REVIEW

Biologia futura: the role of polyamine in plant science

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Abstract

Polyamines (PAs) are positively charged amines such as putrescine, spermidine and spermine that ubiquitously exist in all organisms. They have been considered as a new type of plant biostimulants, with pivotal roles in many physiological processes. Polyamine levels are controlled by intricate regulatory feedback mechanisms. PAs are directly or indirectly regulated through interaction with signaling metabolites (H_2O_2, NO), aminobutyric acid (GABA), phytohormones (abscisic acid, gibberellins, ethylene, cytokinins, auxin, jasmonic acid and brassinosteroids) and nitrogen metabolism (maintaining the balance of C:N in plants). Exogenous applications of PAs enhance the stress resistance, flowering and fruit set, synthesis of bioactive compounds and extension of agricultural crops shelf life. Up-regulation of PAs biosynthesis by genetic manipulation can be a novel strategy to increase the productivity of agricultural crops. Recently, the role of PAs in symbiosis relationships between plants and beneficial microorganisms has been confirmed. PA metabolism has also been targeted to design new harmless fungicides.

Keywords Biomarker · Fungicide · Polyamines · Shelf life · Stress resistance

Introduction

Polyamines (PAs), including putrescine, spermidine and spermine, have been known as aliphatic biogenic amines which are present in most prokaryotes and all eukaryotic organisms [100]. PAs have been used in a wide range of biological processes in plant growth and development, such as seed germination, root growth, embryogenesis, rhizogenesis, organogenesis, floral initiation and development, vascular development, fruit development, biofilm formation, ripening, leaf senescence and programmed cell death [46, 75]. PAs also play important roles in resistance against different abiotic stresses, including low and high temperatures, salt, drought, wounding, ozone, flooding, acid, heavy metals (Cu,

Cr, Fe and Ni) and oxidative stresses [106]. In plant, PAs interplay with a variety of fundamental cellular processes, including membrane stabilization, nucleic acids and protein synthesis, modulating RNAses, proteases and other enzymes activities, gene expression, DNA replication, transcription, RNA modification, ion-channel regulation, cation–anion balance, free radical scavenging activity, cell cycle regulation, protein modification, interaction with phytohormones, regulation of buffering mechanism, ethylene biosynthesis and N metabolism (they serve as N reserve, play a role in proline synthesis and N: C ratio regulation) [70].

Polyamine biosynthesis

Metabolic pathways and numerous enzymes involved in PA synthesis and conversion of Put into the higher polyamines have been discovered over the last two decades. The process of synthesis is carried out by two aminopropyl transferase enzymes: Spermidine and spermine synthase S-adenosyl-methionine (SAM) is also needed for ethylene biosynthesis which is made by ACC synthase and ACC oxidase [109]. Thus, both ethylene and polyamine biosynthetic pathway compete for SAM as substrate.

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Regulatory feedback mechanisms of polyamines

Ornithine as a non-proteinogenic amino acid plays an important role in regulation of PAs biosynthesis. De-Olivera et al. [25] showed that arginine (Arg) or ornithine (Orn) act as regulators of PA metabolites in *Araucaria angustifolia* cell lines. Exogenous Arg and Orn led to the increase in cellular PAs contents and expression of genes related to PAs biosynthesis and catabolism. Also, these compounds demonstrate distinct roles in embryogenesis of plants. Exogenous D-Orn promotes the expression of genes involved in Orn, Arg and S-adenosyl methionine metabolisms [32]. PA levels are controlled by intricate regulatory feedback mechanisms [55]. PAs control the level of OAZ (ODC antizyme) through multiple mechanisms that provide a homeostatic feedback regulation of PA levels [116]. Az1 temporally attaches to ODC then, Az1 binding triggers ODC degradation by increasing the breakdown of cryptic proteasome-interacting surface of ODC. Yordanova et al. [120] reported that some cis-acting elements in antizyme mRNAs such as specific RNA structures are needed to induce the frame-shifting efficiency. In fact, a nascent polypeptide stimulates frame-shifting efficiency in response to PAs within the ribosome exit tunnel. A feedback in PA-dependent translational regulation indicated that the synthesis of full-length OAZ requires a ribosomal frame-shifting (RFS) event that leads to the translation beyond the interrupting STOP codon [39]. Feedback in PA-dependent translational regulation indicated that AZIN1, a repressor of OAZ, is modulated by PA at the translational level. The more the PA level increases, the more the translation of AZIN1 decreases. Thus, synthesis of full-length OAZ is stimulated by high PA concentrations. In another study, Yordanova et al. [120] reported a new mechanism, indicating that an amount of gene translation inhibits further translation of the signal message by creating a ''queue'' in ribosomes which eventually interrupts the translation of AMD1 coding sequences and shows a regulatory feedback mechanism of PAs.

