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REVIEW

Mechanism of Phytohormone Responses Against Salt Stress: a Review

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Abiotic stress is defined as the negative impact of non-living factors on living organisms in a specific environment. An unfavourable environmental condition comprising extreme low and high temperature, salinity, drought, water logging, heavy metals etc. pose a complex set of stress condition. Plant responses to those environmental stresses are also complex. The effects of stress are usually measured in terms of plant survival, crop yield, growth (biomass) or primary assimilatory processes which are related to overall growth of plants. Various physiological stimuli and/or stresses control the synthesis of phytohormones in many ways. Again all the molecular biological phenomenon including growth and development of the plants are controlled by the phytohormones at very low concentration. During abiotic stress the biosynthesis and accumulation of different molecules thought to have protective functions in the cells. Some plant growth promoting rhizobacteria (PGPR) may exert a direct stimulation on plant growth and development by providing plants with some of the phytohormones. Among the all abiotic stresses salinity limits the crop’s growth and productivity worldwide. Salinity affects many of the physiological processes starting from seed germination, enzymatic activity, food production to DNA and protein synthesis. Many of the researchers work on the effect of salinity on the physiological activity of the plants, but the mechanism of phytohormones response against salinity are still not assembled in a systematic manner. An attempt is made to establish the comprehensive mechanism of phytohormones responses against salt stress and to know about the adaptation/tolerance of plants in the molecular level as well as systematic approaches during this post genomic era with 164 references.

Key words: Abiotic stress, salinity, phytohormones, physiological activity, molecular mechanism

Plants are constantly confronting a variety of abiotic stresses (e. g. drought, salinity, extreme high and low temperature, metal toxicity etc.) that negatively influence plant growth, productivity, reproductive capability or survival. Plant responses to that stresses are complex and involve numerous physiological, molecular and cellular adaptations. When plants are exposed to a variety of abiotic stresses such as salinity, drought, temperature, the growth of the plants and biomass production are unexpectedly changed (Ahmad *et al*., 2019). Among abiotic stresses, salinity limits crop growth and productivity worldwide (Abdel Latef *et al*., 2020). Many physico-chemical processes in plants including seed germination and seed establishment (Dash *et al*., 2001), enzymatic activities (Seckin *et al*., 2009), transcription and translation (Anuradha *et al*., 2001) are obstructed by salinity. According to some scientist, one-third of the world's food producing areas are salt-affected (Gregory *et al*., 2018). Saline areas are expanding at a rate of 10% annually which would be amplified by increased global warming and climate changes (Shrivastava *et al*., 2015). Initially osmotic stress in plants is caused by salinity and the metabolic processes are directly affected (Khan *et al*., 2019). Later the over-accumulation of NH^+ + Cl^- ions in cells cause ionic toxicity due to salinity (Khan *et al*., 2019). Water insufficiency and nutrient such as Ca^{2+}, K^+, Fe^{2+} and Zn^{2+} deficiency within plants due to salinity caused to disruption of photosynthesis and oxidation stress (Rahman *et al*., 2019). Salinity reduces leaf area, stomatal conductance and chlorophyll levels in the plant and generates reactive oxygen species (ROS) (Khan *et al*., 2018); it also reduces germination percentage, length of root-shoot and fresh weight of plant tissues (El-Shaieny, 2015; Nasri *et al*., 2017). In plants, there are various modified and adaptive methods of salt tolerance to win the worst conditions of high soil salinity (Wang *et al*., 2019). Some researchers used plant growth regulators (PGRs) to alleviate the adverse effect of salinity on plants (Khan *et al*., 2019; Khan *et al*., 2020). In both non-stress and stressful conditions, plants synthesized phytohormones, also known as PGRs, which are small bio active compounds that can work locally or transport to the distant sites of the plant body to accelerate growth and development (Peleg *et al*., 2011; Iqbal *et al*., 2014). PGRs can mitigate the negative effects of salt stress by increasing seed germination, growth, development and yield (Bielach *et al*., 2017). Auxin, Cytokinin (CK), Gibberellic acid (GA), Abscisic acid and ethylene play crucial roles during high-salinity exposure and their responses are supported by other hormones like Salicylic acid (SA), Jasmonate (JA) Triazoles (Fahad *et al*., 2015).

This review discusses about the mechanism of phytohormone actions as well as responses of plants under salt stress condition.

Response of auxin against salinity

Auxin plays a crucial role as a plant development propeller of various physiological processes (Teale *et al*., 2006; Zhao, 2010); it regulates root-shoot architecture, lateral and adventitious root formation, controlling of root-shoot meristems, establishment of apical dominance, leaf morphogenesis, flowering, and senescence (Aloni *et al*., 2003; Okushima *et al*., 2005).

