



Roles of Polyamines in Growth and Development of the Solanaceous Crops Under Normal and Stressful Conditions

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Abstract

Polyamines (PAs) namely putrescine, spermidine, spermine and cadaverine are low molecular weight polycations found in all living organisms. In plants, considerable progress has been made on PA metabolism. As evident from the multiple research articles and reviews, PAs are known to stimulate various aspects of growth and development such as seed germination, organogenesis, pollination, flower and fruit development and senescence. In these processes, they could exhibit mostly synergistic and in some cases antagonistic effects with the phytohormone-mediated interactions. Various PAs are also closely related to both abiotic and biotic stress responses in plants. Currently, PAs are significantly gaining importance as substitutes of the plant growth regulators, and being used as media supplements for plant tissue culture. Both endogenous levels of PAs and their exogenous applications are known to influence various stages of plant life cycle under both normal and stressful conditions. The major objective of this review is to highlight the demonstrated effects of PAs, particularly on the commercially important solanaceous crops. Relationships between PAs and various stress responses are exceedingly complex in terms of involvement of the multiple processes. In-depth understanding of such biological processes would help to develop useful designer crops.

Keywords Polyamines · *Solanaceae* family · Growth and development · Abiotic and biotic stresses · Exogenous applications

Introduction

Polyamines (PAs) are ubiquitous and low molecular weight nitrogenous aliphatic compounds that occur in different tissues and cell types as examined in animals and plants (Pascalidis et al. 2005). They exist as water-soluble polycations at biological pH. PAs play crucial roles in various cellular, biochemical and metabolic processes such as cell growth and division, morphogenesis, stabilization of nucleic acids and membranes, protein synthesis, dynamic modifications of chromatin architecture. Apart from growth and development under normal conditions, PAs are also crucial under stresses and senescence responses in plants. With regard to human/animal health and disease, the role(s) of PAs are

well-recognized in gastroenterology, programmed cell death (PCD), parasitology, cerebral stroke, oxidative stress and oncology (Hussain et al. 2011; Liu et al. 2017; Vuosku et al. 2018; Handa et al. 2018). Over the last few decades, many researchers were involved in understanding various aspects of PA metabolism and their stimulatory roles in different plant species under laboratory, field and importantly stressful conditions.

Putrescine (Put), spermidine (Spd), spermine (Spm), thermospermine (Tspm) and cadaverine (Cad) are the most common types of PAs in plants predominantly present in the free forms (F-PAs) (Kim et al. 2014; Sobieszczuk-Nowicka 2017; Takahashi et al. 2017; Mustafavi et al. 2018). They also exist as covalently conjugated (CC-PAs) and/or non-covalently conjugated (NCC-PAs) forms depending on the status of cellular metabolism (Gholami et al. 2013). PAs are found in several subcellular compartments viz. cell wall, vacuoles, mitochondria and chloroplasts at varying levels suggesting their functional specializations. They can covalently bind to biomolecules such as DNA, RNA and protein structures that induce conformational changes ultimately resulting in

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altered gene expression impacting plant growth and development (Kusano et al. 2008; Mattoo and Handa 2008). For instance, enhanced PA levels in the transgenic tomato plants could induce expression of multiple genes associated with signal transduction pathways, chaperone family, stress responses and biosynthesis of various molecules such as amino acids, ethylene, isoprenoids and flavonoids (Handa and Mattoo 2010). In *Arabidopsis*, Spm was reported to stimulate the expression of heat shock related (HSR) genes to protect plant cells at elevated temperatures (Sagor et al. 2013). Put was known to modulate abscisic acid (ABA) biosynthesis and gene expression as well in *Arabidopsis* plants exposed to cold stress (Cuevas et al. 2008). Usually, Put levels are notably higher in leaves as compared to other PAs, whereas intracellular Spm and Spd could be higher in other organs (Takahashi et al. 2017). In tobacco (*Nicotiana tabacum*), Spd and Spm are predominantly synthesized in the shoot apical meristem, whereas Put is synthesized in the roots (Moschou et al. 2008). Cad could be detected at all the stages of embryogenesis in pepper (*Capsicum annuum*) (Regla-Márquez et al. 2016). Usually, higher PA levels are noticed in the metabolically active growing cells. Liu et al. (2007) reported relatively higher levels of PAs in developing fruits as compared to the mature ones. Multiple research and review articles reported the importance of PAs as bioactive compounds impacting various aspects of plant life cycle (Moschou et al. 2012; Bordenave et al. 2019; Chen et al. 2019; Wang et al. 2019), also presented in Fig. 1 and Table 1. Significant progress has been made in understanding the roles of PAs by fluctuating their levels through both exogenous applications and genetic manipulations (Meng et al. 2021; Raziq et al. 2022; Tavallali et al. 2022).

Polyamines were known to play crucial roles during stress conditions (Bitrián et al. 2012; Gupta et al. 2013; Minocha et al. 2014; Pál and Janda 2017; Ali et al. 2020). They help in overcoming various stresses in plants as shown in Fig. 2. Put

plays a major role in abiotic stress (Groppa et al. 2007; Yang et al. 2013). Sagor et al. (2015) reported the role of Spm in a cellular stress response, i.e. unfolded protein response (UPR) by modulating the expression and splicing of bZIP-type transcription factors. Put triggered dark-induced leaf senescence through GABA production in barley; Spd and Spm participated in senescence-dependent degradation processes (Sobieszczuk-Nowicka et al. 2017). Cad had also been implicated in both biotic and abiotic stress responses (Masson et al. 2017). Exogenous applications of Spd and Put alleviated the chlorophyll loss, and enhanced the Rubisco levels in wheat exposed to drought stress (Hassan et al. 2020). Spm or Spd treatment improved growth, relative water content (RWC), chlorophyll content and stomatal conductance in water stress-induced oxidative stress in Damask rose (Hassan et al. 2018). Pál et al. (2015) reported that PAs could upregulate the activities of protein kinases in plants exposed to stress. Elevated Put level was noticed in maize under cold stress (Lee et al. 2012). Glutamine, arginine, ornithine and Put were found to accumulate in *Medicago truncatula* due to ammonium stress resulting in the changes of PA metabolism (Urrea et al. 2022). Effects of exogenous PAs on plants under stresses are presented in Table 2.

Many studies indicated the cross-talks between the PAs and several phytohormones. The most abundant PAs like Put, Spd and Spm were known to regulate the expression of phytohormone biosynthesis genes and the related metabolic pathways. For example, overexpression of PA biosynthesis gene *SPMSYN* in *Arabidopsis* has been shown to differentially regulate YUCCA family genes related to auxin biosynthesis. PAs were involved in complex interactions with the phytohormone-mediated signalling networks. The cross-talks between PAs, ABA and NO were known to be crucial for plant responses to biotic stresses. Ethylene in concert with PAs could effectively act in developing tolerance towards abiotic stresses. PA-derived H₂O₂ could mediate

Fig. 1 Polyamines (PAs) like putrescine (Put), spermidine (Spd), spermine (Spm) and cadaverine (Cad) have positive effects on various physiological processes of plant life cycle. PAs are also used in plant tissue culture media as biostimulants

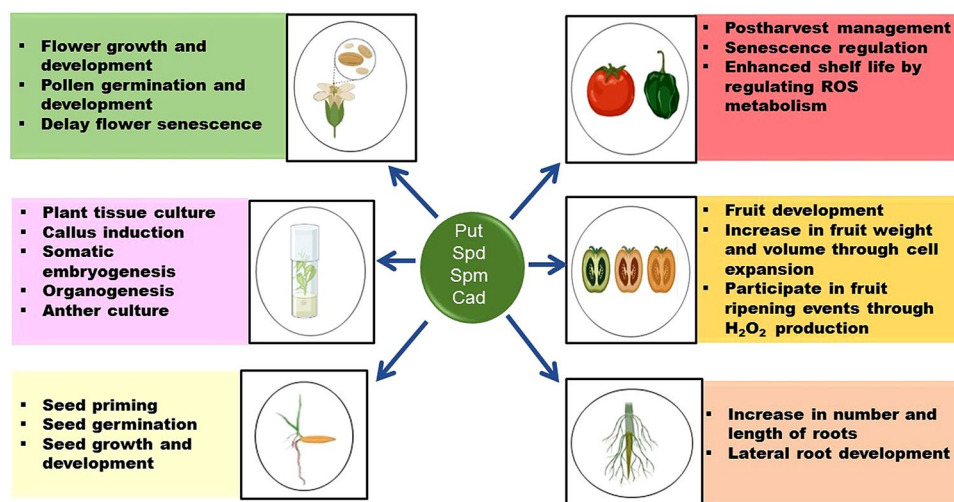


Table 1 Demonstrated effects of PAs on growth and development in different plant species

