Review Article

Phytohormones: Important Participators in Plant Salt Tolerance

Ling Zheng[1*], Haiyan Ma[1], Qiqing Jiao[2], Changle Ma[1*] and Pingping Wang[1*]

[1]*Shandong Provincial Key Laboratory of Plant Stress, College of Life Sciences, Shandong Normal University, Wenhua East Road 88, Jinan 250014, China*
[2]*Shandong Institute of Pomology, Long Tan Road 66, Tai'an 271000, China*
*For correspondence: changlema@yahoo.com; zhengling0000@sina.com; pingping.wang@sdnu.edu.cn

Abstract

Salt stress is an abiotic stress that can be deleterious to plant growth. Currently, one third of the soil in the world is affected by salt stress. Under saline conditions, plants suffer from stress toxicity, such as ion toxicity, osmotic stress and oxidative stress, resulting in inhibition of plant growth and decreases in crop yield. Phytohormones play an important role in stress resistance in plants. Phytohormones, such as auxin, gibberellin, cytokinin, ethylene, abscisic acid and brassinosteroids, are pivotal regulators in triggering tolerance against salt stress by remodeling ion homeostasis, regulating osmolyte synthesis and activating antioxidant enzymes. Understanding how hormone function is regulated during the salt stress response will be critical for enhancing the salt tolerance of crops and can provide guidance for curbing soil salinization. Here, we review salt stress toxicity and discuss the important regulatory roles of hormones in plant adaption to salt stress. © 2020 Friends Science Publishers

Keywords: Osmotic stress; Oxidative stress; Phytohormones; Salt stress; Soil salinity

Introduction

Salt stress is a very destructive abiotic stress throughout the world. One third of the world's fields, across more than 100 countries, have saline-alkali soil (Szabo *et al.* 2016; Yang and Guo 2018; Morton *et al.* 2019). Seed germination and plant growth are inhibited significantly when plants are grown in a saline environment. Thus, salt stress is a widespread environmental stress factor which significantly hinders crop productivity.

Soil is considered saline when the electrical conductivity of the soil extract solution exceeds 20 m*M*. Based on their salt tolerance, plants are divided into halophytes (salt tolerant and can normally grow in at least 200 m*M* NaCl conditions) and non-halophytes (salt intolerant). Halophytes employ various mechanisms to resist salt stress (Yuan *et al.* 2016). For example, many halophytes have salt excretory organs, such as the salt gland of *Limonium bicolor* (Feng *et al.* 2014a) or the salt bladder of Quinoa (Munns and Tester 2008). Other halophytes, such as *Suaeda salsa*, store salt in the vacuoles of their succulent leaves or stems (Sui *et al.* 2010; Guo *et al.* 2015; Song and Wang 2015; Wang *et al.* 2015; Song *et al.* 2016; Zhou *et al.* 2016). But in non-halophytes, salt tolerance is a complex process regulated by multiple genes and various biochemical and physiological mechanisms (Yuan *et al.* 2013; Zhang and Shi 2013; Liang *et al.* 2014). Plant hormones are central integrators involved in plant growth and development and stress response. Plant hormones can sense and respond to stress through their signal transduction pathways. The expression of many genes, such as ATPase, superoxide dismutase (SOD) and catalase (CAT), are regulated by plant hormone signals, which help to partially restore homeostasis during plant growth and development during salt stress (Fig. 1). Thus, understanding the relationship between salt stress and phytohormones may be integral to combating the huge agricultural costs inflicted by saline soil. Here, we review salt stress toxicity and the relationship between salt stress and plant hormones.

Saline Stress Effects on Plant

Ion stress

Plants growing in saline soil absorb and accumulate salt, resulting in high intracellular Na^+ concentrations and disruption of intracellular ion equilibrium (Rengasamy 2010; Feng *et al.* 2014b; Shen *et al.* 2014). For example, Na^+ can competitively inhibit K^+ absorption through the Na^+-K^+ translocator. K^+ promotes the activity of some intracellular enzymes and regulates many physiological functions in plants, including photosynthesis and organic matter synthesis and transport (Ren *et al.* 2013; Leng *et al.* 2018). Thus, decreasing the intracellular K^+ concentration
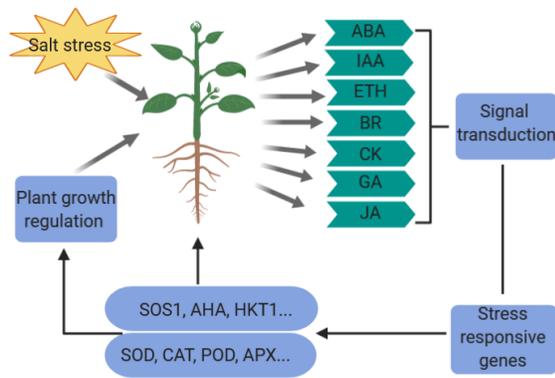
Fig. 1: Salt stress and phytohormones response. Salt stress is detected by plants via various sensors that activate the biogenesis of plant hormones such as abscisic acid (ABA), auxin (IAA), ethylene (ETH), brassinosteroids (BRs), cytokinin (CK), gibberellins (GA), and jasmonates (JA). Hormonal based responses activate their respective signaling pathways and trigger the activation of stress responsive genes. SOS1: salt overly sensitive 1, AHA: plasma membrane (PM) H$^+$-ATPase, HKT1: high affinity potassium transporter 1, SOD: superoxide dismutase, CAT: catalase, POD: peroxidase, APX: ascorbate peroxidase

disturbs the metabolic balance in plants (Liang *et al.* 2017; Duan *et al.* 2018). In addition, Na$^+$ replaces Ca^{2+} in cytomembranes, decreasing the stability and increasing the penetrability of the cell membrane (Han *et al.* 2012). Increasing cell membrane penetrability causes an influx of external Na$^+$ and Cl$^-$ into the cell (Liu *et al.* 2018). Moreover, Ca^{2+} participates in many biological processes (Zheng *et al.* 2017) which may be disturbed by Na$^+$-mediated changes in intracellular Ca^{2+} concentrations. For example, dramatic changes in cytoplasmic Ca^{2+} concentrations will disrupt the Ca^{2+}-mediated calmodulin (CaM) adjustment system. As a result, ion stress caused by saline soil causes wide-ranging adverse effects, including disrupting photosynthesis, phytohormone synthesis and seed germination, speeding up toxic reactions, inhibiting root and stem growth and inhibiting nutrient uptake. Ultimately, this leads to inhibition of plant growth and decreases in crop yield for grains, such as cotton, barley, wheat, rice, and peanut (Liu *et al.* 2012; Hou *et al.* 2014; Kong *et al.* 2016; Hu *et al.* 2018; Sui *et al.* 2018). India, Myanmar and Bangladesh, which are the major contributors to the world's rice production, are currently facing serious threats to food security due to salinization of coastal soil (Abedin *et al.* 2014; Szabo *et al*. 2016). For example, in the Sindh region of Pakistan and Alberta, 31 and 25 percent of crops, respectively, have been lost due to salinity (Ilyas 2017).

Osmotic stress

Saline soil solutions have high ion concentrations leading to

a high osmotic potential (Deng *et al.* 2015). Thus, water influx into the roots, including water efflux from the plasma membrane and vacuole, is suppressed in saline soil. When the salt concentration exceeds the rate of exclusion by the roots or the cell's ability to compartmentalize salt in the vacuoles, osmotic stress occurs. As the initial phase of stress, osmotic stress occurs immediately (within a few minutes) upon contact of the plant with high concentrations of saline soil (Shavrukov 2013). Osmotic stress disrupts cellular structures and disturbs cell turgor. Stomatal conductance is also affected by osmotic stress, causing stomatal closure. Ultimately, the plant growth rate is slowed, followed by leaf senescence and apoptosis (Munns and Tester 2008).

Oxidative stress

In addition to ion imbalance and loss of water availability, salt stress causes a secondary stress, oxidative stress. Salt stress induces overproduction of reactive oxygen species (ROS), such as hydroxyl radicals (OH$^-$), hydrogen peroxide (H$_2$O$_2$) and superoxide (O$_2^-$), in plant cells leading to oxidative stress (Zhu *et al.* 2007; Hazman *et al.* 2015). ROS accumulation triggers oxidative damage by disrupting membrane permeability and reducing protein and enzyme activity (Wu *et al.* 2019). The cell membrane is an important protective barrier necessary for material transport, energy transfer and signal transduction (Liu *et al.* 2017). ROS change membrane permeability which impacts ion selectivity, velocity and transportation and causes leaking of phosphorus and organic matter. Finally, ROS severely damage cellular structures and macromolecules (Golldack *et al.* 2014).

Phytohormones and Salt Tolerance

Plant hormones, also known as phytohormones, are produced in plants and regulate plant growth. They are involved in complex physiological functions, such as cell division, elongation, plant sprouting, flower and fruit maturation, sex determination and seed dormancy. In plants, there are many kinds of phytohormones, such as abscisic acid (ABA), auxin (IAA), ethylene (ETH), brassinosteroids (BRs), cytokinin (CK), gibberellins (GA), and jasmonates (JA).

Phytohormone levels are dynamically regulated according to the growth environment and growth period of the plant. In a saline environment, plants have various mechanisms to cope with the dramatic damage caused by salt stress, including removing salts from the cells or transporting salt to particular areas such as *Limonium bicolor* and *Suaeda salsa* (Golldack *et al.* 2011; Cheng *et al.* 2014). During salt stress, phytohormone levels and activity change, which subsequently modulate plant physiological processes (Yang *et al.* 2017; Zhang *et al.* 2017; Wei *et al.* 2018; Hoang *et al.* 2019; Jang *et al.* 2020; Wang *et al.* 2020).

Abscisic acid (ABA)

ABA is an important small signaling molecule in plants. ABA is synthesized via cleavage of carotenoids and is regulated by several important ABA biosynthesis genes. NCEDs (9-cis-epoxycarotenoid dioxygenases) are the key regulatory enzymes of ABA biosynthesis as they catalyze the rate-limiting carotenoid cleavage reaction. *ZEPs* encode zeathanxin epoxidase that catalyzes the epoxidation of zeaxanthin and antheraxanthin to violaxanthin. *LOSs* encode a sulfurylase that generates the active form of the molybdenum cofactor required by ABA aldehyde oxidase.

ABA is involved in numerous processes including seed dormancy, plant growth and development and stress responses. ABA inhibits seed germination, promotes dormancy and stomata closure, promotes synthesis of storage proteins and lipids and responds to salt stress. In response to salt stress, ABA functions as an important secondary signaling molecule. Salt stress increases the ABA content in plant cells by upregulating expression of ABA synthesis genes (Cramer and Quarrie 2002; Cabot *et al.* 2009). In rice, *OsNCED5* is induced by exposure to salt stress. In the *nced5* mutant, ABA levels are reduced, concomitant with decreased tolerance to salt stress. In contrast, overexpression of *NCED5* leads to increased ABA levels and enhanced salt tolerance (Huang *et al.* 2019). *Arabidopsis ABA1* and *ABA3* are also induced by salt stress (Tan *et al.* 2019). The salt-induced increase of ABA levels may play a role in activating the ABA signaling pathway.

The ABA signal network is highly complex and includes many ABA receptors. In normal conditions, Ca^{2+} and SnRKs/CPK activity are inhibited by type 2C protein phosphatases (PP2Cs). During stress, ABA binds to the receptors PYR/PYL/RCARs (PYRABACTIN RESISTANCE/PYRABACTIN RESISTANCE-LIKE/REGULATORY COMPONENT OF ABA RECEPTORS), causing inhibition of PP2C activity and subsequent activation of SnRK2s (SNF1-RELATED PROTEIN KINASES) (Fujii *et al.* 2009; Wang *et al.* 2018) (Fig. 2). SnRK2s activate several transcription factors, such as ABREs (ABA-RESPONSIVE PROMOTER ELEMENTS) and ABFs (ABRE BINDING FACTORS). SnRK2 kinase activity is increased under salt stress conditions. SnRK2s regulate ABA-responsive physiological processes (Du *et al.* 2012; Golldack *et al.* 2014).

