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PLANTS RESPONSES AND THE ROLE OF PHYTOHORMONES AGAINST SALINITY STRESS

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ABSTRACT

Exposure of plants to diversity of abiotic stresses such as salinity stress retard growth and development of plants which results in huge yield loss worldwide. Plants respond to salinity in unique and complex way that involves many biochemical and physiological changes in plant system. Plant hormones are known to play indispensable roles to elicit an adaptive response in plants under salinity stress. A basic understanding of biological knowledge about the damage that salt stress has on plants and the salt stress tolerance mechanisms is necessary to discover future implications to overcome the effect of salt stress on plants. The main aim of present article is to enhance our knowledge of how salt stress may impact the physiological features of plants and to narrate the potential roles of various phytohormones against the salinity stress at both physiological and molecular grounds.

Keywords: Salinity stress, Stress tolerance, Phytohormones.

INTRODUCTION

Soil salinity involves the build-up of salt in the soil and soil water and is a major agricultural threat affecting most of world's agricultural fields (Yamaguchi-Shinozaki and Shinozaki 2006). Salinity can be defined as excessive concentrations of soluble salts in soils such as Ca^{2+}, Mg^{2+}, Na^{+} etc. Salinity affects severely the development of plants by influencing vital metabolic processes. Salinity restricts the production of crop because of ionic, oxidative and osmotic stresses with adverse effect on growth of plant (Munns and Tester 2008).

Phytohormones, also denoted as plant growth regulators, are recognized to play vibrant roles in the capability of plants to adapt to fluctuating environments. It was clearly defined that salinity causes increase in abscisic acid (ABA) and Jasmonic acid and decrease in indole-3-acetic acid (IAA) and salicylic acid (SA) (Wang *et al.,*2001). Phytohormones are significant endogenic materials that are crucial in harmonizing physiological reactions that ultimately lead to adaptation to salinity.

Effects of Salt Stress on plants

Osmotic Stress

Soil salinity initially represses growth of plant by way of osmotic stress and after which ion toxicity takes place (Rahnama *et al.,* 2010). In initial phase,water absorption by root systems diminishes and loss of water from leaves is enhanced because of osmotic stress of high salt gathering in plants and soil (Munns, 2005). Osmotic stress in the early stage of salt stress causesdifferent physiological changes like interruption of membranes, nutrient inequality, damages the capability to detoxify ROS, reduction in stomatal aperture and reduced photosynthetic activity etc. (Rahnama *et al.,* 2010, Munns and Tester 2008).

Ionic Toxicity

Ionic toxicity by salinity is due to increased concentration of cytosolic Na^{+} as it disrupts the activities of the cytosolic enzymes (Benito *et al.,* 2014). Salinity leads to decrease in K^{+} content (Wu *et al.,* 2013) and an increase in ionic strength within the cells, which cause protein denaturation (Kronzucker *et al.,* 2013). Salt stress leads to the accumulation of reactive oxygen species in plant cells. The plant has to respond to neutralize the excessive ROS and many enzymes are involved in this process (Nxele *et al.,* 2017). The result of ROS formation led to oxidative damages in different cellular constituents like DNA, lipids and proteins, which interrupt the vibrant cellular tasks of plants.

Germination

It has been investigated that greater level of salt stress adversely affects the seed germination while the lesser level of salt stress cause dormancy state (Khan and Weber 2008). Salinity stress decreases germination of seeds of many crops (Carpici *et al.,* 2009, Xu *et al.,* 2011). Under salinity stress, seeds are not able to imbibe water due to low osmotic potential (Khan and Weber 2008) which alters the action of enzymes of nucleic acid and also metabolism of protein (Dantas *et al.,* 2007, Gomes-Filho *et al.,* 2008). Salts affect seed germination by damaging the seed coat, increasing seed aging and dormancy, and decreasing seed vigor index (Panuccio *et al.,* 2014).