Plant species	Polyamines	Effect	Outcome	References
Azalea (<i>R. simsii</i>)	Exogenous GA ₃ and Spd	Endogenous PA↑, flower senescence↓, PA catabolism↓	Flower development	Xu et al. (2022b)
Cucumber (<i>C. sativus</i>)	Endogenous Cad, Spd and Spm	Undifferentiated floral buds (Cad↑, Spd↑ and Spm↑) Sex differentiation (Cad↓) Female flowers (Total PAs↑) Male flowers (Put↑) Macrogametogenesis (Cad↑)	Sex differentiation and unisexual flower development	Kiełkowska and Dziurka (2021)
Olive (<i>O. europaea</i>)	Endogenous total PAs	Undeveloped olive flowers with aborted ovaries and undeveloped stamens (<i>OeSPDS</i> ↓, <i>OeSPMS</i> ↓ and <i>OeADC</i> ↓)	Flower development	Alagna et al. (2016)
Black plum (<i>S. cumini</i>)	Exogenous Put application	Lipid peroxidation↓, spoilage↓, anthocyanins↑, soluble solids content↑, flavonoids↑, ascorbic acid↑ and antioxidant capacity↑	Post-harvest management	Mishra et al. (2022)
Peach (<i>P. persica</i>)	PA catabolism	Total PA↓, PA catabolism↑, <i>PpePAOI</i> ↑	Fruit growth, development and ripening	Wang et al. (2021)
Babchi (<i>P. orylyfolia</i>)	Exogenous Put application	Endogenous Put↑ Root and shoot induction	In vitro rooting and shooting	Gajula et al. (2022)
Arabidopsis (<i>A. thaliana</i>)	Exogenous Spd application	Lateral root primordia to shoot conversion efficiency↑, Spd↑ in roots, ROS↑, <i>AtADC1</i> , 2↑, <i>AtSAMDC2</i> , 4↑, <i>AtSPDS1</i> , 2↑	Meristem conversion	Kaszler et al. (2021)
Flame lily (<i>G. superba</i>)	Exogenous Put/Spd/ Spm application	Shoot multiplication↑, <i>in vitro</i> rooting ↑ and colchicine content↑	In vitro mass propagation	Sivakumar et al. (2019)
Pear (<i>P. ussuriensis</i>)	Exogenous Put/Spd application	Pericarp browning↓, ROS↓, endogenous PA↑ Regulation of mitochondrial physiology and energy status (<i>ADC</i> ↑, <i>ODC</i> ↑, <i>SPDS</i> ↑ and <i>SPMS</i> ↑)	Fruit quality	Li et al. (2021)

↑: indicates and increase, and ↓: indicates decrease of levels

Fig. 2 Diverse roles of polyamines in plants under stresses. Green zone in the meter indicates the stimulatory effects of PAs, whereas red zone means various physiological processes are adversely affected under stresses.

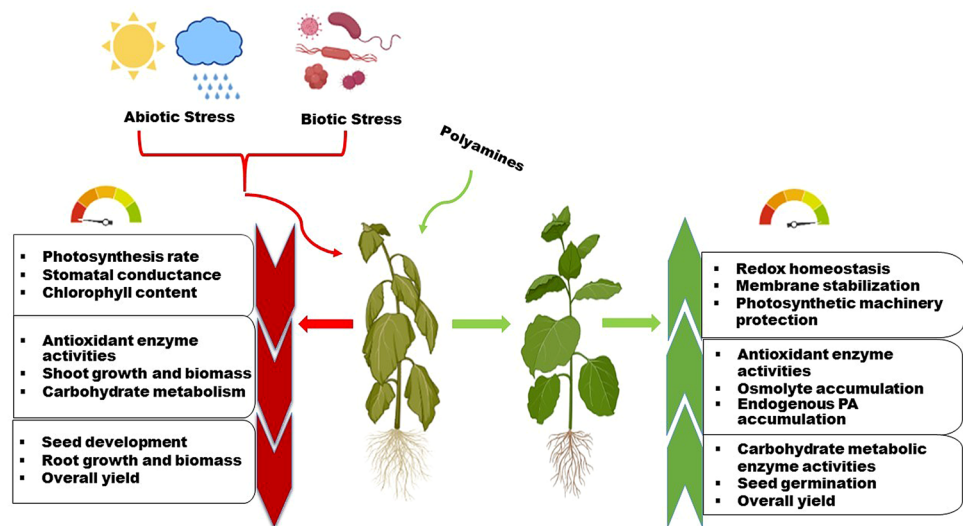


Table 2 Effects of exogenous PAs on abiotic and biotic stresses in plants

Plant species	PA treatment	Stress type	Effects	References
Tea (<i>C. sinensis</i>)	Spd/Spm (0.2 mM)	Drought	Plasma membrane H ⁺ -ATPase activity↑, fatty acid unsaturation↓	Na et al. (2022)
Faba bean (<i>V. faba</i>)	Spd (1.5 mM)	Drought	Antioxidant enzyme activities↑ Differential expression of drought responsive genes <i>VfADC</i> ↑, <i>VfSAMDC</i> ↑ and <i>VfSPDS</i> ↑	Abid et al. (2022)
Maize (<i>Z. mays</i>)	Spd/Spm (1.0 mM)	Drought	Conjugated PAs in plasma membrane↑, cell plasmolysis↓, H ⁺ -ATPase activity↑	Du et al. (2022)
Sugar beet (<i>B. vulgaris</i>)	Put (0.3, 0.6 and 0.9 mM)	Drought	Oxidative stress↓, antioxidant enzymes activities↑ and modulation in biochemical and physiological responses	Islam et al. (2022)
Barley (<i>H. vulgare</i>)	Spm (10 μM)	Drought	Cell cycle and antioxidant enzyme activities↑	Özmen et al. (2022)
Rapeseed (<i>B. napus</i>)	Spm/Spd (0.25 mM)	Salinity	Chl content↑, PSII↑, stomatal conductance↑, ROS scavenging↑, lipid peroxidation↓, antioxidant enzyme activities↑, <i>CuZnSOD2</i> ↑, <i>CAT1</i> ↑, <i>APX</i> ↑, <i>DHAR</i> ↑, <i>GR</i> ↑, <i>DAO</i> ↑, <i>PAO</i> ↑	ElSayed et al. (2022)
Stevia (<i>S. rebaudiana</i>)	Spd (0.75 mM) and endophytic fungus	Salinity	H ₂ O ₂ content and lipid peroxidation↓, Chl content↑, antioxidant enzyme activities↑	Saravi et al. (2022)
Cucumber (<i>C. sativus</i>)	Put (8.0 mM)	Salinity	Endogenous PA↑, stomatal opening, photosynthetic efficiency↑, GSH↑, ABA↓, H ₂ O ₂ ↑	Ma et al. (2022)
Lettuce (<i>L. sativa</i>)	Spd (1.0 mM)	High-temperature	Stomatal conductance↑, chlorophyll a and b↑, oxidative damage↓, net photosynthetic rate↑ and transformation of PBG to urogen III↓	Yang et al. (2022b)
Lettuce (<i>L. sativa</i>)	Spd (1.0 mM)	High-temperature	Photosynthetic pigment content↑, leaf starch and sucrose↑, Yield↑, <i>SS2</i> ↑, <i>SS-like</i> ↑, <i>SPSI</i> ↑, <i>NI</i> ↑ and <i>AI</i> ↑	Yu et al. (2022)
Cauliflower (<i>B. oleracea</i>)	Spd (1.0 mM/4.0 mM)	High temperature	Soluble sugars↑, protein percentage↑, potassium↑, phosphate↑	Collado-González et al. (2021)
Citrus fruits (<i>C. reticulata</i> , <i>C. sinensis</i> , <i>C. paradise</i>)	Put (10.0 mM), and Proline (20.0 mM)	Low temperature	flavonoids↑, phenolic compounds↑, antioxidant capacity↑	Mohammadrezakhani et al. (2021)
Rice (<i>O. sativa</i>)	Put (2.5 and 3.5 mM)	High-temperature	Endogenous PAs in leaf and panicle tissues↑, membrane stability↑, panicle grain yield↑, oxidative damage↓	Das et al. (2021)
Wheat (<i>T. aestivum</i>)	Spm/Spd (1.0 mM)	High-temperature	Grain weight↑, antioxidant enzyme activities↑, MDA↓	Jing et al. (2020)
Oilseed rape (<i>B. napus</i>)	Put/Spm/Spd (1.0 mM)	Low temperature	Free proline↑, plasma membrane H ⁺ -ATPase↑ and ethylene stimulation↓	Jankovska-Bortkevič et al. (2020)

