



REVIEW ARTICLE

Polyamines and Plant Growth Regulators: The Dynamic Duo Alleviating Salinity Stress in Plants a review

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Abstract

Soil salinity is a critical issue that affects plants and leads to decreased productivity worldwide. When soil salinity occurs, it causes the production of reactive oxygen species (ROS), oxidative burst, and ionic imbalance in plant cells. These factors can result in plant death, reduced growth, and low crop yields. To overcome this problem, polyamines such as putrescine, spermine, and spermidine play a crucial role in plant defense against abiotic stress conditions. Polyamines are organic compounds that are naturally present in plants and are involved in various physiological processes such as growth, development, and stress response. Studies have shown that the exogenous application of polyamines can help plants withstand abiotic stress caused by soil salinity. This is because polyamines can regulate the expression of stress-responsive genes and activate various antioxidant enzymes that help scavenge ROS and reduce oxidative stress. Moreover, polyamines also help to maintain ion homeostasis in plant cells and prevent toxic ion accumulation, essential for plant survival under salt stress conditions. This review presents the most illustrious research on strengthening plants against abiotic stress by externally applying polyamines. It also provides some clues about the functions of polyamines and their interaction with other molecules. Overall, the use of exogenous polyamines to improve plant stress tolerance is a promising strategy for sustainable agriculture and food security.

Keywords: Salinity, Polyamines, Crosstalk, Antioxidants, Phytohormones etc.

Introduction

Soil salinity is one of the most important global problems that negatively affect crop productivity. Salinity impairs plant growth and development via water stress, cytotoxicity due to excessive uptake of ions such as sodium (Na⁺) and chloride (Cl⁻), and nutritional imbalance. Additionally, salinity is typically accompanied by oxidative stress due to

generating reactive oxygen species (ROS) (Tsugane *et al.* 1999; Hernandez *et al.* 2001; Isayenkov, 2012). Plant responses to salinity have been divided into two main phases. An ion-independent growth reduction, which takes place within minutes to days, causes stomatal closure and inhibition of cell expansion mainly in the shoot (Munns and Passioura, 1984; Munns and Termaat, 1986; Rajendran *et al.* 2009). A second phase takes place over days or even weeks and pertains to the build-up of cytotoxic ion levels, which slows down metabolic processes, causes premature senescence, and ultimately cell death (Munns and Tester 2008; Roy *et al.* 2014). Tolerance to both types of stress is governed by a multitude of physiological and molecular mechanisms: osmotic tolerance, ionic tolerance, and tissue tolerance (Rajendran *et al.* 200; Roy *et al.* 2014). Osmotic tolerance initiates relatively quickly and includes a rapid decrease in stomatal conductance to preserve water. It employs fast long-distance (root-to-shoot) signaling mechanisms (Ismail *et al.* 2007; Maischak *et al.* 2010; Roy *et al.* 2014). Which largely do not discriminate between osmotic effects created by NaCl, KCl, mannitol, or polyethylene glycol (Yeo *et al.* 1991; Chazen *et al.* 1995).

The entering of salt into the root system triggers the activation of several signal cascades that generate ionic tolerance by restricting (net) Na⁺ influx into the root and

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reducing (net) Na⁺ translocation. Lastly, tissue tolerance is enhanced by the compartmentation of toxic ions into vacuoles to avoid detrimental effects on cytoplasmic processes. The above strategies have been observed in many types of plants, and differences in tolerance between glycophytes and halophytes are predominantly due to the greater robustness of the employed mechanisms in the latter, rather than a qualitative difference (Flowers and Colmer, 2008, 2015; Maathuis *et al.* 2014). Most of these aspects have been covered in previous reviews; here, we will focus particularly on the quantitative role of symplastic and the apoplastic pathways regarding salt influx, an evaluation of how mechanisms of chloride uptake, transport, and distribution, compared to that of sodium and a critical re-evaluation of ion toxicity. Global warming has emerged as a major environmental challenge that modulates diverse environmental factors like temperature extremities, altered oxygen levels, and salt and mineral deficiency including toxicity. In bird's eye view, global warming is being visualized as climate change that transmits cautious signals for living organisms to modulate themselves to withstand the environmental effects. The impact of climate change on plant systems, expressed in a multitude of forms like drought, heat, oxidative burst, salinity, and so forth, has shifted the focus of plant biotechnology more towards the dissection of genetic elements involved in stress tolerance. (Higashi *et al.* 2013). Thus, drought, salinity, and high and low-temperature extremes are among the major stresses that adversely affect plant growth and productivity worldwide. In particular, these events are important for Europe, since four out of the five worldwide extreme heat wave events that occurred within the last 15 years were observed in European regions (Coumou and Rhamstorf, 2012). Land degradation due to soil salinization is also a serious problem, the impact of which increases steadily in many parts of the world, especially in arid and semiarid regions. Most crop species used in agriculture are glycophytes (salt sensitives) and, therefore, their productivity is being severely affected in many regions of the world (Panta, *et al.* 2014). Under water deficit and/or salinity conditions, as well as under cold and heat, plants initiate several physiological and metabolic responses, which are orchestrated by post-translational modifications and changes in gene expression (Pandey, *et al.* 2015). Many plant genes involved in abiotic stress responses have been identified. Among them are genes controlling the synthesis of protective metabolites like osmolytes and Pas (Tiburcio, *et al.* 2014). Excessive salt accumulation in the root zone causes osmotic toxic stress and nutrient imbalance in plant cells (Baker and Rosenqvist, 2004; Desoky *et al.* 2021). Subsequently, salt stress adversely affects cell elongation, metabolic process, and photosynthetic efficacy (Chen and Murata, 2011, Mansour *et al.* 2021). Enhancing seedling vigor is crucial for plant stand establishment and successful