Salt stress triggers ABA synthesis gene expression, inducing ABA signaling which in turn mediates the salt stress response. The salt stress signaling pathway has crosstalk with the ABA signaling pathway. In addition to up-regulating ABA synthesis, salt stress conditions also activate a Ca^{2+} signal. The Ca^{2+} is perceived by Ca^{2+}-dependent protein kinase (CPK) and calcineurin B-like proteins (CBLs)/CBL-interacting protein kinase (CIPK). CBL-CIPK regulates downstream genes such as SnRK2s. The salt overly sensitive (SOS) pathway plays an important role in the plant salt stress response. The *SOS*
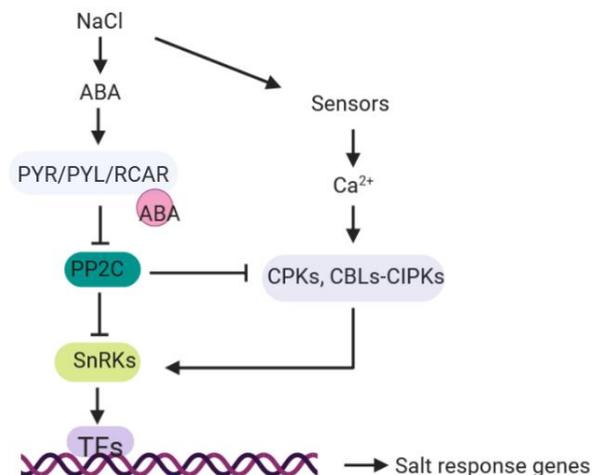

Fig. 2: Salt stress and ABA signaling.
Under normal conditions, the Ca^{2+} signal and SnRKs/CPK activity are inhibited by PP2C. Salt stress causes accumulation of ABA. ABA binds to PYR/PYLs/RCARs which inhibit PP2C activity. Subsequently, SnRKs are activated to phosphorylate transcription Factors (TFs) which regulate the salt response genes. Sensors sense the salt stress stimuli and trigger concentration fluctuations of cytosolic-free Ca^{2+}. The Ca^{2+} serves as second messenger to transmit the salt stress signal to CPK and CBLs-CIPKs. SnRK2s can be activated by CIPK. CBLs-CIPKs phosphorylate effector proteins including TFs to mediate salt tolerance.

genes were discovered by screening for hypersaline sensitive mutants (Wu *et al.* 1996). Calcium-binding protein SOS3 decodes the Ca^{2+} signal by interacting with the protein kinase SOS2 (also named CIPK24) which is activated by SOS3. SOS2 phosphorylates and activates the Na^+/H^+ antiporter SOS1 to transport Na^+ into the cytoplasm. ABI2 (abscisic acid insensitive 2) interacts with SOS2 to inhibit SOS2 activity. The *abi2-1* mutant has increased salt stress tolerance and ABA insensitivity (Ohta *et al.* 2018).

Plants grown on saline soil accumulate Na^+, causing high intracellular Na^+ concentrations. Because of their similar chemical properties, Na^+ competitively inhibits the absorption of K^+, causing K^+ deficiency (Shao *et al.* 2014; Feng *et al.* 2015). During salt stress, increasing ABA levels causes Na^+ exclusion to decrease, while root-shoot Na^+ translocation increases, causing Na^+ concentrations to rise in the leaf (Cabot *et al.* 2009). Enhanced ABA accumulation can regulate the plasma membrane Na^+/H^+ antiporter and water uptake during salt stress. The H^+-ATPase type vacuolar pump (V-ATPase) and vacuolar pyrophosphatase (V-PPase) are the major Na^+/H^+ antiporters which can transport Na^+ into the vacuole (Otoch *et al.* 2001; Xue *et al.* 2019). In wheat, ABA induces the expression of salt tolerant genes, including the Na^+/H^+ antiporter NHX2 and vacuolar H^+-pyrophosphatases HVP1 and HVP10 (Yu *et al.* 2007). These proteins enhance the cell ion selectivity and promote intracellular Na^+ regionalization into the vacuole or extracellular Na^+ export.

ABA accelerates stomata closure in plants to protect against water loss (Murata *et al.* 2001; Yan *et al.* 2010). Stomatal closure also blocks the transport of Na^+ from the root to the shoots which accompanies transpiration. While the closure of stomata weakens ion toxicity, CO_2 absorption and fixation are also reduced resulting in decreased photosynthesis and slower plant growth. NACs are plant-specific transcription factors which may regulate the expression of stress-resistant genes. In peanut, *AhNAC4* expression increases after treatment with ABA (Tang *et al.* 2017). *AhNAC4* transgenic tobacco lines have enhanced salt tolerance associated with more stomatal closure (Casella *et al.* 2017). During the stomatal closure process, *Arabidopsis* CKL2 (casein kinase 1-like protein 2) responds to ABA to aid actin reorganization in the stomata to help close the stomata. *ckl2* mutants alter actin reorganization and decrease ABA-induced stomatal closure compared to wild-type (Zhao *et al.* 2016).

ABA induces synthesis of many osmolytes. Osmolytes can enhance cell turgor and cause the cell to expand to reduce water loss under osmotic stress. Osmotic balance is important for metabolic maintenance and normal plant growth. In plants, many osmolytes regulate the osmotic balance, such as proline, soluble sugar, betaines (Summers *et al.* 1998; Hu *et al.* 2015), polyols (Conde *et al.* 2011; Bertrand *et al.* 2015) and ions (Rodriguez *et al.* 1997). Proline, with a low molecular weight, high water solubility and lack of charge, is a perfect osmolyte. Because of this, proline concentration is positively correlated with stress and increases significantly during salt stress (Guo *et al.* 2012). Betaines also play a role in osmotic balance (Shah *et al.* 2018). As a result, proline, soluble sugar and betaines accumulate under high salt because of the ABA high content (Silva-Ortega *et al.* 2008). These osmolytes enhance cell turgor and cell expansion, maintain protein and cell membrane stability and modulate cellular metabolism (Silva-Ortega *et al.* 2008).

ABA signaling not only enhances the expression of many transcription factors but also enhances antioxidant enzyme activity. The activity of antioxidants like SOD, peroxidase (POD), ascorbate peroxidase (APX) and CAT scavenge ROS to protect lipids, proteins and nucleic acids from oxidative damage (Meloni *et al.* 2003; Pang *et al.* 2011; Li *et al.* 2015; Cao *et al.* 2017; Wang *et al.* 2017). H_2O_2 is generated from the disproportionation reaction of O_2^- by SOD and can be catalyzed to H_2O by CAT (Li *et al.* 2012; Ismail *et al.* 2014; Su *et al.* 2018; Su *et al.* 2019). Increasing endogenous ABA synthesis may maintain the balance between the generation and removal of ROS, circumventing cell membrane damage. This is substantiated by the finding that *Arabidopsis* lines overexpressing tomato *ERF84* have high salt tolerance. SlERF84 is an ethylene-responsive transcription factor which is significantly induced by salt. Moreover, SOD and POD activities are highly induced by oxidative stress in these overexpression lines, demonstrating these transgenic plants possess higher ROS scavenging capability (Li *et al.* 2018).

In summary, salt stress causes ABA accumulation in plants which activates salt-resistance pathways. As a result, ABA regulates plant growth by attenuating the deleterious effects of salt stress on processes like osmosis, ion balance, ROS production and photosynthesis (Chen *et al.* 2013).

Auxin (IAA)

IAA (indole-3-acrtic acid), the main auxin in higher plants, is one of a group of multifunctional phytohormones. Low IAA concentrations promote plant growth, while high concentrations inhibit growth and even cause plant death.

IAA responses to salt stress are modulated by changes to IAA biosynthesis, conjugation and transport (Fig. 3). For example, the levels of IAA in tomato roots decline nearly 75% after treatment with NaCl (Dunlap and Binzel 1996). The tryptophan aminotransferase (TAA)/flavin monooxygenase (YUC) pathway is the predominant IAA biosynthesis pathway. In this pathway, YUCs play an important role in salt tolerance. Plants overexpressing *Arabidopsis YUC6* have higher tolerance to osmotic stress (Kim *et al.* 2013; Ke *et al.* 2015). On the other hand, in *yuc1/yuc2/yuc6* mutants, IAA levels are reduced and stress resistance is decreased (Shi *et al.* 2014).

In plants, most IAA exists in the conjugated form, with the active IAA product being freed when needed. IAA is conjugated sugars and amino acids via UGTs (UDP-glucose transferases) and IAA amino acid conjugate synthetases of the GH3 family (Fig. 3) (Staswick *et al.* 2005; Ludwig-Müller 2011). In cotton, using virus-induced gene silencing (VIGS), *GH3.5* VIGS plants reduced the tolerance to drought and salt stresses compared to the wild types (Kirungu *et al.* 2019). IAR3 hydrolyzes IAA-alanine and releases free, active IAA. Free IAA levels are reduced in *iar3* mutants, which display reduced osmotic stress in roots (Natsuko *et al.* 2012).

Auxin transporters regulate auxin homeostasis. PINs are responsible for auxin efflux from the cell, while AUX1/LAX control auxin influx into the cell. Other auxin carriers include ABCB1,19, PILS and WAT1 (Fig. 3). Salt stress represses *PIN* expression, disrupting the root gravity response (Liu *et al.* 2015). Under salt stress, lateral roots grow away from the saline soil by changing the spatial and temporal distribution of auxin. It has been consistently shown that under directional gradient salt treatment DII-VENUS, an auxin response reporter, has a reduced level and auxin levels highest at the side of the root opposite to the higher salinity (Galvan-Ampudia *et al.* 2013). PIN2 also internalizes at the side of the root facing high salt conditions, thus affecting auxin flow (Sun *et al.* 2008).

