Revisiting the Role of Polyamines in Plant Growth and Abiotic Stress Resilience: Mechanisms, Crosstalk, and Future Perspectives

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Abstract

Phytohormone-like plant growth regulators are becoming hallmarks in plant stress biology since they can offer incredible benefits to plants, such as increased crop output, improved growth features and stress tolerance. Among them polyamines (PAs) such as putrescine (Put), spermidine (Spd), and spermine (Spm), are recognized as important bio-stimulants that can boost plant growth, productivity, and stress tolerance, whether provided exogenously or synthesized endogenously by genetically engineered plants. However, the precise mechanism by which they regulate plant development and stress responses and their interactions with other signaling molecules remains unknown. Hence, unravelling the molecular complexity of PAs signaling in plants can help us to improve crop stress resistance and yield. This review focuses on the distribution, biosynthesis, and role of PAs in plant growth and development, abiotic stress tolerance, and the involvement of a possible novel interlinked signaling cascade between them. Further, we focused on our current understanding and knowledge gaps of how PAs interact with other signaling molecules like hormones and nitric oxide (NO) to regulate plant growth and stress tolerance in a coordinated manner. We also provide an overview of PA signaling in plants, focusing on calcium (Ca^{2+}) and reactive oxygen species (ROS) under abiotic stress, and some key insights into omics and nanotechnology approach for future research.

Introduction

Plants experience continuously changing environmental conditions and various stresses throughout their life cycle. Environmental stresses negatively affect crop growth and development, which reduces their productivity (Ali et al. 2018a). The continuously increasing global population poses a major challenge to achieving agricultural productivity, and the situation is further worsened by the reduction in arable land due to abiotic stresses (Verma 2016). Abiotic stresses such as temperature, drought, and salt are the primary causes behind the decrease in the yield of most crops by > 50% worldwide (Rodríguez et al. 2006). In the current climate change scenario with global warming, abiotic stresses are becoming frequent and more severe (Bano et al. 2020). Unfortunately, climate change has greatly hampered the productivity of important staple crops, including rice, wheat, and maize, presenting considerable challenges in many countries (Syed et al. 2022). It is predicted that developing and underdeveloped countries may experience greater negative effects due to climate change and a lack of adaptation capacity (Farooq et al. 2022). Therefore, it is essential to fill the knowledge gaps between climate change and food security by implementing mitigation and adaptation measures for a climate-smart food production system that ensures food security (Farooq et al. 2022). In addition, the development of climate-smart, multiple stress-tolerant, and high-yielding crops is crucial for the economy and sustainable agriculture.

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In response to stress, plants upregulate various genes involved in synthesis of biological molecules such as secondary metabolites, phytohormones, osmolytes, and PAs, which can mitigate the effects of stress and maintain cellular homeostasis (Tiburcio et al. 2014; Zhu, 2016; Ali et al. 2017). These molecules can act independently or interact with each other to alleviate stress responses. PAs are one of the oldest known substances in biochemistry (Galston 1991). The first PA identified was Spm as phosphate crystals in aging human spermatozoa in ~ 1677 by Antonie van Leeuwenhoek (Leuwenhoek 1677). About 200 years later, in 1885, Put and cadaverine (Cad) were identified from putrefying cadavers by Ludwig Brieger (Brieger 1885). In the 1920s, Harold Ward Dudley and his colleagues reported the chemical composition and synthesis of Put, Spm, and Spd (Dudley et al. 1926, 1927). PAs are aliphatic amines, or nitrogen-containing low molecular weight compounds present ubiquitously in all living organisms (Kaur-Sawhney et al. 2003; Vuosku et al. 2018). The diamine-Put, triamine-Spd, and tetra-amine-Spm are the major PAs produced in plants and animals. Plants also synthesize less abundant PAs such as thermospermine (Tspm, another tetra-amine), Cad, 1,3-diaminopropane, homoSpd, norSpd, homoSpm, norSpm, aminopropyl homoSpd, and methyl-Spd (Martin-Tanguy 2001). Tspm has been detected in archaea, diatoms, and plants but not in animals or bacteria (Michael 2016). The PA biosynthetic pathways have been well established, credit to the availability of mutant eukaryotes and prokaryotes, which lack functional genes involved in PA biosynthesis (Tabor and Tabor 1984). In plants, PAs occur as free aliphatic PAs or as conjugates bound to phenolic compounds and biological macromolecules like deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and proteins due to their cationic nature (Gholami et al., 2013). Plant PA content varies in different species, organs, and developmental stages (Tiburcio et al. 2014). PAs are involved in a wide range of physiological processes such as plant growth and development, including organogenesis, floral initiation, embryogenesis, fruit development and maturation, leaf senescence, and biotic and abiotic stress responses (Fig. 1) (Galston and Sawhney 1990; Liu et al. 2016a; Ebeed et al. 2017; Zhang et al. 2017; Mattoo and Sobieszczuk-Nowicka 2018; Pál et al. 2019). The content of PAs increases multiple folds in response to various abiotic stresses and nutrient deficient conditions (Alcázar et al. 2006a, b; Smith and Richards 1962; Yoshikawa et al. 2007; Gill and Tuteja, 2010; Minocha et al. 2014; Pal et al. 2015; Takahashi et al. 2017; Chen et al. 2019). PAs play a key role in stabilizing membranes, scavenging free radicals, DNA replication, transcription, and translation, affecting the activity of enzymes like RNase, proteases, and others, and interacting with phytohormones, phytochrome, and ethylene (ET) biosynthesis (Slocum et al. 1984; Galston and Sawhney 1990; Alcázar et al. 2010; Qi et al. 2010; Childs et al. 2017). This review provides a comprehensive and critical evaluation/metanalysis of the literature on the role of PAs in plant growth development and stress resilience

Fig. 1 A general illustration highlighting the role of PAs in different physiological processes a) growth and development, b) abiotic stress response, c) defense response, and d) aging in plants
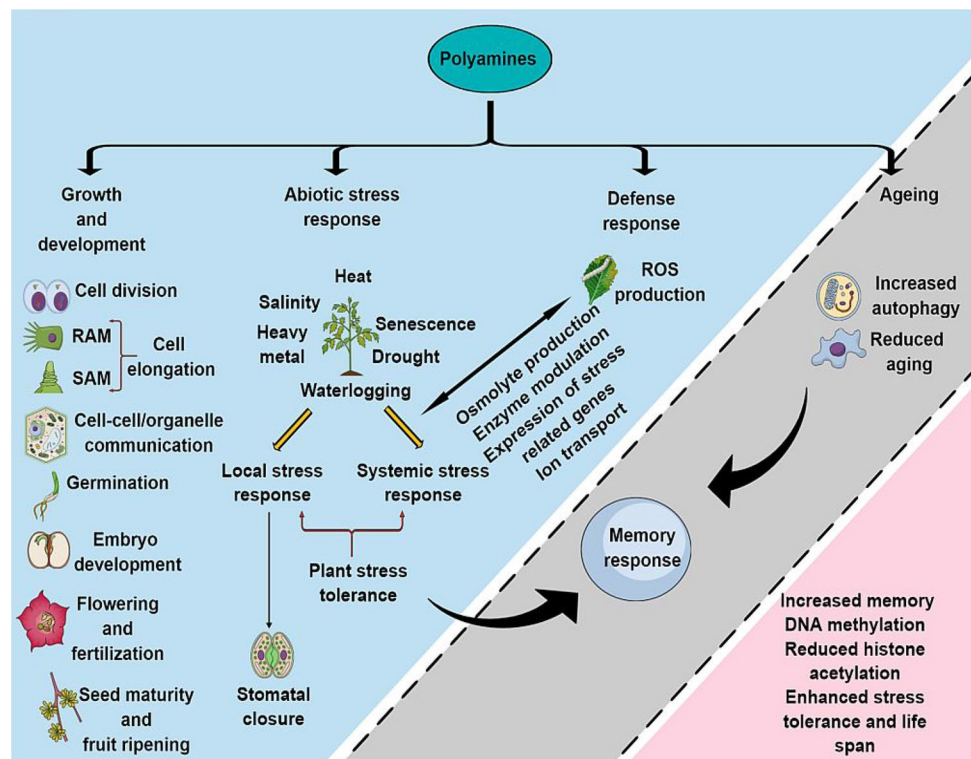
(Fig. 2). This article discusses the distribution, biosynthesis, and function of PAs in plants, emphasizing their involvement in improving growth and abiotic stress tolerance. In addition, we also highlight the crosstalk of PAs with other signaling molecules like NO and hormones. We also emphasize the role of multi-omics in unraveling the molecular complexity of PA signaling in plants. Finally, we highlight the role of nanoparticles in increasing PA delivery and efficacy for crop improvement.

Distribution of Polyamines in Plants

PAs are synthesized ubiquitously in prokaryotes and eukaryotes, including simpler plant RNA viruses, phytoplanktons, and complex plants and animals (Liu et al. 2016a). In higher plants, PAs are predominantly present in their free form. The commonly produced PAs in plants are Put, Spd, Spm, Tspm, and Cad, while the other PAs are only found in a few plant species or under certain conditions (Martin-Tanguy 2001; Sobieszczuk-Nowicka, 2017; Takahashi et al. 2017). PAs show plant tissue-, organ-, and stage-specific distribution (Fig. 3). For example, the total content of major PAs
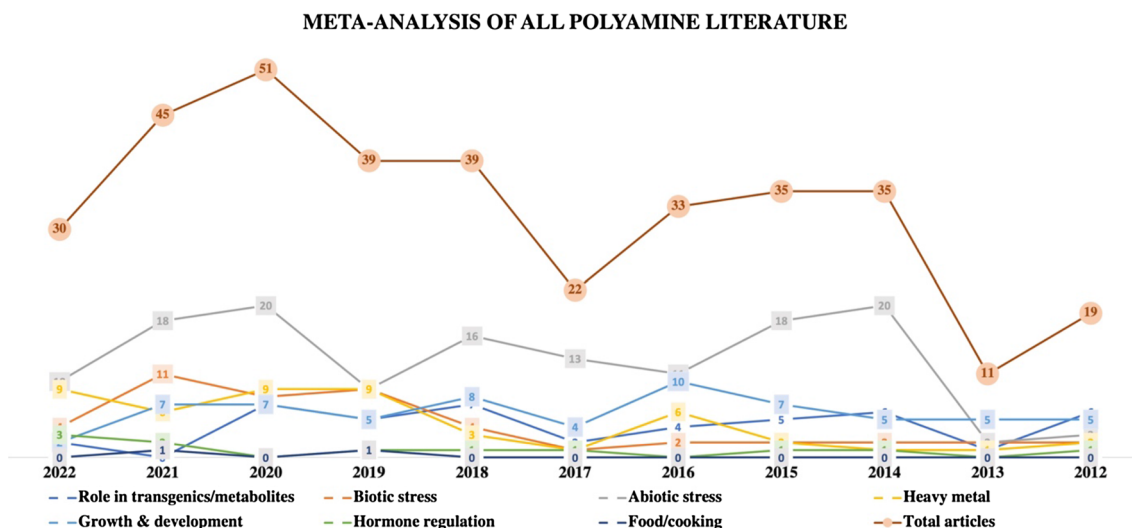