Table 2 (continued)

Plant species	PA treatment	Stress type	Effects	References
Apricot (<i>P. armeniaca</i>)	Spm/Spd/Put (1.5 mM)	Biotic (<i>A. alternata</i>)	Black spot development↓, antioxidant enzyme activities↑	Li et al. (2019)
Oat (<i>A. sativa</i>)	Spd/Spm/Put (1.0 mM)	Biotic (<i>P. coronata</i>)	Appressorium formation↓, endogenous PAs↑, H ₂ O ₂ ↑, ADC↑	Montilla-Bascón et al. (2015)

↑: indicates and increase, and ↓: indicates decrease of levels

DHAR dehydroascorbate reductase, *GR* glutathione reductase, *APX* ascorbate peroxidase, *SS2* sucrose synthase 2, *SS-like* sucrose synthase-like, *SPS* sucrose phosphate synthase, *NI* neutral invertase, *AI* acid invertase, *MDA* malondialdehyde, *PBG* porphobilinogen, *urogen III* uroporphyrinogen III, *Chla* chlorophyll a, *Chlb* chlorophyll b

ABA signalling associated with stomatal closure and antioxidant machineries (Gonzalez et al. 2011; Zapata et al. 2017; Kamiab et al. 2020). PAs and gibberellins (GAs) were known to synergistically promote cell division (Krishnan and Merewitz 2017). PAs are significantly gaining importance as they exhibit stimulatory effects on growth and development of various plants under different conditions, and potentially act as substitutes of the phytohormones (Kumar et al. 2007; Haque and Ghosh 2016; Nandy et al. 2022). The following sections of this review highlight the recent advances and current understanding of the influence of PAs on several physiological processes in plants; however, the major focus remains on the commercially important *Solanaceae* family members; particularly integrating our knowledge to recognize and assess the impacts of PAs at various stages of their life cycles under field, laboratory and stressful conditions.

Historical Perspectives

The presence of crystalline substances, later termed as “spermine”, was first noticed in old semen samples by Antonie van Leeuwenhoek in 1678 (Bachrach 2010). Later, this substance was known to be effective in curing various diseases. Ciamician and Ravenna (1911) first isolated Put from *Datura stramonium*. Herbst and Snell (1948) reported the presence of Put in orange juice. Richards and Coleman (1952) studied the Put biosynthesis pathway in potassium-deficient barley leaves. Galston et al. (1978) reported the importance of PAs in protoplast viability, DNA synthesis, mitosis and senescence in plants. Bertossi et al. (1965) noticed the stimulatory actions of Put and Spm in dormant tubers of *Helianthus tuberosus*. Exogenous applications were found to influence embryo development and cell cycle in apple and *Helianthus tuberosus* (Bagni 1989). Davis et al. (1990) showed that PAs were involved in ripening of tomato fruits. The uses of PA biosynthesis inhibitors had adverse effects on growth and development of plants. The metabolic

aspects of PAs were investigated under stresses; for example, potassium deficiency led to higher Put level in the young oat seedlings (Galston and Sawhney 1987). Salt stress enhanced the ratio of combined Spd and Spm to Put ratio in some plants like spinach, broccoli, pepper and tomato (Zapata et al. 2004).

An Overview of PA Metabolism

Intracellular PA levels depend on the dynamics of their biosynthesis, transport and catabolic aspects. There are several routes for Put synthesis in plants. Commonly, the precursor arginine (Arg) is converted to Put by the sequential actions of arginine decarboxylase (ADC) and N-carbamoylputrescine amidohydrolase (CPA), respectively. The latter one is allosterically regulated by its substrate. Arg can also be converted to ornithine (Orn) by arginase, and then to Put by ornithine decarboxylase (ODC) (Docimo et al. 2012; Pegg 2016). In sesame, citrulline (Cit) is synthesized from Arg, then converted to Put by the enzyme citrulline decarboxylase (CDC) (Chen et al. 2019). Spd synthase (SPDS) catalyses the conversion of Put to Spd followed by the synthesis of Spm by Spm synthase (SPMS). Both SPDS and SPMS are aminopropyltransferases as they require an aminopropyl donor in the form of decarboxylated S-adenosylmethionine (dcAdoMet or deSAM) produced by S-adenosyl-methionine (AdoMet) decarboxylase (SAMDC) (Imamura et al. 2015). Lysine acts as a substrate for the synthesis of Cad (Masson et al. 2017). PA catabolic pathways are equally crucial with regard to plant growth and development. For the catabolism of PAs, the major enzymes include copper-containing amine oxidases (CuAOs) also referred to as diamine oxidases (DAOs) and flavin-containing PA oxidases (PAOs) (Tavladoraki et al. 2016). Put and Cad are preferentially catabolized by DAOs to produce ammonia, H₂O₂ and 4-aminobutanal. This aminoaldehyde is catabolized to γ -aminobutyric acid (GABA), then to succinate followed by further breakdown through Krebs cycle (Cona et al. 2006). Spd, Spm and Tspm

are catabolized by the PAOs to yield several products viz. 4-aminobutanal, 3-aminopropyl-4-aminobutanal, 1, 3-diaminopropane (Dap) and H_2O_2 . The latter acts as a signal in the cellular stress responses (Angelini et al. 2010; Moschou et al. 2012; Liu et al. 2014; Bordenave et al. 2019; Wang et al. 2019). Both biosynthesis and catabolism of PAs are schematically presented in Fig. 3.

PAs as Biostimulants

Like plant growth regulators (PGRs), PAs were extensively used in plant tissue culture as they significantly influenced organogenesis, cell multiplication and embryogenesis (Kevers et al. 2000). Put was known to be crucial at the onset of embryogenesis, whereas Spd and Spm influenced embryo growth and seed germination. Spm is essential in cell division as it acts as a substrate for the synthesis of unusual amino acid hypusine, a residue of eukaryotic translation initiation factor (García-Leon et al. 2019). Tspm could promote stem elongation (Takahashi and Kakehi 2010). PAs are known to promote shoot development in combination with other phytohormones. *Bacopa monnieri* showed improved shoot development in vitro grown in a medium supplemented with 6-benzyl-aminopurine (BAP) (2.0 mg/L) and Spd (1.0 mM) (Dey et al. 2019). Similar effect was noticed in *Dendrobium crepidatum* (Bhattacharyya et al. 2016). Put showed synergistic effects on multiple shoot induction and

proliferation in the micropropagation of some medicinally important plants like *Aristolochia indica* and *Chlorophytum borivillianum* on MS basal medium containing cytokinins (CKs), adenine sulphate, casein hydrolysate (Khatri et al. 2019; Dey et al. 2021). Exogenously added PAs could influence the level of endogenous PAs (Francisco et al. 2008). Viu et al. (2009) reported the effects of exogenously applied PAs during organogenesis in *Curcuma longa*; briefly, the explants showed efficient shoot growth and regeneration in MS media supplemented with PAs, naphthaleneacetic (NAA) and/or BAP at different concentrations. Moreover, endogenous Put, Spd and Spm levels were increased in the calli.

Debiassi et al. (2007) reported that media supplemented with Put had stimulatory effects on cell multiplication and tissue regeneration; whilst exogenously added Spm and Spd resulted in callus formation. Multiple PAs, i.e. Put, Spd and Spm in combination could induce microshoot formation in *Hemerocallis* spp. PAs could replace the conventional plant growth regulators (PGRs) as noticed during in vitro shoot regeneration from internodal segments of *Psoralea corylifolia*. The regenerated plants exhibited 95% survival rate after acclimatization under greenhouse conditions (Gajula et al. 2022). In *Dimocarpus longan*, exogenous 1-aminocyclopropane-1-carboxylic acid (ACC) and D-Arg in combination with PAs regulated the transformation of embryogenic calli (EC) into globular embryos (GE) by altering the levels of endogenous hormones (Lai et al. 2022).

