

Salinity Stress Alleviation Using Phytohormones to Plant Responses and Arbuscular Mycorrhizal Fungi: A Review

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ABSTRACT

Salinization of soil is a serious land degradation problem and is increasing steadily in many parts of the world, particular in arid and semiarid areas. Salinity is often recognized as excess of sodium ions (sodicity) that imparts life threatening consequences in plant due to mal-textured soil hindered porosity and aeration leads to physiological water deficit. Mingling with other edaphic or environmental factors viz. precipitation, temperature, flooding, soil profile, water table exaggerates the catastrophe synergistically. Improper irrigations system, leaching fraction added with land clearing and deforestation have been marked as the major cause. Phytohormones are known to play vital roles in the ability of plants to acclimatize to varying environments, by mediating growth, development, source/sink transitions and nutrient allocation. These signal molecules are produced within the plant, and also referred as plant growth regulators. It described the potential role of different phytohormones and their balances against salinity stress and summarized the research progress regarding plant responses towards salinity at physiological and molecular levels. We emphasized the role of abscisic acid, indole acetic acid, cytokinins, gibberellic acid, salicylic acid, jasmonates and ethylene in mediating plant responses and discussed their crosstalk at various baseline pathways transduced by these phytohormones under salinity. The significance of arbuscular mycorrhizal fungi alleviation of salt stress and their beneficial effects on plant growth and productivity. Although salinity can affect negatively arbuscular mycorrhizal fungi, many reports show improved growth and performance of mycorrhizal plants under salt stress conditions. These positive effects are explained by improved host plant nutrition, higher K⁺/Na⁺ ratios in plant tissues and a better osmotic adjustment by accumulation of compatible solutes such as proline, glycine betaine, or soluble sugars. Arbuscular mycorrhizal plants also improve photosynthetic- and water use efficiency under salt stress. Arbuscular mycorrhizal plants enhance the activity of antioxidant enzymes in order to cope with the reactive oxygen species generated by salinity. The regulation of these genes allows mycorrhizal plants to maintain a better water status in their tissues. Gene expression patterns suggest that mycorrhizal plants are less strained by salt stress than non-mycorrhizal plants. In contrast, scarce information is available on the possible regulation by the arbuscular mycorrhizal symbiosis of plant genes encoding Na⁺/H⁺ antiporters or cyclic nucleotide-gated channels.

Key word: Salinity stress, Abiotic stress, Plant growth regulators, Phytohormones, Salinity stress tolerance and Arbuscular mycorrhizal fungi

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INTRODUCTION

Salinity is one of the most important abiotic stresses, limiting crop production in arid and semi-arid regions, where soil salt content is naturally high and precipitation can be insufficient for leaching⁶⁷. According to the FAO Land and Nutrition Management Service¹⁷, over 6% of the world's land is affected by either salinity or sodicity which accounts for more than 800 million ha of land. Saline soils are defined by Ponnamperna⁴⁶, as those contain sufficient salt in the root zone to impose the growth of crop plants. However, since salt injury depends on species, variety, growth stage, environmental factors, and nature of the salts, it is difficult to define saline soils precisely. The USDA Salinity Laboratory defines a saline soil as having an electrical conductivity of the saturation extract (EC_c) of 4 dS m⁻¹ or more. EC_c is the electrical conductivity of the 'saturated paste extract', that is, of the solution extracted from a soil sample after being mixed with sufficient water to produce a saturated paste. The most widely accepted definition of a saline soil has been adopted from FAO¹⁸, as one that has an EC_c of 4 dS m⁻¹ or more and soils with EC_c's exceeding 15 dS m⁻¹ are considered strongly saline.

Phytohormones, often regarded as plant growth regulators in literature refer to the compounds derived from plant biosynthetic pathways that can act either locally (at the site of their synthesis) or transported to some other site within plant body to mediate growth and development responses of both under ambient and stressful conditions⁴⁴. Growth and development in the sessile plants is regulated in a coordinated fashion by the activity of several phytohormones like abscisic acid (ABA), gibberellins (GA), ethylene (ETHY), auxins (IAA), cytokinins (CKs), and brassinosteroids (BRs), which control many physiological and bio-chemical processes. However, in recent years, new compounds like polyamines, nitric oxide (NO) and strigolactone have also been added to this list²². These hormones may act either close to or remote from their sites of synthesis to regulate responses to environmental stimuli or