Photosynthesis

It is believed that salinity is responsible for lower photosynthesis rate in plants which in turn affects the plant productivity. The reduced photosynthetic rate in plants under high salt concentration is due to imbalance in the osmotic pressure which increases the toxicity of ions in the chloroplasts. Further, high salt concentration affects the photosynthetic electron transport chain by either hindering the carbon metabolism or photon phosphorylation mechanism (Farahbakhsh *et al.,* 2017). Salinity reduces the photosynthesis by affecting biosynthesis of photosynthetic pigment (Maxwell and Johnson 2000). The reduction in Chlorophyll content under salt stress is a normally stated phenomenon (Chutipaijit *et al.,* 2011).

Inhibition of Growth

Salinity reduces the capability of plants to take up water and this quickly causes reduction in growth rate. Saline soil reduces the water holding level in the plant, which in turn decreases the growth of the plant by decreasing the osmotic potential (Munns 2002). Over a prolonged time period after transpiration, ionic toxicity causes the deposition of Na$^+$ and Cl$^-$ ion in leaves which outcomes in senescence of leaves and diminishes the total photosynthetic leaf area which finally alters the productivity (Munns and Tester 2008).

The various responses of plants to the salinity stress are given in Figure **1**.

Mechanisms of tolerance to salinity

Ion Homeostasis

Salinity interrupts homeostasis at cellular and whole plant levels (Tunuturk *et al.,* 2011). NaCl is the most abundant form of salt existing in the soil. When K$^+$ issubstituted by Na$^+$ in biochemical reactions then ion cytotoxicity happens. The presence of Na$^+$/H$^+$antiporter in the plasma membrane of plants is critical for their growth under high salinity as it removes toxic Na$^+$ from the cytoplasm. Salt stress increases the activities of plasma membrane H$^+$-ATPase and Na$^+$/H$^+$antiporter (Zhang *et al.,* 2006). Cytoplasmic Na$^+$ ion is moved to the vacuole via. Na$^+$/H$^+$ antiporter. NHX1 is a Na$^{+/H+}$ antiporter, which can transport Na+into vacuole. The salt stress can induce NHX1's expression (Yokoi *et al.,* 2002). HKT (histidine kinase transporter) transporter, present on the plasma membrane also show an important role in salt stress by managing Na$^+$ and K$^+$ transportation. Stress signaling pathway involving Salt Overly Sensitive (SOS) play crucial role in salt tolerance and ion homeostasis (Hasegawa *et al.,* 2000, Sanders 2000). It comprises of three key proteins, SOS1, SOS2, and SOS3. In plasma membrane, SOS1 encodes Na$^{+/}$H$^+$antiporter. Overexpression of this SOS1 protein confers salt tolerance in plants (Shi *et al.,* 2000, Shi *et al.,* 2002) SOS2 gene encodes serine/threonine kinase. In high salt concentration, it is activated by eliciting Ca^{2+} signals.

ROS Detoxification

ROS must be present at suitable levels in plant cells. Various pathways are involved in controlling the homeostasis of ROS in stress conditions. ROS produced during salt stress are detoxified by antioxidant enzymatic and nonenzymatic compounds (Birben *et al.,* 2012). Stress tolerance in plants is induced by the antioxidants enzymes such as dehydroascorbatereductase (DHAR), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), guaiacol peroxidase (GPX) and catalase (CAT). Glutathione (GSH), tocopherol, Ascorbate, alkaloids, carotenoids and flavonoids are non-enzymatic antioxidants (Bose *et al.,* 2014). Salinity stress initiates activation of MAPK signaling cascade, involved in antioxidant defense responses and regulate ROS homeostasis.

Osmotic Adjustment

One of the strategies employed by plants to counteract water deficit is through osmotic adjustments. For osmotic adjustment plants accumulate uncharged, polar, and soluble compatible solutes (osmolytes) in stress condition which do not affect the cellular metabolism. These osmolytes have been categorized into four major classes: 1) sugars (trehalose) 2) polyols (glycerol inositols, mannitol, sorbitol) 3) amino acids (proline, glycine, betaine) and 4) quaternary ammonium compounds (β-alanine, betaine etc.) (Rontein *et al.,* 2002). The osmolytes do not affect usual biochemical reactions and execute their highly specific protective mechanisms by maintaining the membrane structures and integrity of the enzymes under water deficit. These osmolytes maintain the structure of cells and osmotic balance by continuous water influx (Hasegawa 2013).

