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REVIEW ARTICLE

The role of polyamines in plants: A review

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Abstract

Polyamines (PAs) are linear alkali nitrogenous with two, three or more amino groups that have a low molecular weight. PAs are created by organisms thru metabolism and can be found in nearly wholly cells. They are considered a unique type of plant stimulant because they acts significant roles in many kinds of plant growth and developmental stages as well as stress responses. More evidence suggests that the PA can be produced endogenously or exogenously applied to improve plant reproduction, productivity, and bear stress. While the mechanism of polyamines influencing plant growth and stress responses is still not clear. We are making an attempt to supply an inclusive review of the available literature that explained the association between PAs and flowering, stress responses and senescence. This review aimed at this is focused and abbreviates how PAs enhances and increase plant productivity and then serve as a foundation for forthcoming study on the mechanisms of PAs exploit in plant reproduction and growth.

Keywords

polyamine, polyamine oxidase, growth, proliferation

Introduction

Polyamines (PAs) compounds like that spermine (Spm), spermidine (Spd), cadaverine (Cad) and putrescine (Put) are positively charged aliphatic molecules, play an essential role in the nucleic acid regulation, protein synthesis and structures, interactions of nucleic acid, protein, oxidative balance, and proliferation of the cell. (1,2). They can be found in prokaryotic as well as eukaryotic cells. (3,4). PAs are mostly found in free form in higher plants. Many physiological processes are regulated by them, including flower development(5), cell proliferation embryogenesis, morphology, organogenesis, senescence, root system formation, fruit maturation, architecture, induce a biosynthesis of osmotic alteration substances and responses to abiotic and biotic stresses and as an antioxidant (6,7,8,9), salinity and fruit maturity and development (10) also recognized as being crucial for plant growth (11). They are likewise elaborate in abiotic and biotic stress responses (12). Meanwhile, free polyamines contribute form covalent bonds with biological substances such as nucleic acids and proteins also lignin or phenolic compounds (13). Plants such as potatoes contain numerous phytochemicals like PAs, which are highly required in the diet because of their useful effects on health (14). In addition, PAs can maintain the stability of the membrane and aid in the scavenging of reactive oxygen species (ROS) in chloroplasts (15). it seems that PAs boost the activity of antioxidant enzymes and noticeably lessen the oxidative effects of ROS on membranes (16).

We review the latest research of PAs effects on plant growth, from flowering to salinity, and investigate their characteristics in response to various stresses.

Methodology

The methodology of this article was designed to search and diagnose PAs effectiveness, which depended on the information and evidence available and published on the sciences platforms, Web of Science, Scopus, John Thompson Science Direct etc., for the approximately last 40 years. The article dealt with these compounds from several aspects focusing on the papers on plant king dome only inclusion while excluding all tissues and organisms of humans and animals.

PAs compounds were discussed in terms of the chemical distribution compositions, biosynthesis, degradation and the effects of the products of these vital processes on plant cell divisions, and proliferation. The criteria of the effect of PAs in this article was discussed by searching and collecting information that indicates and confirms the effect of these compounds' free or combined with other negative compounds or ions on the sensitivity of plants towards environmental influences such as temperature, physiological pH or internal influences such as exposure to oxidative stress and their role as antioxidants by combined with membrane phospholipid of the cell to protect it. For obtaining all the information of this review, using some keywords were adopted, namely PAs compounds, types, the relationship of Pas to plant life, and the functions of PAs. It was found that they have an important role in the development and flowering, in addition to their significant role in enhancing plant resistance to environmental conditions.

Results

Distribution of PAs

Polyamines are abundant in eukaryotic and prokaryotic cells (17). PAs are distributed in plants in tissue and organ-specific forms and participate play in photosynthesis (18). The best common PAs in plants are Spm, Spd and Put, with high intracellular concentrations, and the least common are Cad and Dap (19,20). Many studies indicate the presence of polyamine compounds in rice, pistachio, green tea, mangoes, and mushrooms (21-23) noticed clear differences in the concentration of polyamine compounds in a variety of plants, and indicated that some plants contain high levels of Put and Spm in corn, citrus, and peas. Spd was also found at a higher level in soybeans, beans and castor tissues and these levels of plant leaves changed during the life of the leaf (24). Immature citrus seed species also were found to contain high levels of cadaverine (25,26).

On the other hand, an inverse relationship was observed between ascorbic acid with of Put and Spm levels in green peppers and tomatoes respectively (27). High levels of endogenous Put were found to be unfavourable for the accumulation of GA, and endogenous Put was discovered to be strictly interrelated to gibberellin contents (28). The patterns of PA distribution may be linked to their unique functions. Generally, greater PA contents are associated with more robust plant growth and metabolism (29).

