

## Role of Polyamines in the Physiological Responses of Plants

Suman Sen\*

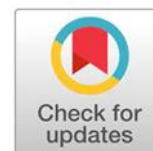
Department of Botany, Ananda Chandra College, University of North Bengal, Jalpaiguri-735101

### Abstract

Polyamines (PAs) are aliphatic nitrogenous bases containing two or more amino groups. These organic compounds have a low molecular weight and play essential role in the growth and development of plants. They contribute to the tolerance of plants against all abiotic and biotic stresses. They occur in the free form as cations, but are often found in the conjugated form to different macromolecules such as proteins and nucleic acids and to small molecules like phenolic acids. They are produced by plants during metabolism and are ubiquitous in plant cells. They are considered to be a new kind of plant biostimulant because they are intimately associated with a wide range of metabolic process in plants, ranging from cell division and organogenesis to protection against abiotic and biotic stress. Their chemistry, biosynthetic pathway and metabolism are now well characterized. Their titer varies and depends on the environmental conditions, especially stress. With the development of molecular biotechnology, genes for several key biosynthetic enzymes of the PA pathway have been cloned from different plants species, and antibodies to some of the genes are now available. The antisense transgenic approaches and over-expressed PA biosynthetic genes have given further evidence that PAs are required for plant growth, productivity and development of stress tolerance. This paper aims to review the various physiological responses of plants to PA with special emphasis to abiotic stress response and to provide a basis for future research on the role of polyamines in plant physiology.

**Keywords:** Abiotic Stress, Embryogenesis, Flowering, Osmolytes, Polyamines, Senescence

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### Introduction

Polyamines are widely distributed in eukaryotic and prokaryotic cells (Liu et al., 2017; Mustafavi et al., 2018). PAs have low molecular weight and are aliphatic nitrogenous bases containing two or more amino groups which have potent biological activity (Xu et al., 2009; Vuoksu et al., 2018). They may exist freely in living organisms (F-PAs) or in covalently conjugated form (CC-PAs) or non-covalently conjugated (NCC-PAs) forms (Gholami et al., 2013). The history of PA biochemistry goes back to more than 300 years. It was Antoni van Leeuwenhoek who first observed depositions of star shaped crystals in aging sperms when he was observing human semen through his primitive microscopic lenses in 1678. Almost more than 200 years later, the basic component of these star shaped phosphate crystals was named Spermine. By

mid 1920s the correct chemical composition and structure was determined. Spermidine was also discovered around the same time. Since then, PAs remained interesting mainly to chemists for about next half a century. Later Cohen's book directed the attention to possible biological importance of these compounds and initiated research in many areas, including plant physiology. A definitive work on plant polyamine biochemistry came from Terence A Smith at Long Ashton Research Station of the University of Bristol. Later in 1973, a paper delivered at plant growth hormone symposium in Tokyo suggested that polyamines have a regulatory action in plants. Since then, research on polyamines has spread to many countries of the world. Polyamines are essential for the growth and development in prokaryotes and eukaryotes (Tabor and Tabor, 1984; Tiburcio et al., 1990). In plant

\* *Correspondence* - [suman.sen0@gmail.com](mailto:suman.sen0@gmail.com)

cells, the diamine putrescine (Put), triamine spermidine (Spd) and tetramine spermine (Spm) constitute the major PAs. They remain associated with macromolecules such as proteins and nucleic acids and stimulate DNA replication and protein synthesis. They participate in wide range of biological processes related to growth and development of plants such as senescence, embryo development, environmental stress and also biotic stress such as infection by fungi and viruses. Their biological activity is mainly attributed to their cationic nature. Recently use of PA biosynthetic inhibitors has shown a causal relationship between changes in the endogenous levels of PA and growth responses in plants. These observations have enhanced further studies in understanding the mode of PA action. Since PAs are involved in numerous biological interactions in plant systems like stabilizing membranes, scavenging free radicals, affecting nucleic acid and protein synthetics, enzyme activities, hormone interactions etc, it has been difficult to determine their precise role in plant growth and development. However recent investigations into the molecular genetics of plant PAs helped to isolate number of genes encoding enzymes of PA biosynthetic pathway. Antibodies of some of the genes have also been developed. Genomic and proteomic approaches are being used to find out the role of PAs in plant developmental processes. This review article highlights the role of PAs in plants with particular emphasis on its role in abiotic stress responses.