genetically programmed developmental changes. Phytohormones thus have a vital role in mediating plant response to a biotic stress, by which the plant may attempt to escape or survive the stressful conditions and may result in reduced growth so that the plant can focus its resources on withstanding the stress. A biotic stresses often lead to alterations in production, distribution or signal transductions of growth as well as stress hormones, which may promote specific protective mechanisms¹⁴. Indeed, perception of a stress signal triggers the signal transduction cascades in plants with phytohormones acting as the base line transducers²⁶. Worldwide, soil salinity has adversely affected about 30 % of the irrigated and 6 % of total land area⁸, with a resultant monetary loss of 12 billion US\$ in agricultural production⁵⁸. Soil salinization is one of major stress affecting more than 831 million hectares of the agricultural lands worldwide¹⁶. Increased incidence of salinity on arable lands suggests the need of a better understanding of the plant tolerance mechanisms in order to sustain crop productivity by modulating growth conditions to the best possible extent. Inhibition of growth and development, reduction in photosynthesis, respiration and protein synthesis in sensitive species have been reported under salinity^{42,63,28}. Excessive generation of reactive oxygen species (ROS) such as superoxide anion, hydrogen peroxide and the hydroxyl radicals, particularly in chloroplasts and mitochondria is an important indication of salinity induced oxidative damage in plants³⁹. To rectify damaging effects of ROS, plants employ antioxidant enzymes to protect nucleic acid, proteins and membrane lipids. Disruption of membrane structure and permeability, metabolic toxicity and damage to ultrastructures due to ROS, and attenuated nutrients are the factors that initiate more catastrophic events in plants subjected to salinity stress. Recent studies mainly focused on understanding the mechanisms of salt tolerance in plant along with general consequences of its harmful effects^{42,10,63}, and control of ionic homeostasis and osmotic shock.

Plants, in their natural environment are colonized both by external and internal microorganisms. Arbuscular mycorrhizal fungi (AMF) are ubiquitous among a wide array of soil microorganisms inhabiting the rhizosphere. These fungi constitute an important integral component of the natural ecosystem and are known to exist in saline environments²¹. The proportion of vascular plant species forming AM is commonly overestimated⁶², probably as a result of the low proportion of species and environments surveyed. Although AMF exist in saline soils, the growth and colonization of plants may be affected by the excess of salinity, which can inhibit the growth of microbes due to osmotic and/or toxic effects of salts³³. AM symbiosis has been demonstrated to increase resistance to soil salinity in a variety of host plants such as maize, clover, tomato, cucumber, and lettuce⁴⁸. Although it is clear that AM fungi mitigate growth reduction caused by salinity, the mechanism involved remains unresolved. So far, studies on salt stress tolerance in mycorrhizal plants have suggested that AM plants grow better due to improved mineral nutrition and physiological processes like photosynthesis or water use efficiency, the production of osmoregulators, higher K⁺/Na⁺ ratios and compartmentalization of sodium within some plant tissues^{54,21}. In this review, we present a comprehensive analysis of nutritional, biochemical, physiological, and molecular changes that occur in plants when colonized by AM and subjected to salt stress.

Causes of salinity

1. Natural cause

Most of the saline sodic soils are developed due to natural geological, hydrological and pedological processes. Some of the parent materials of those soils include intermediate igneous rocks such as phenolytes, basic igneous rocks such as basalt, undifferentiated volcanic rocks, sandstones, alluvium and lagoonal deposits⁶⁶. Climatic factors and water management may accelerate salinization. In arid and semi-arid lands evapo-transpiration plays a very important role in the pedogenesis of saline and sodic soils.

2. Anthropogenically induced salinity

Secondary salt affected soils are those that have been salinized by human caused factors, mainly as a consequence of improper methods of irrigation. Poor quality water is often used for irrigation, so that eventually salt builds up in the soil unless the management of the irrigation system is such that salts are leached from the soil profile. Szaboles⁶⁰. estimated that 50% of all irrigated schemes are salt affected.