Polyamine and phytohormone cross-talk

The interactions among the three main PAs (putrescine, spermidine and spermine) and phytohormones biosynthesis and signaling are quite complex. These PAs regulate the phytohormones gene expression. Studies on different plants have shown that PA-derived H_2O_2 acts as a mediator in ABA signaling during stomatal closure and antioxidant defense system [5]. PA-derived H_2O_2 also acts as a signal and plays key roles in cell wall maturation, stress-induced stiffening, stomata opening and programmed cell death (PCD) [7]. Agurla et al. [3] revealed the possible overlap of signaling components during stomatal closure by ABA and PAs. An increased nitric oxide (NO) and reactive oxygen species (ROS) as essential signaling components in guard cells of a plant were observed during stomatal closure. Increased ROS seems to be a prerequisite for NO production and can be considered as an upstream event of ROS. Similarly, increased levels of ROS and NO were observed when guard cells were exposed to ABA [97]. Also, it has been reported that a certain threshold of PAs may elevate degradation or generation of H_2O_2 [118].

In many studies, the cross-talks among PAs, abscisic acid and NO were confirmed during plant responses to biotic stresses. NO is a mediator in ABA-dependent stomatal closure [5]. Nahar et al. [69] showed that PA and NO cross-talk could alter some physiological processes to promote Cd-toxicity tolerance.

PAs have also showed a positive feedback with gibberellin (GA), and both hormones synergistically promote cell division [47].

Ethylene and PAs can act as inducers of resistance against abiotic stresses [122]. Ethylene triggers salt tolerance by activation of a complex pathway of H_2O_2 signaling that is PA catabolism-dependent. In this sense, a model for cross-talk regulation among ethylene, PAs and H_2O_2 in salt-tolerant maize genotypes has been reported (Fig. 1; [29]).

PA has a strong link with ethylene (Eth). During PA biosynthesis, S-Adenosyl methionine (SAM) is used which is also an Eth precursor. Therefore, PA and Eth compete with each other for SAM [109]. It is reported that PAs and Eth play an important role in the regulation of somatic embryogenesis of cultured cell/tissues, and Eth alone cannot make somatic embryogenesis [9]. Asgher et al. [13] confirmed the PA and Eth cross-talk in plants.

The jasmonate (JA) family acts as signaling molecules that play an important role in regulation of PAs biosynthesis [88]. A relationship between brassinosteroids and PAs was suggested by Choudhary et al. [21] that showed this fact that the interaction of brassinosteroids and PAs improved copper stress tolerance in *Raphanus sativus*. Application of 24-epi-brassinolide (EBL) and spermidine enhanced plant drought tolerance by altering PA, Eth and protein levels in Maize [102]. EBL increased the levels of soluble conjugated and insoluble bound PAs, particularly putrescine, and consequently improved the cucumber growth under Ca $(NO_3)_2$ stress [121].

Fig. 1 Cross-talk regulation model among ethylene, PAs and H_2O_2 in salt-tolerant maize [29]
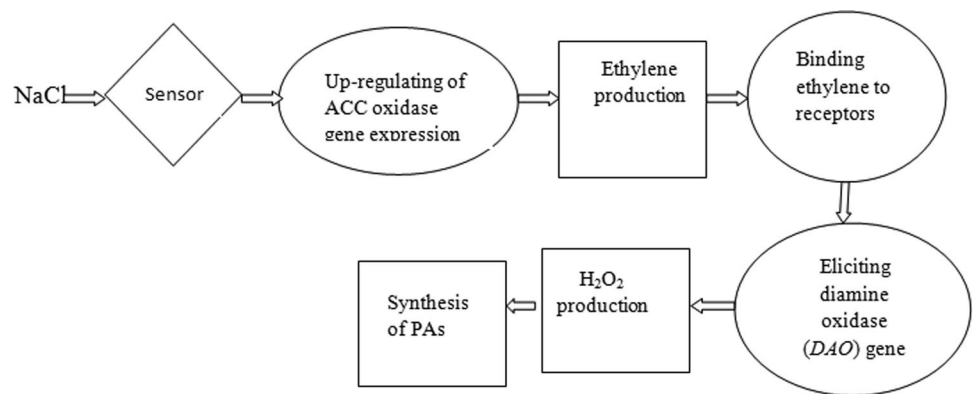
Role of polyamines in biotic and abiotic stresses

