Review article

The role of phytohormones in alleviating salt stress in crop plants

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Abstract

Phytohormones are chemical messengers produced in one part of plant and translocated to the other parts, where they play critical roles in regulating plant responses to stress at extremely low concentration. Phytohormones are natural products and they called plant growth regulators, when they are synthesized chemically. Plants are usually subjected to environmental factors such as drought or high soil and water salinity. The reduction in plant growth exposed to saline environments could be due to either the effects of specific ions on metabolism or adverse water relations. Different strategies are being employed to maximize plant growth under saline conditions. One of them is to produce salt tolerant genotypes of different crops. Attempts to improve tolerance to salinity through conventional plant breeding methods are time consuming, laborious and depended on existing genetic variability. In addition, many attempts have been made to overcome this disorder, including proper management and exogenous application of plant growth regulators. This article presents a review of the role of abscisic acid (ABA), indole acetic acid (IAA), cytokinins (CK), gibberellic acid (GA), brassinosteroids (BR), jasmonates (JA), salicylic acid (SA) and triazoles (TR) in alleviating salt stress in crops.

Keywords: Phytohormone, Plant growth regulator, Salt stress.
Abbreviations: ABA_Abscisic acid; BR_Brassinosteroid; CK_Cytokinin; GA_Gibberellic acid; IAA_Indole-3-acetic acid; JA_ Jasmonic acid; MeJA_Methyl Jasmonate; PGRs_Plant Growth Regulators; SA_Salicylic acid; TR_Triazole.

Introduction

Plants are frequently subjected to the environmental stress such as water deficit, freezing, heat and salt stress. Salinity is one of the most common environmental stress factors. Salinity adversely affects plant growth and development, hindering seed germination (Dash and Panda, 2001), seedling growth (Ashraf et al., 2002), enzyme activity (Seckin et al., 2009), DNA, RNA, protein synthesis (Anuradha and Rao, 2001) and mitosis (Tabur and Demir, 2010). However, plant species differ in their sensitivity or tolerance to salt stress (Ashraf and Harris, 2004). There have been numerous studies of the effects of salinity on plants (Jamil et al., 2007; Duan et al., 2008). Recently, investigations have focused more on the mechanisms of salt tolerance in plants (Dajic, 2006; Munns and Tester, 2008). Some researchers have used PGRs for reducing or eradicating the negative effects of salinity (Kabar, 1987; Mutlu and Bozcuk, 2000). Phytohormones suggested playing important roles in stress responses and adaptation (Sharma et al., 2005; Shaterian et al., 2005). It is thought that the repressive effect of salinity on seed germination and plant growth could be related to a decline in endogenous levels of phytohormones (Zholkevich and Pustovoytova, 1993; Jackson, 1997; Debez et al., 2001). Wang et al. (2001) clearly defined that ABA and JA will be increased in response to salinity, whereas indole-3-acetic acid (IAA) and salicylic acid (SA) are declined. For example, the exogenous application of PGRs, auxins (Khan et al., 2004), gibberellins (Afzal et al., 2005), cytokinins (Gul et al., 2000) produces some benefit in alleviating the adverse effects of salt stress and also improves germination, growth, development and seed yields and yield quality (Egamberdieva, 2009). It has been reported that exogenous application of ABA reduces the release of ethylene and leaf abscission under salt stress in plants, probably by decreasing the accumulation of toxic Cl$^-$ ions in leaves (Gomez et al., 2002). In wheat, seed germination decreased with increasing levels of salinity, while the adverse effect of salinity was alleviated by soaking seed with IAA (Gulnaz et al., 1999). In addition, exogenous IAA showed high stimulatory effect on the root and shoot growth of wheat seedling in saline condition (Egamberdieva, 2009). Growth and yield parameters of rice were significantly increased in response to application of cytokinin under salin stress (Zahir et al., 2001). In this review, the role of some phytohormones in alleviating salinity stress in crop plants has been discussed.