Role of plant growth regulators in salt stress

Auxin

The phytohormone auxin coordinates many important processes in the growth of plant. Several evidences indicate the role of auxin in salinity stress tolerance in plants. A link between salt stress and auxin signaling has been identified (Jung and Park 2011). There are numerous auxin responsive genes and they have been separated into three gene families i.e. GRETCHEN HAGEN3s (GH3s), auxin/indoleacetic acid AUX/IAAs and Small auxin- up regulated RNAs (SAUR*s).* In a study, SAUR*s* family member TaSAUR75 was found to be down regulated in wheat roots under salt stress (Guo *et al.,* 2018). In Arabidopsis, under salt stress, nitric oxide (NO) accumulation led to reduction in auxin level by down-regulating the *PINFORMED* (*PIN*) genes expression. Apart from this, stabilization of AUXIN RESISTANT3 (AXR3)/INDOLE-3-ACETIC ACID17 (IAA17) genes is promoted by salt stress, which are responsible for repressed auxin signaling, led to the inhibition of root meristem growth (Wen *et al.,* 2015). 24 auxin signaling pathway genes were up regulated under salt stress which suggest the importance of auxin signaling in salt stress tolerance (Yin *et al.,* 2019). Under Salt Stress in rice GH3 and other auxin-responsive genes were expressed differentially, indicating the presence of crosstalk between salt stress signaling and auxin. Thus, response of plant to salt stress is controlled by auxin.

Abscisic acid (ABA)

Abscisic acid is well-known to be involved in responses to multiple stresses. It is a major signal that enables plants to survive under stress conditions such as salt stress (Keskin *et al.,* 2010). Increase in the concentrations of abscisic acid (ABA) upon exposure to high NaCl was found in rice. ABA activates various transcription factors like *AREB1/ABF2, AREB2/ABF4, ABF3,* secondary messengers, and