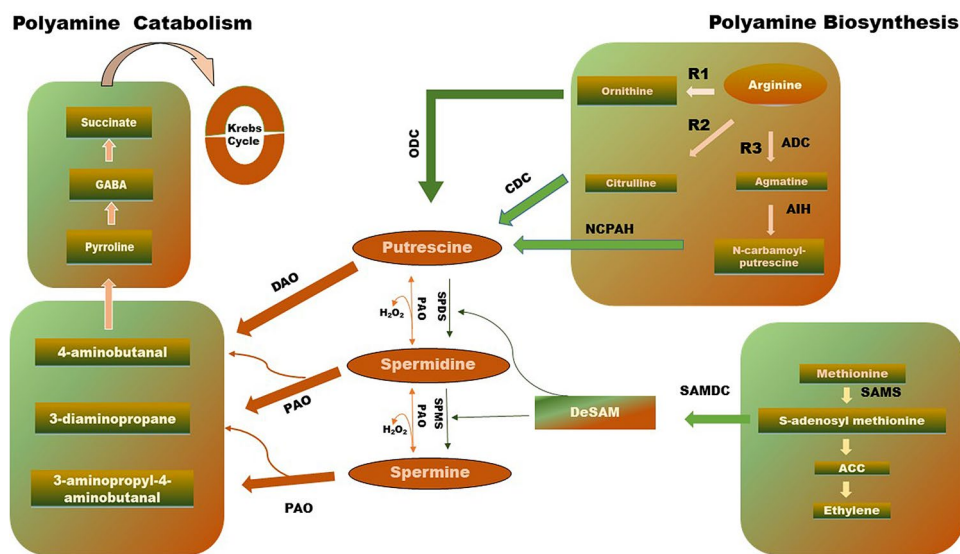


Fig. 3 A schematic view of polyamines (PAs) biosynthesis and catabolism. R1, R2 and R3 in the right panel refer to three different routes of putrescine biosynthesis. Spermidine and spermine are also produced from putrescine and aminopropyl residues (in the form of deSAM) generated from ethylene biosynthesis. Catabolic pathways for PAs are depicted in the left panel. ADC arginine decarboxylase, AIH agmatine iminohydrolase, NCPAH N-carbamoylputrescine ami-

dohydrolase, CDC citrulline decarboxylase, ODC ornithine decarboxylase, SAMS S-adenosylmethionine synthase, ACC 1-amino-1-carboxycyclopropane, SAMDC S-adenosylmethionine decarboxylase, DeSAM decarboxylated s-adenosylmethionine, SPDS spermidine synthase, SPMS spermine synthase, PAO polyamine oxidase, DAO diamine oxidase, GABA γ -aminobutyric acid

All these studies suggested that PAs had prominent effects on plant growth *in vitro*. PAs were also known to influence the development of floral organs. Exogenously applied PAs induced flowering in *Pharbitis nil* cv. Kidachi and *Sinapis alba* (Wada et al. 1994; Havelange et al. 1996). Probably, the fluctuations of the levels of PAs and its conjugates in the xylem and phloem exudates were responsible for such flowering transitions (Ohe et al. 2005). The importance of PAs in flowering was also supported by other reports. Use of difluoromethylornithine (DFMO), an inhibitor of ODC, affected flowering in rose (Sood and Nagar 2005). Similar effect was noticed in *Arabidopsis*; interestingly, the flowering was restored if the plants were transferred to media without inhibitors (Applewhite et al. 2010; Chen et al. 2019). Chen and Shen (1999) reported the stimulatory effects of Spd in the formation of flower primordium in *Dianthus chinensis*. Presence of different PAs was noticed during flower development in *Rosa damascene* and *Rosa bourboniana*. Free Put and Spd forms were prevalent during early stages, whereas their conjugated forms were at peak in mature flowers. Spd and Cad were considered as flower bud differentiation markers (Huang et al. 2004). PAs were known to influence *in vitro* pollen germination and pollen tube growth in almond; individually, 0.05 mM Put, 0.005 mM Spd and 0.025 mM Spm could promote longer pollen tube growth as compared to the control ones (Sorkheh et al. 2011). Exogenous applications of Spm resulted in improved flower quality and vase life. In *Gentiana triflora*, overexpression of *GtSPDS* and *GtSPMS* genes induced early flowering (Imamura et al. 2015). The PA-mediated regulation of flowering was confirmed by altering the expression of PA-transporter in *Arabidopsis* (Ahmed et al. 2017). Delayed flowering in plants transformed with *OsPUT1* under the control of *PUT5* promoter was reported. Spd conjugates such as hydroxycinnamoyl-spermidine (HCSpd) in *Arabidopsis* are involved in pollen development (Wu et al. 2010).

Effects of PAs on Growth and Development of the *Solanaceae* Family Members

An Overview of the *Solanaceae* Family

The *Solanaceae* family consists of approximately 4000 species in about 90 genera. The largest genera *Solanum* comprises nearly 1500 different species representing a major diversity of the *Solanaceae* family (Knapp et al. 2004). Some of the commercially important crops in this family include potato (*Solanum tuberosum*), tomato (*Solanum lycopersicum*), eggplant (*Solanum melongena*), pepper (*Capsicum annuum*) and tobacco (*Nicotiana tabacum*). *Datura*, *Petunia* and poisonous plants such as mandrake (*Mandragora officinarum*), henbane (*Hyoscyamus niger*) and deadly

nightshade (*Atropa belladonna*) also belong to this family (Bohs 2007). Members of the *Solanaceae* family have typically conical or funnel-shaped flowers with five fused petals and persistent sepals. They have bithecate and usually longitudinally or poricidal dehiscent stamens; ovaries are superior and biloculate. They have usually small, round and flat seeds along with berries, wolfberry drupes or dehiscent capsules as fruits (Simmonds et al. 1974). *Solanaceae* members exhibit polyploidy levels, e.g. tomato, eggplant and pepper are diploid ($2n=2x=24$) with basic chromosome number of $x=12$, whereas the cultivated species of *S. tuberosum* is allotetraploid ($2n=4x=48$), and *N. tabacum* is autotetraploid.

From an agronomical perspective potato, tomato, capsicum and eggplant are nutritionally rich food crops for human consumption. Globally, total produce of potatoes, tomatoes, eggplants and capsicum was approx. 540 million tonnes in 2010 (Samuels 2015). Pharmaceutically important bioactive compounds like nicotine, scopolamine, atropine and hyoscyamine are produced from other members of this family. Tobacco occupies a distinct position in plant research because of its short generation time and ease of genetic transformation. Multiple signalling pathways and their crosstalk profoundly influence both primary and secondary metabolism in plants which control their overall growth, development and productivity. Expression patterns of multiple genes and the cognate transcription factors, phytohormones and elicitors and signalling pathways were known to be crucial at various stages of life cycle of the solanaceous crops (Jin et al. 2018; Jon et al. 2020; Qin et al. 2020; Saidi et al. 2021). Moreover, environmental factors influence their geographic distribution, growth and yield (Jin et al. 2018). Both quality and crop yield are compromised under various biotic and abiotic stresses. Plants under stresses develop defence strategies through accumulation of sugars, amino acids, PAs and modified amino acids such as betaine for survival. PAs function through osmotic modulation, maintaining membrane integrity and balancing stomatal movement (Alsamir et al. 2021). As discussed earlier about the stimulatory effects of major PAs in different plant species, many laboratories also demonstrated their diverse visible effects on the solanaceous crops under normal and stressful conditions by changing endogenous levels through modulation of the metabolic pathways, adding them as media supplements usually in combination with PGRs, and exogenous applications. The salient findings of these studies are precisely discussed in the following sub-sections.

Effects of PAs on Seed Germination

In plants, dormant seeds begin to sprout and grow into seedlings under favourable conditions. Seed dormancy and germination are influenced by the environmental factors and phytohormones (Kucera et al. 2005). Abscisic acid (ABA)

controls the seed dormancy by inhibiting germination; in contrast, Gibberellic acids (GAs) promote seed germination (Yamaguchi et al. 2007; Seo et al. 2019). Ethylene counteracts ABA effects and serves as an inducer in the process of seed germination. CKs stimulate ethylene synthesis during seed germination (Lieberman 1979). The final stages of this process are associated with cell elongation, replication and mitosis that occur sequentially in the radicle. PAs are known to be crucial for initiating cell division, and tissue regeneration in plants. PAs could improve seed germination by enhancing metabolic activities such as improved genetic repair and effective mobilization of seed reserves (Vondráková et al. 2015).