TIR1/AFB and Aux/IAA are auxin receptors which recognize intracellular auxin. Aux/IAA and ARF are two important protein families which mediate the auxin response. Aux/IAA and ARFs interact with each other to form dimers. Under salt stress, the interaction of TIR1/AFB
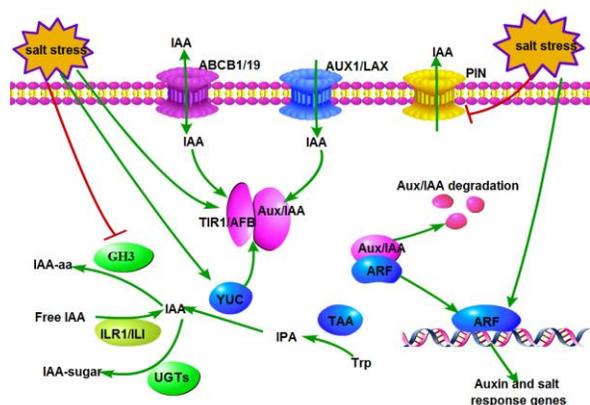
Fig. 3: Proposed model of IAA biosynthesis and signaling responses in response to salt stress. Under salt stress, IAA biosynthesis genes YUCs play an important role in salt tolerance. PINs (PINFORMED), AUX1/LAX (AUXIN TRANSPORTER CARRIER1/AUXIN TRANSPORTER-LIKE PROTEINS), ABCB1,19 (P-glycoproteins/ATP-binding cassette class B proteins), PILS (PIN-LIKES) and WAT1 (WALLS ARE THIN1) are IAA carriers. Auxin is recognized by TIR1/AFB (TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX PROTEIN) and Aux/IAA (AUXIN/INDOLE-3-ACETIC ACID). Aux/IAA and ARF (AUXIN RESPONSE FACTOR) mediate the auxin response. Aux/IAA and ARFs interact with each other to form a dimer. Under salt stress, auxin promotes the interaction of TIR1/AFB and Aux/IAA, leading to Aux/IAA degradation and release of ARF. The released ARF activates auxin and salt response genes

and Aux/IAA leads to degradation of Aux/IAA and subsequent release of free ARF. The released ARF induces expression of auxin and salt response genes (Fig. 3). PLTs (PLETHORAs) are auxin-responsive transcription factors responsible for maintenance of the stem cell niche and cell proliferation. In *Arabidopsis*, ARF2 positively mediates the expression of *PLT1* but negatively mediates *PLT2*. In rice, *Aux/IAA* and *ARF* are induced by salt stress (Jain and Khurana 2010). Additionally, overexpression of *Aux/IAA6* improves drought tolerance in rice (Jung *et al.* 2015). Overexpression of *mTIR1* also improves salt tolerance by decreasing H_2O_2 and O^{2-} levels (Iglesias *et al.* 2010; Chen *et al.* 2014). The *tir1 afb2* mutant has higher salt tolerance because of the high activity of POD and CAT (Iglesias *et al.* 2010). Many auxin transport mutants show stomatal clustering, demonstrating that auxin is a regulator of stomata (Balcerowicz and Hoecker 2014; Balcerowicz *et al.* 2014; Zhang *et al.* 2014). Overexpression of the auxin responsive gene *OsGH/3-2* in rice reduces auxin and ABA levels, increases the rate of water loss, and weakens stress tolerance (Du *et al.* 2012). Together these data demonstrate that auxin regulates plant growth by alleviating osmotic and oxidative stress.

During salt stress, auxin induces the transcription of many genes (Hou *et al.* 2012; Wang *et al.* 2017). Although many of these auxin response genes have been studied in

various plants such as *Arabidopsis*, soybean and rice (Javid *et al.* 2011), many are novel genes which require further investigation.

Ethylene (ETH)

Ethylene (ETH) is a gaseous phytohormone which regulates plant growth and development by breaking seed dormancy, promoting flowering and fruit maturation and regulating plant resistance (Morgan and Drew 2010). Under saline conditions, the synthesis of ACC (1-aminocyclopropane-1-carboxylic acid, the direct precursor of ethylene) and ethylene are increased. ACC synthase (ACS) is the major enzyme responsible for regulation of ethylene production under salt stresses (Sun 2005; Shen *et al.* 2014). Exogenously applied ACC significantly increases the salt tolerance of rice (Liang *et al.* 2019). Overexpression of the tobacco type II ethylene receptor *NTHK1* increases tobacco salt sensitivity, concomitant with changes in salt-related functional gene expression, which can be rescued by exogenously applied ACC (Tao *et al.* 2015). Many *ACS* genes, like *ACS2* and *ACS6-8* in *Arabidopsis* and *ACS1* and *ACS12* in cotton (Achard *et al.* 2006; Peng *et al.* 2014a; Shen *et al.* 2014), are more highly expressed during salt stress, hinting at their important function in stress regulation. ETHYLENE INSENSITIVE 3 (EIN3) is an important participator in the ETH signal pathway. The *ein3-1* mutant is salt-sensitive during seed germination and seedling development, with the survival rate of *ein3-1* seedlings in 200 m*M* NaCl being only 20% (Yoo *et al.* 2008). However, the *eto1* mutant has higher ethylene concentrations and increases soil-salinity tolerance (Jiang *et al.* 2013). Furthermore, the *eto1* mutant reduces Na^+ influx and the Na^+ concentration in xylem, enhancing K^+ balance. Some research has shown that increased ETH content can cause higher salt sensitivity while decreased ETH content can cause higher salt tolerance (Xu *et al.* 2008; Hui *et al.* 2011; Chen *et al.* 2014). Thus, the relationship of ETH and salt resistance remains ambiguous as ETH seems to have both a positive and negative impact.

Salt stress induces ROS overproduction. Many ETH functions are related to ROS scavenging. ETH enhances the expression of *SIEDs* and *PODs* by stabilizing EIN3/EIL1, thus promoting ROS scavenging (Peng *et al.* 2014b). A large number of ethylene-responsive secondary transcription factors (ERFs) have been found in *Arabidopsis*. AtERF74 promotes a ROS burst in the early stages of various stresses and AtERF98 regulates the expression of *VTC1* (ascorbic acid synthase). Ascorbic acid is an important antioxidant in plants, which can remove ROS through a redox reaction (Zhang *et al.* 2012). As mentioned earlier, loss of function of ETO1 causes improved Na^+/K^+ homeostasis and increased saline tolerance (Jiang *et al.* 2013). However, overexpression of *JERF3* (ETH response factor protein) reduces ROS production and promotes expression of osmotic stress genes, resulting in increased salt tolerance

(Wu *et al.* 2008). *etr1-1*, a functionally acquired mutant whose ethylene signal pathway is blocked, is insensitive to ethylene and shows higher sensitivity to salt. In contrast, the functionally deficient mutant *etr1-7* shows higher salt tolerance (Wang *et al.* 2008). Another functionally acquired mutant *ein4-1* also shows increased sensitivity to salt (Cao *et al.* 2007). Under salt stress, *etr1* and *etr4* mutants inhibit seed germination, while *etr2* promote germination.

ETH has crosstalk with other phytohormones. BRs increase the expression and stability of the ETH synthesis genes. During salt stress, BRs induce generation of H_2O_2, which acts as a secondary messenger to activateMKK9. Activation of MKK9 triggers the MPK3/MPK6 signaling pathway, which is required for the stabilization and activation of *ACS* genes and *EIN3* (Yoo *et al.* 2008). ETR1 and EIN4 induce accumulation of ABA to inhibit germination, but ETR2 suppresses ETR1 and EIN4, reducing ETH levels and inducing germination (Wilson *et al.* 2014). Thus, the mechanisms underlying the role of ETH in salt resistance appears to be complex and warrants further study.

Brassinosteroids (BRs)

Brassinosteroids (BRs) are a group of plant-specific polyhydroxylated steroid hormones derived from the isoprenoid squalene. BRs are widely distributed throughout plants and are synthesized in every plant organ. BRs do not undergo long-distance transport. Among the BRs, only the end-product of BR biosynthesis, brassinolide (BL), and its precursor castasterone (CS) have bioactivity *in vivo* (Wei *et al.* 2017). Many detailed biochemical studies have identified various biosynthesis routes for BRs. Numerous key enzymes of BR biosynthesis have been identified, such as BR6OX1 (brassinosteroid-6-oxidase 1), CPD (constitutive photomorphogenesis and dwarfism), DET2 (de-etiolated-2), DWF4 (dwarf4), and ROT3 (rotundifolia 3), which catalyze the main rate limiting step in BR biosynthesis. BRs play numerous important roles in plant growth, including in seed germination, cell growth, flowering and fruiting (Kim *et al.* 2009). BRs have positive roles in tolerance to many stresses, including drought (Li *et al.* 2008), high temperature (Li *et al.* 2007) and salinity (Zhu 2002). In stress environments, the biosynthesis of BRs is increased and plant stress tolerance enhanced.

Exogenous application of BRs can increase betaine and GSH content and improve saline tolerance in beans and barley (Ali and Abdel-Fattah 2006). BRs also induce expression of soluble proteins which reduce oxidative stress and reduce chloroplast damage during salt stress (Krishna 2003; Özdemir *et al.* 2004). BRs increase nitrate reductase activity and restore chlorophyll levels as a means to regulate plant growth under salt stress (Bajguz and Hayat 2009). Exogenous applications of BRs reduce Na^+ content and increase the absorption of K^+ and Ca^{2+}, concomitant with higher saline tolerance (Qayyum *et al.* 2007; Shahbaz *et al.*
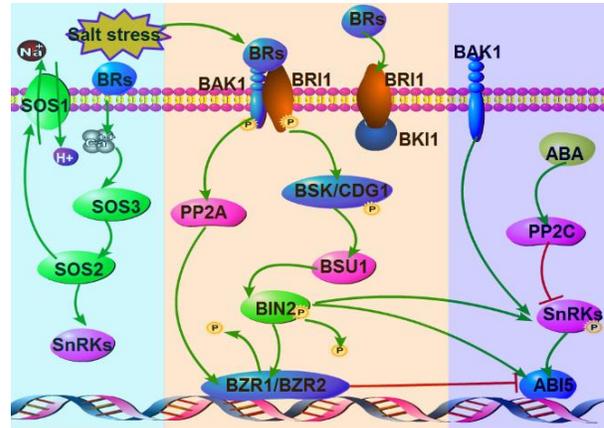

Fig. 4: Salt stress triggers the BRs signaling transduction pathway The biogenesis of BRs is triggered by salt stress and the increased BRs enhance salt tolerance by inducing the expression of salt stress response genes. Under salt stress, the levels of BRs are increased due to high expression of the synthesis genes. The BRs bind to BRI1 (BR-INSENSITIVE 1) and BAK1 (BRI1 associated receptor Kinase 1), triggering formation of a cross-phosphorylating complex. BRI1 rapidly phosphorylates BKI1 (BRI1 kinase inhibitor), causing BKI1 to be released from the plasma membrane. BRI1 also phosphorylates BR-SIGNALING KINASE (BSK)/CONSTITUTIVE DIFFERENTIAL GROWTH 1 (CDG1) which in turn activates BRI1 SUPPRESSOR1 (BSU1) which phosphorylates BR ASSINOSTEROID-INSENSITIVE2 (BIN2). Phosphorylated BIN2 loses its ability to suppress the functions of BR ASSINAZOLE-RESISTANT1 (BZR1) and BRI1-EMS-SUPPRESSOR1 (BES1/BZR2), causing dephosphorylation of BES1/BZR1. As a result, PROTEIN PHOSPHATASE 2A (PP2A) dephosphorylates and thus activates the transcription factors BZR1 and BES1/BZR2 leading to down-stream gene expression of salt responsive genes. BRs have crosstalk with the ABA pathway as BIN2 and BAK1 regulate the SnRKs. Green background represents the SOS pathway. Pink background represents the BR pathway. Purple background represents the ABA pathway

2008; Karlidag *et al.* 2011). BRs respond to stresses via different mechanisms, such as key enzymatic activation or suppression, protein synthesis, and osmolyte production (Bajguz and Hayat 2009).

Transcription factors BRASSINAZOLE-RESISTANT1 (BZR1) and BRI1-EMS-SUPPRESSOR1 in the BR response pathway modulate multiple developmental and environmental stress response genes (Fig. 4) (Wang *et al.* 2011; Fàbregas *et al*. 2018). Overexpression of *Arabidopsis BRL3* (a BR receptor, *BRI1-Like 3*) causes high drought tolerance. *BRL3* overexpression lines exhibit increased accumulation of osmolytes including proline and sugars (Fàbregas *et al.* 2018).

During the salt response, BRs cross talk with other phytohormones, such as ABA. In addition to PP2C, the BR receptor BAK1 also regulates SnRK2.6 and to modulate stomatal closure (Acharya *et al.* 2013). BIN2 also phosphorylates and activates SnRK2.2 and the transcription

factor ABI5 (Cai *et al.* 2014). Conversely, BZR1/BZR2 inhibits ABI5 expression (Yang *et al.* 2016) (Fig. 4). A group of salt response genes is positively regulated by ABI5 under salt stress conditions. In another example of BR-ABA cross talk, BRs induce Ca^{2+} accumulation, which activates the SOS pathway to enhance salt tolerance (Fig. 2). The Ca^{2+} binds to calcium sensor proteins, such as SOS3, and activates SOS2 activity. SOS2 interacts with and activates the plasma membrane Na^+/H^+ antiporter, SOS1, which causes Na^+ exclusion from the cytoplasm. BRs activate SOS1 activity by increasing the cytoplasmic concentration of Ca^{2+}, thus maintaining ionic homeostasis in cells under salt stress.