plant development, particularly under stressful growing conditions (El-Sanatawy *et al.* 2021).

Various efficient, cost-effective, and ecologically friendly strategies have been explored to mitigate the effects of environmental stresses, including salt, by plant growth regulators application, osmoprotectants, and different nutrition applications (Ahanger *et al.* 2017, Yakhin *et al.* 2017). The beneficial influences of growth regulators such as polyamines (PAs), amino acids, and phytohormones in mitigating salinity stress on plants have been deduced in various studies (ElSayed *et al.* 2018). Polyamines are polycationic low molecular weight compounds detected in all organisms and include spermine (Spm), putrescine (Put), and spermidine (Spd). Polyamines play an essential role in different development stages including cell division, acid stability, embryogenesis, dormancy termination, aging regulation, plant growth, and stress resistance (Todorova *et al.* 2007). Polyamine accumulation is essential in the plant reaction to salt stress and accordingly, PAs have a decisive importance in salinity tolerance (Chen *et al.* 2019). Exogenous PAs of various types and concentrations displayed significant attenuation of the influences of salt stress in various crops and reduced resultant damage (Verma and Mishra, 2005). The most abundant plant polyamines include putrescine (Put, 1, 4-diaminobutane), spermidine (Spd, N-3-aminopropyl-1, 4-diaminobutane) and spermine (Spm, bis (N-3-aminopropyl)-1,4-diaminobutane). Besides these, cadaverine (Cad, 1, 5-diaminopentane) has also been detected in several plant species, in particular in Gramineae, Leguminosae, and Solanaceae (Lutts *et al.* 2013). Another polyamine, thermospermine—a structural isomer of spermine—is synthesized by the action of thermospermine synthase (Takano *et al.* 2012). Putrescine (Put) is primarily synthesized by ornithine decarboxylase using ornithine as a substrate. Another alternative pathway for Put synthesis occurs through the action of arginine decarboxylase (ADC) followed by two successive steps catalyzed by agmatine iminohydrolase (AIH) and N-carbamoyl-Put amidohydrolase (CPA) (Fuell *et al.* 2010). Put can be used as a substrate to generate Spd by spermidine synthase (SPDS) and Spd can then be converted to Spm by spermine synthase (SPMS). Other polyamine oxidation products include hydrogen peroxide and γ -aminobutyric acid, which are involved in plant development and stress responses (Tiburcio *et al.* 2014). The interactions between polyamines, ROS and antioxidants are complex and induce diverse and apparently contradictory physiological effects during stress (Bhattacharjee, 2005; Gill and Tuteja, 2010; Pottosin *et al.* 2012, 2014; Velarde-Buendia *et al.* 2012). In particular, increased levels of cellular polyamines during abiotic stress (e.g., salinity) have shown dual effects. On one hand, exogenous polyamine application was correlated with higher plant tolerance to abiotic stress, partly due to the increased ability to inactivate oxidative radicals. On the other