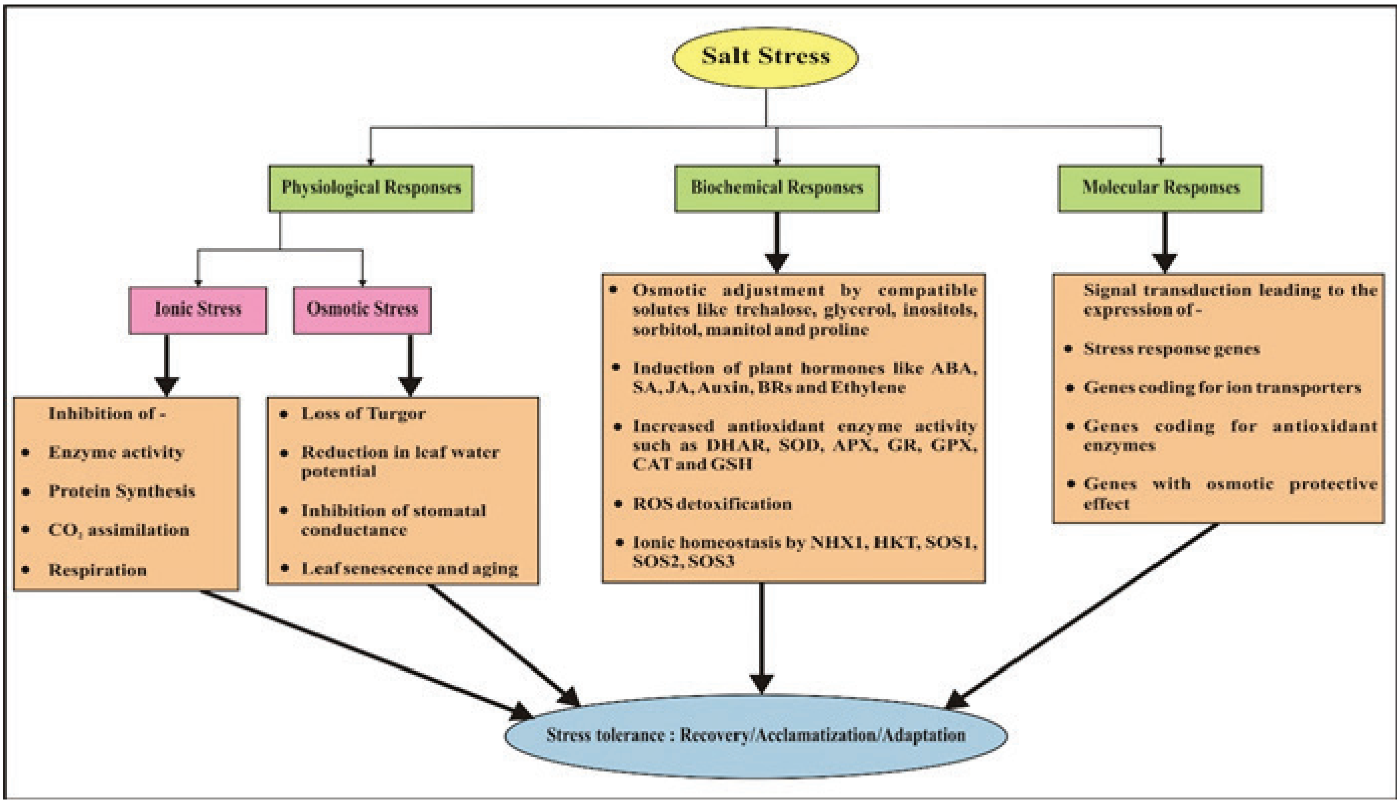

Figure 1. Responses of plants to salt stress

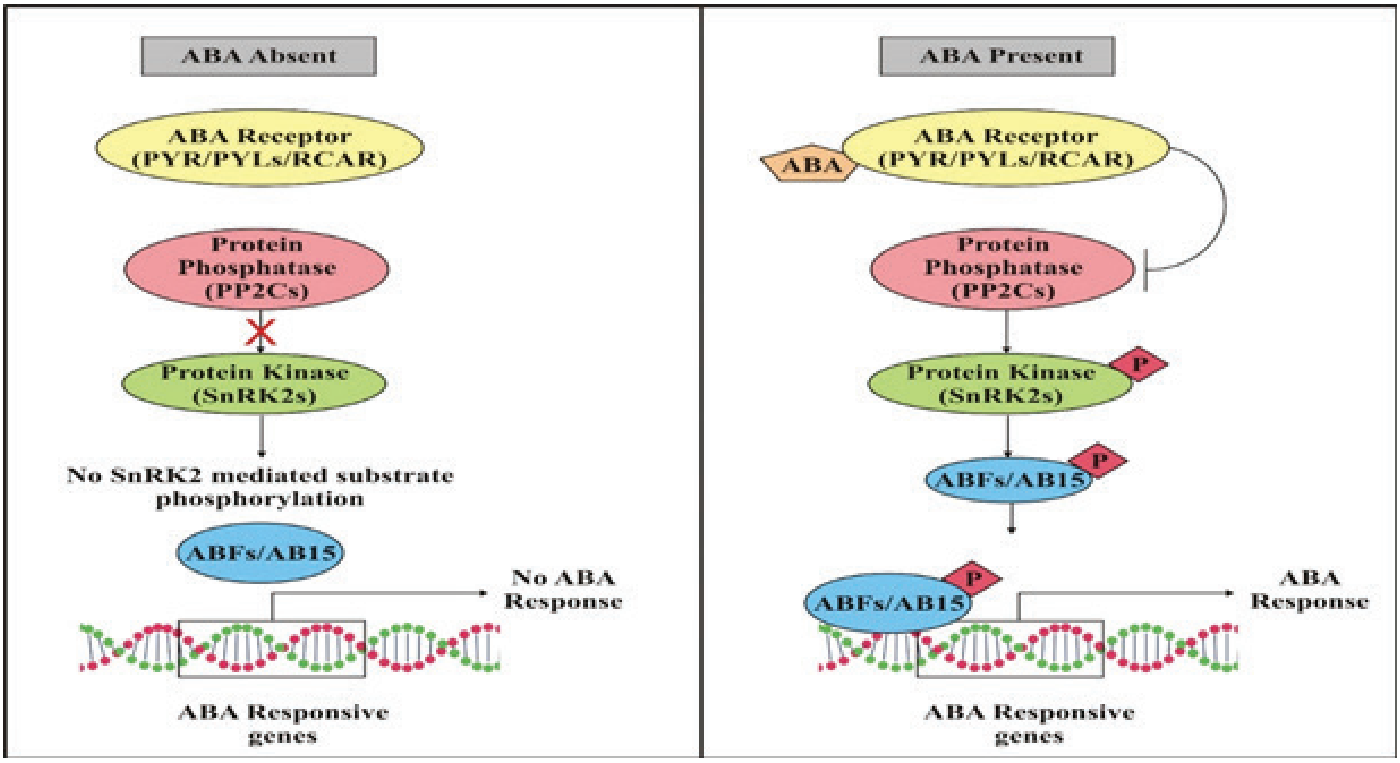

Figure 2. ABA-mediated stress response. Activation of ABA-by-ABA receptor PYL induce the inhibition of PP2Cs. Inhibition of PP2C activate SnRK2 which mediate phosphorylation of downstream target in response to ABA

protein kinases (SnRK2) under salt stress in vegetative organs of plant (Fujita *et al.,* 2011). The proteins which are expressed in ABA-dependent manner have important role in osmotic tolerance. ABF3 and ABI5 are b ZIP TFs that are known to be important in abscisic acid (ABA) signaling. ABI5 activates transcription of LEA proteins. LEA proteins also have a role in salt stress tolerance (Chen *et al.,* 2012). A case showed that primary root growth inhibition and lateral root growth recovery is mediated by the PYL8 /RCAR3 ABA receptor upon exposure to ABA. (Zhao *et al.,* 2014 and Antoni *et al.,* 2013). In addition, ABA has been implicated in histone H3 acetylation and methylation, thereby regulating stress-inducible gene expression at the epigenetic level (Chen *et al.,* 2010). ABA mediated salt stress response is given in Figure 2.

