FUNCTIONS OF POLYAMINES IN THE REGULATION OF ABIOTIC STRESS TOLERANCE IN PLANTS

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Abstract. The growth, development, and productivity of plants are significantly impacted by environmental stress factors. Consequently, plants have evolved a variety of adaptation techniques to maintain their survival in adverse environmental conditions. One such method is the use of metabolites to improve stress tolerance. Polyamines (PAs), a class of metabolites, have distinguished themselves as significant players in this area and they are organic growth agents that take part in a variety of biological processes. They modulate plant metabolism, thereby influencing the growth and development of plants. Several common polyamines, including spermine, spermidine, and putrescine, have been identified as important regulators in controlling and modulating stress tolerance in plants. Accumulation and increasing activity of these polyamines, together with their synthesizing enzymes, have been proven to improve stress tolerance in plants. In this review, a comprehensive summary is provided on the role of polyamines in enhancing stress tolerance against various abiotic stress factors in plants. Also, polyamines have been shown to play a role in stress tolerance by altering the homeostasis of reactive oxygen species (ROS) through their direct or indirect actions in regulating antioxidant systems or decreasing ROS generation.
Keywords: *polyamines, environmental stresses, resistance, reactive oxygen species*

Introduction

Polyamines (PAs) are critical for defense and playing essential roles in increasing plants' resistance to under harsh abiotic circumstances, although their molecular interaction in this is unknown (Shao et al., 2022). Polyamines have been demonstrated to be involved in a variety of plant growth and development processes and polyamines have also been shown to play a role in stress tolerance by altering the homeostasis of reactive oxygen species (ROS) through their direct or indirect actions in regulating antioxidant systems or decreasing ROS generation (Liu et al., 2015).The growth and development of flowers, stems, leaves, leaf shedding, and grain maturity are regulated and standardized. In contrast, hormones could have been absent or present in very minute concentrations in plants, causing them to remain a clump of undifferentiated cells (Islam et al., 2023). In several plant developmental stages, polyamines are essential, such as cell division, embryogenesis, reproductive organ development, root growth, tuberization, floral initiation and development, fruit development and ripening, as well as leaf senescence and response to abiotic stresses (Nambeesan et al., 2008). PAs and their biosynthetic enzymes are involved in a wide range of metabolic processes in plants, including cell division, organogenesis, and protection against environmental stresses (Pedraza et al., 2007). Under biotic and abiotic stress conditions, PAs, with their positively charged amino groups, can interact with macromolecules such as nucleic acids, proteins, and lipids (Menendez et al., 2012). The major types of PAs found in plant cells are diamine putrescine (PUT), triamine spermidine (SPD), and tetramine spermine (SPM) (endogenous polyamines structure).

In higher plant chloroplasts, the intracellular levels of PAs increase in response to oxidative stress, indicating a protective role for PAs (Pál et al., 2015). To counteract

photoinhibition under abiotic stress, plants have developed an adaptive system that includes the involvement of PAs. Under light stress, endogenous PAs concentration also rises in plants. For instance, tobacco chloroplasts exposed to UV-B irradiation show a significant increase, around 900%, in spermidine (SPD) levels (Lütz et al., 2005). This substantial increase suggests an important role of endogenous PAs in the plant's response to light stress. Previous studies (Kuznetsov and Shevyakova, 2010; Radyukina et al., 2017) have reported the significant role of PUT in protecting the leaves of *Thellungiella salsuginea* and other species from UV-B irradiation, and the contribution of both bound and free PAs was found to be species and organ-specific. Additionally, it is known that the primary enzyme in PA catabolism, polyamine oxidase, may catalyze the reverse conversion of Spd and Spm into PUT (Korolkova et al., 2014).

