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Review Article

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Role of Some Phytohormones in Plant Response to Salt Stress

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Abstract

Plants are extremely subjected to environmental stress, which includes drought, low or high temperatures, and salt stress. The most common environmental stress factor is salinity, primarily in arid and semi-arid regions. Salinity stress is the most limiting factor for seed germination and plant productivity; therefore, most plants are susceptible to adverse effects because of the high concentration of salt in the soil, which affects plant growth and productivity. Phytohormone, considered an endogenous defense factor under stress conditions, has an important role in plant growth and survival, particularly under abiotic stress. Phytohormones influence a wide spectrum of processes in plants in both normal and stressful environments. The phytohormones stimulate plant responses to stress conditions, such as jasmonic acid, while there are other phytohormones that include Proline, Gibberellic acid, Cytokinins and Auxins. Exogenous application of plant growth regulators could be an alternate strategy to improve salt stress tolerance. The use of auxin or gibberellin has been shown to mitigate the violent effects of abiotic stresses on seed germination, plant growth, and productivity. Furthermore, proline induces plant tolerance against various abiotic stresses by increasing their endogenous levels and their intermediate enzymes in plants. Moreover, exogenous application of proline may be a good approach to reducing the unfavorable effects of salinity stress on plants.

Keywords: Auxin; Cytokinins; Gibberellin; Phytohormones; Proline; Salinity

Abbreviations: ACC: 1-Amino Cyclopropane 1-Carboxylic Acid; ACO: ACC Oxidase; ACS: ACC Synthase; ATPS: ATP-Sulfurylase; AVG: Amino Ethoxy Vinyl Glycine; BR: Brassinosteroids; Ca: Calcium; CAT: Catalase; CBL: Calcineurin B-Like Protein; CK: Cytokinins; EBL: Epibrassinolide; GA: Gibberellins; GS: Glutamine Synthase; GSA: Glutamate-Semialdehyde; IAA: Indole Acetic Acid; JA: Jasmonate; MDA: Malondialdehyde; MeJA: Methyl Jasmonate; N: Nitrogen; NiR: Nitrite Reductase; NO: Nitric Oxide; NR: Nitrate Reductase; NRA: Nitrate Reductase Activity; OAT: Ornithine-Delta-Aminotransferase; P5C: Pyrroline-5-Carboxylate; P5CDH: P5C Dehydrogenase; P5CR: P5C Reductase; P5CS: 1-Pyrroline-5-Carboxylate Synthetase; PDH: Proline Dehydrogenase; POD: Peroxidase; POX: Proline Oxidase; ROS: Reactive Oxygen Species; S: Sulfur; SNP: Sodium Nitroprusside; SOD: Superoxide Dismutase; SOS: Salt Overly Sensitive.

Introduction

Climate change affects soil salinity, particularly in arid and semi-arid regions, due to low precipitation, which has negative impacts on plant growth and development. Fluctuations in climate conditions increase changes in the composition and structure of various metabolite processes. Proteins and RNA molecules that precede signal transduction or stress acclimation events in plants [1]. Furthermore, abiotic stresses affect plant metabolism, physiology, and morphology processes and cause disturbances in various cellular pathways, particularly genetic regulation. One of these significant changes in environmental conditions is salinity. There is about 20% of the cultivated area, and nearly half of the world's irrigated lands are affected by salinity [2]. Salinity is considered one of the main threats that affect plant growth, seedling development, inhibiting seed germination, inhibiting enzyme activity, synthesis of DNA, RNA, and protein, and mitosis, as well as minimizing biomass accumulation [3,4].

In high salinity conditions, plants either decrease their growth and developmental programs in response to stress due to the effects of specific ions on metabolism or reverse water relations [5]. Therefore, under rising salinity, plants use different strategies to adapt to stress conditions, reducing adverse impacts on plant development, in addition to stress conditions pushing plants to regulate growth and development to complete their life cycle [3]. Phytohormones (both endogenous and exogenous applications) mediated the plant response and played an important role in acclimating plants to both biotic and abiotic unfavorable conditions [6].

Plant growth regulators play a paramount role in the growth, flowering, and fruit set of different crops, especially gibberellic acid and naphthalene acetic acid, which promote fruit set and decrease fruit drop in many fruit species and varieties under stress conditions [7].