META-ANALYSIS OF ALL POLYAMINE LITERATURE

Fig. 2 Graph showing an increase in the number of published papers on PAs in the past decade (2012–2022). The graph also shows the maximum number of systemic reviews on PAs modulating abiotic stress tolerance in plant systems

Fig. 3 Distribution and storage of PAs in different organs in plants such as vegetative (leaf, stem, root), reproductive (flower, seed, fruit, tuber) organs and other organelle compartments

Polyamine distribution in plants
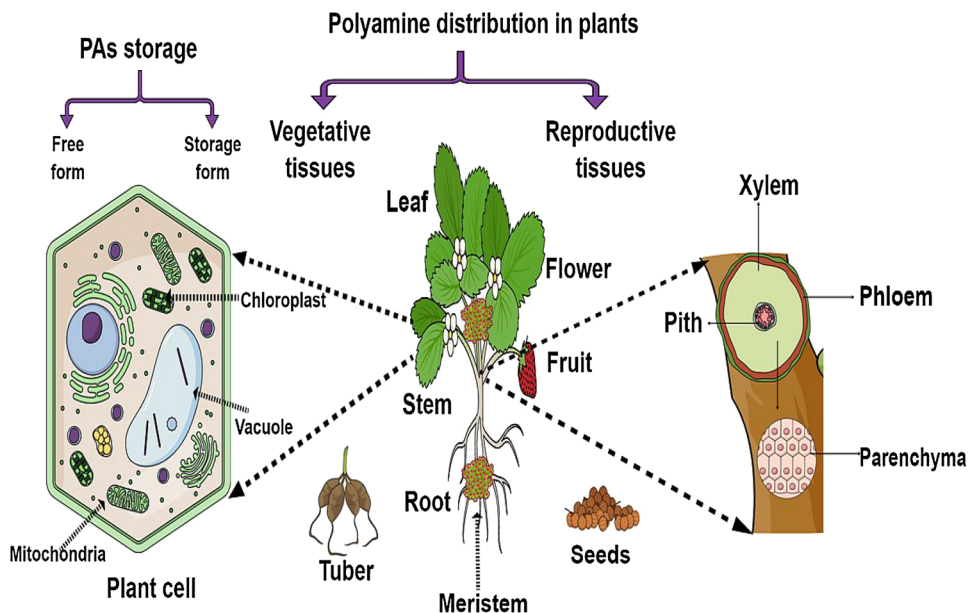
(Put and Spm) in tobacco plants was higher in young leaves and apical meristems than in old/mature leaves, while Spd content showed a contrasting pattern. The higher PAs (Spd and Spm) are mainly synthesized in aerial plant organs like shoot apical meristems, while Put is synthesized in hypogeous (underground) plant organs. Among the major PAs, Spm and Spd are more uniformly distributed across the whole plant than Put (Paschalidis and Roubelakis-Angelakis 2005). The PAs show great variation in their accumulation within the cells. In carrot cells, Put was found mainly in the cytoplasm, while Spm was in the cell wall (Cai et al. 2006). The distribution pattern of PAs in plants correlates with their functional requirement. In general, it was observed that more vigorous plant growth and efficient metabolism are associated with greater PA biosynthesis and higher PA contents (Paschalidis and Roubelakis-Angelakis 2005; Cai et al. 2006).

Biosynthesis of Polyamines and Its Regulatory Mechanisms

PA biosynthesis in plants has been studied in detail and discussed in many reviews (Slocum et al. 1984; Evans and Malmberg 1989; Martin-Tanguy 2001). In plants, biosynthesis of PAs occurs via three different routes, all starting with arginine (Arg). The first and the main route of PA biosynthesis in plants (Hao et al. 2005) involves the conversion of Arg into intermediate agmatine (Agm) by arginine decarboxylase (ADC) (Docimo et al. 2012). Then, Agm loses its $-NH_3$ group to form N-carbamoyl putrescine (NCPA), which is hydrolyzed by N-carbamoyl putrescine amidohydrolase (NCPAH) to form Put, carbon dioxide (CO_2), and ammonia (NH_3). The second route of PA biosynthesis in plants involves hydrolysis of Arg by arginase to form ornithine (Orn), which is then decarboxylated by ornithine decarboxylase (ODC) to produce diamine-Put and CO_2 (Pegg 2016). The absence of the *ODC* gene in *Arabidopsis* and other members of the Brassicaceae indicated that PA synthesis through the ornithine pathway is not essential for normal growth (Hanfrey et al. 2001). In the third route, Arg is first deiminated to citrulline (Cit) by arginine deiminase. Later, the Cit is decarboxylated by citrulline decarboxylase (CDC) to form Put (Hanfrey et al. 2001; Pegg, 2016). Put is further converted into Spd and then to Spm and Tspm by successive addition of an aminopropyl group, and these aminopropyl transfer reactions are catalyzed by Spd-synthase (SPDS), Spm-synthase (SPMS), and Tspm-synthase (TSPMS), respectively (Fig. 4). The aminopropyl groups are derived from methionine in a separate enzymatic process. First, methionine is converted into S-adenosylmethionine (SAM) by methionine adenosyltransferase (MAT), and then SAM is decarboxylated by SAM decarboxylase (SAMDC). The resulting decarboxylated SAM (dSAM) acts as an aminopropyl donor for PA biosynthesis. SAM is a common precursor for both PAs and ET.

An alternative Spd biosynthetic pathway was identified in grass pea (*Lathyrus sativus*), which involves the conversion
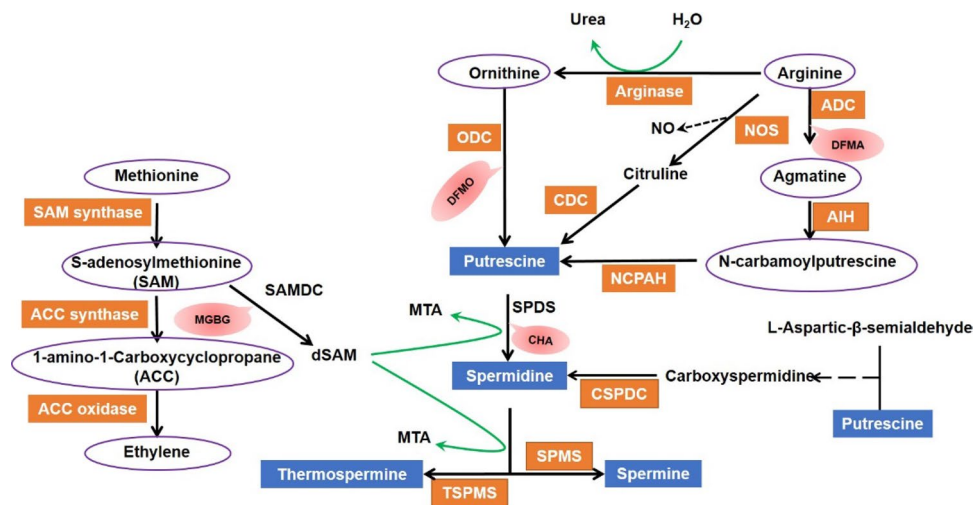

Fig. 4 Biosynthesis pathway of major PAs in plants. NO, Nitric oxide; ODC, ornithine decarboxylase; DFMO, difluoromethylornithine; CDC, citrulline decarboxylase; NOS, nitric oxide synthase; ADC, arginine decarboxylase; DFMA, difluoromethylarginine; AIH, agmatine iminohydrolase; N-carbamoylputreseine amidohydrolase; CHA, clohexylamine, the inhibitor of SPDS; CSPDC, carboxynorspermidine/carboxyspermidine decarboxylase; SPMS, spermine synthase; SPDS, spermidine synthase; TSPMS, thermospermine synthase; SAMDC, S-adenosylmethionine decarboxylase; SAMS, S-adenosylmethionine synthase; ACS, 1-aminocyclopropane-1-carboxylate synthase; ACO, 1-aminocyclopropane-1-carboxylate oxidase; MGBG, Methylglyoxal-bis (guanylhydrazone), the inhibitor of SAMDC; dSAM, decarboxylated SAM; MTA, 5′-methyl-thioadenosine; NCPAH, N-carbamoylputerscine amino hydrolase

of aspartic acid or homoserine into aspartic semialdehyde, which then combines with Put to form a Schiff's base. The Schiff's base is then reduced to Carboxy-Spd, which is later decarboxylated to Spd (Fig. 4). This pathway is an important alternative for Spd biosynthesis when SAM (Propylamine donor) is limited (Srivenugopal and Adiga 1980). Decarboxylases, including ADC, ODC, CDC, and SAMDC, are important enzymes involved in PA biosynthesis and are key regulators of PA content in plants. SAMDC regulates both PA and ET biosynthetic pathways (Fig. 4). Many studies were conducted using inhibitors of key enzymes involved in PA biosynthesis to understand the role of PAs in plant growth and development. The most commonly used enzyme inhibitors of PA synthesis include Difluoromethylornithine (DFMO) and Difluoromethylarginine (DFMA), which are irreversible inhibitors of ODC and ADC, respectively (Bey et al. 1987; Bitonti et al. 1987). Methylglyoxal-bis guanyl hydrazone (MGBG) competitively inhibits SAMDC (Williams-Ashman and Schenone 1972), and Cyclohexylamine (CHA) is a competitive inhibitor of spermidine synthase (Hibasami et al. 1980).

Polyamine Catabolism

Oxidation and back conversion are the only mechanisms identified for the degradation of PA in plants. Higher PAs such as Spd, Spm, and Tspm content in plants is regulated by specific oxidases, including diamine oxidase (DAO) and polyamine oxidase (PAO) (Smith and Barker 1988). The PAOs are mainly involved in the oxidation of major PAs like Spd, Spm, and Tspm, while DAOs catalyze the oxidation of primary PAs like Put. For example, Put is oxidized to form 4-aminobutanal, NH_3, and hydrogen peroxide (H_2O_2). This reaction is catalyzed by DAO, which requires copper (Cu^+) and pyridoxal phosphate as its cofactors. The 4-aminobutal is then spontaneously cyclized to form pyrroline (Pyrr).