The physiological expression of the accumulation of PAs in plant cells in response to abiotic stress or biotic stress is taken into advisement. PAs can act as a barrier against a variety of abiotic stressors, like salt stress, drought, heat, UV, and heavy metals pollution (Alcázar et al., 2010; Nahar et al., 2017). Different types of stresses relate to development at the first stage oxidative stress and an intracellular concentration of polyamines (PAs) enhanced which plays a role antioxidant (Rathinapriya et al., 2020). In cadmium and cooper metal-induced oxidative damage in the sunflower plant tissue, as evidenced by an increment in lipid peroxidation, PAs are related to the protection against this metal-induced oxidative damage (Groppa et al., 2001).

PAs are involved in the inhibition of peroxidation of membrane lipids (Bellé et al., 2004), and heavy metals are involved to catalyze the inhibition of oxidative reactions (Bors et al., 1989). In addition, the catabolism of PAs is accompanied by the release of H_2O_2, which is a signalling molecule involved in the antioxidative mechanism of plants. The overproduction of this chemical, however, might lead to oxidative stress (Groppa and Benavides, 2008). Plants tolerant to certain stress generally can trigger polyamine biosynthesis compared to sensitive plants. Navakoudis (2003) pointed out that tobacco cultivars tolerant to ozone stress can accumulate PAs in their tissues, especially PUT so that the intracellular level of PAs in susceptible cultivars remains unchangeable. Furthermore, the measurement of the intracellular concentration of PAs in rice tolerant cultivars to salt stress showed high levels of PMS and SPD. In contrast, PUT concentration has only increased in susceptible cultivars (Krishnamurthy and Bhagwat, 1989). A high level of PUT followed by a strong activity of ADC and ODC enzymes was observed in the leaf of wheat treated by cadmium (Groppa, 2003).

Salt Stress Induced Physiological Changes Mediated by Polyamines

Plant resistance to salt stress undoubtedly depends in part on the equilibrium between stress-induced polyamine accumulation and ROS (Saha et al., 2015). Recent studies conducted by Napieraj et al. (2020) and Rathinapriya et al. (2020) have shed light on the significant role of exogenous PAs in promoting plant growth under stressful conditions. Specifically, they investigated the use of PAs to boost plant development in the context of salt stress. In their findings, it was observed that the application of lower concentrations of PUT and SPD in foxtail millet (*Setaria italica* L.) under NaCl stress led to a remarkable improvement in endogenous PAs. This enhancement in PAs played a crucial role in enhancing the plant's tolerance to high-salinity stress by effectively detoxifying ROS (Rathinapriya et al., 2020). Similarly, in arabidopsis and rice, the application of SPM has shown promising results in promoting osmotic and salt stress tolerance. This is achieved

through the accumulation of polyphenols and the activation of key antioxidant enzymes such as catalase (CAT) and superoxide dismutase (SOD). SPM treatment has been discovered to increase photosynthetic rates, plant growth, antioxidative enzyme activity, and proline buildup in salt-sensitive cucumber cultivars, thus improving salt tolerance (Duan et al., 2008).

The PUT increases resistance to salt stress by lowering lipid peroxidation, decreasing macromolecule breakdown, and raising quantities of crucial chemicals, such as glutathione (GSH) and carotenoids. Studies have demonstrated that the application of PUT can significantly increase the activity of antioxidant enzymes and carotenoid levels in leaf tissues of salt-stressed *Brassica juncea* seedlings, resulting in enhanced seedling growth compared to untreated controls (Verma and Mishra, 2005). In addition to endogenous PAs, the application of exogenous PAs can also improve plant responses to various stress conditions. For example, the application of exogenous SPM protected arabidopsis mutants (unable to synthesize SPM) against drought (Yamaguchi et al., 2007). Similarly, exogenous SPD application reduced the negative effects of salt stress in barley cultivars sensitive to salt (Liu, 2006a). It has been proposed that maintaining high levels of endogenous PUT, SPD, and SPM as well as their modification is essential for defending plants against salt stress.