Biochemical mechanisms are considered one of the major adaptation techniques. Plant phytohormones are involved as essential components in various metabolic processes in the plant. While the interaction between different phytohormones causes different results, it also plays an important role in plant responses to different abiotic stresses.

The main phytohormones that stimulate plant responses to various stresses are jasmonic acid (JA), salicylic acid (SA), and abscisic acid (ABA), while there are other phytohormones that include triazole (TR), proline, gibberellic acid (GA), cytokinins (CKs), Auxins, Indole-3-acetic acid (IAA), abscisic acid (ABA), and ethylene (ETHY) [8].

Phytohormones play essential roles in enhancing plant adaptation to harsh environmental conditions, such as soil salinity, drought, and rising temperature. They also stimulate the plant to grow under stress. There is crosstalk (antagonisms or associations) amongst different phytohormones depending on the growth stage, severity, and duration of stress conditions [9]. In addition, it has an effective role in controlling growth and nutrient uptake to reduce the negative impacts of salinity on plant growth and complete its life cycle under stress conditions [10].

It is generally clear that the repressive effect of salinity on seed germination and plant growth could be related to a decline in endogenous levels of phytohormones. It is suggested that phytohormones play an important role in stress responses and adaptation, thus, some researchers have used plant growth regulators to reduce the adverse effects of salinity stress [11].

However, plants should manufacture low-molecular-weight non-enzymatic antioxidants like proline to save cells and tissues from oxidative injury, as well as enzymatic antioxidants including peroxidase, superoxide dismutase, ascorbate peroxidase, and catalase to safeguard against oxidative stress [12].

Objectives of this Review

The present work focuses on increasing our understanding of the role of phytohormones in salinity tolerance and improving plant growth and development under salinity stress.

Through discussion of the influence of salinity stress on plant growth and crop productivity, explore the role of phytohormones in reducing the harmful effects of salinity on plant growth and reproduction. In addition, this work further highlights the importance of using phytohormones to develop salinity-tolerant crops in light of the future impact of predicted climate change through an exploration of 200 references and a discussion of 90 references related to the main subject.

Salinity

In arid and semi-arid regions, salinity is one of the most significant abiotic threats influencing plant development and output. Salt problems are more severe in hot, dry weather than in cold, damp weather, moreover, salinity conditions reduce the formation of dry matter that is required for various growth processes [13].

Regularly, the rates of photosynthesis are lower in plants exposed to salinity due to the negative effect of salinity on photosynthesis, this would furthermore lead to restrictions on water availability and an imbalance in nutrient uptake by plants with inhibition in seed germination due to ionic disturbance, osmotic, and toxic effects [14]. While salt-tolerant plants (halophytes) involved fewer Na^+ and Cl^- transport to leaves, were able to preserve lower Na^+/K^+ proportions in their shoots, and developed higher facilities to isolate ions into the cytoplasm or cell wall [15]. However, plant species vary in their sensitivity or tolerance to salinity stress, most of the economic plants are glycophytes, which are sensitive to salt stress. For instance, citrus is generally classified as a salt-sensitive crop because physiological trouble and decreasing growth and fruit yield can occur at relatively low-salinity levels [16].

Both osmotic stress and ionic toxicity are due to salt stress. Salt stress reduces osmotic potential which leads to osmotic stress, which limits the absorption of water from the soil, while ionic stress is caused by the over-accumulation of toxic salt ions within plant cells. Both abiotic stresses and nutrient deficiency affect the various physiological statuses and are responsible for adverse effects on the growth and development of glycophytes crops [17].

Soil salinity affects plant growth through reducing the osmotic potential of the soil solution, interfering with nutrient uptake, inducing ionic toxicity, and associating nutrient imbalances [18]. There are major variations in the morphology and anatomy of plants grown on saline soils, rising salinity reduces the economic productivity of various crops by inhibiting the germination of seeds, decreasing seedling flushing, and fluctuating flowering and fruit set, which affect total yield and fruit quality [19].

High salinity forces ionic and osmotic stresses on plants. In earlier stages of plant responses, a rapid osmotic phase is caused by the osmotic pressure of high salt concentrations in the soil. After salt accumulates above a threshold level in the plant, a slower ionic phase occurs because of the toxic effects of salt ions [20].