Most of the plants produce IAA from tryptophan via IPA and IAN. Salinity can affects some the enzymes activity in this pathway (Fig. 1). Various studies revealed that salt stress conditions reduce auxin levels and decreased expression of auxin transporter (Park, 2007; Du *et al*., 2012; Liu *et al*., 2015) (Fig. 1). Auxin efflux carriers regulate meristem size during slats stress (Liu, 2015). Exogenous applications of indole acetic acid (IAA) increased salt-stress tolerance in several commercial crops (Ashraf and Foolad, 2005; Ashraf, 2010). In *Pisum sativum* L., foliar applications of auxin has enhanced photosynthetic capacity reduce loss of water; mitigate negative regulation induced by salt stress (Husen *et al*., 2016). IAA treated corn plants enhanced membrane permeability and increased nutrient uptake (Kaya *et al*., 2010). In wheat seed, the effect of delayed germination caused by high salt levels can be reversed by IAA pretreatment (Ashraf and Foolad, 2005). Salinity increased the Na^+ content and reduces K^+, Ca^{2+}, Mg^{2+} content in root, stem, leaf, and seed of faba bean plants. IAA treated faba bean plant reduced the accumulation of Na^+ content and improves the accumulation of K^+, Ca^{2+}, Mg^{2+} content under salt stress. (Abdel Latef *et al*., 2021). Foliar application of IAA has changed expression pattern of proteins for better salt adaptation (Abdel Latef *et al*., 2021).

Similarly exogenous application of IAA has shown positive effects in different crops under salt stress such as *Zea mays* (Keya *et al*., 2010), *Oryza sativa* (Javid *et al*., 2011), *Solanum lycopersicum* (Alam *et al*., 2020), *Solanum tuberosum* (Khalid and Aftab, 2020) *Carica papaya* (Sá *et al*., 2020). Changing of the protein expression pattern showed the ability of a plant's tolerance to salt stress and plants synthesize specific polypeptide under salt stress for adaptation (Bavei *et al*., 2011). Compared to non-stressed plant, protein related to salt stresses show a positive indicator of salinity stress. (Sobhania *et al*., 2016). Several researchers showed that over expression of indole pyruvic acid (IPyA) pathway in several species increase salt tolerance (Kim, 2013; Yan, 2016).

There are large number of auxin responsive genes which were identified and characterized from different plant species, such as soybean, *Arabidopsis* sp and rice (Hagen and Guilfoyle, 2002). In cucumber, YUCCA genes are expressed at high and low temperature in response to salinity. Over expression of CsYUC11 gene has increased higher salinity tolerance (Yan, 2016). These auxin responsive genes have been divided into three gene families-i) Auxin (AUX/IAA), ii) GH_3 and iii) small auxin-up RNA (SAUR) gene families (Guilfoyle *et al.*, 1993). These novel genes have involved in salt stress responses and by which researchers can set further genetic strategies to improve more stress tolerance cultivars (Zhu, 2002).

Response of gibberellins against salinity

Gibberellins help seed germination, leaf expansion, stem elongation and flowering (Magome *et al*., 2004). During abiotic stress condition, plants accumulated gibberellic acid (GA) rapidly (Lehmann *et al*., 1995). GA_3 was helpful to enhance the growth of wheat and rice under saline conditions (Parasher and Varma, 1988; Prakash and Prathapasenan, 1990). Stomatal resistance in tomato was reduced and water use in plant was enhanced by GA_3 treatment at low salinity (Maggio *et al*., 2010). With poultry manure, application of GAs has improved the growth and salinity tolerance of piper (*Capsicum annuum*) plants (Al Taey, 2017). Wheat seeds treated with GAs increased germination and seedling parameters under salt stress (Abido *et al*., 2019). Tomato plant treated with GA_3 increased leaf water content, stomatal density and chlorophyll content by alleviating salinity stress (Jayasinghe *et al*., 2019). Maize seed treated with GAs (5 mgL^{-1}) increased the root-shoot length and water content in tissues under salt stress (Ghodrat and Rousta, 2012). Conformational changes of gibberellin insensitive dwarf (GID_1) was induced by binding of bioactive GA to GID_1 and has recruited DELLA growth repressor protein to form a GA-GID_1-DELLA complex and interaction of E_3 ubiquitin ligase F-box protein SLEEPY 1 (SLY1) with DELLAs, 26s proteosome degraded DELLA activity (Bao *et al*., 2020). DELLA protein SLR_1 was survived under salt stress by inhabiting plant growth (Achard *et al*., 2006). Plants have increased their salt tolerance ability through retarding the growth by the activity of related genes like AtGA20X7 (Magome *et al*., 2008), OSGA20X5 (Shan *et al*., 2014) OSMYB92 (Zhu *et al*., 2015) responsible for GA metabolism. Over expression of GA catabolic gene CYP7D8L in transgenic plants was reduced GA accumulation, increase high soluble sugar and chlorophyll content to enhance plant tolerance to salt stress (Zhou *et al*., 2020). Under salt stress, rice plants have increased their tolerance by ectopic expression of PtCyP714A3 (*Populus trichocarpa*) encoding unique group of CyP mono-oxygenase which regulates deactivation of GA (Wang *et al*., 2016). In *Arabidopsis*, ectopic expression of G(h)PLATZ1 was helped quicker germination than in wild type and has suppressed the transcription of ABI4 (Zhang *et al*., 2018). Under salt stress, GhPLATZ1-mediated germination was depended on GA: ABA ratio (Zhang *et al*., 2018).

