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Morpho-Physiological & Biochemical Basis of Regulation of Plant Growth by Polyamines: An Overview of Recent Trends

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ABSTRACT: Polyamines (PAs) play a crucial role in the physiological and biochemical regulation of plant growth. These small, organic molecules, including putrescine (Put), spermidine (Spd), and spermine (Spm), are essential for various cellular processes. They interact with DNA, RNA, proteins, and membranes to affect plant growth. Polyamines are crucial for general growth and development because they play a role in cell division, differentiation, and elongation. These bioactive compounds are actively involved in germination of seeds, shoot and root growth, flowering, and reproductive growth of plants. They contribute to abiotic stress tolerance stress of plant to withstand adverse environmental conditions. Polyamines also act as signaling molecules, modulating gene expression and enzyme activities. Their crosstalk with other growth regulators modulates plant growth and physiology. They are intricately involved in cellular and molecular processes to regulate plant growth and development. Understanding their physiological and biochemical functions provides valuable insights for optimizing agricultural practices and enhancing crop yield.

Keywords: PAs, physiological, biochemical, growth regulation, development.

INTRODUCTION

Polyamines (PAs), which are low molecular weight organic molecules with several amino groups typically substituting hydrogen in alkyl chains, play a variety of roles in plants (Kaur-Sawhney *et al*., 2003). These aliphatic polycations can be found in all cell types and tissues of plants and animals studied extensively (Handa *et al*., 2018). In recent years, significant progress has been made in our understanding of the molecular mechanisms linking these actions to the physiological, biochemical, and molecular functions of both plant and animal systems. It is well known that interactions of PAs with subcellular components are the main mechanism by which these protonated alkylamines modulate cellular functions. According to numerous studies, PAs function as regulatory molecules in key cellular processes such cell division, differentiation, gene expression, DNA and protein synthesis, and apoptosis (Seiler and Raul 2005; Childs *et al*., 2003; Igarashi and Kashiwagi 2010; Alcázar *et al*. 2010). According to Tiburcio *et al*. (2014), PAs such as spermine (Spm), spermidine (Spd), and putrescine (Put) are protonated and have two, three, and four positive charges, respectively. The spermine molecule's charge distribution helps in its ability to bind to the phosphate backbone of DNA outside the major groove (Katz *et al*., 2017). PAs may interact with the minor or major grooves to stabilise the DNA double helix by joining its two strands together. They also support stems and loops in rRNA and mRNA as well as other double-helix structures. PAs can stabilize tRNA conformation through specific binding sites. These interactions with DNA, RNA, and proteins may influence processes like DNA replication, transcription, and translation (Hou *et al*., 2001). PAs can bind to negatively charged phospholipid head groups or other anionic sites on membranes. This binding alters the stability and permeability of these membranes (Tiburcio *et al*., 1993). Exogenous application of polyamines was found to have a significant impact on the development and productivity of plants. In plants, polyamines such spermine, spermidine, and putrescine are crucial for cell division, growth, and proliferation (Handa *et al*., 2018; Chen *et al*., 2019). PAs are universally present in prokaryotic and eukaryotic cells. In living organisms, PAs are most commonly found in three different states viz. free (F-PAs), covalently conjugated (CC-PAs), and non-covalently conjugated (NCC-PAs) (Gholami *et al*., 2013). Higher plants mostly contain PAs in their free form. The most prevalent PAs in higher plants are Put, Spd, Spm, cadaverine (Cad) and thermospermine (Tspm). In plants, polyamines are distributed peculiarly to various tissues and organs. Put was the most common PA in leaves, with levels three times higher than those of Spd and Spm, but Spd was the most common PA in other organs (Chen *et al*., 2019). Exogenous application of polyamines is known to have diverse effects on the growth and development of plants (Table 1).