The decrease in leaf area, stomatal conductance, and chlorophyll levels in the plants and the generation of reactive oxygen species (ROS) in all these aspects are due to salinity stress [21].

The reduction of photosynthetic ability under salinity is due to stomata closure, loss of chlorophyll, and the deactivation of specific enzymes, which are involved in the synthesis of photosynthetic pigments. The decrease in chlorophyll contents is mainly due to the demolition of chlorophyll biosynthesis, chlorine accumulation, and reductions in magnesium, iron, and manganese [22]. Furthermore, increasing salt concentrations in the soil reduce plant water absorption capacity, hurt metabolic processes, and affect negatively osmotic balance, nutrient absorbance, hydraulic conductivity, net photosynthetic rate, and intercellular CO2 concentrations, all of which inhibit plant growth and development [23].

Phytohormones in Plant

Recent studies have revealed that different signaling networks, especially those involving phytohormones, ROS, and RNS, arrange many abiotic stress responses [15,24]. Phytohormones are endogenous chemical components that act at the location of synthesis or translocate to different tissues to induce plant growth and enhance crop yield both quantity and quality under different abiotic stress. There are main phytohormones produced in plant tissue (Figure 1).

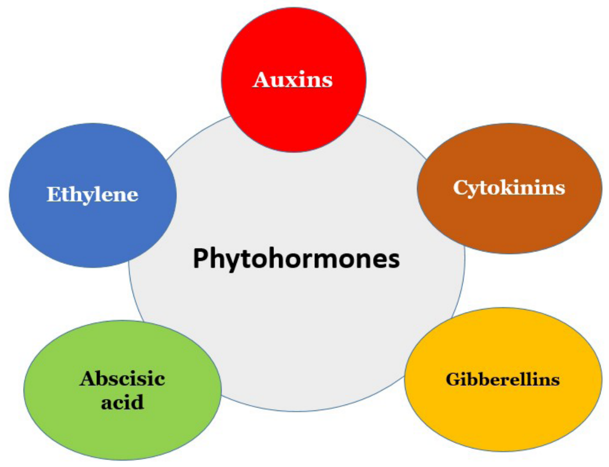

Figure 1: Main phytohormones produced in plant tissue.

Furthermore, phytohormones are paramount for plants as they use them to regulate their own processes and are implicated in plant interactions with their environment. Phytohormones modulate physiological responses in plant tissues to stimulate adaptation to various abiotic stresses [13].

In recent years, there has been more attention given to the role of phytohormones in parallel with rising salinity stress in different regions worldwide. At salinity stress, various signaling pathways such as phospholipids, plant hormones, and calcium ions are coordinately activated to organize an osmotic modulation or homeostasis regulating plant growth and development [3]. In addition, plant hormonal regulation and calcium ion-dependent modification of enzymatic activities are independently integrated into the stress signaling pathways [5].

Phytohormones play a critical role in plants' capacity to respond to abiotic stresses by regulating a variety of adaptive restraints. They frequently modify gene expression quickly by stimulating or inhibiting the degradation of transcriptional regulators via the ubiquitin-proteasome system [25].

How Plant Hormones Mediate Salt Stress Responses

Rising salinity is considered one of the main abiotic stresses that restrict the growth of numerous crops. Plants developing various adaptation tactics to cope with salinity stress, which including reduce water loss by regulate stomata closing and minimizing growth to maintain plant survival under stress [15,26].

Phytohormones are endogenous substances that regulate plant response and balancing plant growth under salt stress. Phytohormones have an important role in adapting growth and defense trade-offs under stress [27]. There is a significant role for phytohormones in the regulation of plant responses to salinity stress and adaptive plant growth under stress, therefore, exogenous application of phytohormones to plants ameliorates the adverse effect of stress condition [6].

Jasmonates (JA)

Jasmonic acid (JA) is one of the endogenous plant hormones that are synthesized by plants and play a significant role in adaptable plant responses under stress conditions. JA or the related substances (methyl jasmonate, MeJA) are involved in various physiological processes in plants [28].