Response of cytokinin against salinity

Cytokinin (CKs) promotes cell division, affects apical dominance, auxiliary bud growth, chloroplast biogenesis, nutrient mobilization, leaf senescence, shoot differentiation, Photo-morphogenic development, anthocyanin production, vascular differentiation (Mok and Mok, 2001; Davies, 2004). CKs has helped to increase plant resistance power to salinity and high temperature (Barciszewski *et al*., 2000). Seed treated with cytokinin has increased plant's salt tolerance (Iqbal *et al*., 2006a). By interacting with other plant hormones, cytokinin has enhanced salt tolerance in wheat plants (Iqbal *et al*., 2006b). Exogenous application of kinetin has inhibited negative effect of salinity stress on the growth of wheat seedlings (Naqvi *et al*., 1982). Prior to salt stress, if the potato plants are treated with kinetin, it alters salt-related growth inhibition (Abdullah and Ahmad, 1990). Under salt stress, Na^+ accumulated in plants to make the disorder of ion homeostasis, the imbalance of K^+ / Na^+ ratio causes oxidative stress (Song and Wang, 2015; Guo *et al*., 2018; Liu *et al*., 2017). Ion stress and oxidative stress caused leaf senescence (Han *et al*., 2011; Li *et al*., 2012) in plants. Cytokinin has the role against the negative effect of salt on plants such as radish and tobacco (Vnakova *et al*., 2010). Some studies have shown that tomato seedling measures cytokinin level under salt stress (Keshishian *et al*., 2018). If INCYDE is sprayed on tomato under salt stress to increase antioxidant enzymes activity, it enhances plant salt tolerance (Aremu *et al*., 2014). On the other hand when 42 bp in promoter region of IPT_5 has deleted, the cytokinin content of apple rootstock "robusta" has enhanced salt tolerance capacity (Feng *et al*., 2019). It has been established that cytokinin receptor AHK_1 is a positive regulator of salt stress response (Tran *et al*., 2007).

Response of brassinosteroid (BR) against salinity

BRs regulated many physiological processes like growth, leaf abscission, seed germination, rhizogenesis and senescence (Sasse, 1997). Exogenous application of BRs has enhanced growth and yield in many economically useful plant species under salinity. BRs promoted the number of ears along with their length and weight of kernels per year in cereals (Ali *et al*., 2008). BRs removed negative effect of salinity to help seed germination and seedling growth in rice. BRs enhanced nitrate reductase, maintained chlorophyll level under salt stress, and played an important role to supply nitrogen, growth and productivity of plants especially in cereals (Bajgur and Hayat, 2009). The impact of salt stress on rice growth was altered by BRs as a result level of pigment was restored and nitrate reductase activity was increased (Anuradha and Rao, 2001). If leaf segments of barley were incubated in either BR solution or water and then incubated in 0.5 M NaCl solution in presence/absence of BR, there was no effect of BR on the leaf cell ultrastructure under normal condition and damage on nuclei; chloroplast caused by salt stress is altered by treatment of BR (Krishna, 2003). Some key enzymes which are associated with BR synthesis help plant to adopt in salt stress. Due to the over expression of a BR biosynthesis gene of *Spinacia oleracea*, SOCYP85A1 gene was amplified and increased the longevity of plant against high salinity (Duan *et al*., 2017). Under salt stress condition, tomato plants deficient of BR biosynthesis genes were more affected, but it has been altered by exogenous BR application (Zhu *et al*., 2016). Plants were sensitive to salt stress due to leak of BRI 1 or BSK5 (Zhu *et al*., 2016; Li *et al*., 2012a). BZR1, a marker, directly repressed the expression of BR biosynthetic gene DWF4 which cross the normal level at an early stress stage not soon back to normal levels (Geng *et al*., 2013).