There are evidences that confirm the critical role of PAs in stress tolerance such as the increased expression of PAs biosynthetic genes under stress conditions [5]. Also, the elevation of endogenous PA levels by exogenous supply of PAs in stress conditions [5, 51, 52, 53] and the relation of decreased stress tolerance with reduction in endogenous PAs [81]. Evidence indicates that PA-triggered salinity tolerance may be involved in Ca^{2+} signaling [79], various ion-channel activities, especially cation, and K^+ channels [124], activity of PM H^+-ATPase [79], protein post-translational modifications such as S-nitrosylation, carbonylation and tyrosine nitration [103] and enzymatic and non-enzymatic ROS detoxifications [59]. The size of PAs pool can be correlated with the stress tolerance capacity, and it has been confirmed that there is more accumulation of Spd and Spm in tolerant genotypes while the sensitive genotypes of the same plant species accumulated more Put under the same stresses [58].

PAs have important roles in biotic stress tolerance, and PAs association has been demonstrated with both pathogenic and beneficial microorganisms in plants. A relationship between polyamines and disease resistance has been shown in plants. Kim et al. [46] revealed that interplay between PA metabolic enzymes and pathogen effectors could also be used by plants to trigger defense response. In this sense, from cotton genotypes tolerant to *Verticillium* wilt, a PA oxidase (*PAO*) gene was identified and cloned. It has been revealed that *GhPAO* participates in plant resistance against *Verticillium* through the intermediation of Spm and camalexin (a phytoalexin) signaling [67].

Polyamines regulate protein synthesis during stresses

It is reported that PAs regulate the protein synthesis at many steps. Two transcription factors (SoxR and EmrR) and a glutathione synthetic enzyme (GshA) have been found as PAs modulators under oxidative stress conditions. Thus, PAs are involved in reduction in oxidative stress by inducing the synthesis of SoxR, EmrR and GshA [86]. Li et al. [51, 52, 53] also reported that interaction of Spe with phytohormones could modulate differentially expressed proteins (DEPs) that are associated with drought tolerance in white clover. MYB transcription factors are important regulators of plant response to abiotic stress. Li et al. [54] reported that *PbrMYB21* has a significant role in drought tolerance, which may be due to the regulation of PAs synthesis.

Cold-regulated (COR) genes associate with cold stress response [94]. *MfERF1* as a cold effector of ethylene responsive factor (ERF) was isolated from *Medicago falcata*, an important forage legume with great cold tolerance. Overexpression of *MfERF1* increased freezing and chilling tolerance by promoting PA turnover, antioxidant protection and proline accumulation in transgenic tobacco plants [125]. *ICE1* (*Inducer of CBF Expression 1*) encodes a transcription factor that acts as a central regulator of cold response. It was demonstrated that *PtrICE1* has an essential role in cold tolerance in trifoliate orange (*Poncirus trifoliata* L.). It could regulate PA levels through interaction with the arginine decarboxylase (*ADC*) gene [37].

In addition to the transcriptional networks, the *COR* genes are also subjected to post-transcriptional regulation by microRNAs (miRNAs). Gupta et al. [36] reported that over-expression of *ptr-MIR396b* in transgenic lemon (*Citrus limon*) plants caused an enhanced cold tolerance due to the regulation of ACC oxidase gene expression and modulation of ethylene polyamine homeostasis.