So far, most research on BRs and salt resistance have focused on antioxidative metabolism. 24-epibrassinolide (EBL) improves plant growth by regulating redox and osmotic balance under salt stress. Under salt stress, EBL modulates antioxidant activities and increases the levels of plant hormones, like ABA, GA and IAA, and osmolytes (Wang *et al.* 2010; Wu *et al.* 2017). Increased levels of BRs in turn increase the levels of SOD, CAT, POD, GR and APX. The BR biosynthetic mutant has very low ratios of GSH/GSSG (reduced glutathione/oxidized glutathione) and AsA/DHA (reduced ascorbate/oxidized ascorbate), which are restored by exogenous BRs (Zhou *et al.* 2014). 28-Homobrassinolide (28-HBL) increases SOD, POD, CAT and APX activity in corn and bean seeding, thereby reducing the lipid peroxidation of membrane. Similarly, application of SA 28-HBL ameliorates the damage caused by salt stress (Fariduddin *et al.* 2009).

Salicylic acid (SA)

Salicylic acid (SA) is a phenolic growth regulator which plays a critical role in plant seed germination, photosynthesis, flowering, fruit yield, ethylene production, stomatal conductance and abiotic stress response (Kaya *et al.* 2002). SA is synthesized through two pathways, requiring multiple proteins which regulate SA synthesis and metabolism (Klessig *et al.* 2018). First, decarboxylation or hydroxylation of cinnamic acid generates benzoic acid or *O*-coumaric acid, respectively. Then, SA is formed by hydroxylating benzoic acid or decarboxylating *O*-coumaric acid. SA synthesis is induced by abiotic stress and pathogens.

Application of SA ameliorates the deleterious effect of salt stress in *Arabidopsis* (Chen *et al.* 2018) and many crops such as bean, tomato and maize (Gunes *et al.* 2007). Several studies have shown that SA alleviates stress-related damage by modulating ROS metabolism and thus enhancing the antioxidant defense system. SA-treated wheat show higher relative water content, membrane stability index and antioxidant enzyme activities during drought stress (Miura *et al*. 2013; Sedaghat *et al.* 2017). Similarly, in rubber tree, exogenous SA increases CAT and POD activities and enhances the defense capacity to stress
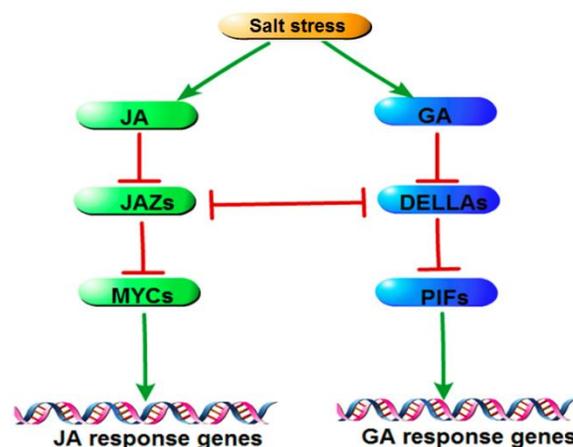

Fig. 5: GAs and JA crosstalk to coordinate the plant stress response. DELLAs, repressors of GAs signaling and JAZs, repressors of JA signaling, interact directly. This interaction allows MYCs to promote expression of JA response genes. The degradation of DELLA causes JAZs to be released from the complex, subsequently attenuating the JA response. Degradation of DELLA releases PHYTOCHROME INTERACTING FACTORS (PIFs) which are responsible for the GAs response

(Deenamo *et al.* 2018). SOD, CAT, APX and dehydroascorbate reductase (DHAR) are induced by application of SA to alleviate the oxidative damage caused by NaCl (Ahanger *et al.* 2019). By modulating expression of antioxidant enzymes and enhancing photosynthesis, *Lablab purpureus* defends itself against adverse environments (Rai *et al.* 2018). Furthermore, under NaCl stress conditions, endogenous SA decreases levels of MDA, H_2O_2 and O_2^-, while also stimulating antioxidant enzymes such as CAT, SOD and APX (Li *et al.* 2019).

Lipid peroxidation and MDA content are also decreased by exogenously applied SA. In maize, SA can also remodel iron balance during salt stress (Gunes *et al.* 2007). In *Arabidopsis* treated with SA, H^+-ATPase activity increases, Na^+ accumulation decreases and K+ retention increases (Jayakannan *et al.* 2013). Shakirova *et al*. reported that exogenous applications of SA caused accumulation of ABA and proline and alleviated the damage of salinity on wheat seedlings (Shakirova *et al.* 2003). In barley, SA protects the photosynthetic pigment and maintains membrane integrity under salinity stress. The positive effects of SA have been demonstrated in many plants, such as maize, wheat, tomato and rice (Stevens *et al.* 2006; Gunes *et al.* 2007; Wahid *et al.* 2007).

Jasmonate (JA)

JA is classified as a cyclopentane fatty acid. Its synthetic substrate is linolenic acid (Jang *et al.* 2020). Linolenic acid is converted to 12-oxo-phytodienoic acid (12-oxo-PDA) through catalysis by lipoxygenase (LOX), allene oxide

synthase (AOS), and allene oxide cyclase (AOC). JA is synthesized from 12-oxo-PDA under the catalysis of 12-oxo-phytodienoic acid reductase (OPR) and 3 cycles of beta-oxidation. The free acid JA can be further metabolized into methyl jasmonate (MeJA) and isoleucine conjugate jasmonyl-isoleucine (JA-Ile) which are the active jasmonate hormones involved in many developmental processes (Pedranzani *et al.* 2007).

Stress conditions dynamically up-regulate the synthesis of linolenic acid and the genes involved in JA biosynthesis and metabolism, leading to changes in endogenous JAs levels and stress responses. Specifically, stresses elevate JA synthesis. JAs are then transported to nucleus by the jasmonic acid transfer protein transporter (JAT1). JAs promote the degradation of jasmonate-zinc finger inflorescence meristem (ZIM) domain proteins (JAZ), which repress expression of JA responsive genes. The degradation of JAZ induces expression of various transcription factors (*NAC, ERF, and WRKY*), resulting in the expression of JA responsive genes (Ali and Baek 2020).

JA is induced by wounding, pathogen infection and abiotic stress. Furthermore, JA is increased under saline conditions in rice, tomato and cultivar *Hellfrucht Frushstamm* (Moons *et al.* 1997; Pedranzani *et al.* 2003). Expression of *TaAOC1*, encoding an allene oxide cyclase (AOC) enzyme, in *Arabidopsis* confers high salt tolerance (Ko *et al.* 2010; Zhao *et al.* 2014). In wheat, overexpression of *TaOPR* (a key gene in JA synthesis) improved salt tolerance in an ABA-dependent manner (Dong *et al.* 2013). Furthermore, *TaOPR1* overexpressing plants had alleviated ROS stress. Additionally, JA enhances the activities of antioxidant enzymes such as SOD, POD, CAT. Post-application of JA in salt stressed plants can alleviate salt stress, concomitant with decreased uptake of Na^+, and increases in Ca^{2+} and Mg^{2+} levels (Kang *et al.* 2010).

Gibberellin (GAs)

GAs constitute a large class of diterpenoid carboxylic acids which play a positive role in the plant stress response. GAs are synthesized in young organizations like buds, tender leaves, immature seeds, immature fruits and root tips. Out of approximately 136 GA forms, only a few are active, including GA1, GA3, GA4 and GA7. The others are intermediate or inactive forms. *ent*-kaurene is converted to GA_{12}, $C_{-19}GAs$ and $C_{-20}GAs$ under the catalytic action of terpene synthases, cytochrome P450 monooxygenases and 2-oxoglutarate-dependent dioxygenases, respectively. GA 20-oxidase, GA 3-oxidase, and GA 2-oxidase are responsible for the metabolism and deactivation of active GAs (Weston *et al.* 2008; O'Neill *et al.* 2010; Hedden and Sponsel 2015).

GAs, through their receptor GIBBERELLIN-INSENSITIVE DWARF (GIDa/b/c), regulates plant growth and responds to stress (Ueguchi-Tanaka *et al.* 2005; Griffiths *et al.* 2006). It has been shown that exogenous GA treatment reduces *GID1* expression, suggesting feedback

regulation. DELLA proteins are important for GA signal transduction as they negatively regulate the expression of GA-signaling downstream genes. For example, in a saline environment, GA biosynthesis decreases whereas DELLA accumulates. In presence of GA, DELLA interacts with GID1, causing a conformational change in DELLA allowing it to be recognized by SLEEPY1 (SLY1) and degraded via the 26S proteasome (Fu *et al.* 2002; Dill *et al.* 2004; Tyler *et al.* 2004). Subsequently, the GA signal pathway is activated.

GAs undergo crosstalk with the ABA and JA signaling pathways during the plant salt stress response (Fig. 5). *XERICO*, a target gene of DELLA, promotes ABA accumulation and suppression of GA biosynthesis (Ko *et al.* 2010; Zeng *et al.* 2015; Shu *et al.* 2017). In addition to DELLA, JAZ (jasmonate ZIM-domain) proteins also participate in the GA and JA signaling pathways. JAZ proteins bind MYC2, a transcription factor which regulates expression of JA-responsive genes, to inhibit JA downstream signaling. JAZs and DELLAs also directly interact to mediate the antagonistic interaction between JA and GA. Formation of the DELLA-JAZ complex promotes the JA response under GA-free conditions. When GA is present, DELLAs are degraded and JAZs are released, attenuating the JA response and causing accumulation of GAs (Yang *et al.* 2012). The findings that JA promotes transcription of *RGA3* (*REPRESSOR OF GA1-3*, a DELLA protein) and MYC2 bindings to the *RGA3* promoter and that JAZ9 directly interacts with the DELLA protein SLR1 (SLENDER RICE 1) further substantiate the crosstalk between GAs and JA (Um *et al.* 2018; Yang *et al.* 2019).

Other phytohormones

In addition to the phytohormones discussed above, there are other plant hormones which regulate plant growth and development. Cytokinins (CKs) got their name from their ability to promote plant cytokinesis. CKs regulate many plant growth and developmental processes, including cytokinesis, chloroplast biogenesis, shoot differentiation and leaf senescence. Because CKs can end seed dormancy, they are considered ABA antagonists. During salt stress, plants decrease the levels of CKs and increase ABA levels to resist the stress (Barciszewski *et al.* 2000; Nishiyama *et al.* 2011). The response of CKs to salt stress involves cross talk between CKs and other hormones, such as ABA, GA, ETH and auxin (O'Brien and Benková 2013).

Exogenous application of CKs results in increased resistance to salt, as seen in wheat and potato (Naqvi *et al.* 1982). In wheat, application of CK reverses seedling growth inhibition caused by salt stress. It has been suggested that CKs may diminish the adverse effects of salinity by promoting osmotic accumulation and inhibiting Na^+/Cl^- accumulation and chlorophyll degradation. In addition, CKs directly or indirectly scavenge peroxide and reduce lipid peroxidation. Thus, CKs resist salt stress by mitigating ionic

and osmotic toxicity.