Polyamine biosynthesis and their association with salt tolerance have been observed in salt-tolerant species or halophytes such as *Atriplex*, which respond to heavy metals in phytoremediation (Bueno and Cordovella, 2019). Exogenous PAs improve resistance to salt stress by increasing levels of free PAs, osmolyte synthesis, and polyamine biosynthetic gene expression (Alcázar et al., 2006, 2020; Ebeed et al., 2017). High levels of both proline (Pro) and PAs (SPD/SPM) have been identified as protective factors in quinoa genotypes adapted to salinity, indicating their potential as indicators of salinity adaptation and improvement of halophyte genotypes for crop enhancement (Ruiz-Carrasco, 2011). Halophytes generally contain higher levels of PAs compared to glycophytes. The expression of genes involved in polyamine biosynthesis is regulated differently in response to salt stress in halophytes and *Solanum lycopersicum* (Gharbi et al., 2016).

According to various research, salt-tolerant plants tend to overexpress genes involved in polyamine production in response to various stressors. For instance, in *Arabidopsis thaliana*, the genes ADC1 and ADC2, encoding the ADC enzyme, are strongly induced by abiotic stress. The ADC2 gene expression increases significantly under salt stress and potassium ion deficiency, while the ADC1 gene is induced by cold stress (Hummel et al., 2004; Alcazar et al., 2006). The genes encoding spermine synthase and S-adenosylmethionine decarboxylase (SAMDC) are also upregulated in response to dehydration and cold stress, respectively (Vergnolle et al., 2005; Alcazar et al., 2006). Molecular approaches targeting the overexpression of genes involved in polyamine biosynthesis have improved defense mechanisms in some sensitive plants, although they may affect the growth and development of these mutant plants (Capell et al., 2004; Kasukabe et al., 2004). Overexpression of genes encoding various polyamine biosynthetic enzymes has also been shown to enhance salt tolerance in different species, such as tobacco lines overexpressing genes encoding PUT and SPM, which exhibited great resistance to salt stress (Waie and Rajam, 2003). It is crucial to increase plant productivity under various environmental stressors. This can be done by creating the newest kinds that are flexible and have a larger output potential and by using proper agricultural techniques (Sadak et al., 2022).

Polyamines: ROS Homeostasis Regulators in Salt Stress

There is little doubt that PAs participate in physiological actions that support plant resistance in response to salt and drought stress (Sequera-Mutiozabal et al., 2017). In order to reduce the buildup of ROS when exposed to salt stress, plants use a variety of enzymatic and non-enzymatic processes. The ascorbate-glutathione cycle is used to control ROS levels through enzymatic antioxidants like SOD, CAT, ascorbate peroxidase (APX), and glutathione reductase (GR). PAs have antioxidant properties in addition to other antioxidants such GSH, ascorbate (AsA), proline, and glycine-betaine (Ozgur, 2013; Todorova, 2013). As plant cells quickly collect ROS in response to salt and other stimuli (Miller, 2010), PAs build up in plants under salt stress to maintain cellular ROS equilibrium. PAs have antioxidant characteristics, and their buildup in stressed plants significantly increases their ability to withstand stress (Alcázar, 2020). With numerous physiological impacts seen under stress, the link between PAs and ROS is complicated. In times of abiotic stress, PAs may serve as regulators of redox homeostasis (Gill and Tuteja, 2010; Saha et al., 2015). PAs can function as antioxidant enzymes and metabolites to detoxify ROS as a result of an increase in PAs anabolism and catabolism in response to abiotic stress (Chen, 2001, 2019).

