbMYB2*, *AbMYB6*, *AbMYB6*, and *R2R3-MYB* is significantly increased under salinity stress (Chen *et al.*, 2019; Wang *et al.*, 2021). *AbMYB12*, *AbMYB18*, *AbMYB28* and *AbMYB30* are also upregulated. These findings suggest that MYB transcription factors are potentially involved in salinity stress tolerance.

#### *NAC transcription factor enhances salinity stress tolerance*

*NAC* (NAM, ATAF and CUC) transcription factor is an important player in abiotic stress tolerance (Nuruzzaman *et al.*, 2013). *NAC* is characterized by a highly conserved DNA-binding *NAC* domain in the N-terminal region, and its C-terminal transcription regulatory domains contain a transmembrane domain that can either activate or repress transcription under environmental stresses (Anwar and Kim, 2020; Yuan *et al.*, 2019). *NAC* proteins interact with ABA-dependent or independent pathways to induce salinity stress tolerance (Yuan *et al.*, 2019). *NAC* family genes induce salinity stress tolerance by regulating plant defense (S. Table 2). *RD26* encodes *NAC* protein in *Arabidopsis* which acts as a transcriptional activator of the ABA signaling pathway to enhance salinity and drought stress tolerance (Fujita *et al.*, 2004).

*TaNAC29* and *TaNAC47* belong to another *NAC* transcription factor family, which repress the ABA pathway and trigger downstream genes (*AtRD29A*, *AtRD29B* and *AtP<sub>5</sub>CS1*) and defense signaling pathways to induce abiotic stress tolerance in *Arabidopsis* (Zhang *et al.*, 2016). Likewise, other *NAC* family members *GmNAC6*, *GmNAC20* and *AtNAC2*, transcription factors downstream of the ethylene and auxin signaling pathways, enhance salinity stress tolerance and lateral root developments in *Arabidopsis* (Faria *et al.*, 2011; Hao *et al.*, 2011; He *et al.*, 2005). These findings suggest that *NAC* acts as a positive regulator in response to salinity and cold stresses (Yuan *et al.*, 2019). In *Solanum lycopersicum*, *SINAC4* responds to salinity and drought stress through regulating MeJA biosynthesis and downregulating ABA biosynthesis (Zhu *et al.*, 2014). These findings suggest that *SINAC4* interacts with the ABA-independent signaling pathway to modulate abiotic stress tolerance. *NAC*-type transcription factors *AtNAC2* and *NAC57* induce salinity stress tolerance in *Arabidopsis* through activating the ethylene and auxin signaling pathway, (Mao *et al.*, 2018). Collectively, the *NAC* transcription factors are potentially involved in salinity stress tolerance.