Triazoles (TR) and Strigolactones (SLs) also act as plant growth regulators (Mayzlishgati *et al.* 2010; Waldie *et al.* 2014). Some studies have shown they are related to salt stress (Quain *et al.* 2015), but their mechanism of regulation is not clear.

Concluding Remarks and Perspectives

Salinity is a serious soil problem to plants, especially crops (Hu *et al.* 2018). Determining the mechanisms of the plant response to salt-stress will lay the foundation for improving crop salt tolerance and will provide guidance on how to curb soil salinization.

Current research has demonstrated that phytohormones can regulate salinity tolerance. During salt stress, the hormone balance is disrupted but rebuilds rapidly. The contents of ABA, IAA, BRs and ETH increase, while those of CK and GAs decline in salt stress. Plants resist salt stress through hormone balance and cross talk (Fig. 4). For example, in *Sesbania cannabina* seedlings, ABA regulates salt tolerance through SLs (Ren *et al.* 2018). Furthermore, EBL can interact with ABA, GA, SA and IAA to regulate plant growth under salt stress (Wu *et al.* 2017). In addition, while ABA is known to regulate stomatal opening, CK, ETH, BR, JA and SA also affect stomatal function during salt stress. Several enzymes involved in ethylene biosynthesis can be regulated by auxin (Tsuchisaka and Theologis 2004). GAs, BRs and SA also interact with each other (Alonso-Ramírez *et al.* 2009).

These various cross talks regulate plant growth and intracellular metabolism to help resist salt stress. As mentioned above, plants in saline soil suffer ion stress, osmotic stress, and oxidative stress. Phytohormones promote the accumulation of osmolytes, selective absorption of ions and removal of reactive oxygen alleviating these deleterious effects. Although a series of studies have reported how plant hormones are regulated in response to salt stress, the mechanism of how the plant cell accurately perceives the stress signal and the extent of cross talk between plant hormone signals remains to be further studied.

Acknowledgements

References

Abedin MA, U Habiba, R Shaw (2014). *Salinity Scenario in Mekong, Ganges and Indus River Deltas Water Insecurity: A Social Dilemma,* pp: 115–138. Emerald Group Publishing Limited, Bingley, UK

Achard P, H Cheng, GL De, J Decat, H Schoutteten, T Moritz, DSD Van, J Peng, NP Harberd (2006). Integration of plant responses to environmentally activated phytohormonal signals. *Science* 311:91–94

Acharya BR, BW Jeon, W Zhang, SM Assmann (2013). Open stomata 1 (*ost1*) is limiting in abscisic acid responses of arabidopsis guard cells. *New Phytol* 200:1049–1063

Ahanger MA, U Aziz, AA Alsahli, MN Alyemeni, P Ahmad (2019). Influence of exogenous salicylic acid and nitric oxide on growth, photosynthesis, and ascorbate-glutathione cycle in salt stressed *Vigna angularis. Biomolecules* 10; Article E42

Ali AA, RI Abdel-Fattah (2006). Osmolytes-antioxidant behaviour in and with brassinosteroid under salt stress. *J Agron* 5:167–174

Ali S, KH Baek (2020). Jasmonic acid signaling pathway in response to abiotic stresses in plants. *Intl J Mol Sci* 21:621

Alonso-Ramírez A, D Rodríguez, D Reyes, J Jiménez, G Nicolás, M López-Climent, A Gómez-Cadenas, C Nicolás (2009). Evidence for a role of gibberellins in salicylic acid-modulated early plant responses to abiotic stress in arabidopsis seeds. *Plant Physiol* 150:1335–1344

Bajguz A, S Hayat (2009). Effects of brassinosteroids on the plant responses to environmental stresses. *Plant Physiol Biochem* 47:1–8

Balcerowicz M, U Hoecker (2014). Auxin – a novel regulator of stomata differentiation. *Trends Plant Sci* 19:747–749

Balcerowicz M, A Ranjan, L Rupprecht, G Fiene, U Hoecker (2014). Auxin represses stomatal development in dark-grown seedlings via *AUX/IAA* proteins. *Development* 141:3165–3176

Barciszewski J, G Siboska, SIS Rattan, BFC Clark (2000). Occurrence, biosynthesis and properties of kinetin (N6-furfuryladenine). *Plant Growth Regul* 32:257–265

Bertrand A, C Dhont, M Bipfubusa, FP Chalifour, P Drouin, CJ Beauchamp (2015). Improving salt stress responses of the symbiosis in alfalfa using salt-tolerant cultivar and rhizobial strain. *Appl Soil Ecol* 87:108–117

Cabot C, JV Sibole, J Barceló, C Poschenrieder (2009). Abscisic acid decreases leaf Na+ exclusion in salt-treated *Phaseolus vulgaris* L. *J Plant Growth Regul* 28:187–192

Cai Z, J Liu, H Wang, C Yang, Y Chen, Y Li (2014). Gsk3-like kinases positively modulate abscisic acid signaling through phosphorylating subgroup iii snrk2s in Arabidopsis. *Proc Natl Acad Sci USA* 111:9651–9656

Cao S, XH Du, LH Li, YD Liu, L Zhang, X Pan, Y Li, H Li, H Lu (2017). Overexpression of *Populus tomentosa* cytosolic ascorbate peroxidase enhances abiotic stress tolerance in tobacco plants. *Russ J Plant Physiol* 64:224–234

Cao WH, J Liu, XJ He, RL Mu, HL Zhou, SY Chen, JS Zhang (2007). Modulation of ethylene responses affects plant salt-stress responses. *Plant Physiol* 143:707–719

Casella S, F Huang, D Mason, G Zhao, G Johnson, C Mullineaux, L Liu (2017). Dissecting the native architecture and dynamics of cyanobacterial photosynthetic machinery. *Mol Plant* 10:1434–1448

Chen C, Y Zhang, P Ye, X Ma, C Zheng, G Zhang (2018). *Eno2* knock-out mutants in arabidopsis modify the regulation of the gene expression response to nacl stress. *Mol Biol Rep* 45:1331–1338

Chen M, WH Zhang, ZW Lv, SL Zhang, J Hidema, FM Shi, LL Liu (2013). Abscisic acid is involved in the response of arabidopsis mutant *sad2-1* to ultraviolet-B radiation by enhancing antioxidant enzymes. *S Afr J Bot* 85:79–86

Chen Z, L Hu, N Han, J Hu, Y Yang, T Xiang, X Zhang, L Wang (2014). Overexpression of a mir393-resistant form of transport inhibitor response protein 1 (*mtir1*) enhances salt tolerance by increased osmoregulation and Na+ exclusion in *Arabidopsis thaliana. Plant Cell Physiol* 56:73–83

Cheng S, Z Yang, MJ Wang, J Song, N Sui, H Fan (2014). Salinity improves chilling resistance in suaeda salsa. *Acta Physiol Plantarum* 36:1823–1830

Conde A, P Silva, A Agasse, C Conde, H Gerós (2011). Mannitol transport and mannitol dehydrogenase activities are coordinated in *Olea europaea* under salt and osmotic stresses. *Plant Cell Physiol* 52:1766–1775

Cramer GR, SA Quarrie (2002). Abscisic acid is correlated with the leaf growth inhibition of four genotypes of maize differing in their response to salinity. *Funct Plant Biol* 29:111–115

Deenamo N, A Kuyyogsuy, K Khompatara, T Chanwun, K Ekchaweng, N Churngchow (2018). Salicylic acid induces resistance in rubber tree against *Phytophthora palmivora. Intl J Mol Sci* 19; Article 1883

Deng YQ, ZT Feng, F Yuan, JR Guo, SS Suo, BS Wang (2015). Identification and functional analysis of the autofluorescent substance in *Limonium bicolor* salt glands. *Plant Physiol Biochem* 97:20–27

Dill A, SG Thomas, J Hu, CM Steber, TP Sun (2004). The arabidopsis f-box protein sleepy1 targets gibberellin signaling repressors for gibberellin-induced degradation. *Plant Cell* 16:1392–1405

Dong W, MC Wang, F Xu, TY Quan, KQ Peng, LT Xiao, GM Xia (2013). Wheat oxophytodienoate reductase gene *taopr1* confers salinity tolerance via enhancement of abscisic acid signaling and reactive oxygen species scavenging. *Plant Physiol* 161:1217–1228

Du SY, XF Zhang, Z Lu, Q Xin, Z Wu, T Jiang, Y Lu, XF Wang, DP Zhang (2012). Roles of the different components of magnesium chelatase in abscisic acid signal transduction. *Plant Mol Biol* 80:519–537

Duan H, Y Ma, R Liu, Q Li, Y Yang, J Song (2018). Effect of combined waterlogging and salinity stresses on euhalophyte *Suaeda glauca*. *Plant Physiol Biochem* 127:231–237

Dunlap JR, ML Binzel (1996). Nacl reduces indole-3-acetic acid levels in the roots of tomato plants independent of stress-induced abscisic acid. *Plant Physiol* 112:379–384

Fariduddin Q, S Khanam, SA Hasan, B Ali, S Hayat, A Ahmad (2009). Effect of 28-homobrassinolide on the drought stress-induced changes in photosynthesis and antioxidant system of brassica junceal. *Acta Physiol Plantarum* 31:889–897

Fàbregas N, F Lozano-Elena, D Blasco-Escámez, T Tohge, C Martínez-Andújar, A Albacete, A I Caño-Delgado (2018). Overexpression of the vascular brassinosteroid receptor BRL3 confers drought resistance without penalizing plant growth. *Nat Commun* 9; Article 4680

Feng ZT, QJ Sun, YQ Deng, SF Sun, JG Zhang, BS Wang (2014a). Study on pathway and characteristics of ion secretion of salt glands of *Limonium bicolor. Acta Physiol Plantarum* 36:2729–2741

Feng ZT, YQ Deng, H Fan, QJ Sun, N Sui, BS Wang (2014b). Effects of nacl stress on the growth and photosynthetic characteristics of *Ulmus pumila* L. seedlings in sand culture. *Photosynthetica* 52:313–320

Feng ZT, YQ Deng, SC Zhang, X Liang, F Yuan, JL Hao, JC Zhang, SF Sun, BS Wang (2015). K$^+$ accumulation in the cytoplasm and nucleus of the salt gland cells of *Limonium bicolor* accompanies increased rates of salt secretion under NaCl treatment using nanosims. *Plant Sci* 238:286–296

Fu X, D Richards, A Tahar, L Hynes, O Helen, J Peng, N Harberd (2002). Gibberellin-mediated proteasome-dependent degradation of the barley della protein sln1 repressor. *Plant Cell* 14: 3191–3200

Fujii H, V Chinnusamy, A Rodrigues, S Rubio, R Antoni, SY Park, SR Cutler, J Sheen, PL Rodriguez, JK Zhu (2009). *In vitro* reconstitution of an abscisic acid signalling pathway. *Nature* 462:660–664

Galvan-Ampudia CS, MM Julkowska, E Darwish, J Gandullo, RA Korver, G Brunoud, MA Haring, T Munnik, T Vernoux, C Testerink (2013). Halotropism is a response of plant roots to avoid a saline environment. *Curr Biol* 23:2044–2050

Golldack D, I Lüking, O Yang (2011). Plant tolerance to drought and salinity: Stress regulating transcription factors and their functional significance in the cellular transcriptional network. *Plant Cell Rep* 30:1383–1391

Golldack D, C Li, H Mohan, N Probst (2014). Tolerance to drought and salt stress in plants: Unraveling the signaling networks. *Front Plant Sci* 5; Article 151

Griffiths J, K Murase, I Rieu, R Zentella, Zhang Z L, SJ Powers, F Gong, AL Phillips, P Hedden, TP Sun, SG Thomas (2006). Genetic characterization and functional analysis of the *gid1* gibberellin receptors in arabidopsis. *Plant Cell* 18:3399–3414

