Abstract
Phytohormones are chemical substances that induce physiological responses in plants in minute concentrations. Apart from the classical five phytohormones viz., auxins, gibberellins, cytokinins, ethylene and abscisic acid, there are other well-known phytohormones like brassinosteroids, methyl jasmonates, salicylic acid, strigolactones etc., that have a profound role during abiotic stress tolerance. Plants are prone to various abiotic stresses like heat, chilling, freezing, drought, flooding, oxidative, salt, allelochemicals, radiation, light, wind, heavy metals stresses etc. Among the various abiotic stresses in plants, salt stress is an important aspect that hinders growth, metabolism and final yields of plants. The roles of above mentioned phytohormones which can alleviate the salt stress are slowly unfolding. The present review deals with the role of the phytohormones on the alleviation of salt stress in plants.

Key words: Phytohormones, Salt stress.

Introduction
Plants are frequently prone to different types of abiotic stresses such as drought, chilling, heat, or salinity stress (1). Other abiotic stress factors such as cold, irradiation, or light stress are also known to adversely affect the crops (2). Salinity usually occurs through natural or human-induced processes which results in the accumulation of dissolved salts in the soil water which in turn inhibits plant growth (3). Salts in the soil water usually inhibit the metabolism by reducing the ability of the plant to take up water which is called as the osmotic or water-deficit effect. The excessive amounts of salt entered into the plant in the transpiration stream will result in the injury to cells and also drastically affect the transpiration. Soil salinity is one of the main factors that limits the spread of plants in their natural habitats and is an ever-increasing problem in arid, semi-arid and also in irrigated regions (4).

Phytohormones have an important role to play in mediating plant responses to abiotic stress. Plants have developed over the years a variety of physiological and biochemical mechanisms through which they survive under the stressful conditions (5). Phytohormones are produced naturally by plants and are essential for physiological responses in plants like formation of leaves and flowers, elongation of stems, development, ripening of fruits etc. The five classical phytohormones are auxins, gibberellins, cytokinins, abscisic acid and ethylene. Plant growth regulators are employed in the modern agriculture to boost the growth and yield of plants. The application of plant growth regulators (auxins, gibberellins, cytokinins, abscisic acid and ethylene) in agriculture started in the early 1930s in the United States of America and the practices are still continuing world-wide. These phytohormones were used for protecting the plants against...
various abiotic stresses. Among the many, the role of abscisic acid on the plants during salt stress has been extensively studied.

In the recent times, other phytohormones like brassinosteroids, methyl jasmonates, salicylic acid, and strigolactones have been shown not only to regulate plant growth and development but also to protect plants from various abiotic stresses like high temperature, low temperature, salt, high light, weak light, drought as well as flooding, heavy metals, herbicide stress, pesticide stress and even biotic stresses. The present article summarizes multiple roles of phytohormones play during salt stress tolerance in various plants.

**Effect of auxins on salt stress tolerance:** Auxins help plants to grow and promote the formation of apical meristems and are responsible for root differentiation. The role of auxins in overcoming various abiotic stresses has been discovered. Salinity stress can influence indole-3-acetic acid (IAA) homeostasis due to the alterations in IAA metabolism and distribution (6). It was observed that a membrane-bound NAC transcription factor NTM2 is a molecular link, and incorporates auxin signal into salt stress signaling during seed germination of *Arabidopsis thaliana*, thus providing a role of auxin in modulating seed germination under high salinity (7).

**Effect of gibberellic acid (GA) on salt stress tolerance:** Gibberellic acid (GA) is the phytohormone that plays pivotal roles in growth and metabolism of plants especially cell elongation. A central role for the GAs in the response to abiotic stresses viz., cold, salt and osmotic is becoming increasingly evident and reduction of GA levels and signaling has been shown to contribute to plant growth under abiotic stresses (8). Gibberellic acid (GA$_3$) reduced NaCl-induced growth inhibition in rice (*Oryza sativa* L. cv. Nipponbare) in a concentration-dependent manner, including the length of root tissue by regulating some salt-regulated proteins like glutamyl-tRNA reductase, enolase, salt stress-induced protein (SALT protein), a hypothetical protein OsJ_014066, putative chaperonin 21 precursor, another hypothetical protein OsJ_025258, ribulose bisphosphate carboxylase, isoflavone reductase-like protein and phosphoglucomutase, providing a new insight to reveal the modulating effect of GA$_3$ on salt stress in rice (9). GA$_3$-priming-induced increase in grain yield of two spring wheat (*Triticum aestivum* L.) cultivars, namely, MH-97 (salt intolerant) and Inqlab-91 (salt tolerant). This increase in yield is attributed to the GA$_3$-priming-induced modulation of ion uptake and partitioning (within shoots and roots) and hormone homeostasis under saline conditions (10). The application of GA$_3$ in combination with CaCl$_2$ mitigated the adverse effect of salinity stress by increasing the growth, physio-biochemical parameters, proline, glycine betaine content, activities of superoxide dismutase and catalase in linseed (*Linum usitatissimum* L.) (11). GA$_3$ ameliorated the adverse effects of salt stress and restored normal growth in terms of plant length and plant fresh/dry biomass and development in other crop plants like soybean also (12).