Under harsh environmental conditions, seed germination might be halted. But there are pre-sowing treatments that prevent seed deterioration with time under adverse conditions. Seed priming refers to the treatments where seeds are exposed to certain solutions in order to break dormancy and improves germination without radicle emergence. It increases pre-germination metabolic processes, allowing seedlings to emerge faster, grow more aggressively and perform better under hostile conditions (Rhaman et al. 2020). PAs could influence the process of seed germination through chemical seed priming (Farooq et al. 2008; Sheteiwy et al. 2017). In tomato cultivars Roma and Nagina, exogenously applied Spm and Spd each at 50 mg/L enhanced seed germination, anti-oxidative capacity and seedling vigour (Afzal et al. 2009). Seed priming using 0.01 mM Put for 48 h at 11 °C significantly improved early seedling growth in two tobacco varieties viz. MSK326 and HHDJY (Xu et al. 2011). Khan et al. (2012) investigated the influence of PAs at varying concentrations on seed germination in hot pepper. The seed priming with lower Put concentrations (25–50 mM) remained effective in terms of germination efficiency and seedling growth. The levels of Spd and its conjugates were lowered in tobacco through RNAi-mediated downregulation of *SPDS* gene. The seeds from these plants were unable to germinate indicating the role of Spd in seed germination and development. Usually, PA-conjugates provide free PAs during seed germination. The decline in cellular Spd-conjugates might be associated with diminished seed viability and germination rate (Choubey and Rajam 2018). Seed priming with PAs is a viable strategy for improving seed germination.

Role of PAs in Flower Induction and Development

In plants, transition from vegetative growth to reproductive phase is triggered by various exogenous and endogenous factors (Andrés and Coupland 2012). GAs, CKs, ABA, jasmonate, salicylic acid, brassinosteroids, ethylene and NO were known to influence flower induction and development (Davis et al. 2009). Like plant growth regulators (PGRs),

importance of PAs was also recognized in flower induction, floral organ differentiation and control of male sterility in various plant species namely *Arabidopsis*, *Xanthium strumarium*, *Pharbitis nil* and *Sinapis alba* (Tiburcio and Alcazer 2018; Chen et al. 2019). Aberrant PA metabolism affected anther and ovule development in tobacco (Malmberg and McIndoo 1983). In tomato, male and female reproductive organs showed differential PA profiles. PAs in anthers were mostly in free form, whereas perchloric acid (PCA)-soluble fraction of Spm conjugates were found in ovaries. The PA conjugates were considered as markers for the reproductive stages (Martin-Tanguy 1997; Aloisi et al. 2016).

PA homeostasis is important at various stages of pollen development under both normal and stress conditions. Tapetal-specific silenced SAMDC lines in tomato produced aborted and sterile pollen with fertile female organs. Only cross-pollination resulted in proper fruit setting indicating the necessity of PA biosynthesis for male fertility (Sinha and Rajam 2013). The enzymes involved in PA biosynthesis and oxidative metabolism could occur precociously. For example, in tobacco the transcripts corresponding to Put metabolism, in particular, were identified during uninucleate microspore stage (Bokvaj et al. 2015). Several conjugated Spm forms were predominantly found at the early stages of pollen development, but their levels were notably reduced at the later stages (Chaturvedi et al. 2013). In tobacco, the genes encoding ODC and agmatinase (AGMAT) were upregulated in the microspore; in contrast, the genes encoding S-adenosylmethionine synthetase (SAMS) and SPDS were downregulated during pollen development. Pollen tube growth in tobacco was correlated with Spd-derived H₂O₂ production (Ma et al. 2012). H₂O₂ activates calcium ion (Ca²⁺) channels. Ca²⁺ accumulation in cytosol was associated with pollen tube growth (Paupière et al. 2017). Xu et al. (2017) reported the role of conjugated PAs in anther cuticle and sporopollenin development in plants. The SPDS-hpRNAi construct-mediated silenced tobacco lines produced flowers with reduced pollen viability (Choubey and Rajam 2018). The yeast spermidine synthase gene (*γSpdSyn*) under the constitutive CaMV35S promoter was used to produce transgenic tomato lines. Around half of the lines exhibited normal flower set with significantly higher Spd/Put and Spd/Spm ratios; whilst the other half produced flowers without fruit and seed set with lower levels of Spd suggesting altered levels of PAs could lead to abnormal development of floral organs (Nambeesan et al. 2019).

Spd-hydroxycinnamoyl transferase (SHT) is an enzyme responsible for synthesis of a PA conjugate, hydroxycinnamic acid amides (HCAAs) reported in eggplant (*Solanum melongena*) and its wild relative *Solanum richardii*. This enzyme function was associated with flower development (Peng et al. 2016). Ectopic overexpression of cotton

SAMDC1 in tobacco showed early flowering with rapid vegetative growth. Simultaneously *NtSPDS4* gene was down-regulated, and *NtSPMS* gene was upregulated in tobacco. An increase in total PAs including Spm but decrease in Spd were noticed during vegetative development and early flowering (Zhu et al. 2020). PAs were known to be responsible for the delay in senescence and maintaining postharvest quality of *Nicotiana plumbaginifolia* flowers. They also regulate protein and carbohydrate contents in the petals (Nisar et al. 2015). All these results suggest that the PAs could influence various aspects of flower development such as microsporogenesis, pollen-pistil interactions, pollen viability and ovary development.

Influence of PAs on Fruit Architecture

Fruits are distinct with regard to their morphological features. PAs influence fruit architecture (Tiburcio et al. 2018). PAs were found to affect cell division and expansion by regulating the expression of cell cycle genes in plants such as *CYCA* and *CYCB* in tobacco (Jang et al. 2006). Tomato lines overexpressing the yeast Spd synthase (*ySpdSyn*) produced obovoid fruits as compared to the spherical ones from the control plants (Nambeesan et al. 2010). Cytological studies revealed the association of PAs in periclinal cell division. Decrease of both cell layers and the cell count in medial–lateral direction of pericarp resulted in architectural changes of fruits. Moreover, the expression patterns of various fruit shape-regulating genes were altered (Anwar et al. 2019).

PA Contents During Fruit Maturation and Ripening

Fruits undergo various stages of development such as fruit set, fruit growth, maturation and ripening. Fruit growth is associated with series of active cell division and cell expansion. PAs are maintained at a high level during the early stages of fruit development associated with rapid cell division. In eggplant, PAs accumulated at the early stage of fruit growth followed by sudden drop at the later stages including ripening (Rodriguez et al. 1999). Ripening leads to nutritionally rich coloured fruits (Kumar et al. 2013). PA metabolism significantly contributed to fruit ripening and shelf life as well (Wang et al. 2017). Ripening events are predominantly controlled by ethylene and ABA (McAtee et al. 2013). S-Adenosyl-L-methionine (SAM) is a substrate for the biosynthesis of ethylene, Spd, Spm and TSpM. PAs were known to act as anti-senescence and anti-ripening regulators by inhibiting ethylene biosynthesis in fruit and vegetative tissues (Mehta et al. 2002). It was proposed that both the pathways could operate simultaneously in tomato (van de Poel et al. 2013). The idea was further substantiated by analysing substrate flux in the transgenic tomato lines

overexpressing *ySAMDC* gene. There was no effect on ethylene production owing to increased flux of SAM towards the PA biosynthesis pathway in the transgenic fruits. The cellular flux of SAM depends on its demand for the competing pathways (Lasanajak et al. 2014).

During the early stages of fruit development, Put and Spm levels were found to be higher in bell pepper and tomato, respectively followed by gradual decrease towards maturity (Zhang et al. 2014). Put in tomato fruit increased consistently till senescence. Put was known to influence the efficacy of ATP production (Ioannidis and Kotzabasis 2014). Tsaniklidis et al. (2016) studied the expression patterns and transcript levels of the genes related to Put metabolism in tomato. Although, basal Put levels were maintained during all the stages of fruit development but sudden increase during early immature stage indicated its role in cell expansion and regulation of sink strength of the developing organs. In hot pepper, PA content was determined at different stages of fruit development. At the initial stages, high Put accumulation occurred through ODC mediated pathway, whereas there was gradual drop in the later stages (Jang et al. 2015). As pepper is non-climacteric fruit, PA biosynthesis mostly occurred through SAM metabolism (Osorio et al. 2012). In tomato, overexpression of the yeast *ySAMdc* gene resulted in increased accumulation of Spd and Spm that led to increased lycopene content, prolonged shelf life and enhanced juice quality (Kolotilin et al. 2011). Pandey et al. (2015) generated transgenic tomato lines overexpressing the mouse *ODC* gene under the control of fruit-specific promoter. The genetically modified fruits showed enhanced levels of Put, Spd and Spm along with reduction in ethylene levels. These fruits exhibited prolonged shelf life. The transgenic tomato lines with higher Spd and Spm levels considerably influenced biogenesis, transcription, processing and stability of rRNA genes in tomato fruits (Shukla et al. 2020).