Abscisic acid (ABA)

The abscisic acid (ABA) has been proposed to act as a mediator in plant responses to a range of stresses, including drought and salt stress. ABA is also the major internal signal enabling plants to survive adverse environmental conditions such as salt stress (Keskin et al., 2010). Exposure of plants to salinity is known to induce a proportional increase in ABA concentration, that is in most cases correlated with leaf or soil

water potential, suggesting that salt-induced endogenous ABA is due to water deficit rather than specific salt effects (Zhang et al., 2006). This may not resemble the prolonged increasing of endogenous ABA levels that can occur in association with slowly increasing salinity stresses in nature or field situations (Etehadnia et al., 2008). Increases of the endogenous ABA concentration in leaf tissue for salt stressed *Brassica* (He and Cramer, 1996), *Phaseolus volgaris* (Cabot et al., 2009) and *Zea mays* (Cramer and Quarrie, 2002) strongly correlated with growth inhibition. Salt stress led to a sharp increase in the concentrations of abscisic acid (ABA) in rice under 20 and 40 mm NaCl, compare to the control values (Kang et al., 2005). The increase of ABA concentration in roots (Jia et al., 2002), when root growth continues, suggests that these tissues may have different sensitivities to the localized concentration of ABA either in endogenous form, or when exogenously applied (Creelman et al., 1990). Stress responses of the root and shoot tissues appear to be coordinated by increased amounts of hormones moving in the xylem sap by 'root-to-shoot' communication (Davies et al., 1994). However, some doubt remains concerning the ability of ABA to act as a signal that mediates the effects of root-zone stress (Jia et al., 2002). There is significant evidence that ABA acts as the root-to-shoot stress signal. A study has demonstrated that ABA contributes to the increase of xylem water potential as well as water uptake to the plant in the presence of salt (Fricke et al., 2004). Jeschke et al. (1997) reported that increase of ABA concentration in the xylem is correlated with reduced leaf conductance and general inhibition of leaf growth. Salt stress stimulated ABA synthesis in roots and its xylem transport and well correlated to the stomatal reactions. This may be explained by the fact, when roots are directly exposed to the salt, ABA in roots stimulates ion accumulation in vacuoles of barley roots which may be necessary for adaptation to saline conditions (Jeschke et al., 1997). Jae-Ung and Youngsook (2001) reported that ABA, as a signal for stomatal closure, induces rapid depolymerization of cortical actin filaments and the slower formation of a new type actin which is randomly oriented throughout the cell. This change in actin organisation has been suggested to be basic in signaling pathways involved in stomatal closing movement, since actin antagonists interfere with normal stomatal closing responses to ABA. It has been reported that exogenous application ABA reduces ethylene release and leaf abscission under salt stress in citrus, probably by decreasing the accumulation of toxic Cl⁻ ions in leaves (Gomez et al., 2002). In addition, Cabot et al. (2009) reported that salt-induced ABA mediated the inhibition of leaf expansion and limited the accumulation of Na and Cl in leaves. ABA delayed the deleterious effect of NaCl and improved tolerance of ionic stress in sorghum (Amzallag et al., 1990). The generic stress hormone ABA is up-regulated by salinity and induces genes involved in salt and osmotic alleviation (Wang et al., 2001). Shi and Zhu (2002) have reported the tissue distribution and regulation of AtNHX1 expression by ABA and salt stress. Fukuda and Tanaka (2006) discussed effects of ABA on the expression of two genes *HVP1* and *HVP10* for vacuolar H⁺-inorganic pyrophosphatase and one *HvVHA-A* for the catalytic subunit (subunit A) of vacuolar H⁺_ATPase. It was accomplished by quantification of the transcript levels, to identify the hormones responsible for regulating the expression of these genes in barley (*Hordeum vulgare* L.) in response to salt stress. Keksin et al. (2010) reported that the *MAPK4*-like, *TIP1* and *GLP1* genes were induced much faster in response to ABA treatment in wheat. This result could be evidence for the possible role of these genes in the ABA-induced

pathways. Thus, in many ways ABA plays vital roles in whole plant responses to salt stress.

Indole acetic acid (IAA)