PAs in high-temperature conditions influence the synthesis of heat shock proteins and also affect cell membrane properties [1]. Nucleic acid degeneration is increased by high temperature. It has been reported that PAs could adjust heat responsive genes expression by enhancing mRNA stability under heat stress conditions [93]. It was reported that PAs could protect nucleic acids against thermal depurination induced by high temperature and decrease depurination of nucleic acids (DNA and RNA) depending on the types of

PAs [107]. Longer and complicated PAs play important roles to preserve the functional conformation of nucleic acids at high temperatures compared to standard PAs and Mg^{2+}. Similarly, unique polycation, N^4-bis (aminopropyl) spermidine 3(3)(3)4, was found in the hyperthermophilic archaeon *Thermococcus kodakarensis*, which grows at temperatures between 60 and 100 °C [72].

Genetic engineering of polyamines in stress resistant plants

Genetic engineering of genes involved in the PAs biosynthesis or degradation has been used for the development of stress-resistant plants. Reverse genetics enables the identification of novel genes in the PA pathway. Atanasov et al. [14] generated a basic protocol for ethylmethanesulfonate (EMS)-mutagenized populations of *Arabidopsis thaliana* to use it in reverse genetics for PAs genes mutation.

Over-expression of PA biosynthesis genes has been successfully applied for the manipulation of PA levels in plants [28]. It was also reported that transgenic centipede grass (*Eremochloa ophiuroides* [Munro] Hack.) with over-expression of *S-Adenosylmethionine decarboxylase* (*SAMDC*) gene had the increased cold tolerance associated with the polyamine oxidase (PAO)-catalyzed production of H_2O_2 [60]. In turn, this causes the NR-derived NO production and promoted antioxidant enzyme activities in transgenic plants. Furthermore, over-expression of *S-adenosyl-L-methionine synthetase* enhanced tomato tolerance to alkaline soil stress through PAs metabolism [34]. Similarly, over-expression of *S-adenosylmethionine synthetase 1* of tomato transgenic callus enhanced alkaline stress tolerance that was positively correlated with PAs and H_2O_2 accumulation [33]. Isolation of PA catabolism mutant genes could be utilized as another suitable method for the accumulation of PAs. Sagor et al. [85] indicated that silencing the cytoplasmic PAOs of Arabidopsis plants increased salinity tolerance by decreasing ROS generation and induced defense genes expression. Various results have demonstrated the precise insight of PAO genes in cotton and sweet orange responses to biotic stress [115]. Wang and Liu [114] revealed that the down-regulation of PAO gene of orange is involved in PA terminal catabolism which could be used as an alternative approach to improve salt stress tolerance. The *AtPAO5* gene which catalyzes the conversion of tSpm to Spd is found as a member of the *PAO* gene family with the highest transcriptional responsivity to salinity stress. Also, salt tolerance in *AtPAO5* mutant was associated with early increase of ABA biosynthesis and enhanced jasmonic acid (JA) content. Thus, the results of this experiment indicated that tSpm has a protective role against salt stress in Arabidopsis. It was reported that *AtPAO5* modulates Therm-Spm homeostasis and is involved in interaction between auxin and cytokinins that is essential for differentiation of xylem [4]. Regulation of the key genes in biosynthesis pathways is an interesting way to improve stress tolerance in plants.

Altered PA/H_2O_2 homeostasis due to over/under-expression of the *ZmPAO* gene in modified *Nicotiana tabacum* plants showed that under-expression of *ZmPAO* increased thermotolerance, whereas *ZmPAO* over-expression decreased thermotolerance. Reduction in PA catabolism in HS response can be used as an attractive strategy for increasing tolerance to HS [66]. Gémes et al. [30] reported that the level of *PAO* expression showed multifaceted effects under long-term salinity by affecting plant vigor via the modulation of ion homeostasis, antioxidant system, phenolics and proline contents and ethylene biosynthesis. Therefore, regulation of the apoplastic PAO can be further utilized as a potential method to improve plants with enhanced/tolerance to abiotic stress.

Exogenous application of polyamines

The exogenous PAs or the elevated levels of endogenous PAs can quickly be converted into each other. The enzymes involved in biosynthesis and catabolism are also affected by PA treatment. Also, PA production and transport mechanisms may be tissue and age specifics. On the other hand, the effect of treatment may also be genotype-dependent [74].