BIOSYNTHESIS OF POLYAMINES

Polyamines are synthesized through a series of enzymatic reactions from amino acids, primarily arginine and ornithine. The biosynthesis of polyamines in plants involves several key steps, and the three primary polyamines found in plants are putrescine, spermidine, and spermine. The biosynthesis of polyamines typically starts with the amino acid ornithine. Ornithine is derived from another amino acid, arginine, through the action of the enzyme arginase. Arginase catalyzes the hydrolysis of arginine to produce ornithine and urea. Ornithine is then decarboxylated by the enzyme ornithine decarboxylase (ODC), which removes a carboxyl group and converts ornithine into putrescine (Chen *et al*., 2019). Putrescine is the simplest polyamine and serves as the precursor for the more complex polyamines, spermidine, and spermine (Xu *et al*., 2009). Putrescine can be further converted into spermidine through a series of enzymatic reactions. The key enzyme involved in this conversion is spermidine synthase, which transfers an aminopropyl group (from decarboxylated S-adenosylmethionine, or dcSAM) to putrescine to form spermidine. Spermine is synthesized from spermidine through the action of another enzyme called spermine synthase Spermine synthase adds another aminopropyl group to spermidine, using dcSAM as the donor molecule (Soda, 2018). The biosynthesis of polyamines is tightly regulated in plants (Carbonell and Blázquez 2009).

ROLE IN SHOOT AND ROOT GROWTH

Polyamines play a significant role in the growth and development of plants by aiding in cell division, differentiation, and root elongation, (Shi and Chan 2014). Polyamines may be found in root systems in three different forms: free (agmatine, putrescine, spermidine, and spermine), conjugated (such as hydroxycinnamate conjugates), and attached to macromolecules. Treatment with inhibitor, mutation, gene manipulation, or exogenous treatment that alters their endogenous levels can have a significant impact on root growth and subsequent architecture. Polyamines control of cell division and differentiation which play important role in in root apex, lateral and adventitious root formation (Couée *et al*., 2004). Exogenous application of PA was found to increase the root length, root surface area and root volume and number of lateral roots numbers of citrus seedling (Yao *et al*., 2008). According to Kakehi *et al*. (2008), polyamines, notably thermospermine (Tspm) promote stem elongation. Polyamines are known to regulate the embryogenesis process in both angiosperms and gymnosperms (de Oliveira *et al*., 2016). According to Chen *et al*. (2019), a dynamic balance of PAs in vivo must be maintained for the normal development of plant embryos. Exogenous application of polyamines like spermine and spermidine was found to increase the height and number of branches of rose plants (Tatte *et al*., 2016). Foliar application of putrescine was found to increase the plant height, number of branches per plant of chilli (Ghosh *et al*., 2020a). Exogenous foliar spray of Put enhanced plant height, leaf area and grain yield of in wheat under moisture stress (Gupta *et al*., 2012). Exogenous application of Spermidine was found to promote adventitious root formation in apple rootstock by increasing the concentration of endogenous IAA and GA_3 and by decreasing the ABA and JA contents (Wang *et al*., 2020). It was proposed that the increased plant growth by PAs might be attributed to their role as hormonal second messengers of cell proliferation and differentiation in numerous processes or regulating plant sensitivity to auxin/CKs ratio. Furthermore, the metabolism of PAs is thought to be associated with the formation of NO, which is an important signalling component for plant growth (Pál *et al*., 2015).

ROLE IN CELL DIVISION

Polyamines play important roles in cell division, and their effects are primarily related to their involvement in regulating various cellular processes. In higher plants, they can be found not only free but also conjugates bound to phenolic acids (hydroxycinnamic, coumaric, caffeic, or ferulic acid) or biomacromolecules such as proteins and nucleic acids to control enzyme activity, DNA replication, gene transcription, cell division, and membrane stability (Chen *et al*., 2019; González-Hernández *et al*., 2022). They play vital role in regeneration of plant tissues and cell culture. There is a higher prevalence of endogenous polyamines in embryogenic callus, somatic, and zygotic immature embryos as compared to mature and germinating embryos (Chen *et al*., 2019). They are essential for normal cell growth and division, and their levels are tightly regulated in cells. Polyamines interact with DNA molecules and stabilize their structure (Molnar *et al*., 2019). Polyamines can influence the expression of genes involved in cell cycle regulation. Polyamines are known to play a role in the G_1 to S phase transition of the cell cycle. They can affect the transcription of specific genes that control cell division, such as those encoding cyclins, cyclin-dependent kinases (CDKs), and cell cycle inhibitors (Alm and Oredsson 2009) Polyamines can alter chromatin structure by binding to histone proteins (Hou *et al*., 2001).