Then, pyrroline dehydrogenase (Pyrr-DH) converts Pyrr into γ-aminobutyric acid (GABA), which is further converted into succinate that enters the Krebs cycle (Fig. 5). A high amount of DAOs was observed in dicots, but very few species were reported to contain DAO encoding genes. PAOs belong to the flavoprotein superfamily and non-covalently bind to flavin adenine dinucleotide (FAD). Monocots are found to have high levels of PAOs. The oxidation of Spm by PAO results in the production of 1,3-diaminopropane, H_2O_2, and 1-(3-aminopropyl)-4-aminobutanal, which later spontaneously cyclizes to form 1,5-diazobicyclo [4.3.0.] nonane. The oxidation of Spd by PAO produces 1,3-diaminopropane, H_2O_2, and 4-aminobutanal, which spontaneously cyclizes to yield Pyrr (Lennarz and Lane 2013). The oxidation of PAs by PAOs does not produce ammonia. It was also reported that some plant PAOs could reverse catalyze PA biosynthesis. It was observed that exogenously applied Spd was converted into Put in *Arabidopsis* and sunflower (*Helianthus tuberosus*). In *Arabidopsis*, *AtPAO1* and *AtPAO4* can convert Spm to Spd, while *AtPAO2* and *AtPAO3* can transform Spm to Spd and then to Put. Similarly, in the false brome (*Brachypodium distachyon*), *BdPAO2* converts Spm or Tspm to Spd and then to Put, but *BdPAO3* preferentially catalyzes the conversion of Spm to Spd. PAs can bind to nucleic acids and proteins and regulate replication, transcription, translation, and various physiological processes in plants. Therefore, it is necessary to understand the role and functional mechanism of PAs in plant growth and development under biotic and abiotic stress conditions.

Role of Polyamines in Plant Growth and Development

Polyamines are involved in plant growth and development, including seed germination, organogenesis, tissue lignification, abscission, senescence, embryogenesis, flowering,

Fig. 5 Oxidation mechanism of major PAs in plants. PAO, polyamine oxidase; Pyrr, pyrroline; GABA, γ-aminobutyric acid; Pyrr-DH, pyrroline dehydrogenase; H_2O_2: hydrogen peroxide; O_2, oxygen; H_2O, water; NH_3, ammonia; DAO, diamine oxidase
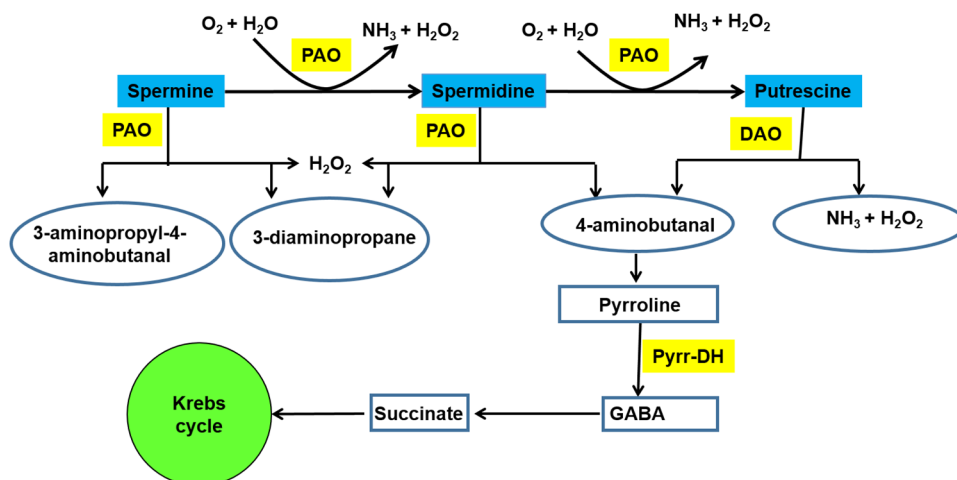
pollination, fruit development, and ripening (Fig. 1). Transgenic methods, exogenous PAs, and PA synthetic inhibitors have been used to validate the role of PAs in plants. In this review, we summarize recent research on the effects of PAs on plants and provide a foundation for future studies on the mechanisms of action of PAs in plant growth and development.

Polyamines Enhance Seed Germination and Vegetative Growth

Seed germination is one of the most complex physiological processes in the plant life cycle. According to previous reports, the PA content increases in the growing tissue during the early stages of germination. It was reported that considerable amounts of Cad and Put accumulated in the hypocotyl and radicle during soybean seed germination and diminished in the cotyledons. Spd was observed to be synthesized and accumulated in the embryonic axis, while Spm was completely undetectable in the germinating seeds (Lin 1984). Similarly, the growing embryo of maize (*Zea mays*) showed an increase in Put content while Spd and Spm contents were decreased (Sepúlveda and Sánchez de Jiménez 1988). PAs play a significant role in cell division and elongation; they are necessary for the plant's vegetative growth, including leaf area, fresh and dry weight of shoots and roots, and flower number. In strawberry (*Fragaria ananassa*), the application of Spd increased the chlorophyll content, while Put had no effect or decreased the chlorophyll content (Movahed et al. 2012). The application of Spd and Put negatively affected the number of runners but positively increased specific leaf weight, fresh and dry weight of shoot and root, truss number, flower per truss, and yield per plant (Movahed et al. 2012). Similarly, the foliar application of Put and Spd showed significant improvement in the vegetative characters of gerbera (*Gerbera jamesonii*) (Saeed et al. 2019). Transgenic overexpression of *GhSAMDC* in tobacco (*Nicotiana tabacum*) plants resulted in rapid vegetative

growth, including a larger leaf area and greater plant height than wild-type plants (Zhu et al. 2020). Some examples of the exogenous application of PAs and transgenic expression of PA biosynthetic genes are provided in Tables 1 and 2, respectively.

Role of Polyamines in Flower Development, Fertilization, Self-Incompatibility, and Embryo Development

The flower bud differentiation is a complex morphogenetic process regulated by various factors, including photoperiod, vernalization, nutrition, and water availability, and is achieved by interaction and coordination of phytohormones and PAs (Xu 2015). In mums (*Chrysanthemum indicum*), a higher content of PAs promoted floral bud differentiation (Guo et al. 2015). The exogenous application of 1.0 mM Spm accelerated the vegetative growth and promoted early flowering in tobacco (Zhu et al. 2020). Further, the transgenic overexpression of *GhSAMDC* caused early flowering by five days compared with flowering time of wild-type plants (Zhu et al. 2020). Similarly, foliar application of 100 mg L^{-1} Spd causes early flowering, and 100 mg L^{-1} Put increases the number and size of flowers in gerbera (Saeed et al. 2019). In strawberries, the exogenous application of Put and Spd increased the truss number and number of flowers per truss (Movahed et al. 2012).

The entire process of microsporogenesis and fertilization is well regulated by PA homeostasis. In *N. tabacum,* the transcripts of ADC and ODC mainly involved in the biosynthesis of Put were found in abundance at the uninucleate and the bicellular microspore stage, and transcripts for Put oxidation were increased (Bokvaj et al. 2015). The accumulation of conjugated PAs from the tapetum to the cell wall of the pollen before dehiscence is necessary for pollen structure, pollen tube growth, and fertilization in *Arabidopsis* (Fellenberg et al. 2009). Further, the oxidation of PAs plays a crucial role in pollen development; the H_2O_2 released

Table 1 Studies showing the role of PAs in different plant systems

Plant	PA (concentration)	Outcome	References
Tobacco (*N. tabacum*)	Put (0.01 and 0.1 mM)	Increased germination and seedling vigor	Xu et al. (2011)
Gerbera daisy (*G. jamesonii*)	Spd and Put (100 mg L^{-1})	Increased number and size of the flower	Saeed et al. (2019)
Thyme (*Thymus vulgaris* L)	Put (20 mg L^{-1})	Drought tolerance	Mohammadi et al. (2018)
Wheat (*Triticum aestivum* L)	Spd or Spm (1 mM)	Increased grain filling and grain weight	Yamaguchi et al. (2007)
	Spm and Spd (0.5 mM)	Enhanced waterlogging tolerance	Du et al. (2018)
	Spm (0.5 mM)	Tolerance to Cd and Cu toxicity	Groppa et al. (2007)
Rice (*Oryza sativa*)	Pur (0.1 mM)	Salinity tolerance	Lutts et al. (1996)
Soybean (*Glycine max*)	Spd, Spm, and Put (100, 150, 150 mg L^{-1}, respectively)	Salinity tolerance	Wang and Yin (2014)
Onion (*Allium cepa* L)	Put (20–100 mg L^{-1})	Increased leaf growth and bulb yield	Yamaguchi et al. (2007)

Table 2 Transgenic studies showing the role of PAs in different plant systems

Plant	Gene	Source	Outcome	References
Rice (*O. sativa*)	*ADC* (EC 4.1.1.19)	Oats (*Avena sativa*)	Salt tolerance	Roy and Wu (2001)
		Jimsonweed (*Datura stramonium*)	Drought tolerance	Capell et al. (2004)
	SAMDC (EC 4.1.1.50)	Hybrid crop (*Tritordeum*)	Salt tolerance	Roy and Wu (2002)
Tobacco (*N. tabacum*)	*SAMDC* (EC 4.1.1.50)	Cotton (*Gossipium hirsutum*)	Improved vegetative growth and early flowering	Zhu et al. (2020)
		Human (*Homo sapiens*)	Salinity, drought, and fungal wilts (caused by *Verticillium ahlia* and *Fusarium oxysporum*) stress tolerance	Waie and Rajam (2003)
Tomato (*Solanum lycopersicum* L)	*SPDS* (EC 2.1.5.16) *SAMDC* (EC 4.1.1.50)	Budding yeast (*Saccharomyces cerevisiae*)	Delayed ripening of fruits and heat stress tolerance	Mehta et al. (2002); Cheng et al. (2009); Nambeesan et al. (2010)
	ODC (EC 4.1.1.17)	Mouse (*Mus musculus*)	Enhanced fruit quality	Pandey et al. (2015)
Arabidopsis (*Arabidopsis thaliana*)	*SPDS* (EC 2.1.5.16)	Black seed squash (*Cucurbita ficifolia*)	Enhanced tolerance to chilling, freezing, salinity, and drought	Kasukabe et al. (2004)

during oxidation of Spd and Spm is involved in cell wall stiffening in pollen development (Fincato et al. 2012). Similarly, RNAi-mediated downregulation of tapetal SAMDC in tomato (*S. lycopersicum*) resulted in partial or complete sterility in transgenic plants (Sinha and Rajam 2013). Competitive inhibition of enzymes involved in PA biosynthesis resulted in the formation of abnormal pollen grains with reduced viability in many plants (Falasca et al. 2010). Further, a germination medium supplemented with exogenous PAs resulted in the restoration of germination and fertilization of aged pollen grains (Song and Tachibana 2007). High PA biosynthesis enzyme activities were observed during the early stages of pollen germination in many plants, and competitive inhibition of PA biosynthetic enzymes by bis (guanylhydrazones) severely affected pollen germination (Antognoni and Bagni 2008).