Put catabolism yields H_2O_2 and ammonia as by-products. H_2O_2 plays active role in fruit ripening by regulating ethylene levels (Steelheart et al. 2019; Tsaniklidis et al. 2021; Gao et al. 2021). Tsaniklidis et al. (2021) reported Put, Spd, Spm and total PA concentrations under different storage temperatures during ripening of tomato fruits. Higher Put levels were noticed in all the ripening stages during storage particularly at 5 °C. The decline of PA levels in tomato fruits stored at 25 °C suggested the initiation of abscission-related events. Storage temperature and PAs orchestrated the ripening events that prolonged the shelf life (Tsaniklidis et al. 2020, 2021). Broadly, metabolism and endogenous PA levels were tuned with the various physiological and biochemical processes in plants. It is generally believed that Put is predominately associated with catabolic processes, whereas Spd and Spm are involved in the anabolic processes.

Importance of PAs in Postharvest Management

Excessive softening compromises the firm texture of fruits and vegetables—a major postharvest problem affecting both consumer acceptance and financial returns. Depolymerization and disintegration of cell wall pectin by enzymes, namely polygalacturonase (PG), pectin methyl esterase and galactosidase mostly contribute to fruit softening (Handa et al. 2007). Senescence and the membrane deterioration are enhanced by the reactive oxygen species (ROS) under storage at low temperatures. Efficient ROS scavenging systems can prolong postharvest life by delaying senescence (Cheema et al. 2018). PAs were known to be important in maintaining the quality and firmness of the fruits and vegetables by preventing the processes of postharvest decay. For example, they protect membranes by binding to the negatively charged macromolecules such as pectin. Various postharvest stresses could be overcome by exogenous applications of the PAs (Fortes et al. 2019).

In eggplant, PAs accumulated in the fruits in response to stress-induced damage during storage (Rodriguez et al. 2001). Ectopic expression of yeast SPDS in tomato resulted in the increase of fruit shelf life. Also, senescence was delayed in the transgenic plants in comparison to the wild type plants (Nambeesan et al. 2010). Anti-senescence properties of PAs have been reported in green bell pepper fruits. 1-methylcyclopropene (1-MCP) treatment resulted in the decrease of ethylene content; in contrast, Put, Spd and Spm levels were increased which explained why there was delay in senescence and improved shelf life in these fruits (Cao et al. 2012). Tomato cultivars with high levels of PAs and less ethylene had a longer shelf life (Dibble et al. 1988). Transgenic plants with overexpressing PA biosynthesis genes could produce fruits with prolonged postharvest life (Lasanajak et al. 2014). Overexpression of the mouse *ODC* gene under fruit-specific promoter in the transgenic tomato plants resulted in the higher Put, Spd and Spm and lower ethylene levels with a longer shelf life of the fruits. There was concomitant reduction in respiration rate and physiological loss of water. Enhanced PA levels can potentially form cross-linkages to the carboxyl groups (COO^-) of the cell wall pectic substances thus blocking access to the degrading enzymes namely pectin methyl esterase, pectinesterase and PG. Hence, PAs could be involved in maintenance of cell wall integrity and extending shelf life (Pandey et al. 2014).

Accumulating PAs in the ethylene-suppressed transgenic tomatoes led to longer shelf life of the fruits (Sobolev et al. 2014). Exogenous treatment of Put significantly improved the quality of pepper fruits in two cultivars (Nongda 24 and Jingtian 3) stored at 20 °C as compared to the untreated ones (Wang et al. 2018). Patel et al. (2019) tested the effects of Spd and Put in multiple combinations to extend

the shelf life of pepper cv. yolo wonder during postharvest storage at 4 °C. Shelf life could be extended up to 40 days by such treatments with elevated levels of proline along with catalase (CAT) and ROS scavenging activities; but there was decline in peroxidase activities. Exogenous applications of Put in combination with Chitosan (CHT) improved shelf life of pepper fruits by regulating ROS metabolism, membrane permeability and pigment contents. It was believed that PAs could maintain the quality of healthy fruits by downregulating the respiratory flux, ethylene biosynthesis and the softening process (Ghosh et al. 2021). Tsaniklidis et al. (2021) showed PA homeostasis at different temperatures during postharvest storage. *ADC* biosynthetic pathway led to Put accumulation in tomato fruits stored at 10 and 25 °C. Spd levels were low as compared to Put. Accumulation of Put and higher PAs depends on the genotypes of the individual cultivars (Dibble et al. 1988; Tsaniklidis et al. 2016). These studies suggest that PAs could potentially improve the shelf life of fruits and vegetables during postharvest storage.

Applications of PAs in Plant Tissue Culture

PAs have a wide range of applications in plant tissue culture (Rakesh et al. 2021). In pepper, Put, Spm and Spd induced shoot buds in terms of frequency and regeneration percentage (Kumar et al. 2007). Exogenous addition of Spd and Spm could affect callusing and ethylene synthesis with concomitant increase of total endogenous PA levels (Batista et al. 2013). The cellular levels of PAs and the corresponding metabolic enzymes vary throughout the life cycle of a plant. Both length and number of lateral roots of eggplant were increased by Spd supplements at 0.5 and 1.0 mM concentrations. Exogenous Spd could overcome the adverse effects of PA biosynthesis inhibitors namely difluoromethylarginine (DFMA) and methylglyoxal-bis (guanylhydrazone) (MGBG) indicating role of PAs in root growth and differentiation (Sharma et al. 1997). In tobacco, the PA biosynthesis genes were highly expressed in shoot and root apical meristems. Usually, high PA levels were noticed in the actively growing meristematic tissues associated with rapid cell division during root and shoot developments in plants as influenced by various phytohormones such as indole-3-acetic acid (IAA), CKs, ethylene and ABA (Paschalidis et al. 2005; Smith et al. 2012; Wu et al. 2012).

Kehie et al. (2013) successfully formulated shoot induction media, i.e. MS basal fortified with thidiazuron (TDZ) (4.54 μM) and Put (5.6 μM) for regeneration of plantlets from cotyledon segments of capsicum. Multiple shoot bud induction by the PAs could be due to rapid cell division and/or their inhibitory effects on production of ethylene (Bais et al. 2000; Batista et al. 2013). Sivanandhan et al. (2011) studied the effects of PAs on shoot multiplication

in *Withania somnifera*, a medicinal plant. Spd at 20 mg/L induced multiple shoots (approx. 94% of nodal explants with 46.4 shoots per node). Put has a major effect on root development. Put supplement at 20 mg/L significantly promoted rhizogenesis in *Withania somnifera* (17.8 roots/shoot). The complex morphological changes like rhizogenesis involves multiple metabolic pathways and PAs (Aragao et al. 2017). Recently, Adly et al. (2022) proposed shoot regeneration in potatoes through enhancing endogenous PAs attributed by the addition of AgNO₃ in growth media. Significant increase in PA content resulted in improved shoot regeneration (by 33%). In recent studies, independent ADC and ODC silenced transgenic tomato lines were grown using NO₃⁻ and NH₄⁺ salts to know the effects on root growth. Increase of ADC expression in the silenced ODC lines led to the accumulation of PAs, but there was no PA accumulation in ADC silenced lines. In the silenced ODC lines, root growth was considerably affected as compared to the other organs suggesting the importance of ODC mediated PA biosynthesis in root development (González-Hernández et al. 2022).

In genetic and plant breeding programmes, the production of doubled haploid (DH) plants is a useful technique; nevertheless, sweet pepper is recalcitrant to microspore embryogenesis and DH production. Experiments using varying concentrations of Put in combination with heat treatment were carried out on three cultivars of pepper namely “Inspiration F1,” “Maratus F1,” and “Magno F1”. Microspore embryogenesis was prevented at higher concentration (5.0 mg/L) of Put, whereas significant regeneration % was obtained at lower (0.5 mg/L) Put concentrations in all three cultivars indicating the regulatory role of Put on sweet pepper microspore embryogenesis (Heidari-Zefreh et al. 2019).

PAs either alone or in combination with other phytohormones played stimulatory role at different stages of somatic embryogenesis (SE). Different PAs were active at different phases of embryogenesis. Put was found to be critical during the early stages of rapid cell division, whilst the cellular elongation phase required the synchronized role of Spm and Spd (Santa-Catarina et al. 2007). Elevated PAs during early stages of SE caused accumulation of SAM synthetase and stress-related proteins that suggested the protective role throughout this process (Nandy et al. 2022). Put was mainly found in SE as compared to zygotic embryos (ZE) in the case of Habanero pepper (*Capsicum chinense*). However, Cad was abundant in all the stages of both SE and ZE indicating its common role in this species (Regla-Márquez et al. 2016). Exogenous treatments of Put, Spm and Spd showed stimulatory effects on the formation and development of SE in pepper. Both apex-radicle growth and emergence of tiny cotyledonary leaves in embryos indicated the impeccable role of PAs in plant tissue culture (Gough et al. 2015).