Uptake, sub cellular localization and transport of polyamines

The mechanisms of PA uptake have been studied in many plants. Uptake of Put in petal of Saintpaulia has been reported by Bagni and Pistocchi [15]. PAs are ubiquitous. PAs have been found in the cytoplasm, nucleus, plasma membrane, mitochondria and chloroplasts. They especially have a high concentration in growing tissues during cell division and elongation [108]. It was suggested that the cell wall and vacuole are the largest PAs sink in plants [63]. Bortolotti et al. [17] showed that chloroplast and nucleus are the sinks of ADC in tobacco plants. In photosynthetic tissues, ADC is located mainly in chloroplasts, whereas in non-photosynthetic tissues it is collected in nuclei. ODC is located in the cytoplasm and nucleus but SAMDC, and Spd synthase is just accumulated in the cytoplasm [108].)

Limited knowledge of mechanisms underlying PA transport is obtained from plants, despite early evidence that pointing to the occurrence of this mechanisms and the detection of PAs in phloem and xylem sap in different plant species [8]. On the bases of studies of short- and long-distance transport of PAs in plant tissues, it is suggested that they belong to the group of phytohormones rather than to second massengers.

Periplasmic proteins play a main role in PAs transportation. It has been suggested that the transfer of PAes through membrane is carried out by PotD and PotF (the substrate binding protein). These periplasmic binding proteins are the primary receptors of the polyamine transport system, which regulate the polyamine content in *Escherichia coli*. [98, 111]. It has been reported that plasma membrane proteins are means for transporting spd in plants such as zucchini (*Cucurbita pepo*) and maize (*Zea mays*) [104, 105]. In resent studies, few PA transporters have been identified in plants, mainly in rice and Arabidopsis [68]. A recent research reveals that the evolution of PA transport might be determined by the acquisition of functional novelties induced by random mutations [18]. Evidences showed that in prokaryotes and eukaryotes, PA transport is not a passive mechanism, and selectivity is achieved through specific recognition and translocation that can be affected by induced mutations and natural genetic variation [109].

Polyamines roles in inducing plant stress resistance

The effects of exogenous PAs in plant tolerance under a/biotic stresses and alleviating the negative effects of stress have been studied in many plants (Table 1). However, harmful effects of PAs when they are applied under non-stressful environmental conditions have been reported by Recalde et al. [83] who showed the decreased root and shoot elongation in wheat under this situation. This study showed the complex interactions among PAs-derived ROS and NO that occur after the exogenous application of PAs on wheat plants. This application triggered a plethora of events at different cellular levels which led to growth inhibition. Higher spd and spm levels but not put increased dose-dependent oxidative damage in wheat and maize plants. Furthermore, the higher PAs levels were paralleled with salicylic acid accumulation [99]. Mellidou et al. [65] also reported that SAMDC may act as a regulator of the trade-off between stress tolerance and plant growth and developmental traits. Under natural conditions SAMDC reduction increased plant vigor by affecting photosynthesis, ROS homeostasis and ion content. But, SAMDC depletion led to increased sensitivity during abiotic stress. These results can be used as the basis for designing strategies to increase tolerance to NaCl. Exogenous Spd concentrations affected the PA metabolism, and salt tolerance in Zoysiagrass and high concentration of Spd reduced the growth of this plant under salt stress. Spd and Spm contents and ODC, SAMDC, DAO and antioxidant enzymes activities initially increased and then decreased with increasing concentrations of exogenous Spd [51, 52, 53].

In addition to the exogenous application of PAs, some compounds can influence the PA synthesis and increase stress tolerance. Gong et al. [34] reported that melatonin plays a positive role in plant tolerance to alkaline stress by regulating the biosynthesis enzymes activity of PAs. It was reported that melatonin enhances cold tolerance in cucumber seedlings by up-regulation of *CsZat12* and modulation of PA and abscisic acid metabolisms [125]. It has been shown that melatonin can increase the resistance of plants to Fe deficit in a phenomena dependent on the PA-induced NO production [125]. Exogenous application of γ-aminobutyric acid (GABA) promoted PA synthesis which in turn prevented PA degradation and alleviated Ca$(NO_3)_2$ stress [38]. Exogenous SA application increased shoot growth in two tomato cultivars (sensitive and tolerant to salt stress) and promoted ethylene and PAs production [31]. Szalai et al. [99] suggested that PAs could assist the stress resistance of plants primed with SA.