When pollen grains land on the stigma, they must undergo a non-self- and self-recognition process, also known as self-incompatibility (SI) response. It is the most important evolutionary process in angiosperms to prevent inbreeding (Takayama and Isogai 2005). There are two different types of SI systems recognized in plants. The stigma of the female plant either consists of a cell membrane receptor as in corn poppy (*Papaver rhoeas*) or releases molecules such as a stigma/ style ribonuclease (S-RNase). S-RNase enters the incoming pollen grains and gets degraded in the compatible pollen grains, whereas in the incompatible pollen S-RNase causes degradation of the RNAs of the pollen (Dresselhaus and Franklin-Tong 2013). High concentrations of PAs like Put, Spd, and Spm inhibit the S-RNase activity in apples (*Malus domestica*) and potatoes (*Solanum tuberosum*) (Altman 1982; Speranza et al. 1984).

PAs regulate embryogenesis in both angiosperms and gymnosperms (De Oliveira et al. 2017). Increased PA content is necessary for embryo development. The requirement for the type of PA varies with the embryo growth stage from the multicellular proembryo, globular, heart-shaped, and torpedo stages to the cotyledon stage (Krasuska et al. 2014). Further, efficient somatic embryogenesis and formation of complete plantlets are closely regulated by endogenous phytohormones, such as Indole acetic acid (IAA), cytokinins (Cyt), abscisic acid (ABA), and PAs. Many studies have shown that PAs play a key role in inducing cell division and promoting regeneration in plant tissue and cell cultures (Minocha and Minocha 1995; Yadav and Rajam 1997; Vondráková et al. 2015). In Korean ginseng (*Panax ginseng*) tissue culture, the addition of Spd (1 mM) to the induction and regeneration medium resulted in a 5- and 4- fold increase in embryonic structures, respectively (Kevers et al. 2000). Similarly, the application of appropriate combinations of Put, Spd, and Spm to the culture medium resulted in increased plantlet development or embryo germination rates in seedless grapevine (*Vitis vinifera*) (Jiao et al. 2018).

Role of Polyamines in Seed Maturity, Fruit Ripening, and Senescence

The role of PAs in fruit development and senescence has received much attention because of the probable metabolic relationship between PAs and ET via the propylamine group of SAM. In soybean (*G. max*), the Put content decreased to undetectable levels during seed growth and maturation, while Spm and Spd levels increased continuously (Lin et al. 1984). In the past decade, many reviews have focused on

the role of PAs in fruit development and ripening (Gao et al. 2021). Among climacteric tomato fruits, PA levels vary between cultivars during fruit ripening. The Put, Spd, and Spm content decreased during fruit ripening in the tomatoes, PikRed and Rutgers, whereas fruits from the cultivar Liberty ripened slowly and exhibited a prolonged shelf life, accumulating high quantities of Put during ripening (Dibble et al. 1988; Saftner and Baldi 1990). Similarly, in cherry tomato (*S. lycopersicum* var. *cerasiforme*), the fruits gradually accumulate Put during ripening while the Spd and Spm content decreases (Tsaniklidis et al. 2016). Transgenic overexpression of the yeast SPDS gene in tomatoes results in high quantities of Spd in fruits, which causes delayed ripening and prolonged shelf life (Nambeesan et al. 2010). The Spd and Spm content decreased gradually while Put content increased during ripening of banana (*Musa acuminata*) and peach (*Prunus persica*) (Liu et al. 2006; Borges et al. 2019). In apples, Spd was reported to be the predominant form of PAs during fruit development and ripening (Zhang et al. 2003). PAs also regulate the growth and ripening of non-climacteric fruits. Even though the transcript abundance of ADC, SPDS, and SPMS are high in grapes, the PA content decreases during ripening due to oxidation of PAs, indicating the role of PA catabolism during grape berry ripening (Agudelo-Romero et al. 2013).

In contrast, PA oxidation negatively impacts fruit ripening in strawberries. RNAi-mediated downregulation of *FaPAO5* results in the accumulation of Spd and Spm and fruit ripening (Mo et al. 2020). Plant leaf senescence is the terminal step in the plant's life cycle, involving a multi-layer control, including hormonal cues, predominantly ET. Recently, many studies have been conducted on the role of PAs in leaf senescence. Exogenous applications of PAs were shown to delay senescence in oat (*A. sativa*), and petunia (*Petunia × atkinsiana*) leaves (Mizrahi et al. 1989). The excised oat leaves stored under dark conditions showed a decreased Spm content (Kaur-Sawhney et al. 1982). There was an increase of transcripts corresponding to PA catabolism enzymes, DAOs and PAOs, in response to dark-induced senescence of barley leaves. Further, inhibition of PAOs decreased H_2O_2 levels, indicating a connection between dark-induced senescence and PA catabolism (Ioannidis et al. 2014). Similarly, *Arabidopsis* PA back-conversion oxidase mutants, which cannot process the conversion of Spm to Spd 'or' Spd to Put, showed a delayed dark-induced senescence response (Sequera-Mutiozabal et al. 2016). Lee et al. (1997) found that Spm delayed the senescence of cut carnation flowers and reduced ET production by regulating the transcription and activities of ET biosynthesis enzymes ACC oxidase and ACC synthase in the petals (Lee et al. 1997). The exogenous PAs' ability to prevent senescence may be linked to their ability to block ET production and membrane stability.

Further, some examples of the exogenous application of PAs and transgenic expression of PA biosynthetic genes for improving plant growth traits and stress resilience in different crops are provided in Tables 1 and 2. PAs are important growth regulators whose mechanisms of action are distinct from those of plant hormones. Despite the availability of high-throughput technologies, the molecular processes by which PAs influence growth responses remain unknown. Further research is needed to better understand the PA production and the metabolic pathways and molecular mechanisms regulated by PAs, which will lead to novel strategies for increasing plant growth and survival in changing environments.

Harnessing the Potential of Polyamines in Abiotic Stress Tolerance

PAs modulate plant defense against various abiotic stresses and are essential for plant development and other physiological processes (Choudhary et al. 2022; González-Hernández et al. 2022; Islam et al. 2022). PAs anti-stress properties are attributed to their acid-neutralizing and cell wall-stabilizing abilities and strong antioxidant activities. It has been discovered that both endogenous synthesis and exogenous supply of PAs and genetic transformation of PA biosynthetic genes provide stress resilience against a wide range of abiotic stressors (Tables 1 and 2). In this review, we have discussed in depth the role of PAs against different abiotic stresses with multiple case studies.

Role of Polyamines in Mitigating Heat Stress in Plants

Temperature stress significantly impacts plant traits like photosynthesis and seed germination, as well as causes oxidative stress, which can lead to reduced plant development and agricultural output (Hasanuzzaman et al. 2013; Raza et al. 2021). Temperature stress in plants can be classified into high-temperature (> 25 °C) and low-temperature stress; the latter is further classified into cold stress (0–15 °C) and freezing stress (< 0 °C), all resulting in considerable yield reduction in the majority of key crops (Raza et al. 2021). Climate change is causing more heat waves, wildfires, and desertification, severely threatening food security (Raza et al. 2022). PAs play a significant role in many plant functions, and the physiological mechanism of thermo-tolerance varies among plant species. Hence, the pattern of changes in PA content in response to high-temperature stress differs among plant species. Under high-temperature stress, PAs can promote photosynthesis by increasing the antioxidant capacity and maintaining the osmotic balance of plants. In Chinese kale (*Brassica alboglabra* Bailey), 6 days of heat

stress induced the accumulation of PAs like Spd, Spm, and Put, but the increments were not maintained over longer stress periods (Yang and Yang 2002). It was reported that heat stress tolerance in alfalfa (*Medicago sativa*) was due to high endogenous Spd content and lower Spm and Put content in the leaves (Shao et al. 2015). Transcriptome analysis of pigeon pea (*Cajanus cajan*) and its wild relatives under heat stress conditions showed upregulation of TSPMS (ACL5) and SAMDC genes, indicating the significance of PAs in heat stress tolerance in pigeon pea (Ramakrishna et al. 2021). Similarly, PAs bind to phospholipids in the membrane during cold stress and prevent cell lysis (Li and He 2012). An increase in Put content along with chilling damage was observed in Bell pepper fruit (*Capsicum annuum* L. cv. Lamuyo) and Zucchini fruits (*Cucurbita pepo*) stored at chilling temperature, while the Spd and Spm content remained low in both (Serrano et al. 1997, 1998). CO_2 pretreatment was shown to reduce chilling injury and Put content in zucchini fruits stored at chilling temperature (Serrano et al. 1998). Hence, it was proposed that accumulation of Put caused the chilling damage, while an increase in Spm may be a defense response against low-temperature stress. Further, exogenous application of Spm resulted in high endogenous Spd and Spm and inhibited Put accumulation and reduced chilling damage in Loquat fruits (*Eriobotrya japonica*) (Zheng et al. 2000). Similarly, exogenous application of PAs increased cold tolerance in candy leaf (*Stevia rebaudiana*) plants (Moradi Peynevandi et al. 2018). In contrast, exogenous application of Put reduced the chilling injury in banana fruits stored at 8 °C (Wang et al. 2003). Transgenic overexpression of the SPDS gene cDNA from black seed squash (*C. ficifolia*) in *Arabidopsis* resulted in increased SPDS activity and Spd content in leaves with enhanced tolerance to various abiotic stresses, including chilling, freezing, salinity, and drought (Kasukabe et al. 2004).

Role of Polyamines in Drought and Waterlogging Stress Tolerance

Drought and waterlogging impact crop development and yield substantially, and due to global climate change, their frequency and severity have increased (Tyagi et al. 2022; Ali et al. 2022a). In 2050, for example, 50% of the world's areas will be water-scarce due to global warming (Gupta et al. 2020). Many studies have focused on the relationship between PAs and water stress in plants (drought and waterlogging) (Ebeed et al. 2017). PAs can maintain the osmotic balance of a cell during stress conditions by regulating ion and water transport through potassium channels and stomata, respectively (Liu et al. 2000). The exogenous application of Put (20 mg L^{-1}) to thyme (*T. vulgaris* L.) plants during drought stress showed improved leaf water content, dry

matter accumulation, reduced cell injury, and upregulated antioxidant enzyme activity (Mohammadi et al. 2018). Fruits of grafted tomato plants subjected to drought stress showed high endogenous PA content, which positively influenced the accumulation of osmoprotectants and ROS scavenging enzyme activities (Sánchez-Rodríguez et al. 2016). The exogenous application of Spm resulted in increased tolerance to salt and drought stress in *Arabidopsis* TSPMS/SPMS mutants (deficient in Tspm and Spm), while pretreatment with Put and Spd could not complement the hypersensitivity of the mutants to salt and drought stresses (Yamaguchi et al. 2007). Among the PAs, Spm is strongly related to drought stress tolerance in apple seedlings (Liu et al. 2010). In wheat (*T. aestivum*), both Spd and Spm alleviated the negative effects of drought stress and improved grain filling, while Put aggravated the negative impact of drought stress (Liu et al. 2016b). Similar results were observed in cherry tomato (Montesinos-Pereira et al. 2014). The heterologous expression of the coding sequence of the ADC gene from thorn apple (*D. stramonium*) resulted in a robust recovery from drought stress in transgenic rice plants despite them having an endogenous *ADC* gene (Capell et al. 2004). Transgenic rice (*Oryza sativa*) plants showed increased endogenous Put, Spd, and Spm content. Wheat (*T. aestivum* L.) seedling roots under waterlogging stress accumulated high levels of Spd and Spm. Pretreatments with exogenous Spd and Spm alleviated the waterlogging stress injury in wheat seedlings by increasing endogenous Spd and Spm content (Du et al. 2018). Further, the application of PA biosynthesis enzyme inhibitor methylglyoxal-bis-guanylhydrazone (MGBG) decreased endogenous Spd and Spm content under waterlogging stress and aggravated the stress-induced injury of the seedlings (Du et al. 2018). In alfalfa (*M. sativa*), pretreatment with melatonin increased endogenous PAs (Put, Spd, and Spm) to alleviate waterlogging stress (Zhang et al. 2019). Exogenous application of Put to welsh onion (*Allium fistulosum*) before waterlogging stress reduced the flooding-induced oxidative damage by activating the antioxidant system (Yiu et al. 2009).