**Effect of cytokinins (CKs) on salt stress tolerance:** Cytokinins (CKs) are the phytohormones that regulate plant growth and development and play prominent roles in cell division via a complex network of CK signaling. CKs have been studied for their roles in mitigating various abiotic stresses in plants. The functional analyses with CK-deficient plants to provide direct evidence that CKs negatively regulate salt stress signaling was reported (13). Cytokinins play a significant role during several plant growth and developmental processes including cell division, chloroplast biogenesis, apical dominance, leaf senescence, vascular differentiation, nutrient mobilization, shoot differentiation, anthocyanin production, and photomorphogenic development (14). It was reported that it increases salinity tolerance via increased proline contents in egg plant under exogenous application of CKs (15). Principal component analysis revealed that leaf xylem cytokinins (CKs) control leaf growth and photosystem II efficiency (Fv/Fm) and thus crop
productivity in tomato plants (cv Boludo F1) grafted onto a recombinant inbred line (RIL) population derived from a *Solanum lycopersicum* x *S. cheesmaniae* cross grown under moderate salinity (75 mM NaCl) for 100 days under greenhouse conditions (16). Enhancing the root cytokinin synthesis modified both shoot hormonal and ionic status, thus ameliorating salinity-induced decreases in growth and yield of tomato (*Solanum lycopersicum* L.) plants (17). Cks and CK signaling regulated the plant adaptation to stress by His–Asp phosphorelay, an important component of the CK signal transduction pathway, triggering CK-responsive genes under salt stress (18).

**Effect of ethylene on salt stress tolerance**: Ethylene plays a prominent role in fruit ripening as well as senescence. The ability of ethylene to alleviate various stresses in plants is one of the main ongoing research topics. The application of ethylene improved plant salt tolerance by improving chlorophyll a/b, photosystem II function (Fv/Fm), redox state and retention of K+ in shoots and roots of *Arabidopsis* wild type (Col-0), ethylene insensitive mutants (ein2-5 and ein3-1) and constitutive triple response mutant (ctr1-1) also (19). Ethylene plays an important role in salt-tolerant (Indent-1) and salt-sensitive (Red Ball) genotypes of tomato subjected to salt stress by regulating plant responses viz., chlorophyll content index (CCI), stomatal conductance and ion homeostasis (20).

**Effect of abscisic acid (ABA) on salt stress tolerance**: Abscisic acid (ABA) is a sesqui terpenoid phytohormone discovered in 1960s for its role in promoting leaf abscission-and seed dormancy. ABA plays a major role during many stages of the plant life cycle, including seed development and dormancy, and mediates plant responses to various environmental stresses and also acts as endogenous signal molecules responsible for inducing abiotic stress tolerance in plants (21). ABA has been proposed to play an important role in stress responses and/or adaptation (22). Under saline conditions, there is a rapid and significant accumulation of ABA which is crucial to plant protective mechanisms (23). The biosynthesis and redistribution of ABA is one of the fastest responses of plants to abiotic stresses including salt stress, causing stomatal closure, thereby reducing water loss via transpiration and eventually restricting cellular growth (24). Two varieties of maize, SRO3 (salt resistant) and Lector (salt sensitive) exhibited significantly increased concentrations of ABA (25). Exogenous application of ABA at 100 µM prior to and during the salt-stress period induced salt tolerance in both the salt-susceptible (LPT123) and the genetically related salt-resistant (LPT123-TC171) rice lines. It enhanced the survival rate and triggered proline (an osmoprotectant) accumulation earlier than that by salt-stress alone, supporting a role for induction of proline biosynthetic pathway gene expression in proline accumulation (26). ABA plays an important role in salt-tolerant (Indent-1) and salt-sensitive (Red Ball) genotypes of tomato subjected to salt stress by regulating plant responses like chlorophyll content index (CCI), stomatal conductance and ion homeostasis (20). ABA is a key endogenous messenger in plant responses to salt stress and it unfolded a unique hormone perception mechanism where binding of ABA to the ABA receptors RCARs/PYR1/PYLs lead to inactivation of type 2C protein phosphatases such as ABI1 and ABI2 and these protein phosphatases seem to function as coreceptors and their inactivation launches SNF1-type kinase action which targets ABA-dependent gene expression and ion channels (27). Thus, ABA plays a vital in transducing the signals and in triggering the downstream responses.