H_2O_2 generation and accumulation of ethylene in tomato, exogenous BR treatment on cucumber were regulated positively to promote antioxidant enzyme activities under salt stress (Zhu *et al*., 2016; Wei *et al*., 2015). BR also helped to accumulate nitric oxide (NO) and mitigated oxidative damage which was caused by salt stress (Zhu *et al*., 2016). BR alleviated effect of salt stress on plant through interacting with other plant hormones like ABA (Zhang *et al*., 2009) SA (Divi *et al*., 2010) and GA (Wang *et al*., 2019a). Under NaCl-stressed conditions, oxidative damage in rice and maize seedlings was mitigated when seed has been treated by EBL or HBL (Özdernir *et al*., 2004). Seed treatment with EBL reduced chromosomal abnormalities in root tips of barley plants grown in a NaCl containing medium, (Tabur and Demir, 2009). In wheat cultivars, EBL has leaded to increase the growth of seedling and maintain Ca^{2+}/Na^+ and K^+/ Na^+ ratio to promote uptake of Ca^{2+}, K^+ and reducing Na^+ , which helped to adapt both wheat cultivars under salt stress (Ali *et al*., 2006). Foliar application of EBL to two strawberry cultivars helped to overcome the negative effect of salinity stress on plant growth and enhanced shoot and root dry matters, relative water content of leaf, stomatal conductance, leaf chlorophyll value, macro-micro element content in leaf and root of plants (Karlidag *et al*., 2011). BRs and spermidine can altered the toxic effect of salt stress on *Vigna radiata* plants (Mir *et al*., 2015). The presence of EBL in nutritive solution under NaCl stress enhanced plant fresh weight, shoot dry weight, leaf and root water content, leaf area, sugar concentration, photosynthetic pigments, photosynthetic rate and water use efficiency of *Cajanus Cajan* plants (Durigan *et al*., 2011).

BR treated faba bean plant reduced the accumulation of Na^+ content and improved the accumulation of K^+, Ca^{2+}, Mg^{2+} content under salt stress (Abdel Latef *et al*., 2021). Under salt stress, foliar application of BR has changed the expression pattern of protein for better salt adaptation (Abdel Latef *et al*., 2021).

Response of abscisic acid (ABA) against salinity

The **a**bscisic acid (ABA) helped plants to survive under adverse environmental condition such as salt stress (Keskin *et al*., 2010). In presence of salt, ABA increased xylem water potential as well as water uptake to the plant (Fricke *et al*., 2004). When barley roots are exposed to the salt, ions are accumulated in vacuoles of roots stimulation of ABA in roots which was important for adaptation to saline conditions (Jeschke *et al*., 1997). Exogenous application ABA inhibited leaf abscission and reduced ethylene release under salt stress in citrus by reducing Cl^- ions accumulation in leaves (Gomez *et al*., 2002). ABA inhibited the deleterious effect of NaCl and enhances tolerance of ionic stress in sorghum (Amzallag *et al*., 1990).