Polyamines and Salt Stress Tolerance

Salt stress is the second most significant abiotic factor affecting agricultural productivity globally (Raza et al. 2022). Salt stress affects membrane integrity and reduces photosynthetic efficiency and enzyme activity (Chen et al. 2019). Plants respond to unfavorable conditions like salt stress by modulation of ion homeostasis, accumulating low molecular weight osmoprotectants such as glycine betaine, proline, and PAs, enhancing the antioxidant defense system and production of defense hormones (Raza et al. 2022). PAs play a key role in mitigating plant salinity stress by activating biochemical, physiological, and molecular defense systems (Rathinapriya

et al. 2020). Pretreatments of belladonna (*Atropa bella-donna*) seeds with 0.1 nM Put alleviated the adverse effects of salt stress during germination and early seedling growth by inducing accumulation of secondary metabolites and endogenous Put (Ali 2000). A study observed that upregulation of the *AtADC2* gene in response to salt stress results in the accumulation of endogenous Put in *Arabidopsis*. Further, in *Arabidopsis adc2-1* mutants, the Put levels were reduced to 25% under salt stress conditions, but the plants recovered from salt stress on application of exogenous Put (Urano et al. 2004). Exogenous application of Put (0.1 mM) increased salinity tolerance in rice cultivars (Lutts et al. 1996). An increase in the endogenous Spm content was observed in the leaves of the sunflower plants treated with different concentrations (50, 100, 150 mM) of sodium chloride (NaCl) (Mutlu and Bozcuk 2005). The exogenous application of 100 mg L^{-1} Spd, 150 mg L^{-1} Spm, and 150 mg L^{-1} Put increased the growth rate of roots and shoots, ROS scavenging enzyme activity, and reduced the electrolyte leakage in soybean seedlings subjected to salt stress (Wang and Yin 2014).

Role of Polyamines in Ameliorating Heavy Metal Toxicity in Plants

In the present era of industrialization, heavy metal (HM) contamination in the soil due to natural and anthropogenic activities is a global concern (Ali et al. 2022b). Some heavy metals, like copper (Cu), zinc (Zn), manganese (Mn), etc., are considered essential micronutrients for plant growth. Other heavy metals like mercury (Hg), lead (Pb), cadmium (Cd), chromium (Cr), arsenic (As), etc., are highly toxic for plant growth and development (Ali et al. 2021). HM toxicity causes oxidative damage, which severely affects plant growth and productivity. The exogenous application of PAs to plants under HM stress can modulate antioxidative pathways to scavenge excessive ROS and prevent their bioaccumulation. In carnation (*Dianthus caryophyllus* L.) plants, endogenous free Put levels and total Put/(Spm + Spd) ratios increased while Spd and Spm content decreased in response to Cd toxicity (Serrano-Martínez and Casas 2011). The exogenous application of Spd alleviated the adverse effects of Cd toxicity in the frogbit (*Hydrocharis dubia* (Bl.)) plant by activating antioxidative pathways (Yang et al. 2013). Similar results were reported in other plant species such as sea lettuce (*Ulva lactuca*) (Kumar et al. 2010), *Helianthus annuus* (Groppa et al. 2008), *T. aestivum* (Groppa et al. 2007), and rice (Roychoudhury et al. 2012). Cr is the seventh most abundant metal and is highly toxic to plant growth and metabolism (Shanker et al. 2005). Quinoa (*Chenopodium quinoa*) treated with (0.01–5 mM) chromium chloride ($CrCl_3$) showed higher levels of Put than those of Spd and Spm. All the PAs were increased with the duration of

the stress treatment (Scoccianti et al. 2016). Similarly, PA homeostasis and Cr toxicity were studied in cultivated radish (*Raphanus sativus*), where Cr-treated plants showed a reduction in PA content compared with the control (Choudhary et al. 2010). Cu is an essential metal for many physiological processes but is toxic to plant growth and development at concentrations above the optimal levels (Fargašová 2004; Yruela 2009). In sunflower plants subjected to Cu toxicity, the Put and Spm increased with increase in ADC activity and decrease in ODC activity under all concentrations of Cu treatments. In contrast, Cu toxicity in wheat induced Put accumulation with high ODC activity (Groppa et al. 2003). The exogenous application of Spd enhanced the Cu stress tolerance in *R. sativus* plants (Choudhary et al. 2012).

Polyamines and Abiotic Stress Signaling: Missing Links Between Them

Many studies have found that using either exogenous PA application or genetic manipulation of endogenous PA levels in transgenic plants improves abiotic stress tolerance (Bano et al. 2020; Takahashi 2020; González-Hernández et al. 2022). Furthermore, multiple studies have also indicated that treating plants with a combination of PAs and hormones improves abiotic stress resistance (Table 3). However, the precise molecular mechanism underlying PA-induced stress resistance remains unknown. It is unclear how PAs and hormones influence plant stress resilience at the molecular level. PAs are not only protective compounds, but also important components of a complex signaling system that aids stress tolerance. Abiotic stressors are concomitant with the increased accumulation of different signaling molecules like ROS, calcium (Ca^{2+}), nitric oxide (NO), hydrogen sulfide (H_2S), and hormones (Mohanta et al. 2018). These signaling players modulate an array of defense and growth responses in plants during abiotic stress, either individually or in combination. Many studies have revealed that PAs are also produced during abiotic stressors, suggesting that they may trigger a variety of signaling cascades in plants. For example, PAs have been shown to scavenge ROS, accumulate H_2O_2 and NO during PA metabolism, activate plasma membrane Ca^{2+}-ATPase and alter H^+ pumping, amplify OH-induced K^+ efflux, and interact with and remodel cation and anion conductance at the plasma membrane all of them will regulate various downstream signaling pathways (Pottosin et al. 2012). However, there are limited studies on the above traits modulated by PAs. Hence, more comprehensive studies at the molecular level are required. In plants, H_2O_2 can mediate various processes, such as stomatal closure, directly due to its ability to influence ion channels and regulate the mitogen-activated protein kinase (MAPK) cascade associated with stress responses. However, how PAs trigger H_2O_2

Table 3 Role of PAs and other hormones/ their crosstalk in regulating physiological, biochemical, and molecular changes during abiotic stress in various plant species

PA	Hormone	Abiotic Stress	Physiological and biochemical or molecular changes for stress tolerance	Plant species	References
Put	ABA	Cold	Stress activates biosynthesis gene involved in Put (ADC1 and ADC2) Put induce ABA biosynthesis (NCED3, RD29B, and RD22) Put positively regulates transcript expression of NCED3 in *ABA-defective mutants*	Arabidopsis (*A. thaliana*)	Cuevas et al. (2008)
PAs	JA		MeJA reduce chilling injury on plant by increasing PAs (Reduced percent ion leakage in chilling tolerant plant)	Mango (*Mangifera indica* cv. Tommy Atkins)	González-Aguilar et al. (2000)
Put	SA		Stress activate SA accumulation SA-treated plants represent high level of Put under stress	Maize (*Z. mays*)	Szalai et al. (2016)
Put	ABA		Stress activates accumulation of Put and ABA (Low electrolyte leakage in chilling tolerant plant)	Rice (*O. sativa* L.)	Lee et al. (1995)
Spm	ABA, JA		PDJ-/Spm-treated plants are chilling tolerant by ABA accumulation, low IC_{50} value of O^{2-} radical scavenging activity, and increased ascorbic acid and polyphenol contents	Apple (*Malus sylvestris* (L.) Mill. Var. domestica (Borkh.) Mansf.)	Yoshikawa et al. (2007)
Spd, Spm	ABA, JA		MeJA alleviate chilling stress on plant by regulating endogenous ABA and PAs	Pumpkin (*C. pepo* L.)	Wang and Buta (1994)
Put, Spm	ABA	Heat	Stress activates PAs production and delayed ABA accumulation (It make plant firmness (HSIR))	Lemon (*Citrus limon* L. Burm, cv. Verna)	Valero et al. (1998)

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Table 3 (continued)

Treatment with Polyamines in combination with different hormones		Abiotic Stress	Physiological and biochemical or molecular changes for stress tolerance	Plant species	References
PA	Hormone				
Spd, Spm	ET	Salt/Drought	Stress activates ET production and conversion of Put into Spd and Spm Reduced indexes of stomata aperture, membrane lipid peroxidation, and electrolyte leakage (Increased tolerance to osmotic stress in *overexpressed CsCDPK6 transgenic mutant*)	Tobacco (*Nicotiana benthamiana*)	Zhu et al. (2021)
Put	ABA		ABA-/Put-treated plants are tolerant by regulating proline metabolism, lower stomatal conductance, and transpiration	Wheat (*T. aestivum* L. TC33)	Pál et al. (2018)
Spm	ABA		Spm-treated plant represent reduced lipid peroxidation and induced/persisted SOD activity, GSH, polyphenol, JA, and ABA contents under osmotic stress condition	Soybean (*G. max.* L. Taekwang-kong)	Radhakrishnan and Lee (2013a, b)
PAs	ABA		High number of Total PA and ABA were detected on drought-tolerant plant ABA induce PA accumulation/oxidation	Grape (*V. vinifera*)	Toumi et al. (2010)
PAs	ABA		Stress actives biosynthesis gene involved in PAs (ADC2, SPDS1 and SPMS) (Decreased tolerance to drought in ABA-nulled mutant)	Arabidopsis (*A. thaliana*)	Alcázar et al. (2006a)
Spm	ABA		Spm can modulate response to stress in ABA-dependent/independent way	Arabidopsis (*A. thaliana*)	Marco et al. (2019)
Put, Spm	ET, ABA		ABA induces biosynthesis of Put and Spm by regulating ET biosynthesis pathway (High accumulated ABA contents in tolerant plant)	Poplar (*Populus popularis*)	Chen et al. (2002)
Spd	SA		SA- and Spd-treated plant showed high photosynthesis, antioxidant activity, and proline contents under stress	Cherry tomato (*Lycopersicon esculentum*)	Fariduddin et al. (2018)
PAs	SA		SA regulate PA contents under stress condition by modulating the expression level of biosynthetic genes (ADC, MetDC and MAT)	*Oats* (*A. sativa*)	Canales et al. (2019)
Spd, Spm	GA, ABA		Spm-treated plant showed high osmotic potential and reduced lipid peroxidation by accumulating GA1, GA4, and ABA under stress condition	Grass (*Agrostis stolonifera*)	Krishnan and Merewitz (2017)
Put, Spd	ABA, ET	Water	Stress activates PAs and hormone biosynthesis pathway	Tobacco (*N. tabacum*)	Hurng et al. (1994)