Chemical nature of polyamines

The majority of PAs have a minimum of two positively charged amino or guanidinium groups, distinct by a carbon backbone with a range of lengths (Figure 1) (46). Different from other cations like Mg^{2+} or Ca^{2+}, PAs have no less than two charged groups linked by a flexible carbon chain. By doing this, electrostatic forces of amino or guanidine groups are enhanced by hydrophobic effects. Agmatine (AGM), which is a chemical compound, is a member of the PA family (47).

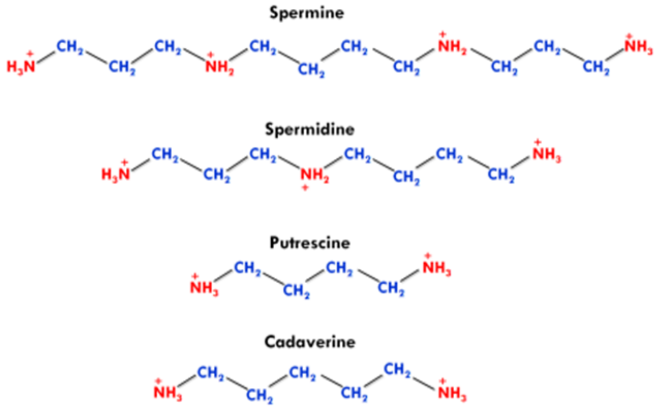

Fig 1. Chemical structure of polyamines (46)

Biosynthesis of Polyamines

In all the kingdoms of living things, the PA biosynthetic pathway has been thoroughly investigated (48,49). The common PA biosynthetic pathway's main output is putrescine, in general. Through three distinct arginine-dependent pathways, plants can produce PAs from the proteinogenic amino acid l-Arginine. (Figure 2)(12). The first pathway is comparable to that of animals and fungi and involves the conversion of l-arginine by the mitochondrial arginase into ornithine, that is next decarboxylated via ornithine decarboxylase (ODC) to yield putrescine. Additionally, plants can produce agmatine by using the arginine decarboxylase (ADC) enzyme, which then catalyzes the conversion of agmatine to N-carbamoyl putrescine and putrescine using the enzymes agmatine iminohydrolase and N-carbamoyl putrescine amidohydrolase, respectively. ADC and agmatine ureohydrolase, respectively, can catalyze the reactions that result in L-arginine and agmatine contributing to the generation of Put (50-53).

The third pathway starts with the conversion of Arg to citrulline, that is before decarboxylated via citrulline decarboxylase to produce Put (54,55). The first two pathways are more prevalent in plants because the Cit pathway has only been discovered so far in sesame. Spermidine synthase (SPDS) generates spermidine from Put and amino-propyl, that is progressively supplied by l-methionine (56). Additionally, putrescine could be transformed into spermidine via the carboxy norspermidine decarboxylase and carboxynors permidine dehydrogenase, respectively, using amide group provided

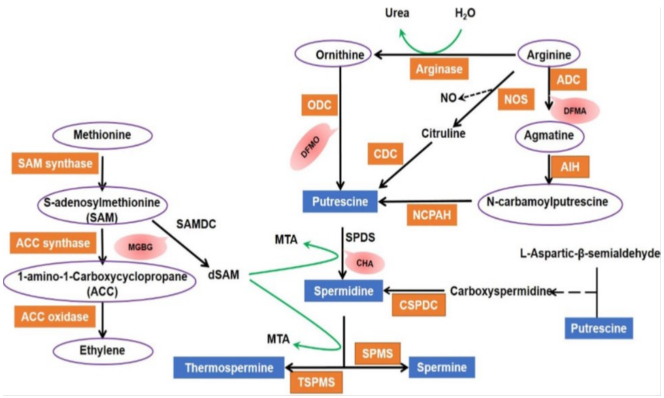

Fig 2. Biosynthesis pathway of main PAs in plants (12)

through the l-aspartate -4- semialdehyde from the glycine catabolism pathway. In the presence of homospermidine synthase, Put and Spd both promote a synthesis of the homospermidine. Finally, by means of the enzymes spermine synthase and thermospermine synthase, respectively, spermidine is transformed into Spm or thermosspermine through a combination of an additional amino-propyl group (57,58). Additionally, some other PAs may be derived from other amino acids that are proteinogenic. For example, lysine decarboxylase (LDC) catalyzes the synthesis of the diamine cadaverine from l-lysine(59). The amino acids L- glycine, L-proline, L-glutamate, and L-methionine are effective sources in the biosynthesis of polyamines (60,61).