Gunes A, A Inal, M Alpaslan, F Eraslan, E Bagci, N Cicek (2007). Salicylic acid induced changes on some physiological parameters symptomatic for oxidative stress and mineral nutrition in maize (*Zea mays* L.) grown under salinity. *J Plant Physiol* 164:728–736

Guo JR, SS Suo, BS Wang (2015). Sodium chloride improves seed vigour of the euhalophyte *Suaeda salsa*. *Seed Sci Res* 25:335–344

Guo YH, WJ Jia, J Song, DA Wang, M Chen, BS Wang (2012). *Thellungila halophila* is more adaptive to salinity than *Arabidopsis thaliana* at stages of seed germination and seedling establishment. *Acta Physiol Plantarum* 34:1287–1294

Han N, WJ Lan, X He, Q Shao, BS Wang, XJ Zhao, (2012). Expression of a *Suaeda salsa* vacuolar H$^+$/Ca^{2+} transporter gene in Arabidopsis contributes to physiological changes in salinity. *Plant Mol Biol Rep* 30:470–477

Hazman M, B Hause, E Eiche, P Nick, M Riemann (2015). Increased tolerance to salt stress in opda-deficient rice allene oxide cyclase mutants is linked to an increased ros-scavenging activity. *J Exp Bot* 66:3339–3352

Hedden P, V Sponsel (2015). A century of gibberellin research. *J Plant Growth Regul* 34:740–760

Hoang XLT, NC Nguyen, YH Nguyen, Y Watanabe, LP Tran, NP Thao (2019). The soybean *GmNAC019* transcription factor mediates drought tolerance in Arabidopsis in an abscisic acid-dependent manner. *Intl J Mol Sci* 21:286

Hou L, L Chen, J Wang, D Xu, L Dai, H Zhang, Y Zhao (2012). Construction of stress responsive synthetic promoters and analysis of their activity in transgenic arabidopsis thaliana. *Plant Mol Biol Rep* 30:1496–1506

Hou L, W Liu, Z Li, C Huang, XL Fang, Q Wang, X Liu (2014). Identification and expression analysis of genes responsive to drought stress in peanut. *Russ J Plant Physiol* 61:842–852

Hu L, Y Xie, S Fan, Z Wang, F Wang, B Zhang, H Li, J Song, L Kong (2018). Comparative analysis of root transcriptome profiles between drought-tolerant and susceptible wheat genotypes in response to water stress. *Plant Sci Intl J Exp Plant Biol* 272:276

Hu L, P Zhang, Y Jiang, J Fu (2015). Metabolomic analysis revealed differential adaptation to salinity and alkalinity stress in kentucky bluegrass (poa pratensis). *Plant Mol Biol Rep* 33:56–68

Huang Y, Y Jiao, N Xie, Y Guo, F Zhang, Z Xiang, R Wang, F Wang, Q Gao, L Tian, D Li, L Chen, M Liang (2019). OsNCED5, a 9-cis-epoxycarotenoid dioxygenase gene, regulates salt and water stress tolerance and leaf senescence in rice. *Plant Sci* 287:110188

Hui D, Z Zhen, J Peng, C Li, Q Gong, NW Ning (2011). Loss of *acs7* confers abiotic stress tolerance by modulating ABA sensitivity and accumulation in Arabidopsis. *J Exp Bot* 62:4875–4887

Iglesias MJ, MC Terrile, CG Bartoli, S D'Ippólito, C Casalongué (2010). Auxin signaling participates in the adaptative response against oxidative stress and salinity by interacting with redox metabolism in arabidopsis. *Plant Mol Biol* 74:215–222

Ilyas F (2017). *Sindh Suffers 31pc Crop Loss Annually Due to Waterlogging, Salinity. Dawn.* Available at: https://www.dawn.com/news/1357033

Ismail A, S Takeda, P Nick (2014). Life and death under salt stress: Same players, different timing? *J Exp Bot* 65:2963–2979

Jang G, Y Yoon, YD Choi (2020). Crosstalk with jasmonic acid integrates multiple responses in plant development. *Intl J Mol Sci* 21:305

Jain M, JP Khurana (2010). Transcript profiling reveals diverse roles of auxin-responsive genes during reproductive development and abiotic stress in rice. *FEBS J* 276:3148–3162

Javid MG, A Sorooshzadeh, F Moradi, SAMM Sanavy, I Allahdadi (2011). The role of phytohormones in alleviating salt stress in crop plants. *Aust J Crop Sci* 5:726–734

Jayakannan M, J Bose, O Babourina, Z Rengel, S Shabala (2013). Salicylic acid improves salinity tolerance in arabidopsis by restoring membrane potential and preventing salt-induced K$^+$ loss via a gork channel. *J Exp Bot* 64:2255–2268

Jiang CF, EJ Belfield, C Yi, JAC Smith, NP Harberd (2013). An Arabidopsis soil-salinity-tolerance mutation confers ethylene-mediated enhancement of sodium/potassium homeostasis. *Plant Cell* 25:3535–3552

Jung H, DK Lee, YD Choi, JK Kim (2015). *Osiaa6*, a member of the rice *Aux/IAA* gene family, is involved in drought tolerance and tiller outgrowth. *Plant Sci* 236:304–312

Kang DJ, YJ Seo, JD Lee, R Ishii, KU Kim, DH Shin, SK Park, SW Jang, IJ Lee (2010). Jasmonic acid differentially affects growth, ion uptake and abscisic acid concentration in salt-tolerant and salt-sensitive rice cultivars. *J Agron Crop Sci* 191:273–282

Karlidag H, E Yildirim, M Turan (2011). Role of 24-epibrassinolide in mitigating the adverse effects of salt stress on stomatal conductance, membrane permeability, and leaf water content, ionic composition in salt stressed strawberry (*Fragaria* x *ananassa*). *Sci Hortic* 130:133–140

Kaya C, H Kirnak, D Higgs, K Saltali (2002). Supplementary calcium enhances plant growth and fruit yield in strawberry cultivars grown at high (NaCl) salinity. *Sci Hortic* 93:65–74

Ke Q, W Zhi, YJ Chang, JC Jeong, HS Lee, H Li, B Xu, X Deng, SS Kwak (2015). Transgenic poplar expressing Arabidopsis *yucca6* exhibits auxin-overproduction phenotypes and increased tolerance to abiotic stress. *Plant Physiol Biochem Ppb* 94:19–27

Kim JI, D Baek, HC Park, HJ Chun, DH Oh, KL Min, JY Cha (2013). Overexpression of arabidopsis yucca6 in potato results in high-auxin developmental phenotypes and enhanced resistance to water deficit. *Plant Signal Behav* 6:337–349

Kim TW, S Guan, Y Sun, Z Deng, W Tang, JX Shang, Y Sun, A Burlingame, ZY Wang (2009). Brassinosteroid signal transduction from cell-surface receptor kinases to nuclear transcription factors. *Nat Cell Biol* 11:1254–1260

Kirungu JN, RO Magwanga, P Lu, X Cai, Z Zhou, XM Wang, F Liu (2019). Functional characterization of Gh_A08G1120 (GH3.5) gene reveal their significant role in enhancing drought and salt stress tolerance in cotton. *BMC Genet* 20; Article 62

Klessig DF, HW Choi, DA Dempsey (2018). Systemic acquired resistance and salicylic acid: Past, present and future. *Mol Plant Microbe Interact* 31:871–888

Ko JH, SH Yang, KH Han (2010). Upregulation of an arabidopsis ring-H_2 gene, xerico, confers drought tolerance through increased abscisic acid biosynthesis. *Plant J* 47:343–355

Kong XQ, T Wang, WJ Li, W Tang, DM Zhang, HZ Dong (2016). Exogenous nitric oxide delays salt-induced leaf senescence in cotton (*Gossypium hirsutum* L.). *Acta Physiol Plantarum* 38; Article 61

Krishna P (2003). Brassinosteroid-mediated stress responses. *J Plant Growth Regul* 22:289–297

Leng BY, F Yuan, XX Dong, J Wang, BS Wang (2018). Distribution pattern and salt excretion rate of salt glands in two recretohalophyte species of limonium (plumbaginaceae). *S Afr J Bot* 115:74–80

Li F, T Asami, X Wu, E Tsang, A Cutler (2007). A putative hydroxysteroid dehydrogenase involved in regulating plant growth and development. *Plant Physiol* 145:87–97

Li J, J Liu, G Wang, J-Y Cha, G Li, S Chen, Z Li, J Guo, C Zhang, Y Yang (2015). A chaperone function of no catalase activity1 is required to maintain catalase activity and for multiple stress responses in arabidopsis. *Plant Cell* 27:908–925

Li KR, HH Wang, G Han, QJ Wang, J Fan (2008). Effects of brassinolide on the survival, growth and drought resistance of robinia pseudoacacia seedlings under water-stress. *New For* 35:255–266

Li Q, G Wang, Y Wang, Y Dan, C Guan, J Ji (2019). Foliar application of salicylic acid alleviate the cadmium toxicity by modulation the reactive oxygen species in potato. *Ecotoxicol Environ Saf* 172:317–325

Li Z, Y Tian, J Xu, X Fu, J Gao, B Wang, H Han, L Wang, R Peng, Q Yao (2018). A tomato ERF transcription factor, SlERF84, confers enhanced tolerance to drought and salt stress but negatively regulates immunity against *Pseudomonas syringae* pv. tomato DC3000. *Plant Physiol Biochem* 132:583–595

Li X, Y Liu, M Chen, YP Song, J Song, BS Wang, G Feng (2012). Relationships between ion and chlorophyll accumulation in seeds and adaptation to saline environments in *Suaeda salsa* populations. *Plant Biosyst* 146:142–149

Liang S, W Xiong, C Yin, X Xie, YJ Jin, S Zhang, B Yang, G Ye, S Chen, WJ Luan (2019). Overexpression of *OsARD1* improves submergence, drought, and salt tolerances of seedling through the enhancement of ethylene synthesis in rice. *Front Plant Sci* 10; Article 1088

Liang W, W Cui, X Ma, W Gang, Z Huang (2014). Function of wheat *Ta-unp* gene in enhancing salt tolerance in transgenic Arabidopsis and rice. *Biochem Biophys Res Commun* 450:794–801

Liang W, X Ma, P Wan, L Liu (2017). Plant salt-tolerance mechanism: A review. *Biochem Biophysical Res Commun* 495:286–291

Liu J, F Zhang, JJ Zhou, F Chen, BS Wang, XZ Xie (2012). Phytochrome b control of total leaf area and stomatal density affects drought tolerance in rice. *Plant Mol Biol* 78:289–300

Liu QQ, RR Liu, YC Ma, J Song (2018). Physiological and molecular evidence for Na^+ and Cl^- exclusion in the roots of two *Suaeda salsa* populations. *Aquat Bot* 146:1–7

Liu S, W Wang, M Li, B Wang, N Sui (2017). Antioxidants and unsaturated fatty acids are involved in salt tolerance in peanut. *Acta Physiol Plantarum* 39; Article 207

Liu W, RJ Li, TT Han, W Cai, ZW Fu, YT Lu (2015). Salt stress reduces root meristem size by nitric oxide-mediated modulation of auxin accumulation and signaling in arabidopsis. *Plant Physiol* 168:343–356

Ludwig-Müller J (2011). Auxin conjugates: Their role for plant development and in the evolution of land plants. *J Exp Bot* 62:1757–1773

Mayzlishgati E, SP Lekkala, N Resnick, S Wininger, C Bhattacharya, JH Lemcoff, Y Kapulnik, H Koltai (2010). Strigolactones are positive regulators of light-harvesting genes in tomato. *J Exp Bot* 61:3129–3136