Table 3 (continued)

Treatment with Polyamines in combination with different hormones		Abiotic Stress	Physiological and biochemical or molecular changes for stress tolerance	Plant species	References
PA	Hormone				
Spm	SA	Drought, Cr	SA and Spm alleviate stress by accumulation of endogenous polyamines, osmolytes (proline), total soluble sugar, total carbohydrate, and antioxidants (APX activity) SA- and Spm-treated plant showed low ROS, lipid peroxidation, and relative membrane permeability under both stresses condition	Maize (*Z. mays* L.)	Naz et al. (2021)
Put, Spm	SA	Cd	Put-treated plant alleviate stress via crosstalk with SA	Wheat (*T. aestivum* L.)	Tajti et al. (2018)
PAs	ET	Cd	Cadmium induces transcript expression of gene involved in metabolism of PA and ET (ACS, DAO, and SAMDC)	Soybean (*G. max*)	Chmielowska-Bak et al. (2013)
Put	ET	Al	Put-treated plant alleviate stress by inhibition of ET production	Wheat (*T. aestivum* L.)	Yu et al. (2016)

to module these responses during abiotic stress is still not fully understood. Further, more research is needed to study how PAs can influence H_2O_2/NO cross talk in plants during abiotic stress. In addition, there are many other questions related to PA-mediated signaling during abiotic stress that need to be addressed further to harness the potential of PAs in stress tolerance and growth improvement: (1) How PAs are sensed by extracellular and intracellular sensors? (2) How they regulate signaling of ROS, H_2O_2, NO, and Ca^{2+} in plants during abiotic stresses? (3) How they interact with different stress hormones to modulate downstream signaling? (4) How can PAs modulate stress responses in plants when exposed to multiple stresses? To address these questions, researchers should focus on PA signal perception and transduction rather than its application. This emphasizes the need for high-throughput molecular and biochemical tools to unravel the complexity of PAs signaling and identify novel players involved in its perception and transduction. This review shows a schematic diagram of a possible regulatory mechanism underlying PA-induced stress tolerance in plants (Fig. 6). This model demonstrates how plants perceive multiple abiotic stresses such as cold, heat, drought, salinity, and heavy metals via cell wall/plasma membrane-associated receptors, increasing endogenous PA levels. Second, it demonstrates how exogenous PAs are perceived by the cell wall or cell membrane sensors, followed by activation of signal transduction pathways linked to abiotic stress resilience. We also discussed how PA signals could be translated via

different signaling pathways (via cytosolic sensors) that target their transcription factors for gene expression and their interactions with other hormones that lead to abiotic stress tolerance in plants. In addition, we have also highlighted the possible inter-organellar signaling activated by cytosolic PA accumulation in plants. Although a definitive picture of PA perception and signal transduction has yet to be established, it is possible that cloning PA biosynthetic genes from more plants and introducing cutting-edge tools (forward and reverse genetics) will help to fill the gaps in PA signaling in plants.

Crosstalk Between Polyamines and Gaseous Signaling Molecules in Plants

PA metabolism in plants plays a significant role in regulating other metabolic pathways. PA and ET biosynthesis are co-regulated as they share a common precursor. L-Arg is the common precursor for both PA and NO biosynthesis. Recalde et al. (2021) highlighted the shared nitrogen network between PAs and NO as a new component of the signaling pathway and how it interacts with other biological processes, primarily the stress response. The H_2O_2 produced during the oxidation of PAs acts as a signaling molecule at lower concentrations to induce biotic and abiotic stress responses, and at higher concentrations, it leads to plant cell death (Quan et al. 2008). Hence, cooperative regulation of
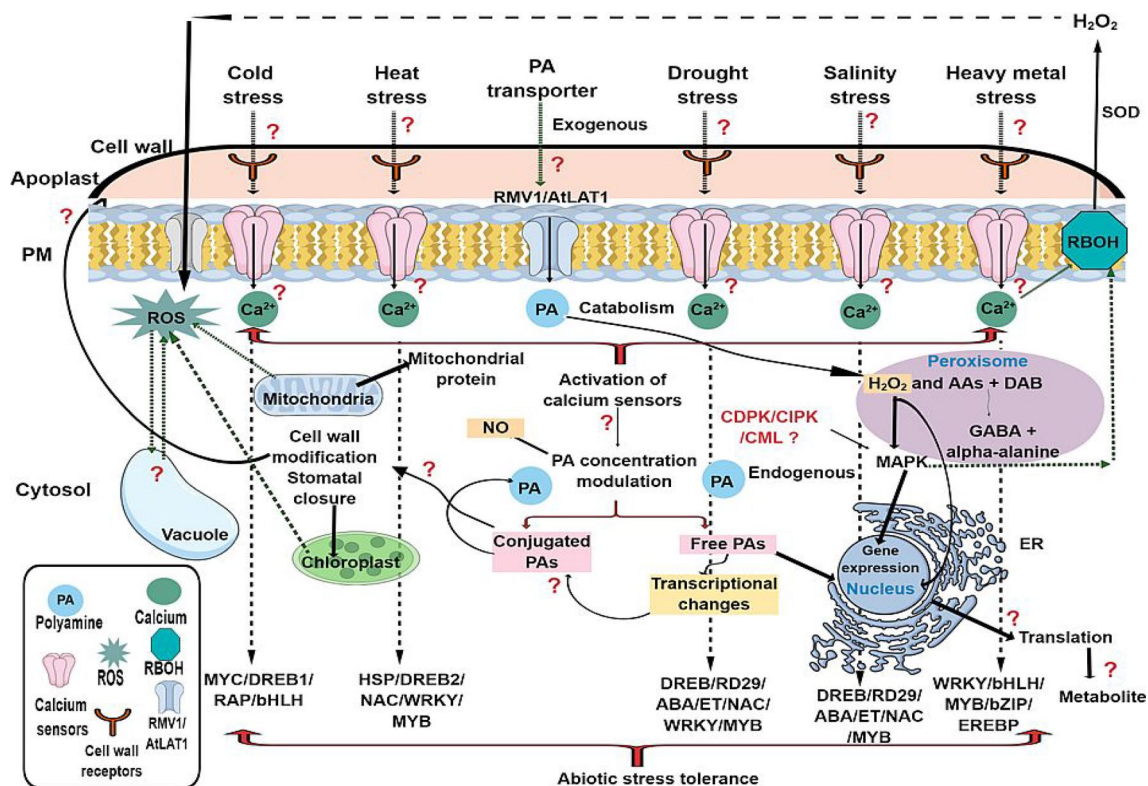
Fig. 6 A hypothetical model highlighting the PA-mediated signaling mechanism regulating abiotic stress tolerance in plants. This model highlights how plants can perceive multiple abiotic stress (using cell wall/ plasma membrane-associated receptors), leading to the elevation of endogenous PA levels. The model highlights how these PA signals can be translated via different signaling pathways (using cytosolic sensors) targeting their respective transcription factors for gene expression and their interplay with other hormones, leading to abiotic stress tolerance in plants. In addition, it highlights the inter-organellar signaling activated by cytosolic PA accumulation in plants. SOD, superoxide dismutase; H_2O_2, hydrogen peroxide; RBOH, NADPH oxidase/respiratory burst oxidase; PA, polyamines; NO, nitric oxide; PM, plasma membrane; ER, endoplasmic reticulum; ROS, reactive oxygen species; AAs, amino aldehydes; GABA, γ-aminobutyric acid

PA, NO, ET biosynthesis, and PA oxidation plays a key role in plant growth and development under abiotic stress conditions. The H_2O_2 produced during PA oxidation induces the nitric oxide synthase (NOS) gene expression, stimulating the ABA-mediated stomatal closure during drought stress (Neill et al. 2008). Transgenic barley plants overexpress the barley non-symbiotic hemoglobin gene (*HvHb1*) that oxidizes NO to NO_3^-, producing less NO during drought stress. This reduced NO level leads to high levels of PAs, mainly Spd accumulation, and decreased ET biosynthesis during drought stress, indicating that NO-ET plays a key regulatory role in PA biosynthesis linked to drought tolerance in barley (Montilla-Bascón et al. 2017). In tomato plants, the exogenous application of Spd and Spm induces a significant increase in the NO and H_2O_2 levels during chilling stress, while Put does not affect the NO content (Groppa et al. 2003). However, the effect of Spd on NO accumulation during chilling stress is greatly reduced by the application of an H_2O_2 inhibitor (DPI; an NADPH oxidase inhibitor) and DMTU (an H_2O_2 and OH· scavenger), indicating the involvement of H_2O_2 in the PA-induced NO production

during chilling stress (Groppa et al. 2003). Tomato seedlings pretreated with sodium nitroprusside (SNP, an NO donor) showed elevated Put and Spd levels throughout the chilling stress treatment period, but SNP did not increase the Spm levels, which remained constant under chilling stress (Groppa et al. 2003). Further, it was also observed that exogenous application of Put induced ABA-mediated chilling stress tolerance in tomato seedlings by maintaining membrane integrity. In ginger (*Zingiber officinale*) Roscoe seedlings, the exogenous application of SNP and Spd increased the chilling stress tolerance by protecting photosystem II (PSII), increasing unsaturated fatty acid levels in membranes, and enhancing ROS scavenging mechanism. The combined application of SNP and Spd had a more significant and positive effect on chilling tolerance in ginger seedlings (Li et al. 2014). Additionally, according to Filippou et al. (2013), the NO donor SNP controls the metabolism of PA and proline in *Medicago tranculata* leaves. Adamipour et al. 2020 investigated how PAs, NO synthase (NOS), and H_2O_2 (secondary messenger) regulate stomatal aperture in response to drought stress in *Rosa canina*. Jahan et al.