Deforestation: It is recognized as a major cause of salinization and alkalinization of soils as a result of the effects of salt migration in both the upper and lower layers. Deforestation leads to the reduction in average rainfall and increased surface temperature²⁷. Top thin soil rapidly gets eroded in the absence of soil green cover. Without the trees there to act as a buffer between the soil and the rain, erosion is practically inevitable. Soil erosion then leads to greater amounts of run-off and increased sedimentation in the rivers and streams. The combination of these factors leads to flooding and increased salinity of the soil^{12,27}.

1. The effect of salinity on plants

Salinization severely affects the agricultural productivity. The disastrous effects of irrigation-induced soil salinization in the Runn of Kachh represent amongst the most extreme examples in India. In agricultural land water-logging and salt accumulations affect plant growth adversely to reduce potential crop production. Plants can be killed in the advanced stages and the land rendered unusable. The salinization of agricultural land at extensive scale causes massive economic loss at the global level.

Salinity directly and indirectly affects the environment by inducing changes in vegetation cover and physical and chemical soil properties. Consequently, loss of biodiversity, shrinking of wildlife². and ecosystems disruption lead to loss of ecosystem resilience³ that affect local climate, water and mineral cycles. Salts in the soil water may inhibit plant growth for two reasons: (i) the presence of salt in the soil solution reduce the ability of the plant to take

up water, and this leads to reduction in growth rate. This is referred to as the osmotic or water deficit effect of salinity (physiological drought). (ii) If excessive amount of salt enters the plant in its transpiration stream there will be injury to cells in the transpiring leaves and this may cause further reductions in growth. This is called the salt specific or ion-excess effect of salinity²³. According to Dubey¹³. and Yeo salt causes both ionic and osmotic effects on plants and most of the known responses of plants to salinity are linked to these effects. The general response of plants to salinity is reduction in growth^{47,20}.

2. Phytohormones and abiotic stresses

Abscisic acid (ABA)

Sharma *et al.*, reported that Abscisic acid has been to play an important role in stress responses and/or adaptation as ABA mediated signaling is known to regulate the expression of salt-responsive-genes under salinity. It plays a significant role during many stages of the plant life cycle, including seed development and dormancy, and mediates plant responses to various environmental stresses. The ABA is often regarded as the stress hormone as it acts as the major internal signal enabling plants to survive adverse environmental conditions. It is now well thought-out as a plant stress hormone because different stresses tend to induce ABA synthesis. It acts as an endogenous messenger to regulate the plant's water status. It plays an important role in regulating plant water status and growth, through guard cells as well as by induction of genes. Zhang *et al.*⁶⁷, reported that plant's exposure to salinity is known to make a proportional increase in ABA concentration that is usually associated with leaf or soil water potential. Concentration of ABA increases in roots, when root continues their growth, which suggests that these tissues may have different responses to the restricted ABA concentration either in endogenous form, or when exogenously applied. Hartung *et al.*, argued that pH changes play a key role in the ABA redistribution in leaf tissues and control the stomata at times when no significant changes in ABA concentration are detected in

the xylem. ABA in conjunction with other phytohormones regulates control of root growth, stress perception triggered expression of responsive genes and proteins (dehydrins and late embryogenesis abundant proteins) as well accumulation of compatible solutes under stress¹⁵. Rapid and significant accumulation of ABA under salinity is pivotal to plant protective mechanisms and synchronizes with expression of early salt induced genes in roots⁴².

2.1: Auxins (IAA)

The IAA is the first identified plant hormone; nevertheless, its biosynthetic pathway at the genetic level has remained unclear¹⁵. The IAA plays a key role in regulating plant growth related processes like cell elongation, vascular tissue development and apical dominance, Although IAA has widely been acknowledged for its implications in plant growth and development yet, it can govern plant growth response to stress or coordinate growth under stressed conditions¹⁴. IAA also responds to salinity in crop plants and a link between auxin signaling and salt stress has been established. They suggested that under salinity, seed germination is modulated by a membrane bound transcription factor (NTM2) that incorporates auxin signal in seed germination. Park *et al.*, reported that salt signaling pathway is mediated by over expression of IAA30 gene of NTM2. Nevertheless, little information is available on the relationship between IAA levels in plants under salinity, and the role of IAA in mitigating salt stress. Abiotic stresses, like salinity can influence IAA homeostasis due to alterations in IAA metabolism and distribution. Moreover, generation of ROS in response to abiotic stresses may also influence auxin response.