ROLE IN ABIOTIC STRESS TOLERANCE

Abiotic stress tolerance in plants is greatly influenced by polyamines. The growth and productivity of plants can be significantly impacted by abiotic factors like drought, salt stress, low and high temperatures and heavy metal toxicity (Chen *et al*., 2019). Polyamines are involved in several physiological and biochemical processes that help plants in overcoming these stresses. The accumulation of reactive oxygen species (ROS) in plant cells as a result of abiotic stresses frequently results in oxidative damage to cellular constituents. Spermine and spermidine in particular function as antioxidants and aid in scavenging ROS. They can either directly neutralise ROS or activate antioxidant enzymes like superoxide dismutase (SOD) and catalase to minimize oxidative stress in plants (Minocha *et al*., 2014). Polyamines contribute to the stabilisation of membranes by preventing lipid peroxidation and preserving membrane fluidity. Maintaining cell structure and function under stressful circumstances depends on this protection of membrane integrity. Maize leaves pretreated with Spm and Put exhibited better resistance to the oxidative stress induced by paraquat, according to Durmu and Kadioglu (2005). Exogenous application of Spd significantly increased the levels of Spd and Spm and lowered the content of Put in the roots of cucumber seedlings under the condition of hypoxia. These changes were linked to increased antioxidant enzyme activity, enhanced ROS scavenging capability, and decreased membrane lipid peroxidation, all of which improved tolerance to hypoxic stress (Jia *et al*., 2008; Wu *et al*., 2018), The homeostasis of ions can be disrupted in plant cells by extreme salinity Putrescine can modify ion transporters and channels, assisting in maintaining the equilibrium of important ions like potassium and sodium. Exogenous application of Spm and Spd improved plant development decreased the inhibitory effects of salt stress by promoting photosynthesis and reactive oxygen metabolism (Meng *et al*., 2015; Baniasadi *et al*., 2018). Similarly, salt injury in soybean seedlings under salinity stress was reduced by exogenous application of polyamines (Wang and Bo 2014). This regulation of ion homeostasis is critical for osmotic adjustment and the prevention of ion toxicity (Saha *et al*., 2015). The efficiency of the photosynthetic system and the activity of photosynthetic enzymes can both be increased by polyamines, hence promoting photosynthesis. Exogenous treatment of polyamines (Spm and Spd) was reported to improve photosynthetic ability, antioxidant defence system, and upregulation of calvin cycle-related genes in rapeseed, reducing the negative effects of salinity stress (ElSayed *et al*., 2022). The expression of stress-responsive genes can be affected by polyamines. They can interact with various transcription factors and proteins involved in stress responses and function as signalling molecules. Plants can adapt to abiotic stress situations owing to this modification of gene expression by polyamines. Polyamines can protect proteins from denaturation and degradation caused by abiotic stress factors (Shao *et al*., 2022). According to Chen *et al*. (2019), polyamines are essential for cell survival because they control several complex physiological processes, including abiotic stress responses. Putrescine was found to reduce stomatal density, maintain chloroplast ultrastructure, and minimise plasmolysis in lettuce, all of which increased drought tolerance and water use efficiency (Zhu *et al*., 2019). Exogenous application of Spd and Spm was found to increase the quantum yield of photosystem II, transpiration, stomatal conductivity, chlorophyll content, antenna conversion efficiency, and photochemical quenching coefficient of flag leaves in high-temperature stressed spring wheat (Jing *et al*., 2019). Under stress conditions, polyamines can improve the absorption of important nutrients like iron and zinc. Polyamines (Spm, Spd, and Put), which have a significant impact on pore opening and shutting, can regulate the size of the potassium channel and the size of the pores in the plasma membrane of guard cells. On account of this, PAs can reduce plant water loss (Liu *et al*., 2000). Salt tolerance may be influenced by the function of Spd in the Calvin cycle, protein folding assembly, and suppression of protein proteolysis under salt stress (Li *et al*., 2013). Exogenous application of polyamines (Put, Spd and Spm) was found to improve salt tolerance in rice, barley, tobacco, cucumber, *Atropa belladonna*, salt and heavy metal (Cu, Fe and Ni) tolerance in *Brassica napus*, chilling tolerance in cucumber, ozone tolerance in tobacco, flooding tolerance in welsh onion, copper stress tolerance in *Nymphoides peltatum* and *Raphanus sativus*, dehydration tolerance in *Citrus reticulate*, and heat stress tolerance in Arabidopsis (Quinet *et al*., 2010; Tavladoraki *et al*., 2012; Li *et al*., 2013; Sagor *et al*., 2013; Shi and Chan 2014).