Jasmonic acid

Jasmonates (JAs), lipid-derived phytohormones, regulate

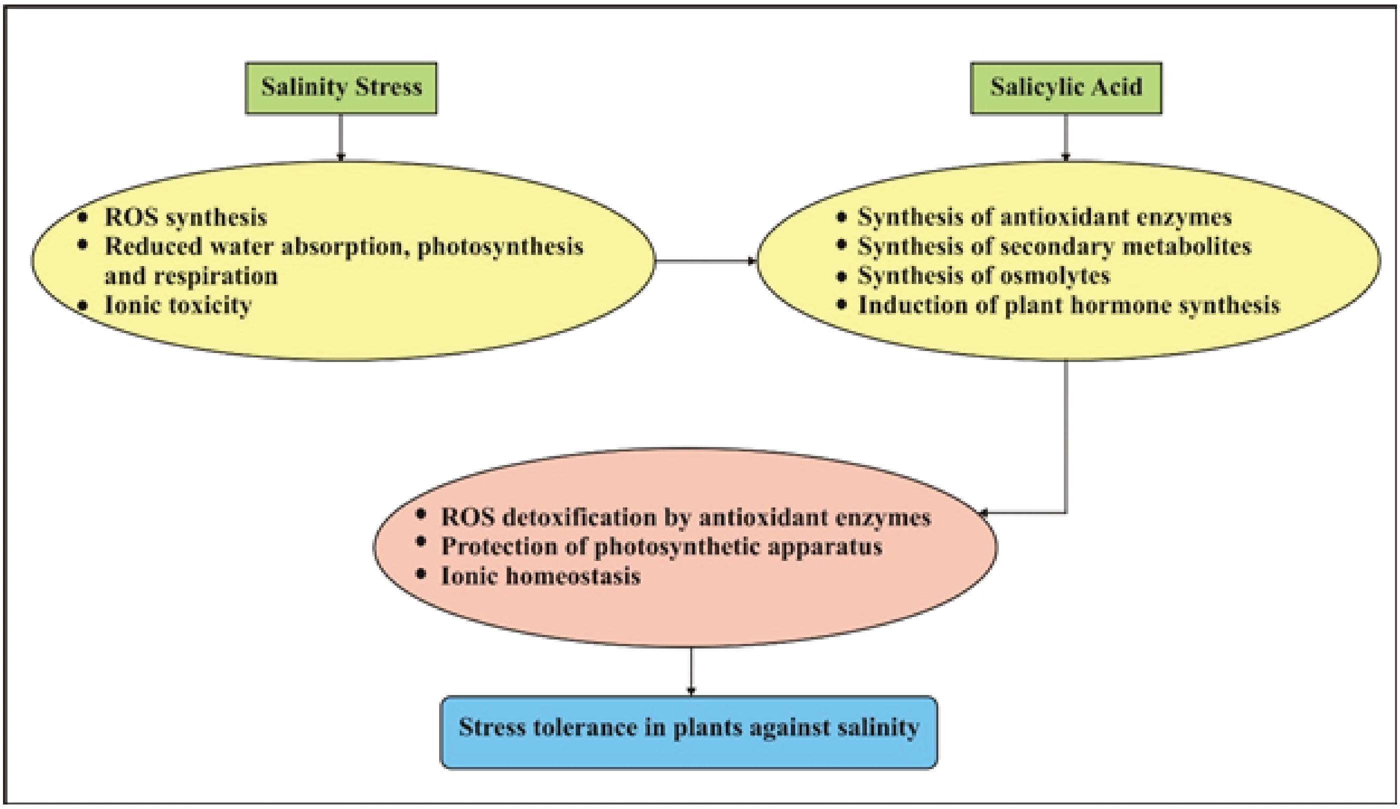

Figure 3. Mechanism of salt stress tolerance induced by salicylic acid in plants

overall plant growth under stress conditions. They upregulate antioxidant metabolism, osmolyte synthesis, and metabolite accumulation upon exposure to high salinity.Level of JA were enhanced in tomato and other plants(Pedranzani *et al.,* 2003, De Domenico *et al.,* 2019). It has been suggested by evidence that salinity tolerance in rice is affected by alterations in the level of JAs (Kurotani *et al.,* 2015). In salt stress exogenous jasmonates (JA) may change the endogenous hormones' level like ABA, which provides a basis for role of JA in protection against salt stress (Kang *et al.,* 2005).Exogenous jasmonate coupled with NaCl showed significantly increased level of antioxidant enzymes in wheat seedlings (Qiun *et al.,* 2014). Jasmonates must be activated by enzymatic coupling to isoleucine amino acid to form JA-Ile. A complex formed between the JAZ proteins and F-box protein COI1, promoted by JA-Ile, resulting in the ubiquitination and subsequent degradation of JAZs (Chini *et al.,* 2007). JAZ proteins play role of transcriptional repressors of stress responsive genes. By formation of this complex, jasmonate relieve JA responsive defense genes from repression. JA-Ile act as a key controller of different aspects of plant immunity/adaptation. While job for jasmonic acid for the immunity to salinity has been recommended (Fujita *et al.,* 2006), molecular pathways for the job of jasmonic acid are still not clear for salt or drought stress-signaling. Suppression of JA signaling repressor, OsJAZ9 generate higher sensitivity to salt and an increased sensitivity to JA (Wu *et al.,* 2015).