(2019) showed that melatonin administration reduces heat-induced damage to tomato seedlings by regulating PA and NO production and restoring redox equilibrium. Similarly, prior exposure to NO increased chilling tolerance in banana (*M. acuminata*) fruits by increasing levels of PAs, GABA, and proline (Wang et al. 2016).

The exogenous application of Put (0.2 mM) and SNP (1 mM) conferred tolerance against Cd toxicity in mung bean (*Vigna radiata* L. cv. BARI Mung-2) seedlings treated with $CdCl_2$, (1.5 mM). The application of Put and SNP reduced Cd uptake, increased phytochelatin content, and reduced oxidative damage by enhancing enzymatic and non-enzymatic ROS scavenging mechanisms. This effect was further improved by the combined application of Put and NO (Li et al. 2014). Adding Put and Spd to apple (*M. domestica* Borkh.) embryos alleviated embryonic dormancy and induced germination by stimulating Arg-dependent NO formation, while the application of Spm inhibited NO formation (Krasuska et al. 2017). Similarly, pretreatment with NO increased endogenous Put content, decreased Spm biosynthesis, and enhanced Spm oxidation (Krasuska et al. 2017). Transgenic tomato plants with overexpression of SAMDC and the yeast SPDS gene, under the control of the E8 promoter, showed high levels of Spd, Spm, and ET, indicating that both ET and PA biosynthesis can occur simultaneously and the effect of high ET content is masked by higher concentrations of Spd and Spm (Mehta et al. 2002). Further, transgenic tomato fruits overexpressing the mouse ODC gene showed delayed on-vine ripening and extended shelf life due to increased PAs and reduced ET production (Pandey et al. 2015). In transgenic *Arabidopsis,* plants overexpressing the *35S:AtADC2* gene showed increased Put content and reduced transcript abundance of genes involved in ET biosynthesis (Alcázar et al. 2005). The improvement in plant tolerance to abiotic stress when their cellular contents are increased by either exogenous treatment with PA or genetic transformation of genes encoding PA biosynthetic enzymes is suggestive of the protective role of PAs.

Crosstalk Between Polyamines and Hormones

Although PAs are not hormones, they have been proposed as a new class of plant growth regulators due to their participation in control of several growth and development processes and responses to abiotic stressors in plants (Chen et al. 2019). Many studies have found that PAs interact synergistically or antagonistically with various plant hormones, suggesting the possibility of crosstalk between hormones and PAs (Bitrián et al. 2012; Milhinhos and Miguel 2013). PAs are generally considered antisenescence growth regulators that appear to exert protective effects against

ET-induced fruit ripening, leaf senescence, and biotic stressors (Nambeesan et al. 2008). The substrate for ET biosynthesis (S -adenosylmethionine (SAM)) is the same as for PAs biosynthesis, which could influence whether ET or Spd/Spm production takes precedence if SAM becomes limited (Lasanajak et al. 2014). Previous studies have shown that PAs and ET show antagonistic interactions with one another, implying that they may distinctly regulate different developmental and physiological responses in plants. ABA is another hormone that interacts with PAs in regulating an array of physiological and biochemical responses, such as Ca^{2+} homeostasis, ROS, and NO, which are important for plant adaptation to stresses (Pal et al. 2018). The relationship between PAs and ABA is reciprocal. Put induces the expression level of the 9-cis-epoxycarotenoid dioxygenase 3 (NCED3) gene involved in ABA synthesis, whereas ABA treatment increases the expression level of the S-adenosyl-l-methionine synthetase 1 (SAM1), SAM3, spermidine synthase (SPDS3), and peroxisomal polyamine oxidase (PAO) (Cuevas et al. 2008; Alcázar et al. 2010; Pál et al. 2018). The positive effects of PAs and ABA in mitigating abiotic stresses have been reported for many plants. For example, under water stress, the transcript levels of ADCs, SPDSs, and spermine synthases (SPMSs) were increased, but not in ABA mutants (Alcázar et al. 2006a, b). Similarly, many drought-tolerant plant species also showed accumulation of ABA and Put, showing that these two components can protect the plant from external challenges (Jiang et al. 2012; Anwar et al. 2015). In transgenic *Arabidopsis* plants, putrescine accumulation hindered gibberellic acid (GA) biosynthesis, resulting in stunted stature and delayed flowering (Alcazar et al. 2005). Furthermore, jasmonic acid (JA) has also been linked to formation of conjugated PAs in plants. This was further proved by RNAi-mediated silencing of R2R3-MYB8, a JA responsive transcription factor, which demonstrated that MeJA induces PA conjugation and involves R2R3-MYB8 (Kaur et al. 2010). Similarly, MeJA stimulates the transcription of Put N-methyltransferase (PMT), an enzyme that converts Put to N-methyl-Put (Shoji et al. 2000). In mango (González-Aguilar et al. 2000) and apples (Yoshikawa et al. 2007), an increase in free Spd and Spm in MeJA-treated fruits correlates with low-temperature stress tolerance, suggesting a role for free Spd and Spm in fruit ripening and low-temperature stress tolerance. However, the effects of PAs on JA synthesis, conjugation, perception, and signal transduction are poorly understood. Auxins are another class of phytohormones that mediate plants' gravitropic and phototropic responses. The link between PAs and auxin and their crosstalk was discovered from transgenic and transcriptomic studies in different crop systems. For example, SPMSYN transgenic leaves showed an upregulation of many auxin-related genes, highlighting PA's positive effect on the auxin pathway. In contrast, no difference in free and

bound amounts of IAA was observed between the control and HM stress conditions in Spd-treated radish seedlings (Choudhary et al. 2011). In *Arabidopsis*, Spm downregulates several auxin carriers, including the ARF, Aux/IAA, and SAUR genes, whereas higher Spd and Spm levels boost the expression of several auxin-regulated genes in tomato fruit (Kolotilin et al. 2011). These results further reveal that individual PAs interact distinctly with plant auxin signaling. However, the effect of PAs on auxin biosynthesis, transportation, and signaling is poorly understood. More research into their role in regulating auxin function is required. The link between PAs and GA was discovered by chance during the analysis of transgenic *Arabidopsis* plants that ectopically expressed arginine decarboxylase (*35S:AtADC2*) and accumulated high levels of free and conjugated Put (Alcazar et al. 2005). Put and GA have an antagonistic relationship, demonstrating that accumulated Put interferes with the final step of the GA biosynthesis pathway in transgenic *Arabidopsis* (Alcázar et al. 2005). Due to a lack of the hormone GA, this transgenic *Arabidopsis* exhibits dwarf phenotype and delayed blooming (Alcázar et al. 2005). In Spm-accumulated *Arabidopsis,* repressed transcript levels of genes engaged in the process of active form GA, GA 13-/20-oxidase, and elevated transcript levels of GA catabolism-related gene, GA 2-oxidase, were also detected (Gonzalez et al. 2011). Further research into the interaction of GA and PAs is needed in both model and crop plants to better understand the mode of crosstalk between these two molecules and how they affect each other at the biosynthetic, transportation, and signaling levels under control and stress conditions.

Salicylic acid has an important role in plant defense signaling under biotic and abiotic stresses such as against pathogens, temperature, salinity, and drought (Agostini et al. 2013; Ali et al. 2017, 2018b). It is well known that plants facing stress start synthesizing endogenous SA mainly via the isochorismate (ICS) pathway in the chloroplasts (Dempsey et al. 2011). Treatment with SA induces the accumulation of Spd, Spm, and Put in various species, including *Arabidopsis*, citrus, tomato, bamboo (*Bambusa vulgaris*), and asparagus (*Asparagus officinalis*) (Zheng and Zhang 2002; Wei et al. 2011; Zhang et al. 2011; Luo et al. 2012). Likewise, Spd and Spm can alter the conjugation of SA. For example, Spm/Spd-overproducing plants revealed a high level of SAM-dependent carboxyl methyltransferase (*SAMT*) and GH3-like phytohormone amino acid synthetase (*GH3.5*), which encode SA-converting enzymes (Lazzarato et al. 2009; Gonzalez et al. 2011). These studies provide evidence of occurrence of PA and hormone crosstalk in plants under stress conditions. However, little is known about the signal transduction pathways regulating this crosstalk at the molecular level. Although tremendous progress has been made in understanding the regulation of biosynthesis and signal transduction pathways for most plant hormones,

research into the molecular mechanisms underlying PA action has begun recently. Here, we have highlighted how PAs interact with several hormonal pathways to maintain growth-defense tradeoffs (Fig. 7). Many questions such as how PAs modulate growth and defense tradeoffs during multiple stresses under field conditions and how PAs interact with different hormones during abiotic stresses and crosstalk with them to provide more effective stress resilience remain to be explored. In future, researchers should also study the effect of PA metabolism on different hormonal signaling pathways and vice versa, which will provide novel avenues for developing future resilient smart crops.

Underpinning Polyamines Signaling and Their Cross Talk in Plants Using Multi-omics

PAs promote plant growth and development and stress tolerance. Unfortunately, little is known about the molecular mechanisms by which PAs regulate or modulate these processes. The crucial participants in PA signal reception and transduction, such as sensors, transporters, transcriptional factors, proteins, and metabolites, remain unexplored. Nonetheless, it is well understood that during biotic or abiotic stresses, application of exogenous PAs or PA synthesized inducers and overexpression of PA genes in plants leads to stress tolerance (Agudelo-Romero et al. 2013; Pál et al. 2018). However, there are many knowledge gaps about how PAs modulate transcriptional, proteomic, metabolic, and ionomic stress adaptive responses and interact with other signaling pathways in plants. Using multi-omics tools and genome editing will be useful to assess the molecular complexity of PA signal perception and transduction and its crosstalk with other signaling players such as hormones, ROS, calcium, NO, and H_2S. This will aid in investigating its role in plant development and stress biology. In addition, it would provide a more comprehensive picture of the consequences of the up- or downregulation of genes associated with stress tolerance and PAs. Similarly, metabolomics, which measures the number of metabolites within an organism, which are usually the end-products of genomic, transcriptomic, and proteomic variations, can be used to determine the overall phenotypic responses to environmental signals (Hong et al. 2016). This high-throughput tool is often combined with nuclear magnetic resonance (NMR), mass spectrometry (MS), liquid chromatography-MS, or gas chromatography-MS (Gathungu et al. 2014). Numerous metabolic processes and end-products direct plants' biochemical and physiological abiotic stress resistance mechanisms. Metabolomics offers a comprehensive approach to identifying PA biosynthetic pathway metabolites to understand biochemically mediated stress resistance. With the growing