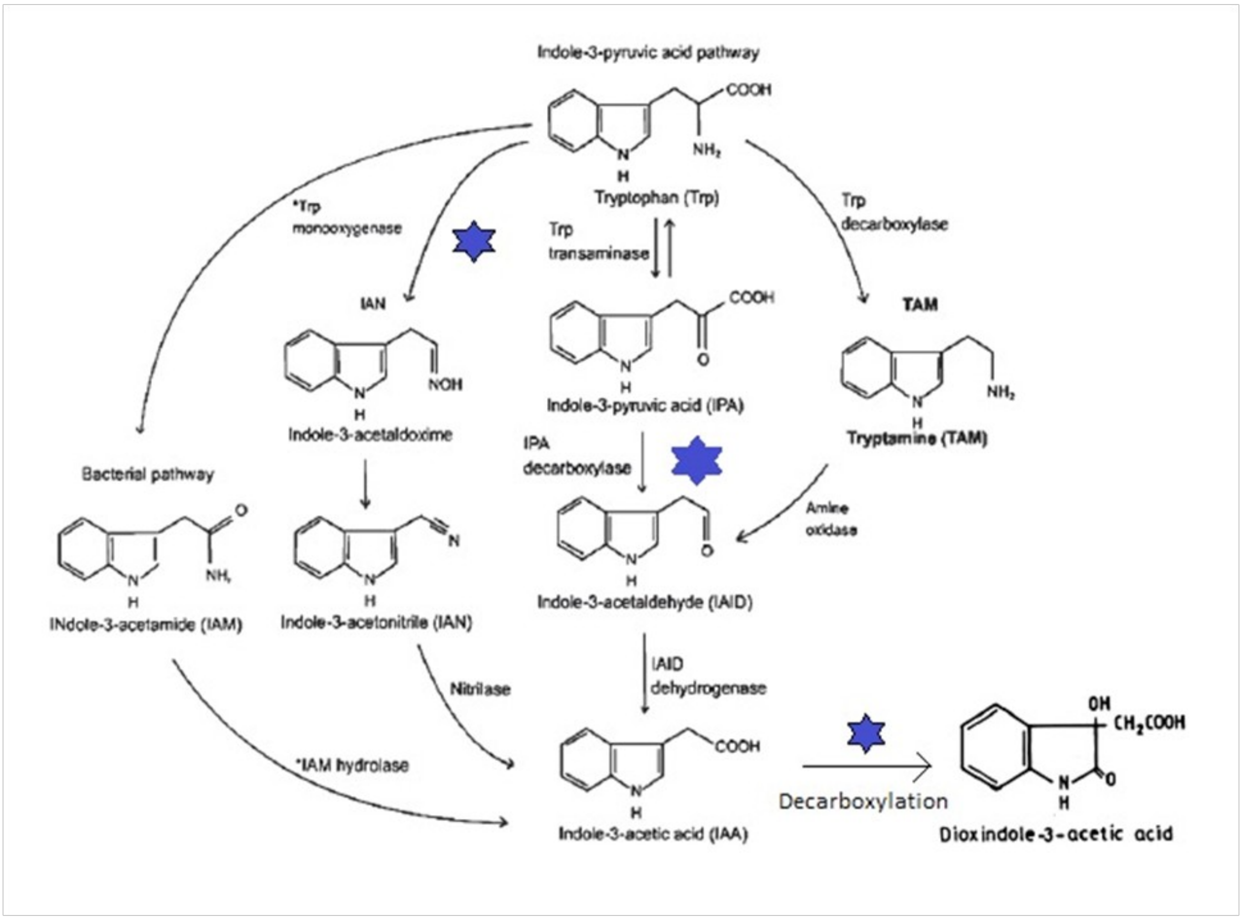

Figure 1. Tryptophan dependent IAA pathway in plants and bacteria. Salinity affects in the asterisk regions.

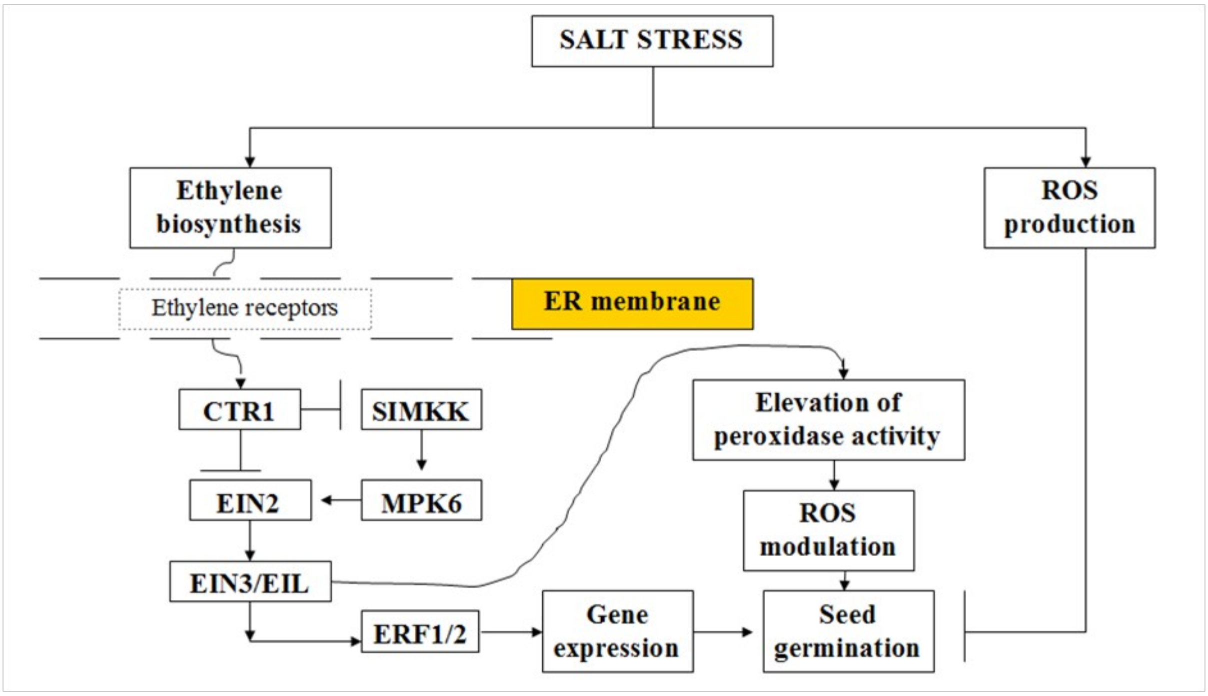

Figure 2. Effect of ethylene signaling on seed germination under salt stress.