IAA plays a major role on regulating plant growth. For example, it controls vascular tissue development, cell elongation, and apical dominance (Wang et al., 2001). IAA also responds to salinity in crop plants. However, little information seems to be available on the relationship between salinity stress and auxin levels in plants and the role of auxin in alleviating salt stress. The variations in IAA content under stress conditions appeared to be similar to those of abscisic acid (Ribaut and Pilet, 1991). The increased level of IAA has reportedly been correlated with reduced growth (Ribaut and Pilet, 1994). Therefore, the reduction in plant growth under stress conditions could be an outcome of altered hormonal balance. Hence, their exogenous application provides an attractive approach to counter the stress conditions. However, Prakash and Prathapasenan (1990) reported that NaCl caused a significant reduction in IAA concentrations in rice leaves. In this experiment, GA₃ application during the salinisation period partly overcomes the effect of salinity on reducing IAA levels and this shows that salinity may influence hormone balances by affecting plant growth and development. There was also a significant reduction in IAA levels in rice five days after NaCl treatment (Nilsen and Orcutt, 1996). Salinity caused 75% reduction in IAA levels of tomato (Dunlap and Binzel, 1996). Sakhabutdinova et al. (2003) reported that salinity causes a progressive decline in the level of IAA in the root system of plants. Other researchers also reported that pre-sowing wheat seeds with plant growth regulators like IAA alleviated the growth inhibiting effect of salt stress (Sastry and Shekhawa, 2001; Afzal et al., 2005). In wheat seed germination decreased with increasing salinity level, while the adverse effect of salinity was alleviated by treatment of seeds with IAA or NAA (Balki and Padole, 1982; Gulnaz et al., 1999). In addition, Akbari et al. (2007) showed that application of auxin increased hypocotyls length, seedling fresh and dry weigh and hypocotyls dry weight of the three cultivars of wheat plants under salinity. As mentioned above further researches should be conducted to understand the real mechanism. Auxin stimulates the transcription of a large number of genes called primary auxin response genes. A large number of auxin-responsive genes have been identified and characterized from different plant species, including soybean, *Arabidopsis* and rice (Hagen and Guilfoyle 2002). These auxin-responsive genes have been classified into three gene families: auxin/indoleacetic acid (*Aux/IAA*), *GH3* and small auxin-up RNA (*SAUR*) gene families (Guilfoyle 1993). Liu et al, (2011) reported that auxin inhibits the outgrowth of tiller buds in rice (*Oryza sativa* L.) by downregulating *OsIPT* expression and cytokinin biosynthesis in nodes. However, the identification of novel genes involved in salt stress responses provides the basis for researchers to set further genetic engineering strategies to improve more stress tolerance cultivars (Zhu 2002).

Cytokinins (CKs)

Cytokinins (CKs) regulate several plant growth aspects and developmental processes, including cell division, apical dominance, chloroplast biogenesis, nutrient mobilization, leaf senescence, vascular differentiation, photomorphogenic development, shoot differentiation and anthocyanin production (Mok and Mok, 2001; Davies, 2004). Cytokinins

can also enhance resistance to salinity and high temperature in plants (Barciszewski et al., 2000). Seed enhancement (seed priming) with cytokinins is reported to increase plant salt tolerance (Iqbal et al., 2006a). CKs are often considered as ABA antagonists and auxins antagonists/synergists in various processes in plants (Pospisilova, 2003). It was hypothesized that cytokinins could increase salt tolerance in wheat plants by interacting with other plant hormones, especially auxins and ABA (Iqbal et al., 2006b). CKs retard senescence. having effect on membrane permeability to mono and divalent ions, and localized induction of metabolic sinks (Letham, 1978). They are generally considered to be antagonists of ABA, with the two hormones having opposing effects in several developmental processes including stomatal opening (Blackman and Davies, 1984), cotyledon expansion and seed germination (Thomas, 1992). A general view has emerged that during stress, a reduction of CK supply from the root alters the gene expression in the shoot and thereby elicits appropriate responses to ameliorate the effects of stress (Hare et al., 1997). Kinetin is capable to break stress-induced dormancy during germination of tomato, barley and cotton seeds (Bozcuk, 1981). Moreover, the observed reduction in endogenous cytokinins under stress conditions points towards the possibility that cytokinin levels could be a limiting factor under stress conditions. It can thus explain the fact that an exogenous application of kinetin resulted in increased growth of chickpea seedlings (Boucaud and Ungar, 1976). It was suggested that the decrease in CK content was an early response to salt stress, but that the effects of NaCl on salt-sensitive varieties is not mediated by CKs since the reduction in growth rate preceded any decline in CK levels (Walker and Dumbroff, 1981). It is generally accepted that cytokinins are produced in the root tips and developing seeds of plants (Zahir et al., 2001). They are translocated to the shoot, by xylem, from roots where they regulate development and senescence processes. However, the involvement of cytokinins in numerous important processes of plant growth and development has been demonstrated by exogenous applications (Arshad and Frankenberger, 1998). Increase in yield and yield components of rice may be discussed with the work of Mathew and Rayan (1995) and Hanada et al. (1994) who reported positive response of rice to cytokinin application. In a field trial, cytokinin application increased the yield of rice by 45.8% compared to control (Zahir et al., 2001). However, endogenous levels of zeatin-type CKs remained unaltered in both roots and leaves during salt-stress in the facultative halophyte *Mesembryanthemum crystallinum* (Thomas et al., 1992). Exogenous application of kinetin overcame the effects of salinity stress on the growth of wheat seedlings (Naqvi et al., 1982) and treatment of potato plants with kinetin prior to salt stress diminished salt-related growth inhibition (Abdullah and Ahmad, 1990). However, earlier studies reported that application of kinetin to bean plants during salinity stress exacerbated its effects (Kirkham et al., 1974). Addition of benzyl adenin (BA) inhibited growth during stress of a salt-sensitive variety of barley, but overcame the decline in growth rate, shoot/root ratio and internal CK content in a salt-tolerant variety (Kuiper et al., 1990). Kinetin acts as a direct free radical scavenger or it may involve in antioxidative mechanism related to the protection of purine breakdown (Chakrabarti and Mukherji, 2003). A possible involvement of genes in stress responses is often inferred from changes in the transcript abundance in response to a given stress trigger. An overview of the many changes in the transcript abundance of cytokinin genes in Arabidopsis in response to environmental factors was given elsewhere (Argueso et al., 2009). Functional analyses of