Table 1 Summary of the effects of exogenous PAs application on abiotic stress tolerance of agricultural crops

Agriculture crops	Effects	Applied polyamines	References
Cucumber	Increase salinity tolerance, induction of antioxidant enzymes and osmoticants, induce *S*-Adenosylmethionine synthase	Spd: 1 mM	Li et al. [50]
Pomegranate	Alleviate growth inhibition and salinity harmful effects, increase potassium and prolin concentrations	Put, Spd: (1 and 2 mM)	Amri et al. [6]
Pistachio	Reduction in severe effects of salt stress, increase activities of superoxide dismutase and catalase, decrease hydrogen peroxide (H_2O_2) activity, lower Na:K ratio	Spm, Spd: (0.1 mM)	Kamiab et al. [42]
Sorghum	Induce salt tolerance and reduce Na^+ accumulation	Spd: 0.5 mM	Yin et al. [119]
Lettuce	Increase antioxidant enzyme activities and drought tolerance	Put: 0.1 mM	Liu et al. [56]
Apple	Alleviate salt stress, increase fresh weight	Put: 5 mM	Liu et al. [57]
Wheat	Osmolyte accumulations, increase free polyamine levels	Put and Spm: 100 μM	Ebeed et al. [26]
Woad	Increase yield and drought tolerance	Put: 0.1, 1 and 2 mM	ÇömlekcIoglu and Arikan [22]

Polyamines roles in postharvest shelf life

PAs act as anti-senescence and anti-ripening regulators by reducing respiration rate and ethylene release, retarding color changes, inducing mechanical resistance and reducing chilling injury symptoms and enhancing the firmness and quality attributes of fruits [92]. Many studies were conducted on the effects of postharvest exogenous application of PAs in order to enhance the storage life of fruits and cut flowers (Table 2). Anti-senescence and ripening effects of PAs have been reported in many climacteric fruits, but there are few studies about this effect on nonclimacteric fruits. Guo et al. [35] showed that the content of Spm increased sharply after the onset of fruit coloration in strawberry compared to Put or Spd. Transcription of a strawberry S-adenosyl-L-methionine decarboxylase gene (*FaSAMDC*) led to Spm dominance in ripe fruit and up- and down-regulation of *FaSAMDC* expression stimulated or inhibited ripening, respectively. Exogenous application of Spm- and Spd-induced fruit coloration, while exogenous Put and SAMDC inhibitors inhibited this process.

The results of this research revealed that Spm could regulate strawberry fruit ripening in an ABA-dominated, IAA-related and ethylene-coordinated manner that was different from the previous experiment on climacteric fruit [61].

It was reported that copper-containing amine oxidases (CuAOs) and PAOs are involved in physiological processes that take place during fruit ripening [110]. There was an association between PA catabolism with fruit ripening in grape and tomato [2, 110]. The up-regulation of *CuAOs/PAOs* during ripening may form ROS signaling events that lead to the promotion of the ripening process [106]. It was reported that PA catabolism participates with plant hormonal pathways, such as ethylene and ABA [2]. It was shown that increased accumulation of Spm in *cPAO4* (*pao4-1* and *pao4-2*) loss-of-function mutants was associated with delayed entry into senescence under dark condition [90].

Biotechnological intermediation by utilizing chimeric gene constructs of PA encoding genes has opened a new means to develop transgenic fruits and vegetables in order to improve shelf life and quality under storage period. Furthermore, nanotechnology-based carriers could be developed for the targeted assimilation of the PAs when used for the

Table 2 Summary of the effects of exogenous PAs application on postharvest physiology and quality of horticultural crops