Meloni DA, MA Oliva, CA Martinez, J Cambraia (2003). Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. *Environ Exp Bot* 49:69–76

Miura K, H Okamoto, E Okuma, H Shiba, H Kamada, PM Hasegawa, Y Murata (2013). SIZ1 deficiency causes reduced stomatal aperture and enhanced drought tolerance via controlling salicylic acid-induced accumulation of reactive oxygen species in Arabidopsis. *Plant J* 73:91–104

Moons A, E Prinsen, G Bauw, MV Montagu (1997). Antagonistic effects of abscisic acid and jasmonates on salt stress-inducible transcripts in rice roots. *Plant Cell* 9:2243–2259

Morgan PW, MC Drew (2010). Ethylene and plant responses to stress. *Physiol Plant* 100:620–630

Morton MJL, M Awlia, N Al-Tamimi, S Saade, Y Pailles, S Negrão, M Tester (2019). Salt stress under the scalpel – dissecting the genetics of salt tolerance. *Plant J* 97:148–163

Munns R, M Tester (2008). Mechanisms of salinity tolerance. *Annu Rev Plant Biol* 59:651–681

Murata Y, ZM Pei, IC Mori, J Schroeder (2001). Abscisic acid activation of plasma membrane ca(2+) channels in guard cells requires cytosolic nad(p)h and is differentially disrupted upstream and downstream of reactive oxygen species production in *abi1-1* and *abi2-1* protein phosphatase 2c mutants. *Plant Cell* 13:2513–2523

Naqvi SSM, R Ansari, AN Khanzada (1982). Response of salt-stressed wheat seedlings to kinetin. *Plant Sci Lett* 26:279–283

Natsuko K, H Wang, K Hiroyuki, J Liu, M Cameron, M Yasunori, K Yuji, MA Hannah, NH Chua (2012). IAA-ALA resistant3, an evolutionarily conserved target of miR167, mediates Arabidopsis root architecture changes during high osmotic stress. *Plant Cell* 24:3590–3602

Nishiyama R, Y Watanabe, Y Fujita, DT Le, M Kojima, T Werner, R Vankova, K Yamaguchi-Shinozaki, Shinozaki, K, T Kakimoto, H Sakakibara, T Schmülling, LS Tran (2011). Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. *Plant Cell* 23:2169–2183

O'Brien JA, E Benková (2013). Cytokinin cross-talking during biotic and abiotic stress responses. *Front Plant Sci* 4; Article 451

O'Neill DP, SE Davidson, VC Clarke, Y Yamauchi, S Yamaguchi, Y Kamiya, JB Reid, JJ Ross (2010). Regulation of the gibberellin pathway by auxin and della proteins. *Planta* 232:1141–1149

Ohta M, Y Guo, U Halfter, JK Zhu (2018). A novel domain in the protein kinase sos2 mediates interaction with the protein phosphatase *2c abi2*. *Proc Nat Acad Sci USA* 100:11771–11776

Otoch MDLO, ACM Sobreira, MEFD Aragão, EG Orellano, MDGS Lima, DFD Melo (2001). Salt modulation of vacuolar H^+-ATPase and H^+-pyrophosphatase activities in *Vigna unguiculata*. *J Plant Physiol* 158:545–551

Özdemir F, M Bor, T Demiral, T İsmail (2004). Effects of 24-epibrassinolide on seed germination, seedling growth, lipid peroxidation, proline content and antioxidative system of rice (*Oryza sativa* L.) under salinity stress. *Plant Growth Regul* 42:203–211

Pang CH, K Li, BS Wang (2011). Overexpression of *sschlapxs* confers protection against oxidative stress induced by high light in transgenic *Arabidopsis thaliana*. *Physiol Plantarum* 143:355–366

Pedranzani H, G Racagni, S Alemano, O Miersch, I Ramírez, H Peña-Cortés, E Taleisnik, E Machado-Domenech, G Abdala (2003). Salt tolerant tomato plants show increased levels of jasmonic acid. *Plant Growth Regul* 41:149–158

Pedranzani H, R Sierra-De-Grado, A Vigliocco, O Miersch, G Abdala (2007). Cold and water stresses produce changes in endogenous jasmonates in two populations of *Pinus pinaster* Ait. *Plant Growth Regul* 52:111–116

Peng J, Z Li, X Wen, W Li, H Shi, L Yang, H Zhu, H Guo (2014b). Salt-induced stabilization of *ein3/eil1* confers salinity tolerance by deterring ROS accumulation in arabidopsis. *PLoS Genet* 10; Article e1004664

Peng Z, S He, W Gong, J Sun, Z Pan, F Xu, Y Lu, X Du (2014a). Comprehensive analysis of differentially expressed genes and transcriptional regulation induced by salt stress in two contrasting cotton genotypes. *BMC Genomics* 15; Article 760

Qayyum B, M Shahbaz, A Nudrat, A Akram (2007). Interactive effect of foliar application of 24-epibrassinolide and root zone salinity on morpho-physiological attributes of wheat (*Triticum aestivum* L.). *Intl J Agric Biol* 9:584–589

Quain MD, ME Makgopa, B Márquez-García, G Comadira, N Fernandez-Garcia, E Olmos, D Schnaubelt, KJ Kunert, CH Foyer (2015). Ectopic phytocystatin expression leads to enhanced drought stress tolerance in soybean (glycine max) and arabidopsis thaliana through effects on strigolactone pathways and can also result in improved seed traits. *Plant Biotechnol J* 12:903–913

Rai KK, N Rai, SP Rai (2018). Salicylic acid and nitric oxide alleviate high temperature induced oxidative damage in *Lablab purpureus* L. plants by regulating bio-physical processes and DNA methylation. *Plant Physiol Biochem* 128:72–88

Ren CG, CC Kong, ZH Xie (2018). Role of abscisic acid in strigolactone-induced salt stress tolerance in arbuscular mycorrhizal *Sesbania cannabina* seedlings. *BMC Plant Biol* 18; Article 74

Ren XL, GN Qi, HQ Feng, S Zhao, SS Zhao, Y Wang, WH Wu (2013). Calcineurin B-like protein *cbl10* directly interacts with *akt1* and modulates K⁺ homeostasis in arabidopsis. *Plant J* 74:258–266

Rengasamy P (2010). Osmotic and ionic effects of various electrolytes on the growth of wheat. *Soil Res* 48:120–124

Rodriguez HG, J Roberts, WR Jordan, MC Drew (1997). Growth, water relations, and accumulation of organic and inorganic solutes in roots of maize seedlings during salt stress. *Plant Physiol* 113:881–893

Sedaghat M, Z Tahmasebi-Sarvestani, Y Emam, A Mokhtassi-Bidgoli (2017). Physiological and antioxidant responses of winter wheat cultivars to strigolactone and salicylic acid in drought. *Plant Physiol Biochem* 119:59–69

Shah N, S Anwar, J Xu, Z Hou, A Salah, S Khan, J Gong, Z Shang, L Qian, C Zhang (2018). The response of transgenic brassica species to salt stress: A Review. *Biotechnol Lett* 40:1159–1165

Shahbaz M, M Ashraf, HUR Athar (2008). Does exogenous application of 24-epibrassinolide ameliorate salt induced growth inhibition in wheat (triticum aestivum l.)? *Plant Growth Regul* 55:51–64

Shakirova FM, AR Sakhabutdinova, MV Bezrukova, RA Fatkhutdinova, DR Fatkhutdinova (2003). Changes in the hormonal status of wheat seedlings induced by salicylic acid and salinity. *Plant Sci* 164:317–322

Shao Q, N Han, T Ding, F Zhou, B Wang (2014). Sshkt1;1 is a potassium transporter of the c3 halophyte *Suaeda salsa* that is involved in salt tolerance. *Funct Plant Biol* 41:790–802

Shavrukov Y (2013). Salt stress or salt shock: Which genes are we studying? *J Exp Bot* 64:119–127

Shen X, Z Wang, X Song, J Xu, C Jiang, Y Zhao, C Ma, H Zhang (2014). Transcriptomic profiling revealed an important role of cell wall remodeling and ethylene signaling pathway during salt acclimation in arabidopsis. *Plant Mol Biol* 86:303–317

Shi H, L Chen, T Ye, X Liu, K Ding, Z Chan (2014). Modulation of auxin content in arabidopsis confers improved drought stress resistance. *Plant Physiol Biochem* 82:209–217

Shu K, Y Qi, F Chen, Y Meng, X Luo, H Shuai, W Zhou, J Ding, J Du, J Liu (2017). Salt stress represses soybean seed germination by negatively regulating ga biosynthesis while positively mediating ABA biosynthesis. *Front Plant Sci* 8; Article 1372

Silva-Ortega CO, AE Ochoa-Alfaro, JA Reyes-Agüero, GA Aguado-Santacruz, JF Jiménez-Bremont (2008). Salt stress increases the expression of gene and induces proline accumulation in cactus pear. *Plant Physiol Biochem* 46:82–92

Song J, BS Wang (2015). Using euhalophytes to understand salt tolerance and to develop saline agriculture: *Suaeda salsa* as a promising model. *Ann Bot* 115:541–553

Song J, JC Zhou, WW Zhao, HL Xu, FX Wang, YG Xu, L Wang, CY Tian (2016). Effects of salinity and nitrate on production and germination of dimorphic seeds applied both through the mother plant and exogenously during germination in suaeda salsa. *Plant Spec Biol* 31:19–28

Staswick PE, BM Serban, I Tiryaki, MT Maldonado, MC Maldonado, W Suza (2005). Characterization of an Arabidopsis enzyme family that conjugates amino acids to indole-3-acetic acid. *Plant Cell* 17:616–627

Stevens J, T Senaratna, K Sivasithamparam (2006). Salicylic acid induces salinity tolerance in tomato (*Lycopersicon esculentum* cv. Roma): Associated changes in gas exchange, water relations and membrane stabilisation. *Plant Growth Regul* 49:77–83

Su T, P Wang, H Li, Y Zhao, Y Lu, P Dai, T Ren, X Wang, X Li, Q Shao (2018). The arabidopsis catalase triple mutant reveals important roles of catalases and peroxisome derived signaling in plant development. *J Integr Plant Biol* 60:591–607

Su T, WJ Li, PP Wang, CL Ma (2019). Dynamics of peroxisome homeostasis and its role in stress response and signaling in plants. *Front Plant Sci* 10; Article 705

Sui N, M Li, K Li, J Song, BS Wang (2010). Increase in unsaturated fatty acids in membrane lipids of *Suaeda salsa* L. Enhances protection of photosystem II under high salinity. *Photosynthetica* 48:623–629

Sui N, Y Wang, SS Liu, Z Yang, F Wang, SB Wan (2018). Transcriptomic and physiological evidence for the relationship between unsaturated fatty acid and salt stress in peanut. *Front Plant Sci* 9; Article 7

Summers PS, KD Nolte, AJL Cooper, H Borgeas, T Leustek, D Rhodes (1998). Identification and stereospecificity of the first three enzymes of3-dimethylsulfoniopropionate biosynthesis in a chlorophyte alga. *Plant Physiol* 116:369–378

Sun F, W Zhang, sheng, H Hu, B Li, Y Wang, Y Zhao, K Li, M Liu, X Li (2008). Salt modulates gravity signaling pathway to regulate growth direction of primary roots in arabidopsis. *Plant Physiol* 146:178–188

Sun MY (2005). The gus reporter-aided analysis of the promoter activities of arabidopsis acc synthase genes *atacs4*, *atacs5*, and *atacs7* induced by hormones and stresses. *J Exp Bot* 56:909–920