hand, polyamines were reported to decrease plant's capacity to withstand stress, possibly due to the increased levels of H_2O_2 resulted from polyamines' catabolism (Minocha *et al.* 2014). PAs exist as polycations at physiological pH that result in their higher electrostatic affinity for negatively charged molecules such as nucleic acids and membrane phospholipids in cells (Aktar *et al.* 2021), which is associated with improving enzyme activity, regulating replication and transcription processes, and modulating cell division and membrane stability, besides a wide range of biological activities related to cell development (Mustafavi *et al.* 2018). Soluble forms of PAs were found to be linked with small phenolic molecules (hydroxycinnamic acid, coumaric acid, caffeic acid, or ferulic acid), which give rise to a large PAs pool (serving as metabolites) in plants (Martin-Tanguy 2017; Luo *et al.* 2009; Bassard *et al.* 2010; DeOliveira *et al.* 2018; Mustafavi *et al.* 2018). Free polyamines combine with macromolecules by covalently bonding with either ionic or hydrogen bonds (proteins, nucleic acids, uronic acids, lignin), generating insoluble bound PAs (Gill and Tuteja, 2010; Chen *et al.* 2019). To overcome the severe impact of environmental stresses, the accumulation of different osmolytes (carbohydrates, betaine, proline, and other amino acids) is found to be an adaptive mechanism that plants use to maintain cellular turgor pressure and respond differently to different abiotic factors; however, alteration of primary metabolism is the most common reaction. It involves alterations in the content of various amino acids, sugars, and tricarboxylic acid cycle intermediates, exhibiting common characteristics in abiotic stress responses. Plants also undergo modification in secondary metabolite content under exposure to abiotic conditions; additionally, these alterations vary according to species and stress type (Khan *et al.* 2018). The PA metabolic pathways are mostly conserved with slight variations from bacteria to plants and animals. In general, prokaryotes primarily synthesize Put and, to a lesser extent, Spd (Tabor and Tabor, 1976; Wortham *et al.* 2007), while Spm is less commonly found (Hamana and Matsuzaki, 1992; Busse, 2011; Michael, 2016). It is universally accepted that transient polyamine synthesis is induced in various species (not just in plants) by heat stress, radiation, and other traumatic stimuli in a process termed the polyamine stress response (Banerjee *et al.* 2021), which was observed in fish and mammals. Thus, it is ubiquitous and universal. Additionally, PAs are versatile compounds, protecting the protein structure and inducing antioxidative mechanisms, which provide tolerance against various unfavorable environmental cues (Alcazar *et al.* 2020). PAs are linked with plant development, stress tolerance, protection of nucleic acids and the cellular membrane, and ultimately, plant growth under stress (Sequera-Multiozabal *et al.* 2016; Pal *et al.* 2018). Osmolyte accumulation plays an important role in scavenging ROS to counteract the adverse effects (Alhaithloul *et al.* 2020) (Figure 1).

Polyamines Biosynthesis

The plant PA biosynthetic pathway has been extensively studied (Kusano *et al.* 2008; Vera-Sirera *et al.* 2010; Pegg and Casero, 2011; Gupta *et al.* 2013). It involves two precursors, L-ornithine and L-arginine, to generate putrescine. Put is produced via the catalytic actions of ornithine decarboxylase (ODC, EC 4.1.1.17) and arginine decarboxylase (ADC, EC 4.1.1.19) in three steps. Put is then converted into Spd by Spd synthase (SPDS, EC 2.5.1.16), with the addition of an aminopropyl moiety donated by decarboxylated S-adenosylmethionine (dcSAM). dcSAM is synthesized from methionine via two sequential reactions that are catalyzed by methionine adenosyltransferase (EC 2.5.1.6) and S-adenosylmethionine decarboxylase (SAMDC, EC 4.1.1.50), respectively. Spd is then converted into Spm or thermospermine, again using dcSAM as an aminopropyl donor, in a reaction catalyzed by Spm synthase (SPMS, EC 2.5.1.22) and thermospermine synthase (ACL5, EC 2.5.1.79), respectively. It should be noted that there is no known gene encoding ODC in the sequenced genome of the model plant *Arabidopsis thaliana* (Hanfrey *et al.* 2001), suggesting that this species may only produce Put via the ADC pathway. Finally, PA synthesis may vary between tissues/organs, one example being that the shoot apical meristem of tobacco (*Nicotiana tabacum*) serves as the predominant site of Spd and Spm synthesis, while it is mostly synthesized in roots (Moschou *et al.* 2008) (Figure 2).

Distribution of Polyamines in Plants

Polyamines are ubiquitous in eukaryotic and prokaryotic cells (Liu *et al.* 2016, 2017), and are found even in plant RNA viruses