PAs as Elicitors of Stress Responses in the Solanaceous Crops

PAs as Signalling Molecules Under Abiotic Stresses

Various abiotic stresses such as drought, extreme temperatures, heavy metals, high salinity, nutrient deficiency and UV-radiation trigger responses orchestrated by various signalling molecules such as phytohormones, hydrogen sulphide (H₂S), nitric oxide (NO), phytochromes and PAs (Slama et al. 2015; Gull et al. 2019). The crucial roles of PAs were studied in many plants under stresses (Liu et al. 2007; Kusano et al. 2008; Alcázar et al. 2010; Hussain et al. 2011; Minocha et al. 2014; Shi and Chan 2014; Tiburcio et al. 2014; Liu et al. 2015; Hasan et al. 2021; Alcázar et al. 2020). The cellular PA levels depend on the type, intensity and duration of a stress and plant species (Kasinathan and Wingler 2004). In comparison to susceptible plants, stress-tolerant plants were found to be better equipped in terms of biosynthesis of PAs with significant increase of their endogenous levels (Cvikrová et al. 2012). They could alleviate stresses by directly acting as ROS scavengers and/or modulating both enzymatic and non-enzymatic antioxidants in order to scavenge harmful free radicals (Duan et al. 2008; Groppa and Benavides 2008; Khare et al. 2018). The following sub-sections focus on the roles of PAs in the *Solanaceae* family members in response to various abiotic stresses.

PAs and Drought Stress

Drought stress is associated with lower water content, reduced leaf water potential, turgor loss, stomata closure, reduction in cell expansion and growth which in turn activate multiple physiological, metabolic and defence systems in plants for their survival (Hussain et al. 2018). Cellular accumulation of PAs was considered as one of the responses under drought stress (Yamaguchi et al. 2007; Hatmi et al. 2015; Sequera-Mutiozabal et al. 2016; Liu et al. 2017; Sadeghipour et al. 2019; Ali et al. 2020). Metabolic aspects of PAs in response to water stress were studied by modulation of signalling pathways through transgenic approaches and exogenous applications (Farooq et al. 2012; Ebeed et al. 2017; Ozturk et al. 2021).

Pepper plants exposed to natural drought conditions were known to exhibit Cad, Put, Spd and Spm accumulations in the leaves. Cad and Put mediated stomatal closure were reported in these plants (Sziderics et al. 2010). Accumulated Cad protected DNA from the damaging effects of oxidative stress, and potentially worked as a free radical scavenger in concert with Spm (Ha et al. 1998; Liu

et al. 2000; Kuznetsov et al. 2007; Tomar et al. 2013). In proline-overproducing tobacco plants under drought, Spm level was considerably higher as compared to Spd and Put levels. Lower Spd level was due to its use in Spm production and/or its oxidation to Dap by PAO. PA-induced antioxidative defence mechanisms were known to reduce stress-related damages (Cvikrová et al. 2012). Proline and PAs were reported to act in tandem in plants exposed to stresses as they had some common intermediates in biosynthetic and catabolic pathways (Pál et al. 2018). Seedlings of two tomato cultivars, Huangguan and Maofen802 under drought exhibited increased level of free PAs. Moreover, rate of both Spd and Spm accumulation was higher as compared to Put in the cultivars, implying their involvement in drought resistance (Zhang and Huang 2013). Drought hardening remained an effective strategy to improve the ability of stress tolerance (Huang et al. 2013). Two potato cultivars viz. *Sullu* and *andigenum* exposed to drought stress showed higher PA accumulation, but the levels gradually declined in response to prolonged stress. Prior drought hardening resulted in the accumulation of PAs that helped plants to endure even prolonged stress indicating stimulatory effects of PAs (Zhang et al. 2018). Exogenous treatment of Spd enhanced stress tolerance under water-deficit conditions in tobacco with simultaneous increase of chlorophyll content, photosynthetic rate and antioxidant enzyme activities (Xu et al. 2022a).

Overexpression of *ADC* gene (*PtADC*) in tomato and tobacco plants considerably affected ROS accumulation in transgenic lines exposed to drought (Wang et al. 2011). *SISAMS1* overexpressing tomato plants under drought and salt stress resulted in the accumulation of Spd, Spm and ethylene which effectively alleviated oxidative damage. The lines showing inhibition of PA biosynthesis were associated with increased water loss; however, PA treatment reversed these effects indicating the crucial role of PA in drought stress tolerance (Zhang et al. 2020a, b). *SPDS*-RNAi transgenic lines of tobacco were raised in order to assess the morphological and physiological implications of this gene function in response to drought stress. Put level was moderately increased in these lines. They were resistant to saline and drought conditions (Choubey and Rajam 2018). Sundararajan et al. (2022) reported the effects of Put in combination with sodium nitroprusside (SNP; a nitric oxide donor) in mitigating stress in tomato seedlings. SNP (150 μ M) in combination with Put (0.3 mM) proved to be effective in alleviating stress symptoms with enhanced growth parameters. The plants showed significant increase in relative water content (RWC) along with more chlorophyll and proline contents suggesting the importance of PAs to withstand drought stress.

PAs and Salt Stress

Salt stress is considered as one of the major challenges in crop productivity as it disrupts the integrity of cellular membranes, functioning of the numerous enzymes involved in the photosynthetic apparatus, thus affecting pigment contents, structure and function of thylakoid membranes and stomatal functions (Geissler et al. 2009; Singh et al. 2021). Spd and Spm levels were found to be significantly increased in response to salinity in plants (Zapata et al. 2004; Mutlu and Bozcuk 2005).

Pepper fruits contain Put, Cad and histamine under normal circumstances. Exogenous supply of NH_4^+ ions to Pepper exposed to salt stress resulted in Put and Cad accumulation that effectively alleviated the detrimental effects (Piñero et al. 2019). Likewise, application of Spd to tomato seedlings facing saline-alkaline stress could induce improved antioxidant systems with enhanced stress tolerance. Both NADPH oxidase and PAO are involved in the generation of H_2O_2 which in turn participates in various physiological and stress responses. The exogenous Spd pre-treatment in the tomato seedlings was responsible for the PAO-mediated H_2O_2 production. Spd treatment were also known to regulate NADPH oxidase activity at post-transcriptional or translational levels (Yang et al. 2022a). Overexpression of *SsSAMS2* gene in tobacco led to an increase of cellular PA level; consequently, increased salt tolerance was noticed (Qi et al. 2010). Exogenous application of Spd in the roots of two tomato cultivars namely Jinpengchaoguan and Zhongza No. 9 growing under mixed salinity-alkalinity stress was found to exhibit varied stress tolerance. The levels of free and soluble conjugated forms of PAs were increased dramatically in these cultivars with concomitant changes in the activities of *ODC*, *SAMDC*, *DAO*, *ADC* and *PAO*. Insoluble bound Put and Spm contents were also increased in the roots of Zhongza No.9. Possibly, insoluble membrane-bound PAs contributed towards stability of plasma membrane, mitochondria, tonoplast of the plant cells under salinity stress (Hu et al. 2012). Pepper seedlings grown under salt stress (0, 50 and 100 mM NaCl) were treated with Put, Spm and Spd. Improvement of plant height, number of leaves, stem diameter, chlorophyll reading value (CRV), stomatal conductance (SC), tissue electrical conductivity (TEC), leaf relative water content (LRWC), enzyme activities of superoxide dismutase (SOD), CAT and peroxidase (POD) of pepper seedlings were noticed (Ekinci et al. 2019). PAs along with other phytohormones showed synergistic effects in improving growth parameters under stress conditions. For instance, application of Spd in combination with salicylic acid (SA) protected tomato seedlings from salt stress by increasing the activities of antioxidant enzymes, levels of osmolytes and mobilization of seed storage proteins (Rajjou et al. 2006; Verslues et al. 2006; Khan and Panda 2008; Sekmen et al. 2012). Spd

also prevented the loss of D1, D2, cytochrome f and Rubisco in leaf tissue (Fariduddin et al. 2018). Transgenic tobacco plants overexpressing *SAMDC* were exposed to salt stress exhibited accumulation of superoxide anions and H_2O_2 in the nucleus indicating the role of PAs in stress tolerance (Seo et al. 2019). Downregulation of apoplastic *PAO* gene affected salt tolerance ability in tobacco (Gémes et al. 2017).

Protective Roles of PAs at High Temperature

High temperature (HT) severely compromise the crop productivity. The endogenous PA levels could fluctuate in response to HT stress. PAs were found to decline during HT in tomato. However, transcript levels of some PA metabolism genes, i.e. *ARG1/2*, *AIHI*, *CPA* (Put biosynthesis), *SISPDS1* (Spd biosynthesis) along with *CuAO4* (a PA catabolic pathway gene) were known to be increased (Upadhyay et al. 2020).