ROLE IN WATER AND MINERAL UPTAKE

Polyamines play a significant role in water and nutrient uptake and transport. Polyamines enhance transpiration and water intake by the root, which in turn increases the uptake and translocation of K^+, Na^+, and Ca^{++} levels that were driven by transpiration (Alcazar *et al*., 2006). Spm application enhanced mineral nutrients content (S, P, K, Ca) in *Phaseolus vulgaris* seedlings (Shah *et al*., 2022). Polyamines can interact with mycorrhizal fungi, forming symbiotic relationships that enhance nutrient uptake. Mycorrhizal fungi can increase the surface area of plant roots available for nutrient absorption, and polyamines may be involved in signaling and nutrient exchange between the plant and fungi (Sharma *et al*., 2021). PAs were found to influence root morphology and arbuscular mycorrhiza (AM) of citrus seedlings. PA application increased root length, root surface area and root volume and number of lateral roots numbers. PAs promoted the fine root length of diameter below 0.4 mm. PAs were found to increase the root colonization by indigenous AM fungi, which implied their beneficial role in nutrient uptake by roots through modified root morphology and mycorrhizal development (Yao *et al*., 2008). Exogenous foliar spray of Put was found to enhance water status in wheat plants under water stress (Gupta *et al*., 2012).

EFFECT ON FLOWERING AND REPRODUCTIVE GROWTH

Polyamines play important roles in the flowering process of plants. Flowering is a complex and highly regulated developmental event in the life cycle of a plant, and polyamines are involved in various aspects of this process (Galston *et al*., 1997). Polyamines, particularly spermidine and spermine, are involved in the regulation of genes associated with flowering. They can influence the expression of flowering-time genes, such as FLOWERING LOCUS T (FT) and CONSTANS (CO), which control the transition from vegetative growth to flowering (Huang *et al*., 2004; Guo *et al*., 2015; Qin *et al*., 2019). Changes in polyamine levels can affect the timing of floral initiation. Polyamines are essential for cell division and differentiation, which are crucial processes during flower bud development Adequate levels of polyamines are necessary for proper floral organ development (Nambeesan *et al*., 2010; Ahmed *et al*., 2017). In Arabidopsis, it was found that flowers contain more PAs than any other organ, and that exogenous PAs significantly enhanced the flowering in plants that were not blossoming well (Applewhite *et al*., 2010). Polyamines are involved in pollen development, maturation, and viability. They play a role in pollen tube growth, which is essential for successful fertilization (Sorkheh *et al*., 2011). Polyamines can delay the senescence of flowers (Nambeesan *et al*., 2010). Increased fruit set and production were seen in vegetable crops when putrescine was applied during the anthesis period (Xu, 2015). Polyamines are known to promote embryogenesis, organogenesis, senescence, and fruit maturation and development (Chen *et al*., 2019)