Under salinity stress, plants synthesize more JA and activate JA signals. Therefore, the exogenous application of JA alleviates abiotic stress tolerance in the plant, it regulates plant growth under salt stress by physiological mechanisms, improving antioxidant enzyme activity, increasing organic solutes such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), APX, and chlorophyll B contents, and reducing H2O2 concentration, consequently improving plant growth under salinity conditions [29]. JA is involved in varied physiological processes, growth, and development, which include root system formation, fruit production, fruit ripening, enhancing oxidative resistance, and interaction with other phytohormones to increase plant tolerance for abiotic stress [30]. In addition, JA has an important role in plant defense against infection by pests, particularly herbivorous insects and diseases like necrotrophic pathogens [31].

Role of Jasmonic Acid in Plant Under Salinity Stress: The essential role of JA as a phytohormone to increase plant tolerance and acclimatize abiotic stress is well documented. JA plays numerous roles in plant cells to regulate adaptation to environmental stresses, therefore, under salinity stress, JA levels increase in plant cells and there is more JA signaling [31].

Previous research has shown that exogenous treatments of JA alleviate salinity stress by improving plant antioxidant responses, enhancing seed germination, stimulating plant growth, and increasing the survival rate of seedlings under abiotic stress Sheteiwy MS, et al. [32], Ghassemi-Golezani, et al. [33] on soybean; Hussain, et al. [34] on rice; Sheyhakinia, et al. [35] on roselle; Ahmad, et al. [36] on maize seedlings.

Furthermore, foliar application of Proline and jasmonic acid enhanced crop yield and improved the fruit quality of the Manzanillo olive tree [37]. In addition, the application of humic acid and jasmonic acid alleviates the adverse effects of salinity on Forage Sorghum by improving antioxidant enzymes [38].

The main effect of JA on plant growth under environmental stresses include:

- Reduce Na cations that enter the cells.
- Enhancing the glycine betaine and soluble protein content.
- Increase antioxidant enzyme activity.
- Improve membrane stability index.
- Increase leaf water content.
- Increase antioxidant enzyme activation.
- Enhancing seed germination.
- Alleviate the negative effects of salinity stress on plant growth.
- Increasing plant acclimation under improper conditions.
- Decreased the amount of herbicide residue.

Cytokinin (CK)

Cytokinin (CK) is one of the main five phytohormones produced in plant tissue, CK has numerous functions in plant metabolism, and it has a significant role in enhancing plant response to various adverse conditions and increasing plant tolerance of both abiotic and biotic stress as well. CKs have the opposing influence of ABA and act as antagonists of ABA in numerous physiological aspects in plants [39]. Cytokinin considered a master phytohormones regulate different processing in plants, particularly cell division, flower bud initiation and differentiation, and delaying senescence. Moreover, CKs synthesis in the root system and transported to the vegetative part through the xylem, under abiotic stress some aerial organs synthesize CK, particularly young tissues, and the influence on root CKs occurs via transport basipetal phloem CK [40]. Cytokinins are vital components in plants for numerous biological functions, like flowering, cell division, seed germination, regulating apical dominance, translocating of nutrients, chloroplast development, senescence, and acclimatization to environmental stresses [41].

Under salinity conditions, the synthesis of cytokinin stimulates metabolisms in plants particularly hormonal and ionic status. Maintaining cytokinin homeostasis is essential for plants experiencing salt stress to enhance plant growth, as well as plant adaptation to abiotic stresses [42].

Furthermore, exogenous application of CKs enhances plant growth and reduces the adverse effect of salinity on the growth and productivity of various crop [33] and Latef, et al. [43] on faba bean; Azadi, et al. [44] on black cumin plants; Feng, et al. [45] on apple seedlings; Sa, et al. [46] on papaya plants). In addition, cytokinin improves the yield crop of rice under abiotic stress conditions by regulating floral primordial activity and modulating rice grain yield [47]. Furthermore, CK stimulates photosynthesis and enhances flower production [48].

Cytokinin-mediated stimulation of ethylene production appears to be of particular importance during water stress. CKs are indispensable for the temporal and differential biosynthesis of SA and JA, which in turn serve as endogenous inducers for distinct classes of PR proteins. CK plays an important role in the regulation of stress-related genes in different plants under adverse environmental conditions.

There is more evidence from previous work that CK has more responses to various stresses. There are important functions for CK in plant responses to biotic stress and improving photosynthesis under salinity stress [49].