cytokinin receptor mutants in stress-response assays showed that all three cytokinin receptors of Arabidopsis act as negative regulators in ABA signaling and in the osmotic stress responses. For *CRE1/AHK4* cytokinin dependence of this activity was demonstrated (Tran et al., 2007). Cytokinin receptor genes of other species are regulated by changes in the osmotic conditions as well, indicating that their function in the osmotic stress response might be common although mechanistically not well understood (Merchan et al., 2007).

Gibberellic acid (GA)

Gibberellins (GAs) are generally involved in growth and development. They control seed germination, leaf expansion, stem elongation and flowering (Magome et al., 2004). Recently, elongated uppermost internode (EUI) is identified in rice, which encodes a cytochrome P450 monooxygenase and epoxidizes GA_1 and GA_4 in deactivation reaction (Zhu et al., 2006). GA metabolism and signaling (Sun and Gubler, 2004), tightly control the GA homeostasis. However, this homeostatic mechanism is still unclear. In addition, it has been long known that there is cross-talking between GA action and other hormones signaling or environmental stresses to control the plant growth and development, although the real mechanism remains unclear. Recently, the GA-promoted destabilization of DELLA proteins is modulated by environmental signals (such as salt and light) and other plant hormone signaling (such as auxin and ethylene), which reveals the mechanisms of this cross-talking at the molecular level (Achard et al., 2006). The biosynthesis of GAs is regulated by both developmental and environmental stimuli (Yamaguchi and Kamiya, 2000; Olszewski et al., 2002). Gibberellic acid (GA) accumulates rapidly when plants are exposed to both biotic (McConn et al., 1997) and abiotic stresses (Lehmann et al., 1995). In order to alleviate deleterious effects of salinity, different types of phytohormones have been used. Among them, gibberellins have been the main focus of some plant scientists (Basalah and Mohammad, 1999; Hisamatsu et al., 2000). For instance, gibberellic acid (GA_3) has been reported to be helpful in enhancing wheat and rice growth under saline conditions (Parasher and Varma, 1988; Prakash and Prathapasenan, 1990). Maggio et al. (2010) reported that GA_3 treatment in tomato reduced stomatal resistance and enhanced plant water use at low salinity. GA_3-priming-induced increase in wheat grain yield was attributed to the GA_3-priming-induced modulation of ions uptake and partitioning (within shoots and roots) and hormones homeostasis under saline conditions (Iqbal and Ashraf, 2010). Under saline conditions, seed germination has been improved by application of GA_3 and in this experiment, growth and grain yield of wheat were decreased with increasing salinity levels, but increased relatively by seed treatment with GA_3 (Kumar and Singh, 1996). In another study, wheat seeds, after treatment with various growth regulators including GA_3, showed highest percent germination when treated with 20 mg/l GA_3 (Nayyar et al., 1995). Free radicals induced lipid peroxidations inhibition by GA (Choudhuri, 1988). These results show that GA_3 application could improve salinity tolerance in crop plants grown under saline condition. In addition, GAs interacts with other hormones to regulate various metabolic processes in the plants. However, many conflicting theories have been put forward concerning their interactions (Yang et al., 1996; Van Huizen et al., 1997). It has recently been discovered in different species that the auxin (IAA) promotes GA biosynthesis (Wolbang et al., 2004). On the other hand, GA