2.2: Cytokinins (CKs)

Naturally occurring CKs are N6-substituted adenine derivatives containing either aromatic or isoprenoid side chain. This phytohormone 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 photo-morphogenic development¹⁵. The CKs are also known to alleviate the adverse effects of salinity on plant growth. Seed priming with CKs was reported to increase plant tolerance to salinity stress²⁹. These authors inferred that decreased concentration of ABA in plants developing from kinetin primed seeds was possibly responsible for alleviation of salt stress in wheat. Application of CKs can reverse leaf and fruit abscission that are induced by ABA or water stress. Contrary to ABA that inhibits germination; CKs release seed dormancy. They act as ABA antagonists and IAA antagonists/synergists in various plant processes and help alleviating salinity stress³⁰. Decrease in CKs level has been suggested as an early response to salt stress; nevertheless, influence of salinity on salt-sensitive variety of tomato was not mediated by Cks since reduction in growth preceded any decline in Cks⁶⁴. During plant growth and development, CKs are master regulators, and were recently shown to control plant adaptation to salt stress. Wu *et al.*, reported increased salinity tolerance via increased proline contents in egg plant under exogenous application of CKs. Under salinity, CKs play an important role by acting as an intermediate in the demonstration of protective role of epibrassinolide and methyl jasmonate in wheat. Inhibition of K-shuttle activity limits CKs transport under salinity and decreased level of CKs have been reported in root and shoot of resistant barley plants just after addition of 65 mM NaCl to the nutrient solution. Nevertheless, adverse influence of salinity on growth of salt-sensitive plants preceded the lowering of CKs in levels suggesting genotypic specificity. The concentrations of zeatin (Z), zeatin riboside (ZR), isopentenyl adenine (iP), and isopentenyl adenine (iPA) in shoots and roots of barley cultivars decreased significantly after exposure to salinity³⁷. In salt-sensitive variety of barley, addition of benzyl adenin inhibited its growth, but in a salt tolerant variety it overcame the negative impact on growth rate, shoot/root ratio and internal CKs content³⁷.

Chakrabarti and Mukherji⁷, reported that Kinetin acts as a direct free radical scavenger or it may also involve in the anti oxidative mechanism that are related to the safety of purine breakdown. In stress responses, a possible involvement of genes is often inferred from changes in the transcript abundance in response to a given stress trigger. In stress-response assays functional analyses of CKs receptor mutants exhibited that all three CKs receptors of Arabidopsis act as negative regulators in ABA signaling and in the osmotic stress responses.

2.3: Ethylene (ETHY)

ETHY is a gaseous hormone that regulates plant growth and development. It has been considered as a stress hormone and is induced by many stresses, however, in salt stress its role is equivocal⁶⁵. It was reported that lesser ETHY production was related with salt tolerance. Contrarily, higher production of ETHY was regarded as an indicator of salt tolerance in rice. According to Pierik *et al.*⁴⁵, ETHY has long been known as a growth inhibitor, but it can also promote growth. Achard *et al.*¹, suggest that in Arabidopsis, ETHY signaling promotes salt tolerance. An experiment conducted by Cao *et al.*⁶, suggests that ETHY receptor function leads to salt sensitivity and ACC appears to suppress this salt sensitivity, inferring that for salt tolerance needs ETHY signaling.

2.4: Jasmonates (JA)

The JA are vital cellular regulators involved in diverse plant developmental processes, including seed germination, callus growth, primary root growth, flowering, formation of gum and bulb, and senescence⁴³. Biosynthesis of JA occurs in leaves and there is proof of a similar pathway in roots. As well, cellular organelles such as chloroplasts and peroxisomes are considered to be the main sites of JA biosynthesis⁹. These are known to activate the plant defense responses to various biotic and abiotic stresses⁴⁰. Exogenous application of JA to plants resulted in induction of pathogenesis- or stress-related genes⁴¹.

2.5: Salicylic acid (SA)

The SA plays a critical role in the regulation of plant growth, development, and interaction with other organisms and defense responses to environmental stresses⁴. Its role is evident in seed germination, glycolysis, flowering, fruit yield, ion uptake and transport, photosynthetic rate, stomatal conductance, transpiration, thermo-tolerance, senescence and nodulation. Major role of SA in plant is thought to be the regulation of responses to biotic stresses; however, a large body of literature now suggests that SA is also involved in responses to several abiotic stresses including salt stress¹⁵. It was found that an inhibition in the chlorophyll biosynthesis in sorghum plants because of salt stress. Positive effects of SA on photosynthetic capacity could be attributed to its stimulation of Rubisco activity and pigment contents.