In addition, under abiotic stress, Cytokines stimulate ethylene production and have a significant role in the synthesis of endogenous hormones like SA and JA Brenner WG, et al. [50] on Arabidopsis, and Joshi, et al. [47] on Rice. Maintaining biosynthesis and cytokinin balance is very important for plant growth and acclimatization of plants to abiotic stresses. Therefore, CK levels in plants are considered an indicator of salt tolerance particularly in various crops [51].

There is crosstalk with other phytohormones particularly JA, and there is a correlation between Cytokinin and Jasmonic acid. JA inhibits the activity of oxidative enzyme-like cytokinin oxidase (CKX) and cytokinin oxidase/dehydrogenase, consequently, increasing the level of Cytokinin [52].

There are emerging roles of cytokinin as follow:

- Priming agent for meristems growth.
- Regulator of plant Defense growth.
- Required factor against biotic stress.
- Improve photosynthesis.
- Increase flowering of tomato plants.
- Increase seed yield of sensitive rice varieties.

Auxin

It is certainly true that auxin plays numerous roles in plant growth and development. Local concentration gradients of auxin (indole-3-acetic acid [IAA]) are thought to instruct the positioning of organ primordia and stem cell functions and to direct cell division, expansion, and differentiation. It also plays a role in plant responses to biotic and abiotic stresses. Furthermore, it has been shown that auxin affects several plant stages, including root hair, stem cell formation, and elongation, and has a great and important function in plant growth under salinity stress [53].

It was noticed that the lower levels of active auxin that exist in Arabidopsis mutants exhibit a reduction in plant growth and show enhanced resistance to environmental stresses. Auxin has also been implicated in seed germination under salinity conditions [54].

Numerous references indicate the involvement of auxin in response to salinity stress in plants, but little information is available regarding the mechanisms of salt stress regulation. Moreover, the pathway of auxin signaling is closely related to the early seedling developmental processes of plants [55].

Higher auxin concentrations caused by overexpression of the auxin biosynthetically correlated YUCCA3 (YUC3) gene, which encodes an auxin biosynthetic enzyme, caused hypersensitivity to salinity stress [56]. Interestingly, high salt stress greatly remodeled root architecture by altering auxin accumulation and its redistribution. So, the redistribution of auxin maxima formation in plant tissues is associated with decreased growth [57].

Foliar application of indole-3-acetic acid improved the growth characteristics of salinized fava bean due to increasing the uptake of some nutrients like K^+, $Ca2^+$, and $Mg2^+$ ions, accumulation of free amino acids, soluble sugars, and soluble proteins, as well as the activity of many enzymes such as superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase [58].

Exogenous applications of auxin compounds such as indole-3-acetic acid or indole-3-butyric acid before grafting could promote the growth characteristics of grafted cucumber seedlings and their performance after transplanting in saline conditions [59].

Under high salinity conditions, exogenous application of auxin further suppressed the reduced germination rate of Arabidopsis seeds as compared with control. In contrast, the auxin effects disappeared in the ntm2-1 mutant. These observations indicate that ntm 2-1 is a molecular link that incorporates auxin signal into salt stress signaling during seed germination, providing a role for auxin in modulating seed germination under high salinity [60].

Foliar application of indole-3-acetic acid (IAA) or 6-benzyl adenine (BA) combined with salt stress, creates a major change in the plant protein profile with various intensities. There are better adaptations and increased saline tolerance, which was confirmed by the exhibited new protein profiles under both saline and treated with IAA or BA conditions. The IAA-applied plants produced more new protein bands than BA, indicating that IAA has more ability to rescue the faba bean from salt stress and adapt to the salt stress condition [58].

Ghibellines

It is known that gibberellins are plant growth regulators that induce various physiological restraints in plants. Generally, gibberellins are phytohormones implicated in the growth and developmental processes of plants like seed germination, leaf expansion, photo-morphogenesis, stem elongation, and flowering [61].

Plant hormones have a role in regulating the expression of genes, especially abscisic acid, gibberellic acid, and mRNA is strongly induced by high salinity stress and the possible relation between the contents of endogenous GA3 and the acquisition of stress protection [62].

It was noticed that bioactive gibberellins are rapidly decreased when plants are exposed to both biotic and abiotic stress. Moreover, under environmental stress, there is a crosstalk between gibberellin action and other hormones signaling the dominance of plant growth and development. However, the underlying molecular mechanism remains to be demonstrated [63].