Under stress, PAs help to deactivate ROS by scavenging free radicals and activating antioxidant enzymes (Wu et al., 2020). Previous studies by Kubiś (2008) demonstrated that free PAs directly contribute to the detoxification of superoxide anions and H_2O_2, while conjugated PAs are involved in scavenging other ROS molecules. Conjugated or bound PAs have been shown to exhibit a higher ability to stabilize or activate antioxidant enzyme activity compared to free PAs through their interaction with these enzymes (Saha et al., 2015). Additionally, PAs stimulate ROS generation in the apoplast via polyamine catabolism (Campestre et al., 2011). The plants have a variety of sophisticated detoxifying systems that convert the extremely destructive ROS into non-toxic chemicals in order to limit the oxidative damage (Chauhan et al., 2022). The net accumulation of ROS at the cellular level increases under abiotic stresses, and the elevated levels of PAs act as antioxidant enzymes and metabolites to detoxify ROS (Thomas et al., 2020). However, the catabolism of PAs can increase the concentration of H_2O_2, resulting in decreased stress tolerance in plants (Gupta et al., 2016). The supply of exogenous PAs is directly correlated with plant tolerance to abiotic stress, as they effectively inactivate oxidative radicals. Wu et al. (2020) concluded that through scavenging free radicals and activating antioxidant enzymes, PAs under stress increase the breakdown of ROS. Variant ROS scavengers and antioxidants can increase plants' tolerance to salt stress while reducing oxidative stress (Javeed et al., 2021). Although, PAs can promote ROS production through PA catabolism in the apoplast (Campestre et al., 2011; Wang et al., 2019), several studies have reported that polyamine biosynthetic pathways are associated with abiotic stress resistance. Islam (2019) found that salt treatment significantly downregulated polyamine biosynthesis-related genes such as ADC1, ODC, and Arginase, while SAMDC was upregulated in rice, leading to reduced salt tolerance by facilitating ROS production. Genes involved in polyamine biosynthesis can enhance stress tolerance in rice plants by preventing the accumulation of ROS (Jang et al., 2012).

Plant Drought Tolerance is Promoted by Polyamines

PAs have a significant regulatory role in plants during various growth and development phases as well as in responses to biotic and abiotic stress (Nandy et al.,

2022). Different ways are now being used to reduce drought stress in crop plants. Exogenous use of polyamines (PAs) is one such technique (Wasaya et al., 2023). Although their exact involvement in protecting plants from drought stress is still being researched, PAs have a well-established protective role in reducing the effects of stressful situations. There is no denying, however, that PAs are essential for physiological mechanisms that increase plant resistance to salt and drought stress. In order to increase a plant's ability to withstand drought stress, PAs affect a variety of processes in plant organs, including roots and leaves (Sequera-Mutiozabal et al., 2017). In numerous species, including *Lotus tenuis* (Espasandin et al., 2014), *Theobroma cacao* (Bae et al., 2008), and *Valeriana officinalis* L. (Mustafavi et al., 2016), PAs have been shown to impart drought stress tolerance via a variety of mechanisms. Drought stress has been shown to reduce wheat growth, and alter the levels of osmoprotectants and endogenous PAs, as well as the expression of PAs biosynthetic genes (Ebeed et al., 2017). However, Exogenous PAs have been shown to considerably boost yield under salt stress. In apple seedlings, treatment with exogenous PAs under drought conditions resulted in increased activity of SOD and CAT, while reducing malondialdehyde (MDA) content. Foliar spray of PAs has the potential to alleviate some of the detrimental effects of drought stress and enhance the physiological performance of spring safflower. Their function as ROS scavengers and osmolytes has been highlighted (Khosrowshahi et al., 2020). Drought-tolerant wheat cultivar Chinese Spring, when subjected to drought stress, exhibited significant accumulation of antioxidants due to the application of PAs, supporting the assumption that PAs are involved in the signaling pathway determining the antioxidative response and tolerance of wheat to drought stress (Marcińska et al., 2020).

Protection for Photosynthetic Apparatus and Polyamines

Although evidence suggests that polyamines play an important role in growth regulation, their specific physiological function and mode of action are unknown (Ioannidis and Kotzabasis. 2007). Numerous studies have emphasised how PAs help higher plants preserve their photosynthetic systems from abiotic stress. A typical stressor, increased salinity, has an impact on the photosynthetic apparatus' structure and operation (Mbarki et al., 2018). According to Kotakis et al. (2014), the buildup of PAs in response to this stress is thought to reduce oxidative stress and preserve the maximum photochemical efficiency of photosystem II (PS II). By improving energy dissipation through the xanthophyll cycle, SPD applied exogenously has been demonstrated to reduce salt-induced loss in photosynthetic efficiency, thereby repairing damage to cucumber seedlings and controlling endogenous polyamine levels (Shu et al., 2012).