3. Salinity effects on arbuscular mycorrhizal fungi

Salinity, not only affects negatively the host plant but also the AMF. It can hamper colonization capacity, spore germination and growth of fungal hyphae⁵⁹. Colonization of plant roots by some AMF is reduced in the presence of Sodium chloride. It is probably due to the direct effect of Sodium chloride on the fungi³³. indicating that salinity can suppress the formation of arbuscular mycorrhiza⁶¹. The varying levels of AM colonization under saline conditions may also be related to the different behaviour of each AM fungal species, even in similar ecosystems³⁶ or to the influence of different environmental conditions. In the presence of Sodium chloride, germination of spores is delayed rather than prevented. The rate of germination and maximum germination of AMF spores may also depend on the salt type. According to Juniper and Abbott, the different salts NaNO₃ and Na₂SO₄ with similar osmotic potentials impart differential effects on the rate and maximum germination of spores. They attributed the difference to a higher concentration of Na⁺ in the latter. Jahromi *et al.*³¹, studied in vitro the effects of salinity on the AM fungus, *Glomus intraradices*. They observed that there was no

significant difference in hyphal length and BAS between control (no salt) and 50 Mm Sodium Chloride, though there was a significant decrease in hyphal length and the number of BAS at 100 Mm Sodium Chloride.

3.1: Arbuscular mycorrhizal effects on plant biomass and nutrient uptake

Several studies investigating that the role of AMF in protection against salt stress have demonstrated that the symbiosis often results in increased nutrient uptake, accumulation of osmoregulator compounds, and increase in photosynthetic rate and water use efficiency, suggesting that salt stress alleviation by AMF results from a combination of nutritional, biochemical, physiological, and molecular effects. However, this positive effect on plant development depends on the AMF species involved³⁸. Hence, mycorrhization was found to increase the fitness of the host plant by enhancing its growth. Several researchers have reported that AMF-inoculated plants grow better than non-inoculated plants under salt stress⁵⁷. For instance, Hajiboland *et al.*²⁴, have recently reported that although high salinity reduced dry matter production by two tomato cultivars, in all treatments mycorrhizal plants grew better than nonmycorrhizal plants. The mycorrhizal association is well known to increase host nutrient acquisition, particularly phosphorous element. The improved growth of mycorrhizal plants in saline conditions is primarily related to mycorrhiza-mediated enhancement of host plant P nutrition²⁵.

3.2: Biochemical changes

The best characterized biochemical response of plant cells to osmotic stress is accumulation of some inorganic ions such as Na⁺ and compatible organic solutes like proline, glycine betaine, and soluble sugars¹⁹. These compatible solutes can accumulate to high levels without disturbing intracellular biochemistry⁵, protecting sub-cellular structures, mitigating oxidative damage caused by free radicals, and maintaining the enzyme activities under salt stress.

CONCLUSIONS

Upcoming years in future may incorporate the integrated efforts considering planning of soil and site specific requirements of deploying strategies discussed above enhance the yield considering sustainable agriculture incorporating resistant varieties within the reach of farmers. Attempts have sought and being sought to look for future food security at physiological and biochemical level. However an integrative and feasible management still required to meet with presently available plant preventive strategies for 'salt amalgamated with stress hindered production'. In present article we summarized the regulatory circuits of different phytohormones and cross talks amongst ABA, indole ABA, CKs, GA, SA, BRs, JA, ETHY and TR at physiological on exposure to salinity. We found that all these phytohormones are directly or indirectly are involved in modulating plant responses to salt stress and their relative balances changes in response to salinity due to crosstalk between these phytohormones. The arbuscular mycorrhizal symbiosis under salinity is a promising field that should shed further light on new mechanisms involved in the enhanced tolerance of AM plants to salt stress. Indeed, these studies would allow understanding if the arbuscular mycorrhizal symbiosis affects sodium uptake, distribution, and compartmentation within the plant cell. Overall, these investigations should open new research lines aimed at obtaining maximum benefit from the AM symbiosis under salinity or other osmotic stress conditions.

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