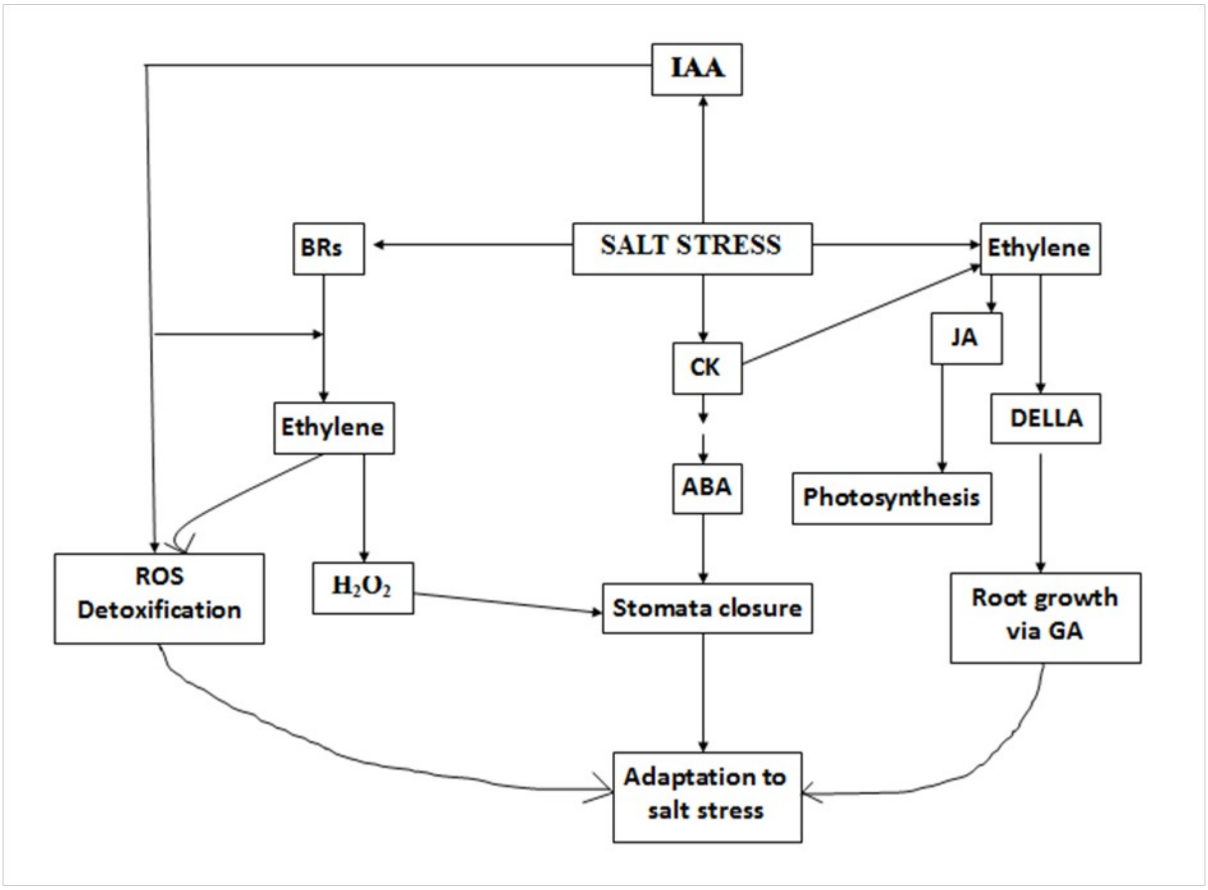

Figure 3. Interrelationship of phytohormone responses is represented by a schematic diagram under salt stress.

Salinity up regulated stress hormone ABA, promoted gene to mitigate salt and osmotic stress (Wang *et al*., 2011). The rice seed treated with ABA increased seedling growth and yield under saline soil by balancing nutrient uptake (Gurmani *et al*., 2013; Li *et al*., 2010). Rice treated with ABA at 10^{-5} M enhance osmoregulation by reduced Na^+ concentration in cells and increased proline and sugar accumulation in rice leaves under salt stress (Gurmani *et al*., 2011). ABA also helped the tolerance power against salt stress in wheat plant (Zongshuai *et al*., 2017). The mustard seeds treated with ABA (100 µm) enhanced germination rate by 25% compared to the control under salt stress (Srivastava *et al*., 2010).

CED_1 (9 CIS EPOXYCAROTENOID DIOXYGENASE DEFECTIVE 1) is an important protein in biogenesis of cuticle. A mutant of CED_1 protein was unable to promote ABA biosynthesis under osmotic stress (Wang *et al*., 2011). During salt stress, ABA acts as a signaling molecule to suppress the growth of lateral roots as in quiescent stage. Lateral roots form a thick, well-developed casparian strip which has reduced diffusion of Na^+ ions through the endodermis and in presence of Na^+ ions, endodermal cells enhanced ABA signaling and inhibited growth of lateral roots under high saline environment (Duan *et al*., 2013). LEA proteins produced in an ABA-dependent manner, were highly hydrophilic small proteins, have an osmoprotectant role against cellular dehydration during late embryogenesis. LEA proteins also played an important role in salt stress tolerance (Bhardwaj *et al*., 2013). In *Arabidopsis,* 51 LEP proteins were identified from nine different groups (Hundertmark *et al*., 2008). *Arabidopsis* can able to mitigate salt stress by over activation of salt stress inducible genes such as RD29B through over expression of AtLEA 14 which belongs to the LEA group-2 proteins (Jia *et al*., 2014).