application enhances the catabolism of ABA (Gonai et al., 2004). However, the mechanisms by which GA$_3$-priming could induce salt tolerance in plants are not yet clear. Salinity perturbs the hormonal balance in plants. Therefore, hormonal homeostasis under salt stress might be the possible mechanism of GA$_3$-induced plant salt tolerance (Iqbal and Ashraf, 2010).

Brassinosteroids (BR)

Brassinosteroids are a new group of phytohormones with significant growth promoting properties (Bishop and Yokota, 2001; Clouse and Sasse, 1998). Brassinosteroids are plant hormones with pleiotropic effects, as they influence diverse physiological processes such as growth, seed germination, rhizogenesis, senescence and leaf abscission (Sasse, 1997). In addition, BRs are implicated in plant responses to abiotic environmental stresses. The CPD gene of Arabidopsis encodes a cytochrome P450 protein (CYP90) that shares sequence similarity with mammalian steroid hydroxylases. Feeding experiments with different BRs indicate that CYP90 acts at the C-23 hydroxylation step in the BR biosynthetic pathway (Krishna, 2003). BR regulated stress response because of a complex sequence of biochemical reactions such as activation or suppression of key enzymatic reactions, induction of protein synthesis, and the production of various chemical defence compounds (Bajguz and Hayat, 2009). Exogenous applications of BRs under salinity have long been known to increase growth and yield in many economically useful plant species. In cereals, BRs promote the number of ears and in some cases also their length, and the number and weight of kernels per ear (Ali et al., 2008). In leguminous crops, the number of pods per plant and total seed yield increases after the application of exogenous BRs (Rao et al., 2002). Growth and seed yield of rapeseed plants are also promoted by their treatment with BRs (Hayat et al. 2000) and the same applications for seed yield in cotton (Ramraj et al., 1997). BRs removed the salinity-induced inhibition of seed germination and seedling growth in case of rice (*Oryza sativa*). BRs also restored the level of chlorophylls and increased nitrate reductase activity under salt stress. The activity of this enzyme plays a pivotal role in the supply of nitrogen and the growth and productivity of plants, especially in cereals (Bajguz and Hayat, 2009). In addition, Anuradha and Rao (2001) reported that Brassinosteroids considerably reduced the impact of salt stress on rice growth, restored pigment levels and increased the nitrate reductase activity. The effect of BR on barley leaf cell ultrastructure was examined under salt stress. Leaf segments were pre-incubated in either BR solution or water and then incubated in 0.5 M NaCl solution in the presence or absence of BR. BR had no effect on the leaf cell ultrastructure under normal conditions. However, damages imposed by salt stress on nuclei and chloroplasts were significantly reduced by BR treatment (Krishna, 2003). In another study, rice seeds soaked in water or 150 mM NaCl, in the presence or absence of BR, were tested for germination and seed growth. When the salt solution was supplemented with BR, the inhibitory effect of salt on germination was considerably reduced. The promotion of growth by BR under salt stress conditions was associated with enhanced levels of nucleic acids and soluble proteins (Anuradha and Rao, 2001). The present findings clearly demonstrate the ability of brassinosteroids to alleviate the inhibitory effects of salinity on germination, seedling growth and plant yield. However further studies are required to unravel the tolerance mechanism conferred by brassinosteroids in the case of salinity stress.

Jasmonates (JA)