PUT application increases endogenous PAs, particularly SPD and SPM, resulting in increased fatty acid mobilization and photosynthetic apparatus stabilization (Shu et al., 2015). The reciprocal reorganization of the photosynthetic apparatus induced by exogenous PUT can compensate for these changes, and confer resistance against enhanced NaCl salinity, enabling cell growth even under normally toxic NaCl concentrations. Changes in endogenous PAs, such as PUT reduction, in green algae under high stress are associated with alterations in the structure and function of the photosynthetic apparatus, including an increase in the functional size of the antenna and a reduction in the density of active PS II reaction centers (Demetriou et al., 2007). Mix solutions of PAs applied during wheat seed priming or as a foliar spray under drought stress have been found to improve chloroplast ultrastructure, suggesting the involvement

of Rubisco and photosynthetic pigments in PA-mediated maintenance of chloroplast stability (Hassan et al., 2020).

PUT, cadaverine, SPD, and SPM are among the PAs that play critical roles in cell development, division, and differentiation; their significance in environmental stress defense mechanisms should also be recognized (Ibarra et al., 2015). In corn, top dressings of PUT, cadaverine, and SPM significantly increase dry matter production under salt stress, as well as chloroplast-bound polyamine contents, net photosynthetic rate, and PSII photochemical efficiency, while reduce MDA content. This suggests that PAs alleviate salt damage by increasing chloroplast-bound PA contents and enhancing antioxidative enzyme activities, thereby improving the photosynthetic capacity of corn under salt stress (Liu et al., 2006b). Pre-treatment with PAs has been shown to enhance the drought tolerance of young forest tree seedlings, such as *Toona ciliate* (Meliaceae) by improving photosynthetic capacity and reducing water loss through changes in leaflet anatomical structure (Liu et al., 2019). The SPD has also been found to protect the structure and function of chloroplasts in rice under salt stress, maintaining chloroplast stability by preserving thylakoid membrane protein components, photosynthetic pigments, and reducing reactive oxygen species and MDA accumulation through enhanced antioxidant enzyme activities (Jiang et al., 2020).

Polyamines and the Ethylene Hormone

PAs are universal phytohormones present in prokaryotic and eukaryotic cells, including plant RNA viruses, with low molecular weight, positively charged polycations (Khan et al., 2022). The biosynthesis of PAs in plant growth processes is regulated by plant hormones, such as auxins, 2,4-D, gibberellins (GA), and ET. These metabolic modifications occur at both endogenous levels of PAs and their biosynthetic enzymes, which are specific to different plant tissues. PAs, whether mobile or non-mobile in plants, can serve as intracellular mediators of hormone actions, thus influencing various physiological processes (Kaur-Sawhney et al., 2003; Sieckmann and Kirschner, 2020). Among the plant hormones, ET has been extensively studied in relation to PA metabolism. PAs and ET play antagonistic roles as metabolites in plant processes. PAs inhibit leaf senescence (Sood and Nagar, 2003; Guo et al., 2018) and fruit ripening (Nambeesan et al., 2008), while ET promotes these processes. Both PAs and ET share interconnected biosynthetic pathways, with S-adenosylmethionine (SAM) serving as a common precursor. Despite their shared routes, their physiological roles are unique and occasionally antagonistic, particularly during leaf and flower withering and fruit ripening (Pandey et al., 2000).