Horticultural crops	Effects	Applied polyamines	References
Grape	Inhibition of chlorophyll degradation and reduction of color changes	Spm, Put: (0.5 mM)	Champa et al. [20]
Apricot	Increase shelf life, reduce respiration rate and ethylene release, stabilize color and firmness of fruits, lower cellular juice leakage and browning	Put: (1 mM)	Davarynejad et al. [24]
Mango	Improve fruit retention, shelf life, yield and quality, regulate fruit softening and antioxidative enzyme systems	Spm: 0.5 mM, Spm (3 ppm), put (150 ppm)	Malik and Singh [62], Venu and Ramdevputra [112]
Kiwifruit	Improve postharvest quality	Put (1 mM)	Petkou et al. [78]
Apple	Decrease weight loss and increase firmness	Put (1and 2 mM)	Asgarpour et al. [12]
Strawberry	Increase vitamin C, anthocyanin, phenolic contents, and antioxidant capacity, reduce color change	Put (2 mM)	Siruieneja et al. [95]
Peach	Delay ethylene emission and maintain flesh firmness	Put (1 mM)	Serrano et al. [91]
Pomegranet	Alleviate chilling injury, enhance shelf life and preserve fruit quality	Put (2 mM)	Barman et al. [16]
Zucchini	Maintain fruit quality	Put (1 mM)	Palma et al. [73]
Broccoli	Prevent chlorophyll degradation, maintain antioxidant compounds and delay senescence	Put (0.25 mM)	Zheng et al. [123]
Green bell pepper	Increase vitamin C content and antioxidant capacity, reduce color changes	Spd (20 μM)and Put (20 μM)	Patel et al. [76]
Cucumber	Inhibit chlorophyll degradation and reduce color changes	Put (0.4 mM)	Jia et al. [40]
Gladiolus	increase fresh weight, uptake of vase solution, flower opening and vase life	put (100 PPM), spd (100 PPM)	Raju Dantuluri et al. [82]
Chrysanthemum	Enhance quality and vase life, increase superoxide dismutase, decrease ACC-oxidase enzyme activity	Spd: 3 mM	Kamiab and Zamanibahramabadi [43]

shelf life extension in perishable horticultural crops. Studies have been carried out to investigate the over-expression of genes encoding PAs for maintaining quality and shelf life in tomato transgenic plants [61, 96].

Polyamines role on symbiosis relationships between plants and beneficial microorganisms

Association of plant roots with microorganisms plays a fundamental role in plant nutrition, health and productivity [117]. Studies have shown that the relationships between PAs and biofilm (multicellular communities of bacteria that their formation is necessary for the plant root colonization) formation by plant growth-promoting rhizobacteria (PGPR) have an essential role in plant protection [117]. Another research showed that PA biosynthesis inhibitors enhanced anti-biofilm activity of amphotericin B (AmB) against *Candida albicans* biofilms [49].

PA has also been known as a component involved in mycorrhizal development [48]. On the other hand, modern breeding programs might have caused decreased plant responsiveness to arbuscular mycorrhizal fungi (AMF) [77]. Symbiosis relationship between plants and beneficial microorganisms such as plant growth-promoting rhizobacteria (PGPR) and mycorrhiza depends on PA metabolism [41]. Also, it has been revealed that exogenous PAs have important roles to induce mycorrhizal colonization and development in in vitro and greenhouse cultivation systems [84]. Niemi et al. [71] revealed that PA content and localization of *Pinus sylvestris* ADC and *Suillus variegatus* ODC mRNA transcripts during the formation of mycorrhizal interaction increased in infected tissues after microbial inoculation. Dual applications of arbuscular mycorrhizal fungi and Put have increased nutrients uptake and growth of trifoliate citrus (*Poncirus trifoliate*) Seedlings [80].

It has been reported that effective microorganism application could mitigate salt toxicity and help plant growth and productivity owing to the PA pool modification in common bean [101].

PAs role as fungicides

Inhibition of the ornithine decarboxylase (ODC) activity by α-difluoromethylornithine (DFMO) inhibitor has been known as the main strategy often used to manipulate and control PAs metabolism. DFMO targets ODC activity in pathogens, whereas the plant utilizes another pathway of PAs biosynthesis. Thus, this method can solve the problem of resistance to fungicide [23];).

Estiarte et al. [27] utilized D, L-α-difluoromethylornithine (DFMO) on *Alternaria alternate* and showed the reduced fungal growth and mycotoxin production in in vitro condition. PA biosynthesis pathways are blocked in fungal cells, but they are able to uptake the PAs from the host plant in field condition. PA analogs for inhibiting the cellular PA transport have been introduced by Burns et al. [19] who designed a group of lipophilic PA analogs. Estiarte et al. [27] tested two PA analogs, AMXT-2455 and AMXT-3016 and observed that they partially control *A. alternata* viability in vitro and in vivo using tomato plants. This method can be used to reduce aflatoxin in susceptible crops. Guazatine is a potent inhibitor of PA oxidase (PAO) activity and is used as a fungicide in agriculture. But, application of this compound has toxicity effects on plants. Thus, Atanasov et al. [14] identified a genome-wide association mapping for the tolerance to guazatine in *Arabidopsis thaliana* and introduced a natural method for *Arabidopsis* populations that can reduce the toxicity of guazatine fungicide.