**Effect of brassinosteroids (BRs) on salt stress tolerance**: Brassinosteroids (BRs) are a new type of polyhydroxy steroidal phytohormones with significant growth-promoting influence (28). Mitchell and his co-workers (29) discovered BRs, but were later extracted from the pollen of *Brassica napus* L. (30). The widely used bioactive BRs, brassinolide (BL), 24-epibrassinolide (24-EpiBL), 28-homobrassinolide (28-HomoBL),
castasterone (CS) and 24-epicatasterone (24-EpiCS). BRs played important roles in monitoring the stress-protective properties in plants against a number of abiotic stresses like low temperature/chilling, freezing, salt, high temperature/heat stress, water/drought/water logging, heavy metals and biotic stresses (31). BRs confer salt tolerance to plants by mitigating its negative effects on the physiological, biochemical and molecular processes in plants (32). Exogenous application of BRs offered tolerance to salinity by altering stress responses in rice variety Pusa Basmati-1 (33). BRs enhanced the physiological mechanisms for enhancing the salt tolerance in oilseed rape plants (34). Further, the ameliorative effect of BRs on germination of cucumber seeds in the presence of sodium chloride was reported (35). The alleviating effects of brassinolides (BLs) on cucumber seedlings grown under NaCl stress was also studied (36). BLs improved the physiological characteristics of rice (Oryza sativa L.) under different salinity levels (37). BL improved the growth, yield and chemical composition of berseem (Trifolium alexandrinum L.) grown in saline soils (38). Further, it was reported that BL not only alleviated the salt stress but also increased the antioxidant activity of cowpea plants (Vigna sinensis) subjected to saline conditions (39).

24-epibrassinolides (24-epiBL) enhanced the physiological and genetic changes in two varieties of pepper under salt stress conditions (40). They have increased the growth and alleviated the deleterious effects induced by salt stress in pea (Pisum sativum L.) and treatment with 5 μM epiBL detoxified the stress generated by sodium chloride and significantly improved the growth, the level of pigment parameters, green pod yield and pod protein in Phaseolus vulgaris L. (41-42). 24-EpiBL regulated photosynthesis, antioxidant enzyme activities and proline content of Cucumis sativus under salt stress (43-44). Further, it was reported that supplementation of 24-EpiBL trigger physiological and biochemical responses for the salt stress mitigation in Cucumis sativus L. (45). Seed treatment and foliar application of 24-epiBL to lettuce (Lactuca sativa L. var. Crispa) mitigated the negative impact of salt stress by enhancing the growth, chlorophyll and mineral contents (46). 24-epiBL application ameliorated the salt-induced oxidative stress in eggplant (47) and also the adverse effects of salt stress on the stomatal conductance, membrane permeability, leaf water content, and ionic composition in strawberry (48). 24-EpiBL also restored the nitrogen metabolism of pigeon pea under saline stress (49). It played a pivotal role in pea protein tyrosine phosphorylation after salinity treatment (50) and alleviated the salt-induced inhibition of productivity by increasing nutrients, compatible solute accumulation as well as enhancing antioxidant system in wheat (Triticum aestivum L.) (51). Supplementation of 24-epiBL played pivotal roles on the hormonal status of wheat plants under sodium chloride stress (52).

28-homoBL alleviated the negative impact of salt stress on Vigna radiata by enhancing the rate of photosynthesis, fluorescence and antioxidant system (53). Foliar application of 28-homoBL mitigated salinity stress in Brassica juncea by increasing its photosynthetic efficiency (54). BR-analouges improved the genotypes of Oryza sativa L. grown under salinity stress (55). It was reported that a BR-analogue prevented the negative effect of salt stress on ethylene synthesis in lettuce plants (56). However, the exact mechanism how epibrassinolides or 28-homobrassinilides alleviate the salt stress and improve the antioxidant capacity of plants under salt stress is not clear.