Cold acclimation (CA) increases the levels of PAs in turfgrass species as well as the activity of related enzymes (Shu et al., 2020). ET also rises in the later stages of CA. The increased levels of PAs during biosynthesis may be defensive responses that contribute to the freezing tolerance of zoysia grass. Thus, PAs and ET are involved in CA in zoysia grass. PAs inhibit ET biosynthesis, potentially by blocking the conversion of SAM to ACC and ACC to ET (Sawhney et al., 2003). Conversely, ET effectively inhibits key enzymes, such as ADC and SAMDC, in the PA biosynthetic pathway (Sawhney et al., 2003; Shi and Chan, 2014). Alvarez (2003) suggested a close relationship between proline, PAs, ET, and salt stress tolerance in sunflower. Additionally, the coordination between PA and ET biosynthesis machinery could be beneficial for plants in enhancing plant developmental processes, such as root-to-shoot ratio, nutrient uptake, modulation

of major signaling compounds, and maintenance of optimal cellular metabolism under heavy metal stress (Asgher et al., 2018). However, further research is needed to identify the genes and receptor families involved in ET and PA synthesis and transport within plants, as well as their roles in influencing other physiological processes.

Interfering with the Physiological and Biochemical Mechanisms of Polyamine-, ROS-, NO-, and ABA-Induced Stress Tolerance

Numerous studies have shown that PAs play a crucial role in the physiology of plant stress because they activate genes that respond to stress and interact with other metabolic pathways (Pál et al., 2015; Llanes et al., 2018). PAs exhibit apparent coaction with abscisic acid (ABA), ROS, and nitrogen compounds, thereby establishing synergistic relationships with these components. This highlights the role of PAs as emerging metabolic hubs in plant stress signaling, where they modulate nitro-oxidative homeostasis and ABA signaling (Pál et al., 2015; Llanes et al., 2018). ROS produced by the oxidation of PAs are essential for starting the stress response (Shevyakova, 2013). ABA has been shown to regulate the levels of Pro, PAs, and cytokinin, demonstrating its defensive role. Under saline conditions, exogenous ABA increases the content of free PAs in roots, while promoting the formation of conjugated forms of PAs in leaves, thereby regulating various biological functions (Shevyakova, 2013). Additionally, the movement of cadmium from roots to leaves may be aided by ABA. Different methods of stress tolerance were found when the glycophyte *Solanum lycopersicum* was compared to its wild relative, the halophyte *S. chilense* (Gharbi, 2016). Higher salicylic acid, ethylene (ET), and PAs levels were linked to higher tolerance.

Numerous studies have examined how PAs work in situations like these to reduce salt stress and increase polyamine synthesis. Nitric oxide (NO) and PAs have been found to interact strongly when subjected to salt stress (Napieraj et al., 2020). As a result, stress tolerance is supported (Andronis et al., 2014; Napieraj et al., 2020). NO fills in the knowledge gaps about a number of physiological impacts of PAs. In the root tip and primary leaves of Arabidopsis seedlings, PAs such SPD and spermine SPM have been observed to increase NO production (Tun et al., 2006). Investigations into the interplay between PAs and other stress-responsive molecules have provided new insights into the molecular functions of individual PAs under stress conditions (Agudelo-Romero et al., 2014). Studies on white clover have shown that changes in PAs and phytohormones lead to accelerated proline metabolism, elevated ascorbate-glutathione (AsA-GSH) cycle, and upregulation of relevant genes, resulting in improved drought tolerance. The effectiveness of PAs in reducing oxidative stress, preventing leaf senescence, and preserving growth under drought stress are well known.

Conclusion

The role of polyamines (PAs) in improving plant stress tolerance is significant. In order to comprehend the significance of polyamines under stressful circumstances, numerous study investigations have been conducted. The PA-biosynthetic genes that are activated in stressful environments have been studied using genetic, physiological, and even molecular methods. Important information about using both exogenous application and transgenic PA manipulation to combat environmental stress. In spite of this, many concerns about PAs remain unresolved, including the connection between stress tolerance

and PA accumulation, PA transit, cellular compartmentation, and the signalling cascade that connects PA genes and stress tolerance. Future studies on several prospective research topics can be conducted in relation to these points.

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