Fig. 7 A proposed model showing how PAs can modulate growth and defense tradeoffs during multiple stresses by interaction with several hormonal pathways. The crosstalk between PAs and hormonal regulation has been demonstrated in some experiments, with downregulation of JA (Jasmonic acid) leading to cold tolerance, GA (Gibberellic acid) leading to stunted growth and delay in flowering, ET (Ethylene) leading to delay in ripening and leaf senescence, and ABA (Abscisic acid) leading to Ca^{2+} homeostasis and ROS and NO production, while upregulation of SA (Salicylic acid) and Auxin delay in flowering. Some signaling pathways regulating cytokinin and BR (Brassinosteroid) and their interaction with different hormones are still unknown
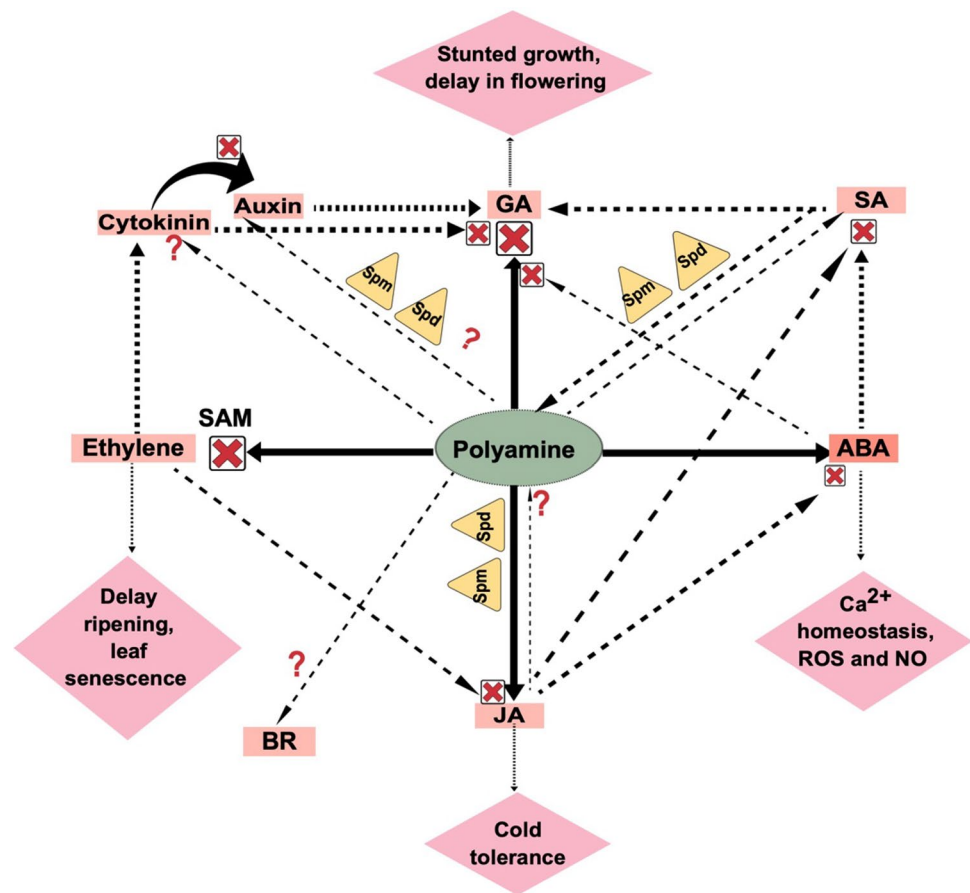
interest in plant metabolic engineering using genetic manipulation and gene editing technologies to improve growth, nutritional value, and environmental adaptation, one major concern is the possibility of unintended broad and far-reaching consequences of manipulating the target gene or metabolic step in the resulting plant. In future, metabolomics and molecular networking studies are required to identify the interaction of PA and novel metabolites that will provide novel avenues for metabolic engineering in crops to develop future stress and higher yielding smart crops. Finally, identifying distinct or shared regulatory nodes of metabolic pathways and crosstalk between the various pathways affected by genetic manipulation of PA metabolism will give us effective targets for development of genetically engineering plants resistant to multiple abiotic stresses.

Furthermore, when PA synthesis is increased, either chemically or through transgenic manipulation, there is an increase in PA catabolism and increased excretion and/or transport. Many studies have primarily focused on animal cells, and there is limited information on increased PA production and catabolism in plants. Only a few studies have looked into the influence of PA overproduction on turnover and catabolism in transgenic plants expressing genes for PA biosynthetic enzymes and the subsequent increases in

cellular PA levels (Kumar and Minocha 1998). For example, Page et al. (2016) showed that cellular transcriptome and metabolome are reprogrammed due to genetic manipulation of Put biosynthesis in black poplar (*Populus nigra*). Their findings showed that increased expression of a single molecule in the PA biosynthetic pathway (ornithine putrescine) changed the expression of a wide range of genes, many of which were involved in transcription, translation, osmoregulation, cell wall metabolism, membrane transport, and stress responses. Similar studies can be targeted for important traits (biotic or abiotic stress tolerance, nutritional improvement), and the results could be implemented in molecular-assisted breeding and metabolomics or metabolic networking for sustainable improvement of different crops. Furthermore, PA biosynthetic genes will be valuable candidates for genetic manipulation to create novel germplasm with better stress tolerance to combat adverse environments for agricultural crop sustainability.

Role of Nanoparticles in Increasing Polyamine Delivery and Efficacy for Crop Improvement

The integration of nanotechnology and plant biology has been used in crop improvement. It is gaining much attention owing to its multifaceted traits. Current advancements in this field are paving the way for a long-term increase in agricultural productivity while reducing negative environmental consequences. Nanotechnology has helped improve soil quality (e.g., Nanofertilizers), accelerate plant growth (e.g,. seed primers, photosynthesis enhancers, growth promoters), and protect plants from biotic (nanopesticides, nanofungicides) and abiotic stresses. In addition, nanotechnology can potentially increase crop productivity by targeted delivery, improve crop tolerance, and reduce pollution. Exogenous chemicals such as brassinolide, nitric acid, melatonin, silicon, polyamines, growth hormones, and selenium have been used to boost plant stress tolerance for salinity, heat, microbes, and heavy metals (Serna et al. 2015; Zhan et al. 2019). However, their stability, target distribution, effectiveness, and transportation remain the primary concerns in fully exploiting their potential for crop development. In this regard, nanobased engineering provides new opportunities for developing highly potent nanobased bio-stimulants that can be more effective and stable crop enhancement agents.

Nanoparticles can improve plant resistance to abiotic stress by scavenging ROS and enhancing antioxidant enzyme activity, improving photosynthetic rates and photoprotection (Jalil and Ansari 2019; Rajput et al. 2021). Furthermore, NPs can activate stress-related genes and increase the number of many target proteins involved in stress resilience (Jalil and Ansari 2019; Rajput et al. 2021). Several studies have found that the application of various nanomaterials, such as zinc oxide (ZnO NPs), titanium oxide (TiO$_2$ NPs), iron oxide (Fe$_2$O$_3$ NPs), and silicon (Si-NPs), reduces the negative effects of abiotic stresses in various crop species (Das et al. 2018; Rani et al. 2020; Rostamizadeh et al. 2020). However, few studies have explored the role of nanocoated PAs in ameliorating abiotic stress resilience in sustainable agriculture. There are reports showing that NPs significantly increase the accumulation of PAs in plants. For instance, Mushtaq et al. (2020) have highlighted that iron oxide nanoparticles (IONPs) and *Bacillus subtilis* S4 exert a synergistic anti-arsenic toxicity function in *Cucurbita moschata* by improving stress-relieving PA production, such as that of Spd and Put. In addition, their co-application increases the activity of antioxidant enzymes such as peroxidase (POD) and superoxide dismutase (SOD) while reducing levels of H$_2$O$_2$, malondialdehyde (MDA), and electrolyte leakage (EL). Another study has revealed that MgONPs lead to the accumulation of PAs, which are critical for plant growth

and development (Faiz et al. 2022). These studies provide the roadmap for harnessing the potential of NPs and PAs (co-application) and coated PAs for mitigating abiotic stress resilience in sustainable agriculture. Although PA coating has gained technological significance for human gene therapy applications, it is yet to be explored in plants. Hence, there is a need to further study NP-coated PAs' role in plant stress tolerance and growth development.

Conclusions and Future Prospects

PAs are involved in plant growth and development, including seed germination, organogenesis, tissue lignification, abscission, senescence embryogenesis, flowering, pollination, fruit development, and ripening. Synergistic and antagonistic interactions with distinct plant hormones have been seen in all these processes, but the molecular mechanisms by which PAs regulate these processes and interact with different hormones remain unknown. The signal transduction pathways that regulate a wide range of PA-triggered growth responses in plants are poorly understood. As a result, further research is needed to better understand the molecular mechanisms by which PAs regulate various plant development features and how their interactions with hormones and other growth-promoting substances work together to improve plant growth and development. Second, PAs have been shown to enhance abiotic stress tolerance in plants by activating a multifaceted defense system. However, there is limited information on PAs signal perception and transduction in plants. For example, sensors, transporters, transcriptional factors, proteins, and metabolites involved in PAs perception and transduction are still unknown. In addition, how PAs regulates or triggers various signaling cascades like Ca^{2+}, ROS, NO, and different hormones during abiotic stresses remains unknown. Furthermore, how PAs trigger transcriptional, proteomic, metabolic, and ionomic reprogramming in plants remains obscure. Moreover, fundamental questions about PA transport between organelles and cells and their role in epigenetic modifications also remain unanswered. Utilizing multi-omics and genome editing tools to assess the molecular complexity of PAs signal perception and transduction, and its crosstalk with other signaling players such as hormones, ROS, calcium, NO, and H$_2$S, will aid in an in-depth investigation of its role in plant developmental and stress biology and the development of future stress resilient smart crops. Plant stress tolerance and high yield may be mutually exclusive results because both are energy-intensive processes with unknown tradeoffs. For example, PAs can alter various morphological, physiological, and biochemical features in response to abiotic stresses to allow plant survival, but this might harm growth circumstances. For example,

closing stomata for prolonged periods during drought stress can limit crops' photosynthetic ability, resulting in reduced growth.

Thus, researchers utilizing PAs must balance two potentially competing processes to improve stress tolerance and yield by focusing on growth and stress tradeoffs. Recently, molecular priming has emerged as a novel and cost-effective method of improving stress resilience in plants. Seed priming with different PAs has significantly improved the abiotic stress tolerance and germinating seedling growth performance. However, some factors, such as stability, target distribution, effectiveness, and transportation, limit the ability to fully exploit their potential for crop improvement. In this regard, nanobased engineering opens new avenues for developing highly potent nanobased PAs bio-stimulants that can be more effective and stable for crop enhancement agents. Finally, yet importantly, future studies should focus on elucidating the molecular mechanisms that regulate PAs during abiotic stresses and their impact on adaptive signaling cascades to provide a more practical means of their involvement in plant stress biology.

Declarations

Conflict of interest All the authors have no competing interest to declare that is relevant to the content of this article.

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