#### *WRKY transcription factors enhance salinity stress tolerance*

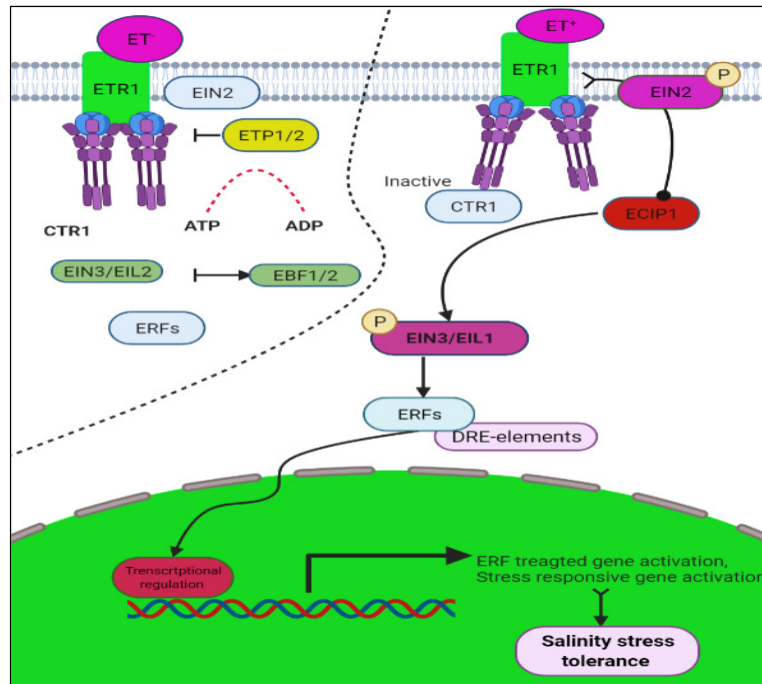
*WRKY* transcription factors are a major transcriptional regulator in plants, which act as repressors or activators for several signaling networks in modulating abiotic stress tolerance (Jiang *et al.*, 2017). Whether the signaling pathways are repressed or activated depends on the strength, intensity and types of environmental stresses (Anwar and Kim, 2020; Anwar *et al.*, 2018). Many *WRKY* candidate genes have been reported in salinity stress tolerance (S. Table 3). The *AtWRKT25* and *AtWRKY33* double mutant of *Arabidopsis* is more sensitive to salinity, while the overexpression line exhibits elevated tolerance to salt stresses (Jiang *et al.*, 2017; Li *et al.*, 2013).

The overexpression of *DgWRK1*, *DgWRK2*, *DgWRKY3*, *DgWRK5* in *Chrysanthemum* increases antioxidant enzyme activities, and decreases ROS accumulation under salinity stress (He *et al.*, 2018; Liang *et al.*, 2017). *OsWRKY45* and *OsWRKY72* overexpression in *Oryza sativa* enhances salinity and drought stress tolerance through modulating ABA and auxin signaling pathways (Qiu and Yu, 2009). Likewise, *ZmWRKY58*, *ZmWRKY23*, *ZmWRKY86* and *ZmWRKY48* in maize also enhance salinity and drought tolerance by activating the ABA signaling pathway to stimulate plant defense (Cai *et al.*, 2014; Fang *et al.*, 2021). Overexpression of these genes leads to delayed germination and suppressed post-germination development with a high survival rate, high relative water contents, and reduced MDA accumulation compared

with the wild type (Cai *et al.*, 2014). *TaWRKY10* significantly enhances salinity and drought stress tolerance in tobacco. Overexpression of *TaWRKY10* enhances osmotic balance, promotes the expression of defense genes and antioxidant enzymes and minimizes ROS contents in wheat (Wang *et al.*, 2013a). *BcWRKY46* from *Brassica campestris* ssp. *chinensis* improves dehydration, cold and salinity stress tolerance in tobacco (Wang *et al.*, 2012). Similarly, *MxWRKY53* in *Malus xiaojinensis* induces salinity stress tolerance in the model plant *Arabidopsis* (Jiang *et al.*, 2017). These findings suggest that *TaWRKY10* stimulates the plant defense system under abiotic stress.

#### *ERF transcription factor*

Plant hormones play major roles in mediating plant defense responses to abiotic stresses (Khan *et al.*, 2017). Among various plant hormones, ethylene (ET) plays a key role in response to environmental factors, as presented in Figure 4 (Iqbal *et al.*, 2017). ERF (Ethylene responsive factor) transcription factor is a key regulator of ethylene biosynthesis and signaling pathways, and thus enhances abiotic stress tolerance. Many ERF genes have been identified in modulating salinity stress tolerance in various of plants (S. Table 4). *TaERF3* overexpression enhances NaCl and drought stress tolerance in wheat by modulating stress-responsive genes (Rong *et al.*, 2014). *ERF1* is a key regulator of JA and ET signaling pathways. In *Arabidopsis*, the *ERF1* overexpression line enhances salinity stress and drought stress tolerance through activating antioxidant enzyme activities and stabilizing ROS production under salinity stress (Cheng *et al.*, 2013). These results confirm that *ERF1* up-regulates specific suites of genes involved in abiotic stress tolerance by stress-specific binding to GCC or DRE/CRT motif and activating ABA, ET and JA genes (Cheng *et al.*, 2013). Ethylene insensitive 3 interacts with ERF1 and ESEs under salinity stress, and downregulates genes involved in stress tolerance (Asensi-Fabado *et al.*, 2012). These findings suggest ET is a fundamental plant hormone for plant growth and development, and plays an important role in response to environmental stresses.