PAs role in flowering, fruit set and embryogenesis

PAs are essential for plant reproduction including flowering [10], fruit set and development [1]. Increased ovule longevity and fruit set were associated with increased foliar and flower N and B levels in Putrescine treated plants. Arias et al. [11] reported that PAs may act as a nitrogen source rather than a regulator of fruit set. Increased nutrients in leaves and decreased fruit abscission could increase fruit set after exogenous application of PAs.

5'-Methylthioadenosine (MTA) cycle is the main S recycling pathway in plants. This compound is produced as a by-product during ethylene, PA and nicotianamine synthesis [89]. Zierer et al. [126] analyzed *Arabidopsis thaliana* mutants with defects in the Met cycle enzymes and showed that the reproductive inability was due to the reduction in PA levels in mutant inflorescences. Phloem-specific S recycling during periods of S deficiency is necessary for the biosynthesis of PAs needed for flowering and seed development.

The reduced fruit drop due to the exogenous application of PAs has been reported [64]. Khezri et al. [44] showed the decreased abscission of inflorescence buds and increased fruit set in pistachio trees with application of Spm. Spm dominantly plays a key role in the growth and development of pistachio nuts.

Kim et al. [45] indicated that *AtPAO5*gene is a T-Spm oxidase and recombinant AtPAO5 catalyzes the conversion of T-Spm and Spm to Spd. This gene delayed the transition from vegetative to reproductive growth, and also it was observed in AtPAO5 loss-of-function mutants (pao5). Liu et al. [57] reported that the PA level decreased during fruit

set to ripening in peach fruit. Thus, the above results indicated that there is an antagonistic effect between PAs and senescence. Vondráková et al. [113] reported that exogenous Put increased endogenous PA levels and caused the somatic embryos development of *Picea abies.* Also it has been indicated that stress responses and specific changes in PA metabolism could influence on Scots pine somatic embryogenesis. Thus, the manipulation of stress response pathways may be a novel strategy for somatic embryo production in recalcitrant Scots pine lines [87].

Conclusions for future biology

Considerable evidences indicate that PAs are involved in a wide array of plant processes. PA levels are controlled by intricate regulatory feedback mechanisms. PA levels are modified during cell growth and differentiation through the interaction between the enzyme ornithine decarboxylase (ODC) and two regulatory proteins: antizyme (Az) and antizyme inhibitor (AzIN).

There are complex and differential relationships among the three main PAs in regard to the regulation of plant hormone biosynthesis and signaling. These PAs could be positively or negatively linked to the expression of genes regulating plant hormone biosynthesis. The most abundant PAs, namely Put, Spm and Spd, are able to influence several physiological processes, including photosynthesis, the antioxidant system and ion channels under stress conditions. PAs cooperate with NO signaling to respond to various a/biotic stresses through interactions with cell metabolic pathway, *S*-nitrosylation of stress responsive proteins and ABA and (ROS) signaling. Genetic engineering of genes involved in the PAs biosynthesis or degradation has been used for the development of stress-resistant plants. Thus, reverse genetics enables the identification of novel genes in the PA pathway.

Anti-senescence and anti-ripening effect of polyamines has been reported in many climacteric fruits. CuAOs and PAOs involves in physiological processes taking place during fruit ripening. Nanotechnology-based carriers can be developed for the targeted assimilation of the PAs to extend the shelf life of agricultural products. Studies showed that there is a positive correlation between PAs and beneficial microorganisms. Furthermore, PAs can be utilized as fungicide which is novel approach to reduce the fungicide resistance. PAs are essential for flowering and fruit set; therefore, by exogenous application of them or genetic manipulation of genes involve in PAs biosynthesis pathways we can significantly improve the performance and yield of agricultural crops.

Author contribution All the authors have equally contributed to collecting the information and writing the manuscript.

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