



Review Article

Phytohormones: Important Participators in Plant Salt Tolerance

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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 adaptation 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 mM. Based on their salt tolerance, plants are divided into halophytes (salt tolerant and can normally grow in at least 200 mM 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

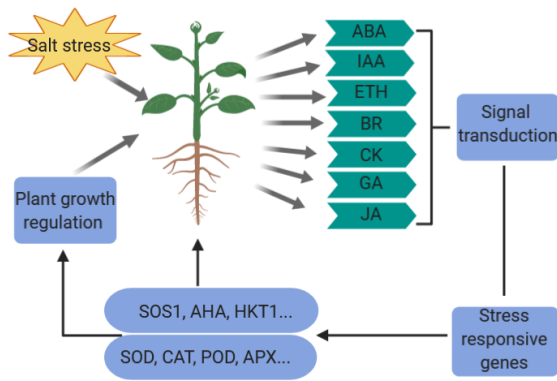


Fig. 1: Salt stress and phytohormones response. Salt stress is detected by plants via various sensors that activate the biogenesis of plant hormones such as abscisic acid (ABA), auxin (IAA), ethylene (ETH), brassinosteroids (BRs), cytokinin (CK), gibberellins (GA), and jasmonates (JA). Hormonal based 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^\cdot), hydrogen peroxide (H_2O_2) and superoxide (O_2^\cdot), 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 zeaxanthin 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; Gollack *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*

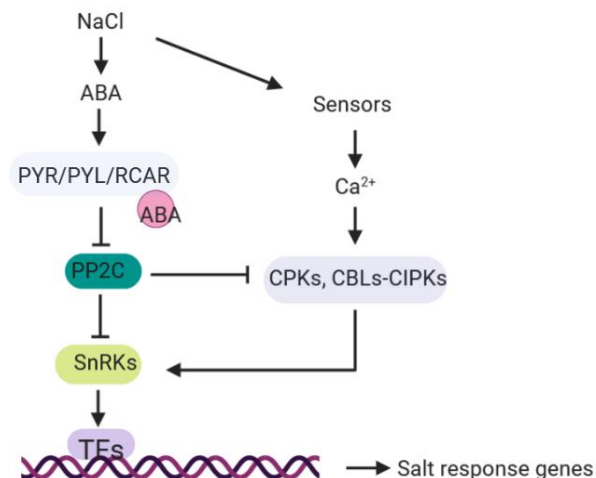


Fig. 2: Salt stress and ABA signaling.

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, CO₂ 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). H₂O₂ is generated from the disproportionation reaction of O₂⁻ by SOD and can be catalyzed to H₂O 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. SIERF84 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-acetic 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

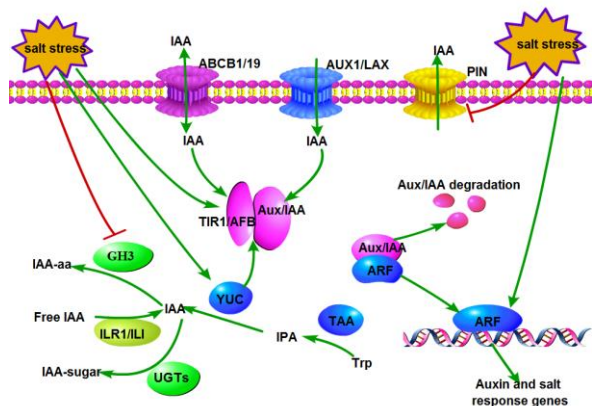


Fig. 3: Proposed model of IAA biosynthesis and signaling responses in response to salt stress. Under salt stress, IAA biosynthesis genes YUCs play an important role in salt tolerance. PINs (PINFORMED), AUX1/LAX (AUXIN TRANSPORTER CARRIER1/AUXIN TRANSPORTER-LIKE PROTEINS), ABCB1,19 (P-glycoproteins/ATP-binding 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 *OsGH3-2* 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 (Achar *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 mM 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 *VTCl* (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 H₂O₂, which acts as a secondary messenger to activate MKK9. 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 Ca²⁺, concomitant with higher saline tolerance (Qayyum *et al.* 2007; Shahbaz *et al.*

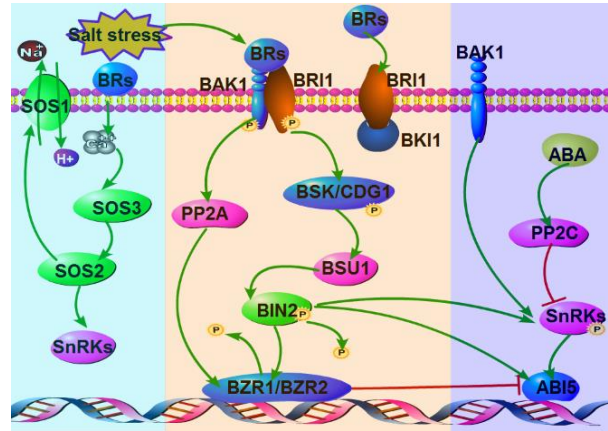


Fig. 4: Salt stress triggers the BRs signaling transduction pathway. The biogenesis of BRs is triggered by salt stress and the increased BRs enhance salt tolerance by inducing the expression of salt stress response genes. Under salt stress, the levels of BRs are increased due to high expression of the 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 downstream 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

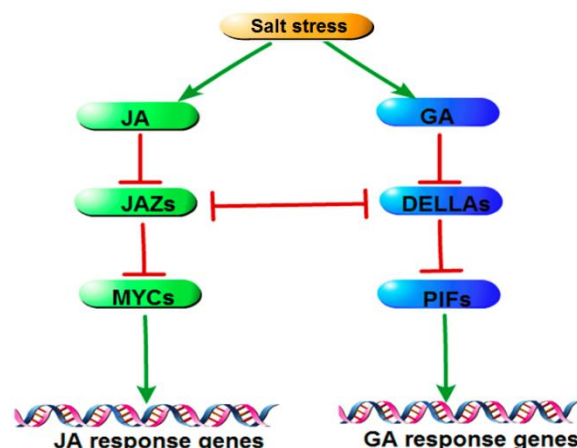


Fig. 5: GAs and JA crosstalk to coordinate the plant stress response. DELLAs, repressors of GAs signaling and JAZs, repressors of JA signaling, interact directly. This interaction allows MYCs to promote expression of JA response genes. The degradation of DELLA causes JAZs to be released from the complex, 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 GA₁₂, C₁₉GAs and C₂₀GAs 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.

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