**Figure 4.** The molecular mechanism of ERF under NaCl stress. By activating the ERF signaling pathway through *ETR1*, *EIN* is phosphorylated, which in turn activates *ECIP1*. The ERF transcription factor is activated, which then activates its target proteins and downstream genes in response to salinity stress

*bZIP transcription factor*

The basic leucine zipper transcription factor (bZIP) is considered a crucial gene which regulates plant developmental processes and abiotic stress tolerance (Dröge-Laser *et al.*, 2018). The highly conserved dimerization domain of bZIP contains a basic region, where a nuclear localization signal is resided, followed by a 16 amino acid sequence with an N-x7-R/K motif that binds to DNA (Wang *et al.*, 2015). A less conserved leucine zipper domain of bZIP is responsible for the dimerization ability of bZIP (Amoutzias *et al.*, 2007). Basically, the bZIP cis-element contains A-box (TACGTA), C-box (GACGTC), G-box (CACGTG), GLM (GTGAGCAT) and PB-like (TGAAAA) sequence that are responsible for abiotic stress tolerance (Dröge-Laser *et al.*, 2018; Wang *et al.*, 2015). A number of bZIP genes have been identified in different plants associated with various biological activities, including developmental processes and abiotic stress tolerance, as mentioned in S. Table 5.

The overexpression of bZIP members can enhance salinity stress tolerance in plants. Salt stress in *Solanum lycopersicum* and *oryza sativa* can be improved by the overexpression of *SlbZIP38* and *OsbZIP42*, respectively (Wang *et al.*, 2018). *Solanum lycopersicum* *SlbZIP1* overexpression lines are more sensitive to drought and salinity stress, which induces high MDA contents and low chlorophyll and proline contents (Zhu *et al.*, 2018), and the transcription levels of ABA biosynthesis genes are downregulated in response to salt stress. Similarly, the ABA signaling pathways are greatly activated in *Oryza sativa* overexpression lines *OsbZIP42* and *ZEP252*, which leads to enhanced abiotic stress tolerance (Joo *et al.*, 2019; Xu *et al.*, 2008). Recent studies reported that wheat bZIP transcription factors *TabZIP60* and *TaZIP14-B* significantly enhance salinity, drought, and freezing stress tolerance in Arabidopsis (Baillo *et al.*, 2019). It was reported that *TabZIP60* binds to the ABA-responsive cis-element, and thus enhances abiotic stress tolerance (S. Table 5). These findings conclude that bZIP and ABA have strong interaction during salinity stress tolerance.