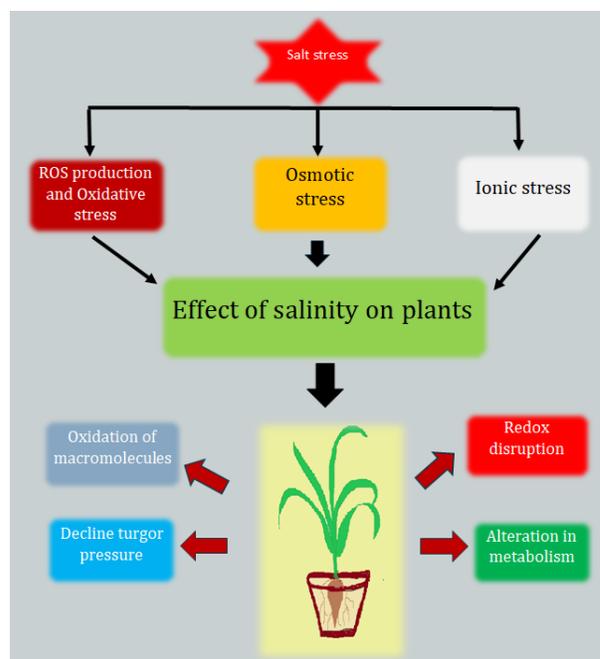


Figure 1: Adverse effects induced on plants by high salinity stress

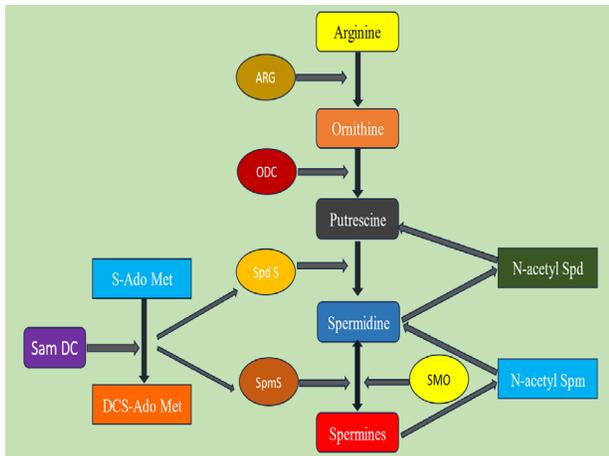


Figure 2: Biosynthesis of polyamines

and plant tumors. They have potent biological activities. There are numerous forms of PAs. In higher plants, PAs are predominantly present in their free form. The most common PAs in higher plants are Put, Spd, Spm, thermospermine (Tspm) (Kim *et al.* 2014; Sobieszczuk-Nowicka, 2017; Takahashi *et al.* 2017b), and cadaverine (Cad) (Regla-Márquez *et al.* 2015; Nahar *et al.* 2016). Polyamines show tissue- and organ-specific distribution patterns in plants. For example, the most abundant PA in leaves was found to be Put, and its levels were three times higher than those of Spd and Spm, whereas Spd was found to be the most abundant PA in other organs (Takahashi *et al.* 2017b). Different types of PAs also show different localization patterns within cells. In carrot cells, Put was found to accumulate in the cytoplasm, and Spm in the cell wall (Cai *et al.* 2006). The distribution patterns of PAs may be related to their unique functions. In general, more vigorous plant growth and metabolism are associated with greater PA biosynthesis and higher PA contents (Zhao *et al.* 2004; Cai *et al.* 2006).

Polyamines: One of the Eminent Regulators in ROS Homeostasis During Salt Stress

Plant polyamines are thought to contribute to cellular responses during salt stress through the modulation of ROS homeostasis via two distinct mechanisms (Takahashi and Kakehi, 2010). First, polyamines promote ROS degradation by scavenging free radicals and activating antioxidant enzymes during stress conditions (Gupta *et al.* 2013). ROS include singlet oxygen (1O_2), superoxide radical ($O_2^{\cdot-}$), hydroxyl radical (HO^{\cdot}), hydrogen peroxide (H_2O_2), alkoxyl radicals (RO^{\cdot}), and peroxy radicals (ROO^{\cdot}). They are generated under normal growth conditions (Mehla, N., *et al.* 2017) (Hasanuzzaman, M *et al.* 2019). However, extreme abiotic stress induces the overproduction of ROS (Gill, SS, and Tuteja 2010) which alters cellular and molecular constituents, for instance, oxidizing DNA, proteins, carbohydrates, lipids, and enzymes and leading to

programmed cell death (Singh A *et al.* 2019, Hasanuzzaman, M *et al.* 2012). To prevent injuries, plants precisely control the generation of ROS through different enzymatic and non-enzymatic antioxidants. The enzymatic antioxidant plant defense machinery includes peroxidase (POD), superoxide dismutase (SOD), glutathione reductase (GR), catalase (CAT), dehydroascorbate reductase (DHAR), ascorbate peroxidase (APX), and monodehydroascorbate reductase (MDHAR), while non-enzymatic antioxidants include ascorbate (AsA), flavonoids, carotenoids, stilbenes, tocopherols, and other vitamins. These counteract oxidative stress either by restoring the level of endogenous antioxidants or by directly detoxifying the overproduced ROS, thereby increasing the tolerance to oxidative stress (Raja, V *et al.* 2017, Kaur, N *et al.* 2019, Mittler, R, 2017). The precise regulation of ROS production facilitates communication between cells by amplifying the signals through nicotinamide adenine dinucleotide phosphate oxidase (NADPH) in response to various stresses by modulating the conformation of different proteins and triggering genes involved in stress tolerance (Hasanuzzaman, M *et al.* 2012). Thus, elucidation and understanding of the molecular basis of ROS signaling and of the related downstream pathways would help alleviate stress in plants (Kesawat MS *et al.* 2023) (Table 1 and Figure 3).