Seed germination is one of the plant developmental processes affected by salinity stress. The presence of NaCl during embryogenesis affects the growth balance, moreover, soil salinity suppresses seed germination either by magnificent osmotic stress or by decreasing gibberellin biosynthesis [64].

Under salinity stress, gibberellins act as promoters for plant growth, which can decrease seed dormancy, improve plant gene expression, enhance the synthesis of hydrolase, repair injured cell membranes, and increase seed vitality [65]. Gibberellic acid partially alleviates the felled effect of salinity by increasing wheat vigor, anti-oxidative enzyme activity, and the accumulation of osmolytes [66]. On the contrary.

Application of gibberellin promotes cell division and cell elongation of stressed seedlings and reduces inhibition effects of NaCl, which increases seedling growth on Okra seedlings, moreover, exogenous gibberellic acid application enhanced seedling emergence percentage, seedling growth, and relative water content [67] on Okra seedlings; Yousif, et al. [68] on sorghum. Gibberellic acid significantly affected emergence percentage and alleviated the adverse impact of salinity stress by improving water uptake and increasing cellular membrane plasticity [69], which can stimulate the activity of amylase in cotyledons and the conversion of insoluble starch into soluble sugars for seed germination and promote radical growth [70].

Furthermore, the application of gibberellin caused an increase in the germination percentage of *Tithonia rotundifolia* Black and pulled off the preventive effects of salinity stress on germination. This may be due to the involvement of GA3 in the activation of cytological enzymes, along with an increase in cell wall plasticity and improved water absorption in papaya plants [69].

The exogenous application with GA3 enhanced seed germination rate under salinity stress. In addition, increasing salt stress levels reduced the growth and grain yield of the crop but increased comparatively with seed treatment with gibberellin [71].

Moreover, gibberellic acid treatments increased the development of plant attributes. The fact that they increase the amino acid content in the embryo of olive cultivars and stimulate the synthesis of hydrolytic enzymes required for the digestion of endospermic starch when seeds renew growth at seed germination [72].

In addition, under salinity stress, the decrease in mineral nutrient uptake may due to Na^+ induced blockage or reduced activity of the transporters, resulting in an ionic imbalance of K^+, Ca^{2+}, and Mg^{2+} as compared to Na^+. Whereas, treating two barley cultivars with gibberellin caused a reduction in sodium ion contents [73].

It has been reported that DELLA family proteins, pioneer gibberellin negative regulators, are basically implicated in the modification of environmental signals and other plant hormone signaling pathways Under abiotic stress, the prominent role of GA in arrangement plant growth is due to DELLA protein-mediated growth restraints on exposure to abiotic stress [74].

Exposure to salinity stress induced a decrease in endogenous levels of bioactive GAs, which coincided with a higher accumulation of DELLA proteins. Moreover, among the different types of plant hormones implicated in the alleviation of deleterious effects on salt stress, gibberellin has been especially important in crops [75]. Moreover, under salt stress, the morphological characteristics of barley were suppressed in all plant growth parameters, while this repression was significantly mitigated after gibberellin application [73].

Proline

Proline is an amino acid with numerous functions, and it is also a signaling molecule that works as a plant growth regulator by triggering cascade signaling processes. Moreover, proline is the major compound that protects cells by stabilizing proteins and cellular membranes. Proline surpasses as a popular osmolyte in plants and gets up-regulated against various stresses [76]. Thus, many plants synthesize amino acids and amides such as proline, alanine, glutamine, asparagine, and quaternary ammonium bases, as well as different sugars, polyols, and cyclites as a non-specific reactions to stress from excess salinity, drought, or frost [77]. Plants suffering from salinity or drought stress in their root zone respond physiologically by regulating their metabolism to adjust to negative conditions. Therefore, plants accumulate organic solutes particularly low molecular weight materials like proline, betaine, polyols, polyamines, and sugar.

Among the metabolic responses to salt stress, the synthesis of compatible osmolytes and non-toxic organic compounds is responsible for the osmotic equilibrium between the cytoplasm and various cell compartments. In many plants, free proline accumulates in response to the prescription of a wide range of biotic and abiotic stresses. Proline controls the expression of a number of genes related to antioxidant enzymes in salt conditions. One gene, 1-pyrroline-5-carboxylate synthase, is responsible for up-regulating the stress-stimulated accumulated of proline under salt stress [78].