Szabo S, MS Hossain, WN Adger, Z Matthews, S Ahmed, AN Lázár, S Ahmad (2016). Soil salinity, household wealth and food insecurity in tropical deltas: evidence from south-west coast of Bangladesh. *Sustain Sci* 11:411–421

Tao JJ, HW Chen, B Ma, WK Zhang, SY Chen, JS Zhang (2015). The role of ethylene in plants under salinity stress. *Front Plant Sci* 6; Article 1059

Tan L, Q Liu, Y Song, G Zhou, L Luan, Q Weng, C He (2019). Differential function of endogenous and exogenous abscisic acid during bacterial pattern-induced production of reactive oxygen species in Arabidopsis. *Intl J Mol Sci* 20:2544

Tang GY, FX Shao, PL Xu, L Shan, ZJ Liu (2017). Overexpression of a peanut NAC gene, *AHNAC4*, confers enhanced drought tolerance in tobacco. *Russ J Plant Physiol* 64:525–535

Tsuchisaka A, A Theologis (2004). Unique and overlapping expression patterns among the arabidopsis 1-amino-cyclopropane-1-carboxylate synthase gene family members. *Plant Physiol* 136:2982–3000

Tyler L, SG Thomas, J Hu, A Dill, JM Alonso, JR Ecker, TP Sun (2004). Della proteins and gibberellin-regulated seed germination and floral development in arabidopsis. *Plant Physiol* 135:1008–1019

Ueguchi-Tanaka M, M Ashikari, M Nakajima, H Itoh, E Katoh, M Kobayashi, TY Chow, YI Hsing, H Kitano, I Yamaguchi, M Matsuoka (2005). Gibberellin insensitive dwarf1 encodes a soluble receptor for gibberellin. *Nature* 437:693–698

Um TY, HY Lee, S Lee, SH Chang, PJ Chung, KB Oh, JK Kim, G Jang, YD Choi (2018). *ZIM-DOMAIN PROTEIN 9* interacts with *SLENDER RICE 1* to mediate the antagonistic interaction between jasmonic and gibberellic acid signals in rice. *Front Plant Sci* 9; Article 1866

Wahid A, M Perveen, S Gelani, SMA Basra (2007). Pretreatment of seed with H_2O_2 improves salt tolerance of wheat seedlings by alleviation of oxidative damage and expression of stress proteins. *J Plant Physiol* 164:283–294

Waldie T, H McCulloch, O Leyser (2014). Strigolactones and the control of plant development: Lessons from shoot branching. Strigolactones and the control of plant development: lessons from shoot branching. *Plant J* 79:607–622

Wang C, S Chen, Y Dong, R Ren, D Chen, X Chen (2020). Chloroplastic Os3BGlu6 contributes significantly to cellular ABA pools and impacts drought tolerance and photosynthesis in rice. *New Phytol* doi.org/10.1111/nph.16416

Wang FX, YG Xu, S Wang, WW Shi, RR Liu, G Feng, J Song (2015). Salinity affects production and salt tolerance of dimorphic seeds of suaeda salsa. *Plant Physiol Biochem* 95:41–48

Wang K, J He, Y Zhao, T Wu, X Zhou, Y Ding, L Kong, X Wang, Y Wang, J Li, C Song, B Wang, S Yang, J Zhu, Z Gong (2018). *Ear1* negatively regulates ABA signaling by enhancing 2C protein phosphatase activity. *Plant Cell* 30:815–834

Wang L, Z Wang, Y Xu, S-H Joo, S-K Kim, Z Xue, Z Xu, Z Wang, K Chong (2010). Osgsr1 is involved in crosstalk between gibberellins and brassinosteroids in rice. *Plant J* 57:498–510

Wang X, G Fang, J Yang, Y Li (2017). A thioredoxin-dependent glutathione peroxidase (osgpx5) is required for rice normal development and salt stress tolerance. *Plant Mol Biol Rep* 35:1–10

Wang Y, T Wang, K Li, X Li (2008). Genetic analysis of involvement of etr1 in plant response to salt and osmotic stress. *Plant Growth Regul* 54:261–269

Wang ZY, MY Bai, E Oh, JY Zhu (2011). Brassinosteroid signaling network and regulation of photomorphogenesis. *Annu Rev Genet* 46:701–724

Wei W, MY Cui, H Yang, K Gao, YG Xie, Y Jiang, JY Feng (2018). Ectopic expression of fvwrky42, a wrky transcription factor from the diploid woodland strawberry (fragaria vesca), enhances resistance to powdery mildew, improves osmotic stress resistance and increases abscisic acid sensitivity in Arabidopsis. *Plant Sci* 275:60–74

Wei Z, T Yuan, D Tarkowská, J Kim, HG Nam, O Novák, K He, X Gou, J Li (2017). Brassinosteroid biosynthesis is modulated via a transcription factor cascade of *COG1*, *PIF4*, and *PIF5*. *Plant Physiol* 174:1260–1273

Weston DE, RC Elliott, DR Lester, R Catherine, JB Reid, IC Murfet, JJ Ross (2008). The pea della proteins la and cry are important regulators of gibberellin synthesis and root growth. *Plant Physiol* 147:199–205

Wilson RL, H Kim, A Bakshi, BM Binder (2014). The ethylene receptors ethylene response1 and ethylene response2 have contrasting roles in seed germination of arabidopsis during salt stress. *Plant Physiol* 165:1353–1366

Wu L, Z Zhang, H Zhang, XC Wang, R Huang (2008). Transcriptional modulation of ethylene response factor protein jerf3 in the oxidative stress response enhances tolerance of tobacco seedlings to salt, drought and freezing. *Plant Physiol* 148:1953–1963

Wu G, S Li, X Li, Y Liu, S Zhao, B Liu, H Zhao, H Lin (2019). A functional alternative oxidase modulates plant salt tolerance in physcomitrella patens. *Plant Cell Physiol* 60:1829–1841

Wu SJ, L Ding, Jk Zhu (1996). Sos1, a genetic locus essential for salt tolerance and potassium acquisition. *Plant Cell* 8:617–627

Wu W, Q Zhang, E Ervin, Z Yang, X Zhang (2017). Physiological mechanism of enhancing salt stress tolerance of perennial ryegrass by 24-epibrassinolide. *Front Plant Sci* 8; Article 1017

Xu J, Y Li, Y Wang, H Liu, L Lei, H Yang, G Liu, D Ren (2008). Activation of mapk kinase 9 induces ethylene and camalexin biosynthesis and enhances sensitivity to salt stress in arabidopsis. *J Biol Chem* 283:26996–27006

Xue Y, SS Zhao, ZJ Yang, Y Guo, YQ Yang (2019). Regulation of plasma membrane H^+-ATPase activity by the members of the v-snare *vamp7c* family in *Arabidopsis thaliana*. *Plant Signal Behav* 14; Article e1573097

Yan J, NT Tsuichihara, S Iwai (2010). Reactive oxygen species and nitric oxide are involved in ABA inhibition of stomatal opening. *Plant Cell Environ* 30:1320–1325

Yang DL J Yao, CS Mei, XH Tong, LJ Zeng, Q Li, LT Xiao, TP Sun, J Li, XW Deng (2012). Plant hormone jasmonate prioritizes defense over growth by interfering with gibberellin signaling cascade. *Proc Natl Acad Sci USA* 109:1192–1200

Yang J, G Duan, C Li, L Liu, G Han, Y Zhang, C Wang (2019). The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses. *Front Plant Sci* 10; Article 1349

Yang X, Y Bai, J Shang, R Xin, W Tang (2016). The antagonistic regulation of abscisic acid-inhibited root growth by brassinosteroids is partially mediated via direct suppression of abscisic acid insensitive 5 expression by brassinazole resistant 1. *Plant Cell Environ* 39:1994–2003

Yang Y, Y Guo (2018). Elucidating the molecular mechanisms mediating plant salt-stress responses. *New Phytol* 217:523–539

Yang Z, Y Wang, XC Wei, X Zhao, BS Wang, N Sui (2017). Transcription profiles of genes related to hormonal regulations under salt stress in sweet sorghum. *Plant Mol Biol Rep* 35:586–599

Yoo SD, YH Cho, T Guillaume, X Yan, J Sheen (2008). Dual control of nuclear ein3 by bifurcate mapk cascades in C_2H_4 signalling. *Nature* 451:789–795

Yu JN, J Huang, ZN Wang, JS Zhang, SY Chen (2007). An Na^+/H^+ antiporter gene from wheat plays an important role in stress tolerance. *J Biosci* 32:1153–1161

Yuan F, M Chen, BY Leng, BS Wang (2013). An efficient autofluorescence method for screening limonium bicolor mutants for abnormal salt gland density and salt secretion. *S Afr J Bot* 88:110–117

Yuan F, BY Leng, BS Wang (2016). Progress in studying salt secretion from the salt glands in recretohalophytes: How do plants secrete salt? *Front Plant Sci* 7; Article 977

Zeng DE, P Hou, F Xiao, Y Liu (2015). Overexpression of arabidopsis xerico gene confers enhanced drought and salt stress tolerance in rice (oryza sativa l.). *J Plant Biochem Biotechnol* 24:56–64

Zhang JL, H Shi (2013). Physiological and molecular mechanisms of plant salt tolerance. *Photosyn Res* 115:1–22

Zhang JY, SB He, L Li, HQ Yang (2014). Auxin inhibits stomatal development through monopteros repression of a mobile peptide gene stomagen in mesophyll. *Proc Natl Acad Sci USA* 111:3015–3023

Zhang LY, XJ Zhang, SJ Fan (2017). Meta-analysis of salt-related gene expression profiles identifies common signatures of salt stress responses in arabidopsis. *Plant Syst Evol* 303:757–774

Zhang Z, J Wang, R Zhang, R Huang (2012). The ethylene response factor aterf98 enhances tolerance to salt through the transcriptional activation of ascorbic acid synthesis in arabidopsis. *Plant J Cell Mol Biol* 71:273–287

Zhao SS, YX Jiang, Y Zhao, SJ Huang, M Yuan, YX Zhao, Y Guo (2016). Casein kinase1-like protein2 regulates actin filament stability and stomatal closure via phosphorylation of actin depolymerizing factor. *Plant Cell* 28:1422–1439

Zhao Y, W Dong, NB Zhang, XH Ai, MC Wang, ZG Huang, LG Xiao, GM Xia (2014). A wheat allene oxide cyclase gene enhances salinity tolerance via jasmonate signaling. *Plant Physiol* 164:1068–1076

Zheng Y, CC Liao, SS Zhao, CW Wang, Y Guo (2017). The glycosyltransferase qua1 regulates chloroplast-associated calcium signaling during salt and drought stress in arabidopsis. *Plant Cell Physiol* 58:329–341

Zhou J, J Wang, X Li, X Xia, Y Zhou, K Shi, Z Chen, J Yu (2014). H_2O_2 mediates the crosstalk of brassinosteroid and abscisic acid in tomato responses to heat and oxidative stresses. *J Exp Bot* 65:4371–4383

Zhou JC, TT Fu, N Sui, JR Guo, G Feng, JL Fan, J Song (2016). The role of salinity in seed maturation of the euhalophyte suaeda salsa. *Plant Biosyst* 150:83–90

Zhu Jh, Xm Fu, YD Koo, JK Zhu, FE Jenney, MWW Adams, Ym Zhu, Hz Shi, DJ Yun, PM Hasegawa, RA Bressan (2007). An enhancer mutant of arabidopsis salt overly sensitive 3 mediates both ion homeostasis and the oxidative stress response. *Mol Cell Biol* 27:5214–5224

Zhu JK (2002). Salt and drought stress signal transduction in plants. *Annu Rev Plant Biol* 53:247–273