*MicroRNAs (miRNA)*

miRNAs (MicroRNA) are non-coding single strand small RNAs with 21-24 nucleotides (Zhang *et al.*, 2006). These miRNAs are important regulators of gene expression in plants to control the transcript of target genes involved in plant growth, development, signal transduction, response to adversity, abiotic stress tolerance and other biological processes (Zhang, 2015). Many miRNAs have been identified which significantly enhance tolerance to salinity stress (S. Table 6) (Sun *et al.*, 2015). *MiR393* has recently been reported to enhance salinity stress tolerance by improving the germination rate, water loss, root elongation, and chlorophyll accumulation, thus reducing senescence and cell death (Chen *et al.*, 2015). The plants with *miR394a/b* overexpression are highly hypersensitive to salinity stress, but its *LCR* (*LEAF CURLING RESPONSIVENESS*) mutant (function loss of *miR394* target *LCR*) is salinity stress tolerant (Song *et al.*, 2013). *miR393a/b* promotes the accumulation of ABA-induced H<sub>2</sub>O<sub>2</sub> and O<sub>2</sub>, and downregulates the genes involved in the ABA signaling pathway, stress response, and the expression of *ABI3*, *ABI4*, *ABI5*, *ABF3*, and *AB4* compared with the *LCR* plants (Song *et al.*, 2013). *Osa-mR939* overexpression enhances tillers and early flowering, but reduces the tolerance to salinity and drought stress in *Oryza sativa*. *miRNA396c* overexpression enhances NaCl stress tolerance through the mediation of water retention, chlorophylls accumulation, cell membrane Na<sup>+</sup>/H<sup>+</sup>, antioxidant enzymes and transcription factors, but reduces the tolerance to alkali and salt stress in Arabidopsis and *Oryza sativa* (Zhan *et al.*, 2021).

miRNAs are associated with plant defense during environmental influences, thus increasing stress tolerance. Overexpression of *miR395c* and *miR395e* enhances seed germination and dehydration stress responses, by targeting *APS1*, *APS3*, and *SULTR2*. *miR172c* is associated with plant root sensitivity. Overexpression of *miR172c* increases root sensitivity to salinity stress in soybean (Sahito *et al.*, 2017). miRNAs are potentially involved in the hormonal signaling pathways to regulate physiological and biochemical processes in plants under abiotic stress (Anwar and Kim, 2020; Zhang, 2015). *miR169* overexpression enhances salinity

stress tolerance via the ABA signaling pathway and regulates the biosynthesis of *ABA1*, *ABA2*, *AB11*, and other stress responsive genes. *miR390* is associated with the auxin signaling pathway in regulating salinity stress tolerance. Overexpression of *miR399f*, *miR404*, and *miR408* enhances the tolerance to salt stress, while overexpression of *miR414c*, *miR417* and *miRNVL5* has a negative effect on salt stress responses in Arabidopsis (S. Table 6). These findings imply that miRNA plays a crucial role in salinity stress tolerance and crop production.

## Conclusions

In this review, we focus on the current progress of salt stress on plant growth and development. Salinity is considered a key hurdle for crop production and is expected to be more severe in the coming decades. Salinity stress causes a wide range of harmful effects on plants in different stages from seed germination to senescence, which ultimately leads to significant yield reduction. To overcome these problems, it is urgent to understand the molecular mechanisms of salt stress responses in plants such as Na<sup>+</sup> and Cl<sup>-</sup> ions absorption, translocation and accumulation. Using advanced biotechnologies, such as RNA-seq, ChIP-seq, CRISPR/Cas9, etc., the responses of plant to salt stress have been investigated, such as Na<sup>+</sup> and Cl<sup>-</sup> ion accumulation, ROS overproduction and oxidative stress. A number of candidate genes, such as *OsNAC2*, *OsNAC5*, *OsNAC10*, *ONAC045*, *AtERF1*, *TaERF3*, *BrERF4*, *mERF7*, *TabZIP15*, *ZmbZIP72*, *WRKY39*, *ZmWRKY33*, and *GbWRKY39*, have been reported to play a role in salinity stress tolerance. In addition, RNA-seq has been used to identify salinity stress candidate genes, and ChIP-seq has been used to identify downstream genes, which are validated through protein-protein or promoter interaction under salt stress. Based on these studies, further investigations need to be conducted to allow genetic engineering of crop varieties and improve salt stress tolerance and crop yield.

## Authors' Contributions

AA, ZS and HL conceived and designed the study. AA and ZS wrote the manuscript. HL help to collect the materials and revised the manuscript. GJ review the manuscript. All authors read and approved the final manuscript.

## Ethical approval (for researches involving animals or humans)

Not applicable.

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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