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RESEARCH ARTICLE

POLYAMINES: ROLE IN ATTENUATION OF HEAVY METAL TOXICITY

Barsha Majumder* and Asok K. Biswas
Plant Physiology and Biochemistry Laboratory, Centre of Advanced Studies, Department of Botany, University of Calcutta, Kolkata - 700 019, West Bengal, India.

ABSTRACT

Environmental changes resulted in a variety of stresses in plants of which heavy metal stress holds important position, affect the growth and development and trigger a series of morphological, physiological, biochemical and molecular changes in plants. When exposed heavy metal stress, the complex dynamic kinetics of polyamine biosynthesis was observed. Polyamines are small organic polycations present in all organisms and have a leading role in signaling, plant growth and development and deliver tolerance to a cultivar against stresses. High accumulation of polyamines (putrescine, spermidine and spermine) in plants during heavy metal stress has been well reported and is correlated with increased tolerance to different plants under stressed condition. Genetic engineering of polyamine biosynthetic genes in crop plants is the way to create resistance heavy metal toxicity.

Keywords: Heavy metal, Polyamine, GABA, Tolerance.

1. INTRODUCTION

Plants are sensitive towards a variety of environmental stresses throughout the life cycle which affect plant distribution, growth, development and productivity (1). Losses in the productivity of many of the agriculturally important crops are associated with the depletion in the economic returns of the country. Unprecedented bioaccumulation and biomagnification of heavy metals (HMs) in the environment have become a dilemma for all living organisms including plants. There are several natural ways of self-defense in the plants to cope with these stressful conditions: they can induce several functional or regulatory genes (2) or can undergo different physiological or biochemical changes. The accumulation of some functional substances is an important element of the physiological and biochemical response of plants to the stressful conditions (3,4).

Polyamines (PAs) are small, positively charged, low molecular weight, N-containing polycations found in all living organisms (5). They are known to be essential for growth and development in prokaryotes and eukaryotes (6). In plant cells, the diamine putrescine (Put), triamine spermidine (Spd) and tetramine spermine (Spm) constitute the major PAs. The total PA concentration and the ratios between individual PAs vary markedly. The characteristic feature of PAs structure is that they have methylene groups, participate in hydrophobic interactions, thereby influencing PAs activity. Polyamines are well known for their anti-senescence and anti-stress effects due to their acid neutralizing and antioxidant properties, as well as for their membrane and cell wall stabilizing abilities (7). Furthermore, it has been noted that genetic transformation with polyamine biosynthetic genes encoding arginine decarboxylase (ADC), ornithine decarboxylase (ODC), *S*-adenosylmethionine decarboxylase (SAMDC) or Spd synthase (SPDS) improved environmental stress tolerance in various plant species (3).

In this review, I tried to summarize the knowledge that has been gathered over the last couple of decades concerning the changes in polyamine metabolism (biosynthesis, catabolism and regulation) in plants under heavy metal toxicity.

2. POLYAMINE BIOSYNTHESIS

The PA biosynthetic pathway in plants has been thoroughly investigated (6,8). The biosynthesis of polyamines in plants has been well described (Fig. 1). Put is produced either directly from ornithine by ornithine decarboxylase (ODC, EC 4.1.1.17) or indirectly from arginine by arginine decarboxylase (ADC, EC 4.1.1.19) with two intermediates, agmatine and *N*-carbomoylputrescine, and two corresponding biosynthetic enzymes, agmatine iminohydrolase (EC 3.5.3.12) and *N*-carbamoylputrescine amidohydrolase (EC 3.5.1.53) (8,9). Put is converted into Spd via spermidine synthase (SPDS, EC 2.5.1.16) with the addition of an aminopropyl moiety provided by decarboxylated *S*-adenosylmethionine (dcSAM), which is catalyzed by *S* adenosylmethionine decarboxylase (SAMDC, EC 4.1.1.50) using *S*-adenosylmethionine (SAM) as the substrate. Similarly, Spm is produced from Spd via spermine synthase (SPMS, EC 2.5.1.22) with the same aminopropyl moiety rendered by dcSAM.

*Correspondence: Barsha Majumder, Plant Physiology and Biochemistry Laboratory, Centre of Advanced Studies, Department of Botany, University of Calcutta, Kolkata - 700 019, West Bengal, India. E-mail: barshamjmdr@gmail.com

Apart from biosynthesis, polyamine degradation plays an important role in the regulation of cellular polyamine titers, which is primarily ascribed to two amine oxidases, diamine oxidase (DAO, EC 1.4.3.6) and polyamine oxidase (PAO, EC 1.5.3.11). DAO catalyzesthe oxidation of Put to give pyrroline, which is further metabolized to gamma-aminobutyric acid (10) and PAO catalyzes the conversion of Spd and Spm to pyrroline and 1-(3-aminopropyl)-pyrroline, respectively, along with 1,3-diaminopropane in plants (8).

The biosynthesis of PAs and ethylene share a common precursor in S-adenosylmethionine (AdoMet). Although there is much evidence to suggest that increased biosynthesis of either PAs or ethylene can inhibit synthesis of the other, this is still a contentious issue. It is also important to note that AdoMet is a methyl donor for a variety of transmethylation reactions (5,11).