Response of ethylene against salinity

In many plant species level of ethylene and its precursor ACC are induced by salinity and other abiotic stresses (Morgan and Drew, 1997). On application of ethylene or ACC has enhanced plant tolerance to high salinity (Cao *et al*., 2007). Ethylene was an essential positive mediator of salinity stress tolerance in maize (Freitas *et al*., 2018), tomato (Gharbi *et al*., 2017), grapevine (Xu *et al*., 2019). It is reported in grapevines that melatonin involves in enhancing salinity stress tolerance by inducing MyB108A-mediated ethylene biosynthesis (Xu *et al*., 2019). Ethylene played positive effect under salinity stress by osmotic adjustment, water use efficiency, maintaining stomatal conductance in *Solanum chilense* (Gharbi *et al*., 2017). Under salinity stress, different components of ethylene signaling have played either positively or negatively at the time of seed germination (Fig. 2) and seedling growth (Cao *et al*., 2008). For examples, in *Arabidopsis*, ETR_1 and ETR_4 have inhibited seed germination, but ETR_2 acted as a positive regulator involves in enhancing seed germination during salinity stress conditions (Wilson *et al*., 2014). Under salinity stress, ethylene has maintained Na^+ /K^+ homeostasis to improve tolerance against salinity stress (Jiang *et al*., 2013). *Stylosanthes humillis,* a forage legume grows naturally in saline soils and ethylene produced in seeds of the plants mitigated the effect of salinity stress (Lovato *et al*., 1999; Silva *et al*., 2014; Silva *et al*., 2018). ACC deaminase in plant growth-promoting *Pseudomonas fluorescens* strain improved salinity tolerance in plants and enhanced seed germination in wheat during salinity stress (Safari *et al*., 2018). Over expressing ethylene response factors (ERF 95 and ERF 96) in seeds of the transgenic line promoted better germination and seedling establishment by comparing with the wild under salinity stress conditions (Wang *et al*., 2017).

A novel ethylene responsive transcription factor from *Lycium clinense* Lch ERF helped to improve salinity tolerance in transgenic tobacco in the time of seed germination and vegetative growth (Wu *et al*., 2014). ERF 109, an ethylene responsive transcription factor gene, has retarded programme cell death (PCD) and enhances adaptation under salinity in the wild type tobacco plant (Bahieldin *et al*., 2016). Ethylene along with other phytohormones like auxin (IAA), cytokinin (CK), abscisic acid (ABA) helped the plants to overcome the adverse effect of salinity stress (Tuteja *et al*., 2010).

Response of jasmonates (JAs) against salinity

Methyl jasmonate (MeJA) and its free form jasmonic acid (JA) both are collectively called as Jasmonates (JAs) which regulate many developmental processes like seed germination, fertility, root growth, ripening of fruits and senescence (Wasternack and Hause, 2002). Jasmonates enhanced defense mechanisms in plants under environmental stresses, such as low temperature, drought, salinity and also in response to various pathogens, insects driven wounding (Cheong and Choi, 2003). In tomato cultivars JAs level changed in response to salt stress and in salt tolerant cultivar HF (Hell frucht Fruhstamm). It was observed that JAs level increased from the beginning of salinization, while salt sensitive cultivar Pera treated with salt in 24h, JAs level decreased (Pedranzaini *et al*., 2003). Salt tolerant cultivar plants have high concentration of JAs than salt sensitive cultivar plants (Kang *et al*., 2005). In rice root, MeJA level was significantly increased in 200 mM NaCl (Moons *et al*., 1997). The inhibitory effect of high salt concentrations on growth and photosynthesis of barley are altered by pre-treatment with JAs (Tsonev *et al*., 1998). The balance of endogenous hormones such as ABA was changed by exogenous JAs application after salt treatment which gave the protection mechanisms under salt stress (Kang *et al*., 2005). In barley, the induction of JA-responsive genes played important roles under salinity (Walia *et al*., 2006). Arginine decarboxylase and apoplastic invertase which are activated by three JA regulated genes, involve in salinity tolerance through JAs (Walia *et al*., 2007). Symptoms produced by salinity stress in soybean seedling are mitigated by exogenous application of MeJA (Yoon *et al*., 2009). In tomato, exogenous application of JAs on mitigation of NaCl toxicity by regulating the antioxidant metabolism, accumulation of metabolite, synthesis of osmolyte was reported (Ahmad *et al*., 2018). The pretreatment of maize seedlings with JAs removed toxic effects of Na_2CO_3 on photosynthesis and plant growth (Mir *et al*., 2018). Under salt stress, exogenous application MeJA enhances the growth of *Limonium bicolor* (Yuan *et al*., 2018). Through maintaining ROS or ion homeostasis, exogenous application of JAs removed salt toxicity (Qiu *et al*., 2014; Farhangi-Abriz and Ghassemi-Golezani, 2018). In tomato, with increased K^+ accumulation, the high JA-accumulation resistant mutant exhibited adaptation under salt stress (Garcia-Abellan *et al*., 2015). In tomato and rice, reduced JAs production or accumulation caused hypersensitivity under salinity (Abouelsaad and Renault, 2018; Kurotani *et al*., 2015), whereas elevated JAs biosynthesis helped to overcome adverse effect of salt stress in wheat and *Arabidopsis* (Zhao *et al*., 2014). Due to lower Na^+ accumulation in shoots, two JAs biosynthesis rice mutants, Cpm 2 and hebiba, were resistant to salt but there was no difference to detect in roots (Hazman *et al*., 2015). MYC 2, the master regulator in JAs signaling, helped plants adaptation to osmotic stress through activated expression of the ABA-inducible genes RD 22 and at ADH1 transcriptionally (Abe *et al*., 2003).