### Distribution of Polyamines

Polyamines are ubiquitous in eukaryotic and prokaryotic cells (Liu et al., 2016, 2017). They are also found in plant tumors and in plant RNA viruses. PAs exist in variety of forms with potent biological activities. In higher plants, PAs are present in their free form. The most common types of PAs found in higher plants include Put, Spd, Spm, Tspm (thermospermin) etc. (Kim et al., 2014; Takahashi et al., 2017) and also Cadaverine (cad) (Regla – Marquez et al., 2015; Nahar et al., 2016). Other types of PAs are found only in certain plants or may be under special conditions only. The polyamines are organ specific and tissue specific in distribution. It was found that the most abundant PA in leaves was Put whereas Spd was found at elevated levels in other organs (Takahashi et al., 2017). Different type of PAs shows different localization pattern within cells. In the cells of carrot, Put was found to accumulate in the

cytoplasm and Spm in the cell wall (Cai et al, 2006). It is concluded that the distribution pattern of PAs is very much related to its unique functions. The more vigorous plant growth and metabolism is directly proportional to greater PA biosynthesis (Zhao et al., 2004; Cai et al., 2006).

### Metabolism of polyamines

The central product of the common PA biosynthetic pathway is Putrescine which contains two amino groups and is a synthetic precursor of Spd and Spm (Xu et al., 2009). Basically there are three different routes of Put biosynthesis in plants. In the first route, Arginine (Arg) loses its No. 8 carbon atom by arginine decarboxylase to form agmatine (Agm) and CO<sub>2</sub>. Agmatine next loses Nitrogen at No.2 position to form N- carbamoyl Put (NCPA) and ammonia. NCPA is further hydrolyzed by N-carbamoyl putrescine amidohydrolase (NCPAH) and its carbamoyl is removed to form Put, CO<sub>2</sub> and NH<sub>3</sub>. This is the main Put synthesis pathway in plants (Docimo et al., 2012; Pegg, 2016). In the second route, Arginine is converted to Ornithine (Orn) by Arginase and then ornithine decarboxylase removes the carboxyl group of No.1 carbon atom of ornithine to produce Put and CO<sub>2</sub> (Hanfrey et al., 2010). In the third route Arginine is first converted to Citrulline (Cit) which is further decarboxylated by citrulline decarboxylase to form Put (Han, 2016). The first two pathways are more common in plants. The third Citrulline pathway has been found only in sesame, till date. Spd and Spm are produced from Put and Amino propyl residues, which are gradually provided by methionine (Vuosku et al., 2018). The PAs are broken down in plants by the action of amine oxidases (Agudelo-Romero et al., 2013). The diamine oxidase (DAO) and PA oxidase (PAO) are the key players. DAO catalyses the formation of H<sub>2</sub>O<sub>2</sub>, ammonia and 4-aminobutanal from Put. The 4-aminobutanal undergoes cyclization to form pyrroline (PYRR), which is next converted to  $\gamma$ - amino butyric acid (GABA) by the action of pyrroline dehydrogenase (Hu et al., 2015). Finally GABA is converted into Succinate which enters into Krebs cycle in mitochondria. Dicots contain high levels of DAO (Cona et al., 2006) and PAO is found at elevated levels in Monocots (Tian, 2012; Takahashi et al., 2017). Its substrates are Spd, Spm and Tspm. There are multiple PAO families in plants (Tian, 2012; Liu et al., 2014, Takahashi et al., 2017). The metabolism of PAs in plants has quite significance. The H<sub>2</sub>O<sub>2</sub> produced by oxidation of PA functions in the signal

transduction process in plants during biotic and abiotic stress responses (Freitas et al., 2017; Mellidou et al., 2017). It also affects stomatal closure induced by Abscisic acid. (Cona et al., 2006; Tim et al., 2006; An et al., 2008). The S-adenosyl methionine produced in the PA biosynthesis route is also a precursor for ethylene synthesis (Chen et al., 2014). In addition, PA metabolism is related to NO production (Pal et al., 2015). NO is an essential signaling component for plant growth (Krasuska et al., 2013; Agurla et al., 2017). So the roles of PAs in plant growth and development and the mechanism of how they function can be discovered by studying the relationship of plant hormones and PA metabolism and also the effect of the later on plant signaling substances.