Catabolism of Polyamines

The action of amine oxidases is crucial in the degradation of PAs in plants. Polyamine oxidase (PAO) provokes the formation of PA as metabolic end products. Wheat PAO, oxidizes Spm and Spd to produce 3-aminopropyl-4-amino butanal, 1,3-diamino propane, 4-amino butanal and hydrogen peroxide. The flavin adenine dinucleotide-dependent enzymes known as polyamine oxidases, which work in PA degradation, are essential in the pathway. (62,63). Tassoni (64) discovered that exo-Spd smeared to kinds of sunflower tuberous resulted in Put transformation. The generated H_2O_2 plays a role in plant indication transduction through abiotic and biotic stress responses (65,66). The function of polyamines in helping plants adapt to salt stress conditions has been demonstrated. Under salt stress conditions, *Calendula officinalis* L. plants were given exogenous Spm and Spd to see what effects they had on their development and physiological characteristics (67). Furthermore, PA metabolism is linked to the creation of NO (68), which is an important signalling constituent for plant growth (69). It has been demonstrated that polyamines and plant growth regulators are crucial for the start and control of the programmed cell death process. A variety of secondary metabolites known as phenol amides are produced when a phenolic moiety is conjugated with polyamines or deaminated aromatic amino acids. (70,71). The catabolism of PA compounds is a non-reversible process through which the cells can be supplied with carbon and nitrogen, which are used as precursors for cellular components (72). In order to better understand the functions of PAs in plant growth and development and the mechanisms underlying them, it is important to understand how PA metabolism interacts with plant hormones and how it affects signalling molecules.

Physiological action of polyamines

Polyamines and the Flowering

Higher plants go through a phase of vegetative growth before beginning a phase of proliferation and growth, then leaf and bud tissues undergo differentiate physiological turnover to the tissues of flower bud, which then cultivates into a floral part of plants, it's referred to as flower bud reproduction (73). Putrescine, Spermidine, and Spermine levels were elevated at prior developmental periods, whereas Putrescine and Spermine levels stayed constant (74). Polyamines, which are important and ubiquitous molecules required for cell growth and differentiation, are oxidatively de-aminated by copper amine oxidases and amine oxidases that include flavin (75). PA is thought to be a plant growth regulator (10).

Polyamines and reproductive development appear to be closely related, according to a number of lines of experimental data, it was found that PAs were more prevalent in Arabidopsis flowers in any other organ, and adding invitros PAs to plants that were not flowering significantly increased their flowering response (76). Gibberellic acid (GA3) and spermine (SPM), two plant growth regulators, have been characterized as extending the postharvest life of flowers (77) Spm enhanced the quality of the flower and vase life of cut rose blossoms (78). On the other hand, feeding of Spd is directly correlated to the time of flowering in *Arabidopsis thaliana* (79).

Table 1. Distribution of Polyamines

1	Put	broccoli, cauliflower, eggplant, jiló (scarlet eggplant), tomato, green onion, parsley, spinach, capers, cassava, heart of palm and bean sprouts	30
2	Put, spd, spm	Soybeans	31
3	Spm, Spd, put	Maize grain, Common wheat	32
4	Spm, Spd, put	Fruits: Apple – bananas – cherry – kiwi – pineapple – orange - mandarin - avocados, strawberry	33,34,35,36
5	Spm, Spd, put	Vegetables: Broccoli – cucumber – cauliflower – celeriac – courgette – eggplant - cabbage green beans – lettuce – mushroom - green pepper – onion - potato – carrot – spinach – tomato	37,38
6	Spm, Spd, put	Legumes: lentils - soybean - red beans – peas - soybean milk - tofu – sprouts – miso	34,36,37, 39,40,41,42,43
7	Spm, Spd, put	Cereals: wheat germ – Rice - white bread	34, 35, 37, 44
8	Spm, Spd, put	Nuts: chestnuts - Almonds - pistachios	34, 39
9	Spm, Spd, put	spinach leaf cells - intact chloroplasts- thylakoid membranes	45

Polyamines and Plant Senescence

PAs change as the plant grows. Endogenous PAs were found to be lowest in the senescent tissues in whole plants (80). A decrease in levels of PA appears to be an important precursor to senescence signals (81). Delayed leaf senescence was linked to higher Spm levels and higher NO levels (82). (83) discovered that chlorophyll degraded quickly and Put collected through senescence, whereas exogenous Spm or Spd inhibited protein breakdown and reduced chlorophyll harm. PA synthesis inhibitors in peonies extended the lifespan and delayed flower senescence, but PAs reduced faster flower senescence (84). Even during nematode pathogenesis, the tomato plant's physiological reactions to the polyamines were found to be improved (85).