Response of salicylic acid (SA) against salinity

Salicylic acid which is phenolic in nature, has regulated many physiological processes like photosynthesis, ethylene production, heat production, flowering, growth, nitrate metabolism (Hayat *et al*., 2010) and helped the plants to protect from biotic and abiotic stress such as salinity (Kaya *et al*., 2002). SA increased resistant power of wheat seedlings under salinity (Shakirova *et al*., 2003). After salt stress, the application of 0.05 mM SA enhanced plant growth, accumulation of ABA and protein in wheat (Shakirova *et al*., 2003). Exogenous application of SA increased the photosynthetic rate and regulated the membranes stability and the growth under salinity stress in barley plants. (El-Tayeb, 2005). When SA added to the soil during salt stress, Na^+ and Cl^- accumulation was decreased and also enhanced the survival rate of maize plants (Gunes *et al*., 2007). SA caused lower lipid peroxidation and membrane permeability in plant during salt stress (Horvath *et al*., 2007). SA treatment has increased H_2O_2 level which mitigates the adverse effects on the oxidation damage induced by salt stress in wheat plants (Wahid *et al*., 2007). SA helped nitrogen fixation in salt environment (Palma *et al*., 2013). In *Arabidopsis* application of excess SA (>100µM) exaggerated inhibition of seed germination caused by salt stress, while moderate level of SA (<50µM) treatment alters effect of salt stress on seed germination (Lee *et al*., 2010). In tobacco, through increasing SA signaling, over expression of AtNPR1 or MhNPR1 increased tolerance under oxidative and salt/osmotic stress (Srinivasan *et al*., 2009; Zhang *et al*., 2014). The npr 1-5 mutant did not have NPR1- dependent SA signaling, showing a hypersensitive phenotype to salinity (Jayakannan *et al*., 2015). In wheat, SA promoted growth through inhibiting the decline of auxin and CK, maintain high ABA levels to increase plant salt tolerance (Shakirova *et al*., 2003). In *Limanium bicolor,* SA enhanced seed germination by maintaining a favorable, GA/ABA balance under salt stress (Liu *et al*., 2019).

Response of strigolactones (SLs) against salinity

SLs helped symbiotic interactions with fungi and shoot branching (Gomez-Rolban *et al*., 2008; Zhang *et al*., 2015). Under salt stress condition a synthetic SL, GR24, has increased plant growth by enhancing antioxidant enzyme activities and photosynthetic characteristics (Ma *et al*., 2017). In the germination and vegetative stages, the SL-biosynthetic mutants showed more axillary growth (Ha *et al*., 2013) indicated that SLs were positive regulator of plant salt tolerance. ABA helped the plants to overcome the adverse effect of salt stress through production of SL. Under salt stress, mycorrhiza colonized lettuce roots and ABA content was increased by upregulation of the ABA biosynthetic gene LsNCED2, which was mediated by salt-induced SL production (Aroca *et al*., 2013). In *S. cannabina* seedings, concentration of SL was also affected by ABA through the upregulation of CCD7, CCD8 and MAX2 (Rne *et al*., 2018). In ABA deficient plants, GR24 application restored the salt tolerance (Rne *et al*., 2018).

From the above discussion we may expect that there must be an interrelationship i.e. the phytohormonal cross-talk within the plants under salt stress (Fig. 3) and plants can mitigate the stressful condition by giving responses in various ways.

CONCLUSION

Among the all major environmental stresses salt stress limits the growth and productivity of the plants. On the other hand phytohormones can control plant’s growth and development. Beside many other physiological functions, production of phytohormones in plants can mitigate the salt stress condition in various ways. The levels of phytohormones are elevated against the salt stress among the many plants. Phytohormones regulate ionic toxicity, osmotic stress, oxidative stress and synthesis of many plant genes by controlling the transcription factors during salt stress condition. So there might be some molecular signaling which can induce for the production of phytohormones in salinity to combat the stressful situations. In this review we have discussed the responses of phytohormones during salinity, though the detail molecular signaling mechanism during the salt stress condition in plants is warranted for further research.

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CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

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