Polyamines and Salt Stress

Salt and drought stress are the two major abiotic stresses in agriculture, and both of them lead to reduced water potential in plants. Salinity is a complex environmental constraint. A high salt concentration reduces membrane integrity, decreases the activity of various enzymes, and impairs the function of the photosynthetic apparatus. Plants adapt to such unfavorable environmental conditions by accumulating low molecular weight osmolytes, such as proline and PAs. The application of different types and concentrations of exogenous PAs has been shown to alleviate the effects of NaCl stress on various plants, and

Table 1: Polyamines and their source

Name	Structure	Molecular formula	Source
Put		$C_4H_{12}N_2$	Ubiquitous
Spd		$C_7H_{19}N_3$	Ubiquitous
Spm		$C_{10}H_{26}N_4$	Ubiquitous
Tspm		$C_{10}H_{26}N_4$	Ubiquitous
Cad		$C_5H_{14}N_2$	Legume plants

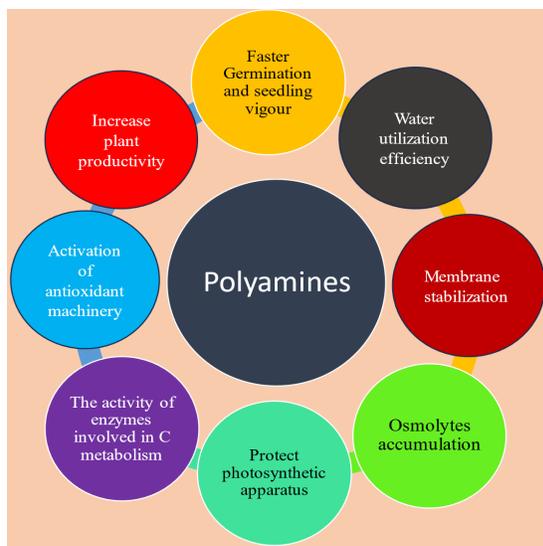


Figure 3: Accumulation and functions of polyamines under abiotic stress

reduce damage (Verma and Mishra, 2005; Li *et al.* 2008). It has been suggested that the level of Spm in plants is an important indicator of salt tolerance (Li and He, 2012). The free, acid-soluble bound, and total Spm contents in leaf tissues of sunflower plants increased under 50, 100, or 150 mM NaCl treatments (Mutlu and Bozcuk, 2005). Exogenous PAs, especially Spm and Spd, resulted in increased reactive oxygen metabolism and photosynthesis, which improved plant growth and reduced the inhibitory effects of salt stress (Meng *et al.* 2015; Baniasadi *et al.* 2018). Similar results were obtained in a study on soybean seedlings (Wang and Bo,

2014). Li *et al.* produced a cucumber line with up-regulated SAMDC expression and down-regulated ADC and ODC expression, resulting in increased accumulation of Spd and Spm and decreased accumulation of Put under salt stress. As a result, the inhibition of plant growth under salt stress was alleviated in the transgenic seedlings (Li *et al.* 2011; Takahashi *et al.* 2017). Several metabolic pathways are affected by Spm and Spd (Paul and Roychoudhury, 2017). Sun *et al.* showed that PAs and ABA together alleviated salt stress in grape seedlings (Sun *et al.* 2018) (Table 2).

Polyamine as Modulator of Ion Homeostasis

Polyamines are also hypothesized to promote salt stress tolerance through their direct or indirect effects on ion transport (Demidchik and Maathuis, 2007; Pandolfi *et al.* 2010; Bose *et al.* 2011). For instance, polyamines including Spd, Spm, and Put affect ion transport indirectly by interacting with plasma membrane phospholipids and enhancing membrane stability. Polyamine-enhanced membrane stability has been shown to have a significant effect on both H⁺/ATPase and Ca²⁺/ATPase transporters during salinity stress (Roy *et al.* 2005; Pottosin and Shabala, 2014). Spm may directly affect ion transport during salt stress by blocking inward-rectifying K⁺ channels (KIRC) and non-selective cation channels (NSCCs), limiting Na⁺ influx, and K⁺ efflux (Liu *et al.* 2000; S; Zhao *et al.* 2007; Zepeda-Jazo *et al.* 2008). Put and Spm have shown strong potential in reducing the hydroxyl radical-induced K (+) efflux and the respective non-selective current. This synergistic effect between ROS and polyamines was much more pronounced in a salt-sensitive barley variety than salt-tolerant one (Velarde-Buendia *et*

Table 2: Effect of polyamines on plants under salinity stress:

Polyamines	Ways of action	Studied plants	References
Put	It relieved the plant from salt stress by maintaining water and nutrition status	Cucumber	Shu <i>et al.</i> 2012
Spd	Promoted gamma-aminobutyric accumulation	Soyabean	Fang <i>et al.</i> 2020
Spd	May participate in the redox homeostasis, hence the stability of chloroplasts against salt stress.	Rice	Jiang <i>et al.</i> 2020
Bound polyamines	Accelerated enzymatic antioxidant mechanisms and regulated TGase to enhance salinity tolerance.	Tomato	Zhong <i>et al.</i> 2020
Spd	Enhanced proline accretion and antioxidant enzyme efficiency for defense against salt stress	Alfalfa	Lou <i>et al.</i> 2018
Spd	Improved the antioxidant system and markedly enhanced Spd and Spm content.	Wheat	El- Sayed <i>et al.</i> 2018
Spd	Helped in the protection of photosynthetic machinery to maintain photosynthesis.	Tomato	Hu <i>et al.</i> 2016
Spd	Amended CAT activity and enhanced the photochemical quantum yield plants	Pot marigold	Baniasadi <i>et al.</i> 2018
Spd	Effectively upregulated the transcription of Calvin cycle genes to improve and regulate the defense response.	Sweet sorghum	Sayed <i>et al.</i> 2019
Put	Reduced salt-induced photosynthetic perturbation of leaf through stomatal-aperture modifications.	Cucumber	Ma <i>et al.</i> 2020

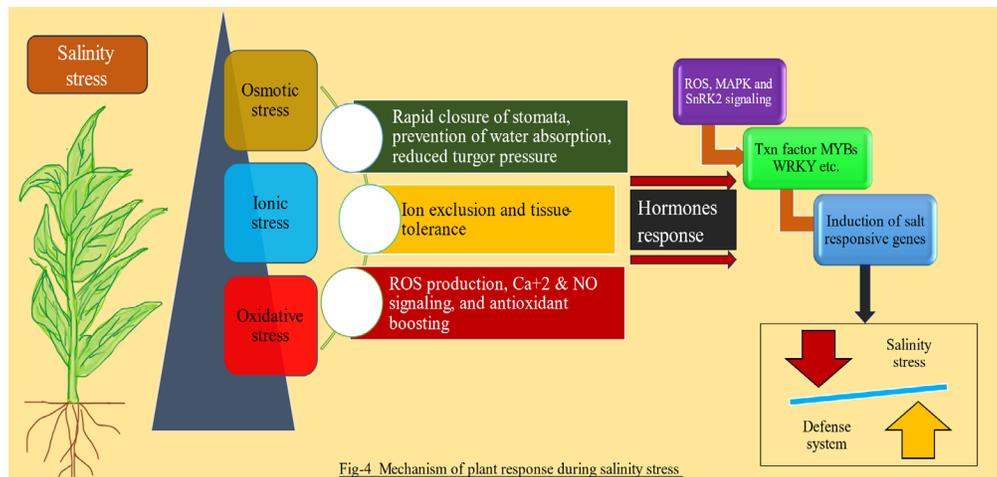


Fig-4 Mechanism of plant response during salinity stress

Figure 4: Mechanism of plant response during salinity stress

al. 2012). Absence of Spm causes an imbalance in Ca²⁺ homeostasis in the *Arabidopsis* mutant plant and showed hypersensitivity to salinity, suggesting its involvement in modulating the activity of certain Ca²⁺-permeable channels and changes in Ca²⁺ allocation compared to unstressed state, which may prevent Na⁺ and K⁺ entry into the cytosol, enhance Na⁺ and K⁺ influx into the vacuole, or suppress Na⁺ and K⁺ release from the vacuole (Yamaguchi *et al.* 2006). Moreover, vacuolar Cation/H⁺ Exchangers (CAX) are found to be over-expressed and both FV and SV channels (FV, fact-activating vacuolar channel; SV, slow-activating vacuolar channel) are suppressed during salinity, resulting in into an overall increase in vacuolar Ca²⁺ (Cheng *et al.* 2004; Pottosin *et al.* 2004). Dobrovinskaya *et al.* (1999) reported that cellular polyamines strongly inhibited FV and SV channels whose reduced activity is essential for conferring salinity tolerance in facultative halophyte *Chenopodium quinoa* (Bonales-Alatorre *et al.* 2013) (Figure 4).

Polyamines- Phytohormones Crosstalk Under Salt Stress

Polyamines play an important role in salinity stress as they interact with plant growth regulators such as ETH, JA, ABA, GA etc.

PA and ETH

Among all plant hormones, the crosstalk between PAs and ETH during salt stress seems to be the most established. It has been suggested that plant tolerance to salinity may be related to ETH biosynthesis and signal transduction pathways. Exogenous application of ETH increased plant tolerance to salinity due to the increased expression of genes involved in ROS scavenging (Zapata, P.J *et al.* 2017). Furthermore, ETH may help regulate Na⁺ and K⁺ concentrations in xylem tissues under salt stress (Sharma A *et al.* 2019). In contrast, the application of ETH biosynthesis inhibitors increases plant sensitivity to salt stress (Zapata, P.J