Cheng et al. (2012) investigated the influence of Spd (1.0 mmol/L) on tomato fruits exposed to HT. Exogenous application of Spd alleviated tissue damage suggesting its role in stress tolerance (Shan et al. 2016). Exogenous Spd could also improve photosynthesis by modulating the gene expression and activity of essential CO_2 fixation enzymes (Shu et al. 2014). Spd application could reduce HT-induced cell damage by regulating PA biosynthesis genes, hormone pathways and redox genes in tomato seedlings (Mostofa et al. 2013). Subsequently, a total of 67 differentially expressed proteins were detected; classified into four categories related to photosynthesis (27%), cell rescue and defence (24%), protein synthesis, folding and degradation (22%) and energy and metabolism (13%). The proteomic analysis confirmed that Spd could activate ROS scavenging enzymes to enhance stress tolerance (Sang et al. 2017). Transgenic tobacco plants with RNAi-mediated *SAMDC* silencing resulted in increased sensitivity and delayed responsiveness to HT. These lines showed excessive injuries with reduced rate of photosynthesis and decreased accumulation of ROS scavenging enzymes (Mellidou et al. 2020). Downregulation of *PAO* in transgenic tobacco lines showed thermotolerant photosynthetic machinery, an increase in biomass accumulation along with enhanced levels of the enzymatic and non-enzymatic antioxidants. PAs may prevent heat damage by preserving thermostability of thylakoid membranes and regulating the synthesis of heat shock proteins (Mellidou et al. 2017).

PAs and Chilling Stress

Exposure to lower temperatures are known to be associated with multiple adverse effects such as micro-organellar disruption, dehydration of cells and tissues, phase transition in cell membrane lipids, ROS production, redox potentials and degradation of essential macromolecules like cellulose. To

combat such stress, the defence machineries gets activated including the accumulation of PAs in plants (Kazemi-Shahandashti et al. 2018).

Chilling-tolerant tomato cultivars had increased levels of *DAO*, *PAO*, soluble sugars and soluble proteins. Cold acclimatization resulted in Put accumulation through modulating *ADC* and *DAO* activities (Song et al. 2015). Increased levels of free and conjugated PAs were found in the leaves of tomato during cold stress (Upadhyay et al. 2020). Ding et al. (2021) reported crosstalk between JA signalling and PA metabolism in tomato plants exposed to cold stress. RNAi-mediated downregulation of *MYC2*, a major regulator of JA signalling, reduced the expression of *ADC1*. Decreased Put accumulation resulted in increased chilling-induced damage in plants. Endogenous PA levels were investigated in tobacco seedlings in response to cold conditions. Put was accumulated in the stressed plants. In the chilling-tolerant tobacco variety, PA accumulation coincided with the corresponding higher biosynthetic and lower catabolic enzyme activities (Wang et al. 2019). Exogenous application of Put (1.0 mM) to tomato seedlings exposed to cold stress resulted in PA accumulation and therefore enhanced chilling tolerance (Song et al. 2015). Tomato cv. Moneymaker was exogenously supplied with Spd to find the role of PAs in chilling stress. The plants showed accumulation of compatible solutes, i.e. soluble sugars and proline along with reduction in ROS. PA anabolism and catabolism enzymes were also upregulated in the leaves (Diao et al. 2015). Application of Put to tomato plants at low temperature induced tolerance by activating the expression of *LeNCED1*, thereby, increasing ABA accumulation. Exogenous Spm and Spd resulted in higher NO and H_2O_2 levels along with the concerned enzymes namely, nitrite reductase (NR), NOS-like and PA-oxidase during chilling stress (Diao et al. 2017). Overexpression of *SAMS* gene enhanced chilling tolerance in tobacco. Transgenic plants exhibited low ion leakage along with thickening of cell wall suggested that PAs were effective in imparting a shield to combat cold stress (Seong et al. 2020).

Protective Roles of PAs Against Pathogens

Biotic stress causes a huge loss in terms of crop yield, a major challenge of global food security. *Phytophthora capsici* adversely affected pepper production (Koc et al. 2017). Recently, onion dry scale extract was used to observe the effect in eggplant infected with *Ralstonia solanacearum*. Elevated PA level could protect the plants from such bacterial infection (Naguib and Abdelraouf 2020). Overexpression of *ADC* gene in eggplants resulted in Put accumulation and conferred resistance to *Fusarium oxysporum* (Prabhavathi and Rajam 2007). Over accumulation of PAs was noticed in response to viral infections, then PA levels were stabilized (Jiménez Bremont et al. 2014). Cucumber Mosaic

Virus (CMV) and Potato Virus Y (PVY)-infected tomato plants showed chilling tolerance induced by PAs. In these plants, elevated PA levels triggered programmed cell death, and hypersensitivity contributed to a ROS burst (Tiburcio et al. 2014). Transgenic tomato lines overexpressing *SAMDC* exhibited resistance to two fungal pathogens namely *Fusarium oxysporum* and *Alternaria solani*. PA accumulation could protect from such pathogens by cell wall lignification and suberization, and preventing them from entering into the cell (Hazarika and Rajam 2011).

The *Cladosporium fulvum* resistant tomato lines became less resistant by virus-induced gene silencing (VIGS) of the *SAMDC* gene indicating the crucial role of the corresponding enzyme under biotic stress (Zhao et al. 2018). RNAi-mediated downregulation of *PAO* in tobacco plants resulted in low hypersensitivity response to cryptogein treatment (Yoda et al. 2006). These observations established a relationship between PA oxidation and stimulation of HR-associated defence-related genes. Overexpression of *PAO* in tobacco transgenic lines induced biotic stress tolerance through H_2O_2 generation against the pathogens namely *Pseudomonas syringae* and *Phytophthora parasitica*. The plants showed enhanced lignin and pectin contents which protected from pathogen entrance due to cell wall hardening (Moschou et al. 2009). Exogenous application of Spm alone, and Spm in combination with proline remained effective in *Phytophthora capsici*-infected capsicum in terms of defence (Koc et al. 2017). Khajuria et al. (2018) revealed that Put application alleviated oxidative stress caused by root knot nematode. Moreover, number of galls, the average gall index, the number of egg masses and the severity level of root knot nematode were known to be significantly reduced. All these data suggested that PAs were promising to fight the biotic stresses in plants.

Concluding Remarks and Future Prospects

Research areas in the field of PAs are significantly gaining importance as evident from a number of published reports in the recent years. The diverse roles of PAs are now well recognized in different plants, animals including human health aspects and microbes. This review provides an integrated knowledge on PAs highlighting their stimulatory roles from seed germination to fruit development in plants. PAs also find their applications in various plant tissue culture aspects since their supplements to the growth media prominently exhibit PGR-like activities in the in vitro grown plantlets. The major focus of this review remained on the commercially important Solanaceous crops. World-wide climate change and pathogen attacks are the major challenges in agriculture. In other words, various abiotic and biotic stresses adversely affect the overall productivity and

nutritional qualities of these crops. PAs are known to be crucial under stresses. As shown in many reports, stress tolerance in the solanaceous crops could be achieved by modulating endogenous levels of PAs and exogenous applications as well. Keeping in view, one section of this review highlights the recent advances regarding the importance of PAs in stress tolerance in these crops. Free PAs can covalently and non-covalently bind to different types of biomacromolecules associated with wide range of biological functions pertaining to plant growth and development; however, underlying molecular mechanisms associated with these processes are yet to be clearly understood. Therefore, modulation of endogenous PA levels and their distribution patterns by the modern biotechnological means will remain attractive areas of applied research for crop improvement. Exogenous applications of PAs are known to enhance antioxidant machineries, reduce ROS and lipid peroxidation and promote plant growth and development; thus, plants survive better without compromising yield under stresses by such practices. Nanotechnology-based carriers for selective PA assimilation could be designed for effective exogenous applications. In plants, relationships between PAs and various abiotic and biotic stress responses are exceedingly complex in terms of involvement of the multiple processes, i.e. stress priming, interactions with ROS, cross-talks with phytohormones and other signal transduction pathways. Still, we do not clearly know the orchestrated molecular mechanisms involved in such processes. Therefore, we need to reinvigorate research activities in these emerging areas to better understand the structure–function relationships of the conjugated PAs, metabolic regulations and distribution of PAs, and their biostimulatory effects on plants. Manipulation of the PA metabolic pathways would be viable alternatives for development of designer crops with desirable traits.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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