EFFECT ON SEED GERMINATION

Polyamines play important roles in seed germination and help in breaking seed dormancy by promoting physiological and biochemical changes within the seed. They activate enzymes that break down inhibitors of germination or promote the synthesis of growth-promoting compounds (Yang *et al*.,2016a).According to Zeid and Shedeed (2006), putrescine treatment of alfalfa under drought stress was observed to enhance seed germination and raise all growth indices (hypocotyl length, root and shoot fresh and dry mass).Polyamines may regulate the enzymatic processes of hydrolysis of carbohydrate, lipids and protein ensuring that the seedling has a sufficient supply of energy and nutrients for initial growth (Yang *et al*., 2016a). According to Khan *et al*. (2012), exogenous PAs enhance the germination of hot pepper seeds. The inhibition of PA biosynthesis delays germination of pea seeds (Villanueva and Huang 1993). In rice and soybean seeds, PA levels rise as the seeds mature (Sen *et al*., 1981; Lin *et al*., 1984). Polyamines can help protect the developing seedling from stresses by acting as antioxidants and stabilizing cell membranes (Parvin *et al*., 2014). Polyamines can influence root growth during germination. They may enhance root elongation, enabling the seedling to anchor itself in the soil and access water and nutrients. The seed treatment with Spermine was found to increase the fresh weight and length of the embryo axis of seedlings grown under excess moisture (Sidhu *et al*., 2020). Polyamines can promote the elongation and emergence of the radicle, which is a critical step in seedling establishment. Polyamines can enhance seed vigor, making seeds more resilient and ensuring successful germination even under adverse environmental conditions (Farooq *et al*., 2008).

EFFECT ON GENE REGULATION

Polyamines play a significant role in the regulation of gene expression in plants. They are involved in a wide range of cellular processes, and their interactions with nucleic acids (DNA and RNA) and various proteins can influence the transcription, translation, and stability of specific genes. Polyamines can modify histone proteins, which are involved in chromatin structure and gene regulation (Molnar *et al*., 2019). By binding to histones, polyamines can influence the packaging of DNA into chromatin, making it accessible to transcription factors and RNA polymerase. Polyamines can stabilize RNA molecules, including both messenger RNA (mRNA) and non-coding RNA (Chai *et al*., 2017). Polyamines bind to the grooves of B-form DNA, owing to their overall net positive charge at physiological pH, The thermal stability of B-DNA is increased by polyamines such putrescine, spermidine, and spermine, which can also cause B-DNA to turn into left-handed Z-DNA (Molnar *et al*., 2019). The biological functions of the NCC-PAs in the growth and development of plants include regulation of gene transcription, cell division, DNA replication, enzyme activity, and membrane stability. According to Chen *et al*. (2019), the physiological activity generally increases with the number of amino groups. Putrescine upregulated the genes responsible for ABA production while downregulating the genes responsible for ethylene, jasmonates, and gibberellin biosynthesis. However, spermidine had the complete opposite effect. Contrarily, spermine upregulated the genes that produce ethylene and jasmonates while downregulating the genes that produce gibberellins and abscisic acid. Spermidine positively controlled salicylic acid signalling genes in terms of hormone signalling pathways, and its activity was associated with auxin and cytokinin signalling genes. Putrescine was found to have a neutral to favourable effect in controlling jasmonate signalling. PAs seem to have no effect on the signalling or biosynthesis of brassinosteroids. Putrescine showed a neutral to beneficial effect in terms of regulation of jasmonate signaling. According to Anwar *et al*. (2015), PAs has no effect on the signalling or biosynthesis of brassinosteroids.

Table 1: Effect of exogenous application of polyamines on growth, physiology, and abiotic stress tolerance in crops.

Type of polyamines	Crop	Effect	References
Putrescine, Spermidine Spermine	*Brassica oleracea* L. var. capitata	Helped in maintaining the viability of protoplasts by alleviating oxidative stress and stimulating mitotic activity	Kiełkowska and Adamus (2021)
Spermidine	Tomato	Improved the heat tolerance, pollen growth and tube germination under high temperature stress condition	Maestri *et al*. (2002)
Spermidine Spermine	Cucumber	Post-harvest dipping of polyamines reduced the chilling injury	Velikova *et al*. (2000)