et al. 2017). PAs can play a role in modulating ETH production during salinity. (Quinet *et al.* 2010). Demonstrated that the application of exogenous Put enhanced ETH synthesis in the salt-resistant cultivar exposed to salinity (Quinet, M *et al.* 2010; Zapata *et al.*). Noticed that under salinity, the ETH, Spd, and Spm contents increased in plant species with different salt sensitivity. PAs and ETH may compete for SAM production. However, the results support that no competence between them occurred, and the SAM pool is high enough to support both PAs and ETH biosynthesis during salt stress (Li, C.Z., and Wang, G.X. 2004; Zapata, P.J *et al.* 2017). PAs catabolism is important in plant responses to stress, the crosstalk between PAs catabolism and ETH signaling has been investigated. In transgenic tobacco plants displaying reduced PAO activity, the transcript levels of genes encoding 1-amino-cyclopropane-carboxylate synthase (ACS) and 1-amino-cyclopropane-carboxylate oxidase (ACO) were higher than those in plants displaying enhanced PAO activity (Gemes, K *et al.* 2017). ACS converts SAM to 1-aminocyclopropane-1-carboxylic acid (ACC), whereas ACO converts ACC to ETH (Yang, S.F., and Hoffman, N.E. 1984). To provide further insight into the link between PAs, ETH, and H₂O₂, (Freitas *et al.* 2018) proposed a detailed model of salinity-induced expression and activity of ACO, leading to enhanced ETH biosynthesis in the salt-tolerant maize genotype.

PA and BR

BRs positively influence plant tolerance to salt stress. In *Arabidopsis*, enhanced BR signaling activity increases salt stress tolerance. In contrast, the BR-defective mutants exhibit hypersensitivity to salinity. Moreover, BRs may control water loss by reducing stomatal density in plants exposed to high salt stress conditions (Ryu, H., & Cho, Y. G. (2015). Co-application of BRs and PAs has a beneficial effect on plants exposed to salt stress (Sharma A *et al.* 2014; Fariduddin, Q *et al.* 2014) Exogenous application of BRs

enhances plant tolerance to salinity by modulating PAs homeostasis and distribution in plants (Parra-Lobato, M. C., & Gomez-Jimenez, M. C. (2011); Serna *et al.* 2015). (Liu *et al.* 2020) described a more advanced model of PAs and BRs interactions during plant response to low and high salt-salinity conditions. EBL promotes tolerance of canola to high salt salinity, but not to low salt stress. The dual effect of EBL on plant responses to low and high salinity is related to H₂O₂ accumulation, which is regulated by PAs metabolism (especially Put oxidation). Under high-salt stress, EBL reduced the accumulation of H₂O₂ and DAO activity. Interestingly, EBL oppositely modulated these parameters in seedlings exposed to low-salt stress (Liu, J *et al.* 2020).

PA and ABA

A high endogenous ABA content is important for increasing plant tolerance to salt stress. ABA induces stomatal closure and accumulation of numerous proteins and osmoprotectants (Ryu, H., & Cho, Y. G. (2015). In the *atpao5-3* mutant, salt stress increased ABA level, up-regulated *NCED* expression and enhanced ABA-inducible *RD29B* expression (Zarza, X *et al.* 2017). On the other hand, the expression of *NCED3* was reduced in Spm-deficient *sperms* mutant and double *acl5/sperms* mutant under salt stress conditions. In addition, in transgenic *Arabidopsis* lines overexpressing *SAMDC1*, two of the five ABA-induced genes (*NCED* and *RD29A*) were up-regulated by salinity (Pal *et al.* 2018).

PA and GA

GAs can also interact with PAs during plant response to salt stress. GAs are tetracyclic diterpenoid carboxylic acids that participate in processes related to plant growth and development (Pal, M *et al.* 2018). GAs positively regulate germination, leaf expansion, and stem elongation. They also initiate flowering, trichome formation, and reproductive development Banerjee, A., & Roychoudhury, A. (2019). Salt stress negatively affects endogenous GAs content in plants. This was accompanied by a higher accumulation of DELLA proteins, which are major GA-negative regulators. Interestingly, studies have shown that GA-deficient biosynthetic or signaling mutants exhibit tolerance to severe salt stress. In contrast, the quadruple DELLA loss-of-function mutant was less tolerant to salt (Ryu, H., & Cho, Y. G. (2015). Recent studies have shown that exogenous GAs improve plant tolerance to salinity. Positive effects of Spd and GA3 on priming-induced physiological and biochemical changes have been reported in salt-tolerant and salt-sensitive rice cultivars (Chunthaburee, S *et al.* 2014). In cucumbers, exogenous Spd up-regulated the expression of genes related to GA biosynthesis and increased the activity of GA3-oxidase and GA20-oxidase. Moreover, in salt-stressed plants, exogenous Spd stimulated the accumulation of GA3 and enhanced the expression of the GT-3b transcription factor, a stress-related protein usually induced by salt stress. Spd-