Methyl jasmonate (MeJA) and its free-acid, jasmonic acid (JA), collectively referred to as jasmonates, are important cellular regulators involved in diverse developmental processes, such as seed germination, root growth, fertility, fruit ripening, and senescence (Wasternack and Hause, 2002). In addition, jasmonates activate plant defense mechanisms in response to insect-driven wounding, various pathogens, and environmental stresses, such as drought, low temperature, and salinity (Cheong and Choi, 2003). Jasmonic acid biosynthesis occurs in leaves and there is evidence of a similar pathway in roots. In addition, cellular organelles such as chloroplasts and peroxisomes are considered to be the primary sites of JA biosynthesis (Cheong and Choi, 2003). Sembdner and Parthier (1993) reported that induction of JA by wounding or pathogens can be attributed to the production of fatty acids by damaging cell membranes, which then metabolizes via lipoxygenase to JA. Allene oxide synthase (AOS) is an enzyme involved in JA synthesis. AOS was shown to be tightly linked with elevated JA content during the wound response in *Arabidopsis thaliana* (Laudert and Weiler, 1998). The expression of AOS genes is also activated by systemin, wounding, 12-oxophytodienoic acid and MeJA in tomato plants (Sivasankar et al., 2000). Another enzyme involved in JA synthesis is lipoxygenases (LOXs), where has been identified and localised within the chloroplasts (Feussner et al., 1995). Phospholipase D (PLD) has also been shown to trigger the release of linolenic acid and to stimulate JA biosynthesis (Creelman and Mullet, 1997). PLD activity has been linked with stress processes playing a main function in membrane deterioration, although there is enough evidence for its role in plant signal transduction (Wang, 1999). Jasmonic acid and its derivatives also respond to salinity (Wang et al., 2001). It has been reported that jasmonate treatments (or endogenous of these compounds) is accompanied by the synthesis of abundant proteins in response to abiotic stress, called JIPs (Sembdner and Parthier, 1993). It has been reported that JA levels in tomato cultivars changed in response to salt-stress and JA increase was observed in salt tolerant cultivar HF (Hellfrucht Fruhstamm) from the beginning of salinisation, while in salt sensitive cultivar Pera, JA level decreased after 24 h of salt treatment (Pedranzani et al., 2003). Kramell et al. (2000) found a rapid increase in endogenous JA content in barley leaf segments subjected to osmotic stress with sorbitol or mannitol; however, endogenous jasmonates did not increase when they were treated with a high NaCl concentration (Kramell et al., 1995). The changes of endogenous JA levels in rice plants under various salt stresses were investigated. Kang et al. (2005) reported that the concentrations of JA in salt-sensitive cultivar plants were lower than in salt-tolerant cultivar plants. In addition, MeJA levels in rice roots increased significantly in 200 mM NaCl (Moons et al., 1997). Therefore, high levels of JA in salt-tolerant plants accumulated after salt treatments can be an effective protection against high salinity. However, there seems to be little information about how salinity affects endogenous JA levels in plants. Kang et al. (2005) reported that post-application with exogenous JA can ameliorate salt-stressed rice seedlings, especially the salt-sensitive rather than the salt-tolerant cultivar. In addition, Sodium concentration dramatically decreased by exogenous JA application. On the contrary, uptake of major ions was partially increased by JA application. At same time, pre-treatment with JA reduced the inhibitory effect of high salt concentrations on growth and photosynthesis of barley (Tsonev et al., 1998). Exogenous JA application after salt

treatment may change the balance of endogenous hormones, such as ABA, which provides an important clue for understanding the protection mechanisms against salt stress (Kang et al., 2005). These results clearly demonstrate that exogenous JA may be involved in the defense not only during wounding and pathogen stress, but also during salt stress.

Salicylic acid (SA)