Polyamines and Temperature Stress

PAs can stimulate photosynthesis while also rising plant antioxidant ability and osmotic adjustment ability under high-temperature stress (86). PAs serve numerous roles in all plants, and the primary physiological processes underlying the tolerance of high-temperature vary between plant species. PAs have the ability to bind to the cell membrane's phospholipid site, increasing cold resistance and preventing cytolysis (87). When the chilling temperature was applied to sweet pepper and zucchini fruits, the Put content expanded rapidly, accompanied by terrifying deterioration (88). Put accumulation, on the other hand, enhanced Spm was a defence reaction to cold damage, which caused chilling damage. They found that the spermidine, spermine, and Put levels eventually rose when loquat fruit was kept at low temperatures (89).

The Role of Polyamines with Oxidative Stress

PAs can activate a variety of enzymes known as antioxidants in plants, permitting them to successful defence against reactive oxygen species and then decrease oxidative stress, which is caused by a diversity of environmental triggers. Spm and Put pretreatment of maize leaves improved their resistance to the oxidative damage caused by paraquat (90). To combat the detrimental impact of different environmental stressors on plant processes polyamines have been advocated as a viable option. (91) Under hypoxia stress, exogenous Spd elevated the amount of Spd and Spm while reducing the amount of Putrescin in cucumber seedling rootstock. (92). It was also discovered that cold-treated or cold polyamine-treated groups had higher specific antioxidant enzyme activity than comparable controls, including catalase and ascorbate peroxidase. The treated plants' H_2O_2 and malondialdehyde levels were significantly reduced as a result (93). The impacts of Cd^{2+} and Cu^{2+} on the peroxidation of lipids were reduced by Spm treatment. (94). PAs have the potential to harm cells under conditions of stress because their degradation generates the powerful oxidizers hydrogen peroxide (H_2O_2) and acrolein. (95). H_2O_2 is, on the other hand, a molecule that signals that may pass through a stressful signal transduction pathway.

As a result, PAs appear to be redox regulators of homeostasis in plants that show a dual role in oxidative stress (96). Numerous studies revealed that polyamine oxidase (PAO) genes are essential for a variety of abiotic and biotic stress responses (97).

Discussion

All living organisms contain polyamines, which are involved in a variety of metabolic processes in plants like cell division, proliferation, expansion, differentiation, and programmed cell death to protect them from various stresses (98). They are important for cells and are known as endogenous growth regulators (99).

The capability of polyamines to interact via negatively charged sites in molecules like lipids, proteins, and nucleic acids is one of the reasons for their wide range of functions, also some natural compounds like phenolic compounds. Additionally, it has been discovered that a few byproducts of polyamine catabolism play important signalling functions in a variety of physiological, cellular, and developing processes (100). For example, transglutaminases (TGases) covalently link polyamines to particular proteins. TGases play a central role in photosynthesis in plants (101). According to Belda-Palazón et al. (102), the spermidine-dependent hypusination pathway may have novel roles in plant improvement and responses to hormonal, dietary, and environmental signals.

According to research by Nambeesan et al. (103), PAs have also been revealed to enhance longevity in a number of organisms, including tomato fruit, and to extend the shelf life of tomato fruit. They also participate in both transcriptional and translational gene regulation (104). In previous research, tomato fruits with high levels of the anabolic biogenic amines Spm and Spd, which are produced as a result of yeast S-adenosyl methionine decarboxylase expression, would increase an expression of SA biosynthesis genes, resulting in increased SA creation.

Putrescine N-methyltransferase is a crucial enzyme of the second metabolism and is involved in the biosynthesis of tropane alkaloids, nicotine and calystegines. An in-silico study demonstrated structural as well as functional characterization and developed three-dimensional computational models of putrescine N-methyltransferase proteins. Recently the number of reports illustrating that crosstalk between PA and phytohormones in plants to respond to abiotic stresses has increased and exposed the favorable influence of the co-application of exogenous PA and phytohormones (105).

Conclusion

In this review, we conclude that polyamines are active natural compounds having at least two positively charged amino groups that play important roles in many biological purposes in plants. .The involvement of polyamines in a variety of plant processes, including DNA replication, gene transcription, organ development, cell division, fruit development and leaves senescence, ripening, and abiotic stresses, is supported by a substantial body of research. As a result, the main genes ADC, ODC, or SAMDC have been overexpressed or down regulated, altering the amount of

PA in cells. Overexpression of heterologous ADC or ODC typically results in increased Put levels without affecting Spd or Spm. In contrast, overexpression of the pathway's genes downstream (SAMDC or Spd synthase) typically results in higher levels of Spd and Spm, demonstrating that the levels of Spm and Spd are tightly regulated by cellular homeostasis. The phytochemical, polyamines have an important impact on the contents of bioactive compounds with antioxidant activity besides in the activity of the key antioxidant enzymes in fruits during the ripening and senescence processes. It can be inferred that polyamines have wide applications due to their effect on the properties of phenolic compounds and flavonoids.

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Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None .

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