### **Polyamines in plant growth and development**

PAs are involved in many plant developmental processes. With the availability of specific inhibitors of PA biosynthesis, it became easy to investigate the mechanisms involved in PA interactions to some extent. Clearly, PAs are involved in developmental processes like cell division, embryo development, reproductive organ development, growth of root, floral initiation and development, fruit development and ripening, leaf senescence and abiotic stresses (Sawhney et al., 2003). It has been found that changes in free and conjugated PAs and their biosynthetic enzymes like ADC, ODC and SAMDC have been found to occur during these developmental processes. In general, cells undergoing division have high levels of free PAs synthesized via ODC, and cells undergoing expansion and elongation contain low level of free PAs synthesized via ADC. High levels of endogenous PAs and their conjugates have also been found in apical shoots and meristems before flowering (Cabbane et al., 1981) and flower parts of many plants (Martin-Tanguy, 1985; Ahmed et al., 2017). Callus cultures derived from explants of tobacco inflorescence show that endogenous Spd increases more rapidly than other PAs in floral buds than in vegetative buds. Addition of Cyclohexylamine (CHA), an inhibitor of Spd synthesis, switches vegetative bud development instead of floral bud (Sawhney et al., 2003). This inhibition could be reversed by addition of exogenous Spd (Kaur-Sawhney et al., 1988). Flower bud differentiation is a complex process of morphogenesis. It is triggered by various factors such as photoperiod, nutrition, vernalization and

water status, and is accomplished by the interaction and coordination of hormones and PAs (Xu, 2015). Exogenous PAs accelerate the process of flower bud differentiation. In *Arabidopsis*, PAs were found to be more abundant in flowers than in other organs and addition of exogenous PAs stimulated flowering response (Applewhite et al., 2010). Lower content of PAs, mainly Put & Spd, were found to lower floral bud initiation in rapeseed while increased PA content promoted differentiation of floral bud. Many growth and developmental processes of plants regulated by phyto hormones such as Auxins, 2, 4-D, GA and ethylene have also been correlated with PA metabolism (Sawhney et al., 2003). These changes occur both on the endogenous levels of PAs and also in the level of their biosynthetic enzymes and appears to be tissue specific. Thus PAs which may or may not migrate can serve as intracellular mediators of hormone actions (Galston and Kaur-Sawhney, 1995). Amongst these, ethylene has been most extensively studied with respect to PA metabolism. PAs and ethylene play antagonistic roles in plant processes. While PAs inhibit senescence in leaves and fruit ripening, ethylene promotes these processes. PAs and ethylene regulates each other's synthesis, either directly or through metabolic competition for SAM, a common precursor for their biosynthesis. PAs inhibit ethylene biosynthesis perhaps by blocking the conversion of SAM to ACC and of ACC to ethylene (Apelbaum et al., 1981; Suttle 1981). During senescence, chlorophyll content decreases, activities of ADC and ODC decrease, while activities of PAO and hydrolases like Proteases and Ribonuclease increases rapidly (Bagni and Tassoni, 2006; Chen et al, 2019). All these changes can be inhibited by application of exogenous PAs (Duan, 2000, Cai, 2009). So polyamines delay senescence by inhibiting ethylene biosynthesis (Woo et al., 2013, Anwar et al., 2015).

Polyamines bind to negatively charged nucleic acids, proteins and phospholipids by ionic and hydrogen bonds through their amino and imino groups and help in establishing the zygote polarity during embryo development and also promotes cell layer differentiation and establishment of the meristem (Chen et al, 2019; Chen and Lv, 2000). Polyamines are considered to regulate the embryogenesis in both gymnosperms and angiosperms (de Oliveira et al., 2016; Kevers et al., 2000) and an increase in PA content is required for the process. However, the types and abundance of PAs vary in different stages of embryonic

development. PAs more abundant in embryogenic callus and somatic and zygotic immature embryos than in mature and germinating embryos (Cao, 2010). Putrescine stimulates somatic embryogenesis and reduced level of Put and Spd result in fewer somatic embryos (Chen et al., 2019). Polyamines and abiotic stress responses: Polyamines play a crucial role in the physiological responses of plant against stress. Stress may be either biotic or abiotic in nature. In fact there are several factors that causes abiotic stress in plants-