Most efforts have been made to consideration of the ability of proline to mediate osmotic adjustment, stabilize subcellular structures, and scavenge toxic oxygen derivatives. High levels of proline synthesized during stress conditions also preserve the NAD $(P)^+$/NAD(P)H ratio [3].

Proline biosynthesis, degeneration, and its accumulation in plants are regulated by various abiotic stresses and salinity has great importance [79].

There is a negative relationship between salt tolerance and proline accumulation. Consequently, accumulation of proline in *Pancratium maritimum* L. may contribute to cellular adaptation to salt stress or be the result of metabolic changes caused by salinity [80]. Furthermore, it was noticed that proline biosynthesis happened because of the disturbance in cell homeostasis or fluctuation in the use of photosynthesis leftover for proline biosynthesis at the expense of plant growth [81].

Plants have developed various saving mechanisms to maintain normal cellular metabolism and prohibit cellular constituent damage including the accumulation of ions and osmolytes such as proline [82].

One of the efficient saving mechanisms of plants against hyperosmotic stress is the increased endogenous level of compatible solutes like proline, ectoine, glycine betaine, and sorbitol, in addition, there is a positive correlation between the endogenous levels of proline and increasing salinity levels [42].

Proline provides tolerance against different abiotic stresses by increasing their endogenous levels and their intermediate enzymes in plants, therefore, the exogenous application of proline increases the endogenous level of proline in bean (*Phaseolus vulgaris* L.) [83].

Many plants accumulate a higher level of proline in contrast to other amino acids when exposed to the high salt content in the soil. When the salt has been accumulated in the vacuole proline acts as a mediator of osmotic adjustment stabilizing, to save cell membranes, several enzymes, and metabolic machinery [84].

Moreover, when plants are subjected to saline conditions, proline plays a very important role in preserving their growth. Therefore, proline contributes to osmotic adjustment, stabilization, and saving the membrane integrity and macromolecules from the harmful effects of salinity and as a hydroxyl radical scavenger. Furthermore, it was suggested that, in saline conditions, proline accumulation in leaves occurred to protect chlorophyll content and turgor to save the photosynthetic activity [85].

Moreover, exogenous application of proline enhances the crop tolerance against different abiotic stresses especially salinity by protecting them from the severe effects of ROS [42]. Foliar application of proline at the rate of 100 mg.l increased plant height, the number of branches as well as fresh and dry weights of leaves of Beta vulgaris L [86]. Exogenous application of proline at the rate of 25 mM increases in Vicia faba growth characters [87]. All proline levels (3, 6, or 9 mM) caused a significant increase in shoot length, number of leaves and branches per plant, and shoot fresh and dry weights per plant of both lupine varieties compared with control [88].

In addition, plants resort to promoting their endogenous level of proline with continuously increasing levels of salinity [89]. Moreover, the exogenous application of proline mitigates the opposite effects of salt by decreasing the accumulation of Na^+ and Cl^- in plants [90].

Conclusion

Plant growth regulators such as auxin and gibberellin improve salt tolerance and mitigate salt stress by stimulating plant growth and development. Recent advances in the research, which is dependent on protein profile, indicated that the disappearance of polypeptide bands in response to stress and foliar applications of phytohormones such as IAA showed a new protein band and newly expressed protein that might diminish the adverse effects of salt stress and increase better adaptation to plants. Moreover, under salinity stress, exogenous application of gibberellins promotes plant growth by improving water uptake, decreasing seed dormancy, activating antioxidant enzymes, and improving plant gene expression. All of these alleviated the negative effects of salinity stress on plants.

In addition, salt stress imposes severe effects on plant growth and productivity by interrupting normal metabolic processes and proline may mitigate the adverse impact of salt by reducing osmotic stress that consequently safeguards the membrane integrity and its function. The exogenous application of proline could offer a simple and economical approach for farmers to decrease the crop loss risk in salt contaminated land. Otherwise, more studies are needed at physiological and molecular levels to gain deeper prudence in understanding the interaction of NaCl persuades oxidative stress and mitigation mechanism of exogenous proline in plants.

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