**Effect of jasmonates (JAs)/methyl-jasmonate (MeJA) on salt stress tolerance**: Methyl jasmonate (MeJA) or its deesterified acid, jasmonic acid (JA) is a lipid-based hormone that regulates a wide spectrum of processes in plants, ranging from growth and photosynthesis to reproductive development. In particular, JAs play pivotal roles for plant defense against herbivory and plant responses to poor environmental conditions and other kinds of abiotic and biotic challenges. Foliar application of methyl-
jasmonate (MeJA) mitigated the salinity stress of broccoli plants (Brassica oleracea L. var. Italica) by enhancing plant dry weight, leaf CO₂ assimilation, and root respiration (57). However, the molecular events leading to salt stress in presence of MeJA or JAs have not yet been elucidated.

**Effect of salicylic acid (SA) on salt stress tolerance:** Salicylic acid (SA) acts as an endogenous signal molecule that is responsible for inducing abiotic stress tolerance in plants. It plays a major role in the regulation of plant growth, development, and interaction with other organisms and defense responses to environmental stresses (21, 58-59). It was observed that, SA is not essential for germination under normal growth conditions, but it plays a promotive role in seed germination in Arabidopsis thaliana under high salinity by reducing oxidative damage (60). Exogenous application of SA led to increased salt tolerance in seedlings of pistachio (59). When mungbean (Vigna radiata L.) cultivar Pusa Vishal plants grown with 50 mMNaCl were sprayed with 0.1, 0.5, or 1.0 mM SA, it mitigated the negative impact of salt stress by increasing nitrogen, phosphorus, potassium (N, P, K), and Ca²⁺ content, and increased the activities of antioxidant enzymes, glutathione content, photosynthesis, and final yield (61). Application of SA mitigated the negative effect of salt stress in plants and improved the physiological, biochemical and molecular events associated with plant growth and development (32). Supplementation of SA improved the biochemical parameters of wheat (Triticum aestivum L.) subjected to salinity stress (62). Ameliorative effects of SA in mitigating the phytotoxicity of NaCl stress in Zea mays L. seedlings by regulating growth traits, content of photosynthetic pigments, proline, relative water content (RWC), electrolyte leakage percent (EC%), antioxidative enzymes and leaf anatomy (63) were noticed. Exogenous application of SA to pearl millet (Pennisetum glaucum (L.) R. Br.) seedlings alleviated salt stress by increasing the length (plant and root), fresh and dry weights as well as glycine betaine and total soluble carbohydrates (64). Application of SA to cucumber seedlings protected them from NaCl-induced stress by increasing the levels of sugars like glucose, fructose, raffinose and stachyose which act as osmotic agents or nutrients and as metabolic signals (65). It was reported that 0.1, 0.5, and 1.0 mM SA alleviated 50 mMNaCl-induced salinity stress in two cultivars of mustard (Brassica juncea L.) viz., Alankar (salt-tolerant) and PBM16 (salt-sensitive) plants by increasing nutrients content, photosynthetic and growth characteristics, and activities of superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR) (66). SA mitigated the toxic effect of salinity stress on tomato (Lycopersicum esculentum Mill.) by regulating sugar, protein and proline contents (67). However, the molecular events leading to the mitigation of salt stress has not yet been unraveled.

**Effect of strigolactones (SLs) on salt stress tolerance:** Strigolactones (SLs) were originally isolated from plant root exudates as germination stimulants for root parasitic plants of the family Orobanchaceae, including witchweeds (Striga spp.), broomrapes (Orobanche and Phelipanche spp.), and Alectra spp., and so were regarded as detrimental to the productivity of plants. SLs are suggested to have other biological functions in rhizosphere communications and in plant growth and development. It was proposed that plants increased strigolactone production in arbuscular mycorrhizal (AM) symbiosis which alleviated salt stress in lettuce plants by increasing plant biomass, stomatal conductance and efficiency of photosystem II (68). It was reported that stigmasterol applied as seed treatment not only alleviated the drastic effect of salt stress but also improved the quality and yield in flax plants (69). SL positively rescued Arabidopsis thaliana SL-deficient and SL-response mutants subjected to high salinity stress by increased leaf stomatal density relative to wild-type and slower abscisic acid (ABA)-induced stomatal closure (70).
Conclusions

Salinity is one of the major abiotic stresses that limit plant growth and productivity in many areas of the world due to increasing use of poor quality of water for irrigation. Plant adaptation or tolerance to salinity stress involves complex physiological, metabolic, and molecular pathways or gene networks. It is an established fact that phytohormones under salinity stress play critical roles in modulating physiological responses that eventually lead to the adaptation of plants. However, it is not clear how different phytohormones alleviate the salt stress in plants. We need to develop hormonal mutants for all different classes and then only it would be possible for us to unravel the mechanisms associated with salt stress alleviation.

References


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