#### *i) Polyamines and Temperature Stress*

Temperature stress is generally of two categories- low and high temperature stress. Low temperature stress is again of two types- cold stress and freezing stress. Few studies have been conducted till date to focus on the physiological functions of PAs in plants under high temperature stress (Chen et al., 2019). High temperature stress affects PA synthesis in the leaves by increasing the Put content but the increase is not sustained for a longer period of time (Yang and Yang, 2002). PAs promote photosynthesis and increases antioxidant capacity and osmotic adjustment capabilities of plants under high temperature stress (Tian, 2012; Guo et al., 2015). The antioxidant enzymes scavenge ROS to prevent membrane lipid per oxidation and stabilize membrane structure (Zhuo et al., 2018). Shao et al. (2015) reported that heat tolerance of alfalfa was because of higher Spd content and lower Put and Spm content (Shao et al., 2015). However, the main physiological mechanism of high temperature tolerance differs among plant species. PAs can bind to the phospholipid site of the cell membrane to prevent cyclosis and improve cold resistance (Li and He, 2012). However, the relationship between Put and plant chilling stress is debatable. Sweet pepper and Zucchini fruits, when stored in chilling temperature, shown an exponential increase in Put content accompanying by chilling damage. Again increased Spm level may be a defense response to cold damage by lowering Put accumulation and thereby reducing chilling damage (Zhan et al., 2000; Roy and Wu, 2001). Sun et al. studied the effect of Put and D-Arg on the physiological and biochemical indexes of *Anthurium andraeanum* under chilling stress at 6° C in winter. They found that Put application resulted in increased antioxidant enzyme activities, nitrogen metabolism, chlorophyll and proline content. Similar results are found in *Stevia* plants where PA supplementation increases tolerance to cold conditions (Peynevandi

et al., 2018). Recent studies suggest that abiotic stress tolerance is mainly affected by role of PAs in signal transduction rather than their accumulation. (Pal et. al., 2015).

#### *ii) Polyamines and Water Stress*

Majority of the work on the relationship between PAs and water stress has focused on drought resistance (Ebeed et al., 2017) and little attention has been given on water logging resistance. Polyamines have been found to regulate the size of K<sup>+</sup> channel and pore size in the plasma membrane of the guard cells, thereby regulating the opening and closing of the pore. This is how PAs can control water loss in plants (Liu et al., 2000). Several other studies have shown that application of Put, at an appropriate level can affect the biosynthesis of osmotic adjustment substances like soluble sugars, amino acids and proline. This may compensate for the negative impacts of drought stress on plant biomass. In alfalfa, treatment with Put have shown to improve seed germination, growth of hypocotyl length etc. under drought stress caused by various concentrations of polyethylene glycol (PEG), both invitro and in a pot experiment (Zeid and Shedeed, 2006). A mutant of *Arabidopsis* *acl5/spms* was cured which is hypersensitive to drought due to Spm deficiency. (Yamaguchi et al., 2007). These results indicate that function of PAs differs amongst different plants and even in different parts of the same plant, whether under osmotic stress of water stress (Sun et al., 2018). It can be concluded that response of plants to exogenous PAs under water stress and osmotic stress is species specific.

#### *iii) Polyamines and Salt Stress*

Like drought stress, salt stress also lead to reduced water potential in plants. Salinity is a complex environmental constraint on plants. A higher concentration of salt reduces membrane integrity, decreases the activity of various enzymes and also harms the function of photosynthesis apparatus. So plants adjust to such extreme environmental conditions by accumulating osmolytes of low molecular weight like PAs and proline. The application of different types of exogenous PAs, at different concentrations, have shown to reverse the effects of NaCl stress and reduce damage in various plants (Verma and Mishra, 2005, Li et al., 2008). Plants rich in PAs have strong salt tolerance. Li and He (2012) suggested that Spm level in plants is

an important indicator of salt tolerance. Exogenous PAs especially Spm and Spd increases the metabolism of reactive oxygen and photosynthesis, thereby improving plant growth and reduces the inhibitory effects of salt stress (Meng et al., 2015; Baniasadi et al., 2018). Li et al. produced a cucumber line with greater SAMDC expression and lower ADC and ODC expression, resulting in greater Put accumulation during salt stress. As a result, inhibition of plant growth under salt stress was reversed in transgenic seedlings (Li et al., 2011; Takahashi et al., 2017; Takahashi et al., 2017b). Sun et al. showed that PAs and ABA together alleviated salt stress in grape seedlings (Sun et al., 2018). Recent studies have discovered the relationship between PAs and salt stress resistance by using genetic engineering techniques. Malabika et al. transformed the ADC gene of oat into rice and found that ADC activity, biological yield and Put contents were higher in transgenic rice and its progeny under NaCl stress (Roy and Wu, 2001).