Salicylic acid

Studies have indicated the role of Salicylic acid in several abiotic stresses including salt stress (Fahad and Bano 2012; Fahad *et al.,* 2014). SA regulate anion and cation uptake through changes in the transmembrane electrical potential of plants. It has also been reported that SA enhance proline accumulation in salt stress (Gautam and Singh 2009). Salinity tolerance is enhanced by SA mediated restoration of membrane potential and checking K^+ loss (Jayakannan *et al.,* 2013) and by accumulating soluble sugars in roots (El-Tayeb 2005).Priming of tomato plants with SA reduced the salt stress injury by increasing activities of antioxidant and osmotic adjustment (Hasanuzzaman *et al.,* 2014). The foliar application SA had stimulatory effects on wheat varieties under salt stress (Mohammadi *et al.,* 2019).Regulation of ROS balance by SA is possibly a mechanism by which SA modulates germination during salt stress (Lee *et al.,* 2010). Arabidopsis mutant with high endogenous SA concentration showed decreased stomatal aperture (Miura *et al.,* 2013) and increased salt tolerance (Miura *et al.,* 2011), suggested that SA-mediated stomatal closure may be beneficial during salt stress. Mechanisms of salt stress tolerance induced by salicylic acid in plants are given in Figure 3.

Brassinosteroids (BRs)

Brassinosteroids are novel steroidal phytohormones that regulate development and growth of plant by several physiological changes (Kartal *et al.,* 2009). To protect the plants by salt stress, the seed treatment with BRs has been used by different researchers. Ali *et al.,* (2007) treated chickpea seeds with solutions of NaCl and then transferred to HBL (28-homobrassinolide), showed that the adverse effects of salt stress were overcome by HBL, although, this treatment was given before or after NaCl treatment. A similar method was also used by Shahid *et al.,* (2011) in pea seeds. They concluded that EBL (24- epibrassinolide) treatments, given prior to NaCl treatment significantly overcame the NaCl-induced deleterious effects. Hayat *et al.,* (2012) demonstrated that the toxic effects of salinity stress were completely counteracted by foliar sprays of HBL and salicylic acid in mustard plants. EBL and HBL application enhanced antioxidant metabolites, compatible solutes accumulation in plants under salt stress (Rattan *et al.,* 2014, Rattan *et al.,* 2020). BRs are perceived by BRI1 (BRASSINOSTEROID INSENSITIVE 1) that in turn enhance the activity of transcription factors BZR1 (BRASSINAZOLE RESISTANT 1) and BES1 (BRI1-EMS-SUPPRESSOR 1) which control the BR-responsive genes.

Ethylene

Gaseous hormone ethylene is also known as a stress-hormone. Ethylene has been known for affecting plant salt stress responses (Cao *et al.,* 2007). It was found that by ROS homeostasis, ethylene regulates the plant growth and stress response (Yang *et al.,* 2017). Ethylene can maintain a low level of ROS under salt stress by enzymatic pathway (Peng *et al.,* 2014; Zhang *et al.,* 2016)or by non-enzymatic pathway (Zhang *et al.,* 2012). However, it has also been reported that ethylene may play a negative role in salinity stress (Albacete *et al.,* 2009). In rice, ROS accumulation and growth inhibition induced by salinity is mediated by MAPK cascades that ultimately led to ethylene production and signaling (Li *et al.,* 2014). The expression of ACSs (ACC synthase) and ACOs (ACC oxidase) are up-regulated under salinity. Salt induced ethylene signaling is carried out mainly by CTR1-EIN2-EIN3 receptor pathway. EIN3/EILs could bind to the ERF1 promoter and enhance its expression. Overexpression of ERF1 led to plant tolerance to salt, drought and heat stress (Cheng *et al.,* 2013). NtTCTP, NEIP2, AtSAURs, and AtARGOS are supposed to responsible for avoiding damage from extreme ethylene responses.

CONCLUSION

Salinity stress is becoming more prevalent that limit the productivity of agricultural crops. High salt mainly affects plants by water stress, ion toxicity, oxidative stress, alteration in metabolism that led to reduced plant growth, development and survival. Plant tolerance to salinity involves change in their physiological traits, metabolic pathways, and molecular networks. Phytohormones play critical roles in helping the plants to resist adverse environmental conditions. We discussed multiple signaling pathways of different phytohormones with several common salt tolerance determinants. However, there are other proteins, signal molecules and other mechanisms involved but not mentioned in this review. Further studies on salt stress signaling pathways are needed to completely understand the mechanisms of plant stress tolerance. This review will be helpful to elevate our understanding of plant salt-resistance mechanisms.

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