Salicylic acid is (SA) an endogenous growth regulator of phenolic nature, which participates in the regulation of physiological processes in plants such as growth, photosynthesis, nitrat metabolism, ethylene production, heat production and flowering (Hayat et al., 2010) and also provides protection against biotic and abiotic stresses such as salinity (Kaya et al., 2002). SA induces acidic pathogen-related (PR) genes and inhibits basic PR genes, whereas JA does the opposite (Wang et al., 2001). SA also reduced the synthesis of tomato proteinase inhibitors. Antagonistic interactions between SA and jasmonic acid affect the expression of PR protein genes in tomato (Thaler et al., 1999). Jumali et al. (2011) showed that most genes responding to acute SA treatment are related to stress and signaling pathways which eventually led to cell death. This include genes encoding chaperone, heatshock proteins (HSPs), antioxidants and genes involved in secondary metabolite biosynthesis, such as sinapyl alcohol dehydrogenase (SAD), cinnamyl alcohol dehydrogenase (CAD) and Cytochrome P450 (CYP 450). Several methods of application (soaking the seeds prior to sowing, adding to the hydroponic solution, irrigating, or spraying with SA solution) have been shown to protect various plant species against abiotic stress factors by inducing a wide range of processes involved in stress tolerance mechanisms (Horvath et al., 2007). The role of SA in defense mechanism to alleviate salt stress in plants was studied (Afzal et al., 2006; Hussein et al., 2007). The ameliorative effects of SA have been well documented including salt tolerance in many crops such as bean (Azooz, 2009), tomato (Tari et al., 2005) and maize (Gunes et al., 2007). Shakirova et al. (2003) reported that SA induced increase of the resistance of wheat seedlings against salinity. In addition, the application of 0.05 mM SA also improved plant growth after salt stress and caused the accumulation of ABA and proline in wheat. Sakhabutdinova et al. (2003) investigated the effect of salicylic acid (SA) on plant resistance against environmental stress factors. Treatment of wheat plants with 0.05mM SA increased the level of cell division within the apical meristem of seedling roots which increased the in plant growth. Exogenous application of salicylic acid enhanced the photosynthetic rate and also maintained the stability of membranes, thereby improved the growth of salinity stressed barley plants (El-Tayeb, 2005). SA added to the soil also had an ameliorating effect on the survival of maize plants during salt stress and decreased the Na^+ and Cl^- accumulation (Gunes et al., 2007). Lipid peroxidation and membrane permeability, which were increased by salt stress, were lower in SA treated plants (Horvath et al., 2007). SA treatment was accompanied by a transient increase in the H_2O_2 level. As seed treatment with H_2O_2 itself had an alleviating effect on the oxidative damage caused by salt stress in wheat plants (Wahid et al., 2007), it seems possible that SA may exert its protective effect partially through the transiently increased level of H_2O_2. Root drenching with 0.1 mM SA protected tomato (*Lycopersicon esculentum*) plants against 200 mM NaCl stress (Stevens et al., 2006). It increased the growth and photosynthetic rate of the plants, as well as the transpiration rate, stomatal conductance and reduced electrolyte leakage by 32%. The endogenous level of SA increased under salt stress in rice seedlings and the activity of the SA biosynthesis enzyme, benzoic acid 2-hydroxylase, was induced (Sawada et al., 2006). Treatment with SA essentially diminished the alteration of phytohormones levels in wheat seedlings under salinity. It was found that the SA treatment caused accumulation of both ABA and IAA in wheat seedlings under salinity. However, the SA treatment did not influence on cytokinin content. Thus, protective SA action includes the development of antistress programs and acceleration of normalization of growth processes after removal stress factors (Sakhabutdinova et al., 2003). The results obtained in the last few years strongly argue that SA could be a very promising compound for the reduction of the abiotic stress sensitivity of crops, because under certain conditions it has been found to mitigate the damaging effects of various stress factors in plants.

Triazoles (TR)

Triazoles are a group of compounds that have been developed to be used as either fungicides or plant growth regulators, although in various degrees they possess both properties (Fletcher et al., 2000). Triazoles can also protect plants against various environmental stresses, including anoxia, air pollutants, drought, salinity, extreme temperatures, and ultra violet light (Fletcher and Hofstra, 1988). Amongst the various triazoles developed as plant growth regulators, uniconazole was the most active stress protectant (Fletcher and Hofstra, 1990; Fletcher et al., 1986). However, its commercial use in agriculture is limited by its residual properties in both soil and plant tissues. Therefore, recent studies have focused on paclobutrazol which is an effective protectant of chilling damage in cucumber seedlings (Whitaker and Wang, 1987). It has been shown that triazole compounds may counteract the effect of salinity e.g., in sunflower and mungbean seedlings it has been observed that the pretreatment of seeds with LAB 150978 (a triazole compound) counteracted the inhibitory effect of salinity on root growth, but it inhibited hypocotyls growth (Saha and Gupta, 1993). Paclobutrazol treatment reduced shoot elongation and leaf length giving thicker vegetative tissues in wheat (Kraus et al., 1995). Paclobutrazol also protects wheat and corn against extreme temperatures, where these effects appears and are associated with enhanced activity of free radical scavenging systems (Kraus and Fletcher, 1994). Although there is substantial evidence about the effects of triazoles on plants, but the information about the role of triazoles in alleviating salt stress in crops is not so much.

Conclusion

It can be concluded that increasing salinity is associated with decreases in auxin, cytokinin, gibberellins and SA in the plant tissues and an increase in ABA and JA. Changes in hormone levels in plant tissue are thought to be an initial process controlling growth reduction due to salinity. Therefore, NaCl-induced reduction in the plant growth can be mitigated by application of plant growth regulators.

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