Spermine	Peanuts (*Arachis hypogaea*)	Alleviated the effects of salt stress	Meng *et al*. (2015)
Putrescine	Punjab Ratta cultivar of tomato	Post harvest application enhanced shelf life and quality	Li *et al*. (2004)
Spermine Spermidine	Rice	Alleviated the effects of salinity stress by reducing the loss of electrolytes and amino acids from the roots and shoots, the degradation of chlorophyll, inhibition of photosynthesis, and the down regulation of genes like psbA, psbB, psbE, and rbcL that are encoded by the chloroplast	Chattopadhayay *et al*. (2002)
Spermidine	Herbaceous Peony (*Paeonia lactiflora*)	Increased antioxidant enzyme activities, raised the contents of zeatin and promoted early development of bulbils	Lv *et al*. (2019)
Putrescine	Lettuce	Alleviated the effects of drought stress by increasing antioxidant enzyme activity	Liu *et al*. (2018)
Putrescine	Onion	Foliar application of Putrescine significantly increased bulb length, bulb diameter and weight, as well as yield of onion and quality of bulbs.	Amin *et al*. (2011)
Putrescine	Chilli	Increased chlorophyll and carotenoids content, nitrate reductase activity and relative water content of leaves	Ghosh *et al*. (2020b)
Putrescine	*Thymus vulgaris* L.	Increased growth and oil yield under water stress conditions by altering anatomical features, maintaining chlorophyll concentrations, accumulating total soluble phenolic compounds, and activating certain enzymes.	Abd Elbar *et al*. (2019)
Putrescine	Carrizo Citrange (*Citrus sinensis* Osb. × *Poncirus trifoliata* Raf.) and Volkameriana (*Citrus volkameriana*) rootstocks	Alleviated flooding stress by decreasing the oxidative damage and improving growth, chlorophyll content, stomatal conductance, chlorophyll fluorescence and CO_2 assimilation rate	Mahdavian *et al*. (2020)
Putrescine	Spinach	Increased PPO and CAT activities and proline content, but decreased POD activity under control condition	Öztürk *et al*. (2003)
Putrescine	Gerbera sp.	Increased mycorrhiza colonization in roots, increased the quality of gerbera cut flowers and reduced ions leakage, hydrogen peroxide, malondialdehyde, and lipoxygenase activity, and increased ascorbate peroxidase activity.	Rakbar *et al*. (2022)
Putrescine	Rice cultivars	Induces tolerance against salt stress and influences ethylene synthesis	Quinet *et al*. (2010)
Spermine	Rose flower	Increased vase life and improved flower quality of cut rose flowers	Tatte *et al*. ((2015)
Putrescine	*Oryza sativa* subsp. indica	improved the growing state of callus of indica rice and enhance the development of embryogenic callus.	Tan *et al*. (2017)
Spermidine Spermine	Wheat	Increased grain weight and grain filling rate	Liu *et al*. (2013)
Spermidine	*Cucumis sativus* seedling	Improved salt tolerance through modulation of H_2O_2 signalling	Wu *et al*. (2018)
Spermidine Spermine	Wheat	Improved grain filling and induced drought tolerance	Yang *et al*. (2016b)
Spermidine	Ginseng	alleviates the growth of saline-stressed seedlings through antioxidative defence mechanism	Parvin *et al*. (2014)
Spermidine	Strawberry (*Fragaria ananassa*)	increased the chlorophyll content of leaves	Movahed *et al*. (2012)
Spermine	Arabidopsis	Protects from heat stress-induced	Sagor *et al*. (2013)

		damage by increasing expression of heat shock-related genes.	
Spermidine	Cucumber seedling	Alleviated the effects of salt stress through higher expressions of proteins involved in the SAMs metabolism, protein biosynthesis, and defense mechanisms on antioxidant and detoxification	Li *et al.* (2013)

CONCLUSIONS

Polyamines play integral role in plant growth regulation, impacting various physiological and biochemical processes. These bioactive compounds have the potential for field use and are also known to protect plants from a variety of biotic and abiotic challenges. Understanding their roles at the molecular level can open avenues for targeted manipulation of polyamine metabolism for crop improvement and stress tolerance.

FUTURE SCOPE

The role polyamines as plant growth regulators can be established by studying their effect on different type of crops. More biochemical and molecular studies are needed to be carried out to understand the physiological basis of growth regulation by polyamines.

Conflict of Interest. None.

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