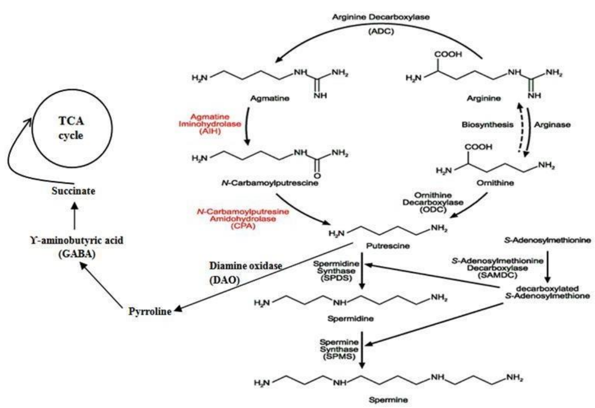

Fig. 1. Schematic representation of the pathway of polyamine-GABA biosynthesis

3. ROLE OF POLYAMINE IN PLANTS

In plant cells, the diamine putrescine (Put), triamine spermidine (Spd) and tetramine spermine (Spm) constitute the major PAs. Cadaverine is also present in legumes. These occur either in the free form or as conjugates bound to phenolic acids and other low molecular weight compounds or to macromolecules such as proteins and nucleic acids owing to their positive charge (12). Besides stimulating DNA replication, transcription and translation, they have contributed to various biological processes in plant growth, embryogenesis, organ development, leaf senescence, stress response (13). Plant polyamines also contribute towards several characteristics of agro-economical importance, such as phytonutrient content, fruiting and fruit quality, vine life, flowering and carnation of plants (14). Some of the observations suggest that PAs can act by stabilizing membranes, scavenging free radicals, affecting nucleic acids and protein synthesis, RNAse, protease and other enzyme activities, and interacting with hormones, phytochromes and ethylene biosynthesis (15,16). Because of these numerous biological interactions of PAs in plant systems, it has been difficult to determine their precise role in plant growth and development (12). PAs are involved in many plant developmental processes, including cell division, embryogenesis, reproductive organ development, root growth, floral initiation and development, fruit development and ripening as well as leaf senescence and in stress management (10,17-19) . It has been observed that cells undergoing division (apical shoots, meristems, flowers, etc) contain higher levels of PAs whereas cells undergoing expansion and elongation contain lower levels of PAs synthesized via ADC (12). Plants are exposed to continuous and rapid changing environmental factors (biotic and abiotic) such as light, temperature, water, nutrient availability and water. These have a major impact on plant growth and productivity. PAs play an important role in heavy metal stress tolerance as briefly discussed below:

4. ROLE OF POLYAMINES IN HEAVY METAL STRESS MANAGEMENT

Most recent reports on plant responses to As, Cu, Cd, Cr, Al, and other heavy metals have focused on the changes in the activities of antioxidant enzymes and more efforts are needed to identify the physiological and molecular significance of PAs in plant heavy metal tolerance (20). Wen *et al.* (21) have recently demonstrated Spd synthase overexpressing transgenic European pear showed tolerance to HMs by exerting antioxidant activities. Heavy metal toxicity leads to oxidative stress, resulted in production of reactive oxygen species such as superoxide free radicals ($O2^{\cdot-}$), hydroxyl free radicals ($OH^{\cdot-}$), or non-free radical species (molecular forms) such as singlet oxygen ($O2^{*}$) and hydrogen peroxide (H_2O_2) as well as cytotoxic compounds like methylglyoxal (MG). PAs are known to have a function in oxidative stresses. The antioxidative effect of PAs is probably due to a combination of their anionic and cationic-binding properties in radical scavenging, inhibiting properties of lipid peroxidation. Phenylpropanoid-PA conjugates can act as antioxidants against ROS and reactive nitrogen species in response to stress conditions (22). Inhibition of DNA oxidative degradation by OH^{-} in the presence of Spm in *Mesembryanthemum crystallinum* proved the efficiency of PAs to function as scavengers of free radicals. So, it may be concluded that plants not only accumulate free PAs to function as scavengers of free radicals, but also produce their conjugates which function as more efficient antioxidants also (23,24). ADC and ODC activity was increased in copper stressed wheat (*Triticum aestivum*) plant led to an increment in put contents, suggesting that polyamines perform a pivotal function in heavy metal stress alleviation.

5. CONCLUSION AND FUTURE OUTLOOK

Heavy metal stresses including the global warming are negatively affecting the plant productivity worldwide. Soil and water contamination by HMs in changing environment poses a serious threat to public and food safety and is now emerging as a major health hazard to humans and plants. On the other hand the demand for food is expected to grow as a result of population growth and rising incomes. It is necessary to obtain stress-tolerant varieties to cope with this upcoming problem of food security. The involvement of PAs in regulation of various cellular processes including growth, development and stress tolerance in plants might have general implications. As much as it is apparent that plants with high PA contents (due to exogenous supply or endogenous production via genetic manipulation) can tolerate short term exposure to a multitude of stress factors, only a handful of studies on the survival and yield (fresh or dry biomass of usable product) in these plants under prolonged stress conditions or repeated exposure to the same stress, have been reported. Most importantly, no viable plant variety has yet been created or selected based upon genetic modification of PAs either via breeding or via transgene expression, which could be evaluated in comparison with other varieties showing similar characteristics. The knowledge gained so far about plant PAs has built a strong case for further studies towards careful analysis of the genes involved in abiotic stress tolerance.

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Abbreviations

ADC-Arginine decarboxylase; AdoMet-S-adenosylmethionine; DAO-Diamine oxidases; dcSAM-decarboxylated *S*-adenosylmethionine; HMs-Heavy metals; ODC-Ornithine decarboxylase; PAs-Polyamines; PAO-Polyamine oxidases; Put-Putrescine; ROS-Reactive oxygen species; SAM-S-Adenosylmethionine; SAMDC-SAM decarboxylase; Spd-Spermidine; Spm-Spermine; SPDS-Spermidine synthase; SPMS-Spermine synthase.