#### *iv) Polyamines and Oxidative Stress*

Polyamines play a very complicated role in plant oxidative stress. (Minocha et al., 2014). Polyamines increase the activity of various antioxidant enzymes in plants which can effectively regulate oxidative stress caused by several environmental factors. Increased tolerance to oxidative stress induced by paraquat was overcome by pretreatment of leaves with Spm and Put in Maize (Durmu and Kadioglu, 2005). Application of Spd significantly increase Spd and Spm levels and reduce Put level in roots of cucumber seedling under hypoxia stress. An increased antioxidant enzyme activity, enhanced ROS scavenging ability and less membrane lipid per oxidation were some of the changes which ultimately led to increased hypoxia stress tolerance (Jia et al., 2008; Wu et al., 2018). It was reported that during cadmium and copper induced oxidative stress, lipid per oxidation increases in sunflower leaf and activities of glutathione reductase and superoxide dismutase decreases (Groppa et al., 2001; Gholami et al., 2013). On the other hand, PAs are also source of ROS because their catabolism produces strong oxidizers  $H_2O_2$  and acrolein. So PAs can cause cellular harm under stress condition (Minocha et al., 2014). However  $H_2O_2$  being a signal molecule enter stress signal transduction chain and activate antioxidant defense response (Groppa and Benavides, 2008). Therefore we can say that PAs are regulators of the redox

homeostasis that play a dual role in plant oxidative stress (Saha et al. 2015). Besides the above mentioned abiotic stresses, plants can be affected by acid, radiation, wound and heavy metal stress. Few studies have been conducted on these topics, but the current idea is that PAs are important in the response to these stresses. Applications of exogenous Put regulates the balance of active oxygen metabolism under acid stress and stabilizes membrane system structure and hence protect plant from acid stress and improve acid resistance (Li et al., 1995). Mechanical injury and wounding of the leaves have shown to increase expression of ADC2 (Perezamador et al., 2002) and increase in free Put content (Cowley and Walters, 2010). Treatment with heavy metals  $Hg^{2+}$  and  $Cr^{6+}$  led to reduction in Spm and Spd content with decreased activities of SOD, catalase and peroxidase leading to excessive accumulation of membrane lipid peroxides and sharp decrease in chlorophyll and soluble protein contents. Application of exogenous Spd helped to overcome these negative effects of  $Hg^{2+}$  and  $Cr^{6+}$  (Wang et al., 2003; Wang and Shi, 2004).

#### **Conclusion**

This article represents a detailed and comprehensive review of the published literature dealing with the relationship between PAs and plant growth, development and abiotic stress tolerance. The role of polyamines in plant developmental processes ranging from flowering to senescence, embryo development has been discussed. These informations will surely provide a reference for future research work on the regulatory mechanism of PAs and on the significance of the use of exogenous PAs to regulate plant growth and production. Application of the technique of endogenous PA production is becoming increasingly popular via genetic manipulation to regulate plant growth. Still many questions are left to be answered regarding the roles of PAs in regulating plant growth and development. Knowledge about the different biosynthetic and catabolic pathways and their regulation at different levels are yet to be deciphered. Further research to uncover the exact mechanism of PA accumulation, in order to improve plant stress resistance needs to be done. Moreover, there is still much left to be discovered about the metabolic relationship between PAs and other phytohormones during growth and development of higher plants, more specifically the relationship between PAs and ethylene. With the advancement of molecular

biology techniques and transgenic methods, PA metabolism can now be manipulated and has become a good tool to study the physiological responses of PAs in higher plants. Besides the known PAs, many unusual PAs are found in nature too like the Tspm from bacteria residing in hot springs having enzymes resistant to heat denaturation. Future research on this aspect could also be eye opener.

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