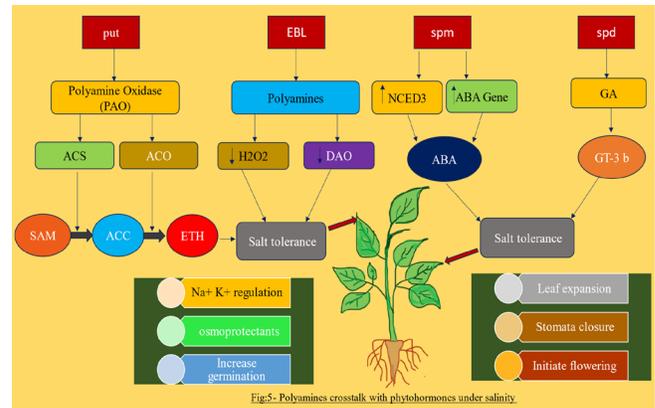


Figure 5: Polyamines crosstalk with phytohormones under salinity

induced salt tolerance was reduced in plants treated with GA biosynthesis inhibitor. This suggests that GA plays a role in Spd-induced salt tolerance in cucumber (Wang Y *et al.* 2020).

PA and JA

In the same species, the application of Spd to salt-treated plants reduced JA content Radhakrishnan, R., & Lee, I. J. (2013). The role of PAs in the regulation of JA content has also been demonstrated in *Arabidopsis* seedlings exposed to salinity. Exposure of the *atpao5-3* mutant to salt stress resulted in strongly enhanced JA accumulation (Zarza, X *et al.* 2017). The relationship between CKs and PAs in plant responses to salt stress has not been well described. CKs such as zeatin (Z) and zeatin ribose (ZR) are involved in plant cell division and growth, morphogenesis, chloroplast biogenesis, nutrient absorption and balance, and vascular differentiation. They also participate in seed germination and delay senescence in plants (Li, L *et al.* 2018; Kapoor, R. T., & Hasanuzzaman, M. 2020; Liu, Y *et al.*, 2016). CKs play an essential role in plant responses to nutrient, drought, salinity, and temperature stresses (Pavlov *et al.* 2018). Simultaneous application of kinetin (KN) and PAs improve tolerance to salt stress in some plant species, such as *Vigna sinensis*, wheat, and *Luffa acutangula* (Aldesuquy, H *et al.* 2014; Kapoor R.T, *et al.* 2020; Alsokary S.S 2011). The positive influence of KN and Spm on photosynthesis parameters has been extensively described in wheat exposed to salt stress. Grain priming with KN, Spm, or KN + Spm alleviated the negative effects of stress by stimulating leaf area expansion, pigment production, photosynthetic activity, and improving chloroplasts ultrastructure (Aldesuquy H *et al.* 2014). Additionally, (Kapoor and Hasanuzzaman, 2020) reported that exogenous KN and Put synergistically mitigate salt stress in sponge gourd (*Luffa acutangula* L.). Simultaneous application of KN and Put to salt-stressed seedlings resulted in a significant enhancement of growth, photosynthetic pigment content, and osmolyte accumulation. Moreover, the co-application of KN and Put up-regulated the antioxidant enzyme activity and increased the content of

the non-enzymatic components of the antioxidant defense machinery. Simultaneous KN and Put treatment was more effective than individual application of KN or Put, suggesting the presence of regulatory crosstalk mechanisms between KN and Put (Kapoor and Hasanuzzaman, 2020). However, the more advanced relationship between PAs and CKs remains unknown (Figure 5).

Conclusion

The effects of climate change are taking a toll on crop production and yield due to the increasing presence of stressful environmental cues. As a result, researchers are putting a greater emphasis on studying resistance mechanisms in plants to provide solutions through the generation of stress-tolerant cultivars. In recent years, there has been a growing interest in the role of polyamines as a defensive mechanism to counteract stress stimuli. However, the interplay between polyamines and stress response pathways is complex and not yet fully understood. This review article aims to provide an overview of recent research on the contributions of abundant polyamines, such as putrescine, spermidine, and spermine, to metabolic and physiological processes that protect plants during climatic adversities. Polyamines are known to be protective molecules, and they play an important role in a complex signaling system that is critical for tolerance mechanisms, depending on their type and concentration under stress conditions. Notably, polyamines are involved in several physiological and metabolic processes, including the defense of photosynthetic pigments, antioxidant systems, hormonal interplay, and ionic homeostasis, which ultimately help to mitigate the negative effects of non-optimal conditions on plants. In addition to the second messengers, such as calcium ions and ROS, which lead to signal transduction pathways, phytohormones, including ABA, SA, JA, and ET, are also synthesized in the early stages of salinity stress. By understanding the crucial role of polyamines in plant stress responses, researchers can develop novel strategies to enhance plant tolerance to adverse climatic conditions and ensure sustainable crop production.

Authors Contributions

First and all authors collected and drafted the literature. The corresponding author edited the manuscript.

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