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Putrescine as a polyamines and its role in abiotic stress tolerance: A Review

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Abstract

Climate change and global warming consequently causes environmental stresses affecting plant growth and productivity worldwide. Latest estimates suggest that two thirds of the yield potential of major crops are lost due to unfavourable environmental factor or abiotic stressors. Food shortage will be the common phenomenon in near future as the world population will reach about 10 billion by 2050. Therefore in order to feed the burgeoning population it is an urgent need to develop crop plants with enhanced vigour and high tolerance to various unfavourable environmental abiotic stressors. Maintaining yield stability under adverse environmental conditions is a major challenge faced by the modern agriculture in which the polyamines play a very important role in mitigating the devastating effect of various environmental factors. Polyamines (PAs) (putrescine, spermidine and spermine) are group of phytohormone-like aliphatic amine natural compounds with aliphatic nitrogen structure and present in almost all living organisms including plants. Among Polyamines, putrescine has more importance since it is the principal component and precursor for tertiary and quaternary PAs. Earlier studies proved that it is having role in diverse physiological processes such as flower development, embryogenesis, organogenesis, senescence, and fruit maturation and biotic and abiotic stress tolerance. Many studies suggested the probable mechanism of abiotic stress tolerance induced by putrescine which includes assisting an compatible solutes proline, glycine betaine and GABA in dehydration tolerance, stabilization of macromolecules and organellar membrane, inducing the production of antioxidant enzymes, playing as signal molecules in ABA regulated stress response pathway, regulators of several on channels, role in metabolic regulation of ammonia toxicity and nitric oxide (NO) production and regulating programmed cell death. Therefore, genetic manipulation of crop plants with genes encoding enzymes of polyamine biosynthetic pathways may provide better stress tolerance to crop plants. Furthermore, the exogenous application of PAs is also another option for increasing the stress tolerance potential in plants. Here, we have described the synthesis and role of various polyamines in abiotic stress tolerance in plants.

Keywords: Putrescine, polyamines and abiotic stress tolerance, climate change and global warming

Introduction

Climate change and global warming consequently causes environmental stresses affecting plant growth and productivity worldwide. Latest estimates suggest that two thirds of the yield potential of major crops are lost due to unfavourable environmental factor or abiotic stressors. Food shortage will be the common phenomenon in near future as the world population will reach about 10 billion by 2050. Therefore in order to feed the burgeoning population it is an urgent need to develop crop plants with enhanced vigour and high tolerance to various unfavourable environmental abiotic stressors. Maintaining yield stability under adverse environmental conditions is a major challenge faced by the modern agriculture in which the polyamines play a very important role in mitigating the devastating effect of various environmental factors. Polyamines (PAs) mainly putrescine (Put), spermidine (Spd) and spermine (Spm) are biogenic amines with aliphatic polycationic properties having roles in wide range of biological processes, including growth, development and apoptosis (Kaur-Sawhney *et al*. 2003; Kuehn and Phillips, 2005) [30, 31]. They are widely distributed in eukaryotic and prokaryotic cells (Liu *et al*., 2017; Mustafavi *et al*., 2018) [34, 42]. Although PAs were discovered more than 300 years ago (Van leeuwen hoek 1978) [65], within the past few decades the significant progress has been made in understanding their role in plant growth and development (Bachrach 2010 ; Martin-Tanguy 2001; Nambeesan *et al*. 2008) [10, 38, 45]. PAs are essential for cell division and proliferation in all organisms and are concerned in diverse growth and development processes including chromatin function, structural integrity of nucleic acids, protein synthesis, and cellular membrane dynamics (Handa and Mattoo 2010; Kusano *et al*. 2008; Theiss *et al*. 2002; Thomas and Thomas 2001; Wallace 2009) [24, 32, 57, 58, 68]. In higher

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plants, PAs are mainly present in their free form. Putrescine (Put), spermidine (Spd), and spermine (Spm) are the main PAs in plants, and they are involved in the regulation of diverse physiological processes (Xu *et al*., 2014b; Mustafavi *et al*., 2018) [72, 42], such as flower development, embryogenesis, organogenesis (Xu, 2015) [71], senescence, and fruit maturation and development. They are also involved in responses to biotic and abiotic stresses (Vuosku *et al*., 2012; de Oliveira *et al*., 2016; Reis *et al*., 2016; Mustafavi *et al*., 2018) [67, 17, 51, 42].

Pharmacological evidence through exogenous application of PAs and recent molecular studies about endogenous PA levels by transgenic approach have demonstrated the important role of PAs in seed germination (Urano *et al*. 2005) [62], organogenesis (Tisi *et al*. 2011) [60], tissue lignification, flowering (Gomez-Jimenez *et al*. 2010) [22], pollination, embryogenesis, fruit development (Mattoo *et al*. 2007) [40], ripening (Torrigiani *et al*. 2008) [61], abscission, senescence, (Nambeesan *et al*. 2008) [45] and stress responses (Minocha *et al*. 2014 ; Takahashi and Kakehi 2010) [41, 55]. Environmental stress responses associated with PAs includes mineral nutrient deficiencies, heat, salinity, drought and osmotic stress, chilling, hypoxia and environmental pollutants (Kuehn and Phillips, 2005; Groppa and Benavides, 2008; Gill and Tuteja 2010; Alcazar *et al*. 2010a) [31, 23, 21, 3, 6].

Among PAs, put has more importance since it is the principal component and precursor for tertiary and quaternary PAs. Earlier studies proved that it is having role in growth, development and abiotic stress tolerance in plants.

Biosynthesis of putrescines

Put can be produced directly from Ornithine by the action of ODC, or indirectly from Arg by Arginine decarboxylase (ADC). In plants, the two alternative pathways appear to have specific roles in growth and development. ADC is the primary enzyme for Put synthesis in non-dividing elongating cells, secondary metabolic processes and in cells under various stresses, while ODC appears to be entailed in the regulation of the cell cycle inactively dividing cells and meristematic zones, (Kakkar and Sawhney 2002; Gerner and Meykens 2004; Alcazar *et al*. 2006a) [28, 3, 6]. ADC is chloroplast localized enzyme but location of ODC is cytoplasm; thus the two biosynthetic pathways leading to Put might be physically separated within the plant cell.

Put is synthesized either directly from ornithine by ornithine decarboxylase (ODC; EC 4.1.1.17) or indirectly from arginine via agmatine. The pathway is initiated by the arginine decarboxylase reaction (ADC; EC 4.1.1.19). Agmatine is consecutively converted to N-carbamoyl putrescine by agmatine imino hydrolase (AIH; EC3.5.3.12) and ultimately to Put by N-carbamoyl putrescine amidohydrolase (CPA; EC 3.5.1.53). Spd and Spm are synthesized from Put by the shift of amino propyl groups from decarboxylated S-adenosyl methionine (SAM). These reactions are catalysed by Spdsynthase (SPD; EC 2.5.1.16) and Spm synthase (SPM; EC2.5.1.22). The decarboxylated SAM precursor is produced from SAM by S-adenosyl methionine decarboxylase (SAMDC; EC 4.1.1.50).

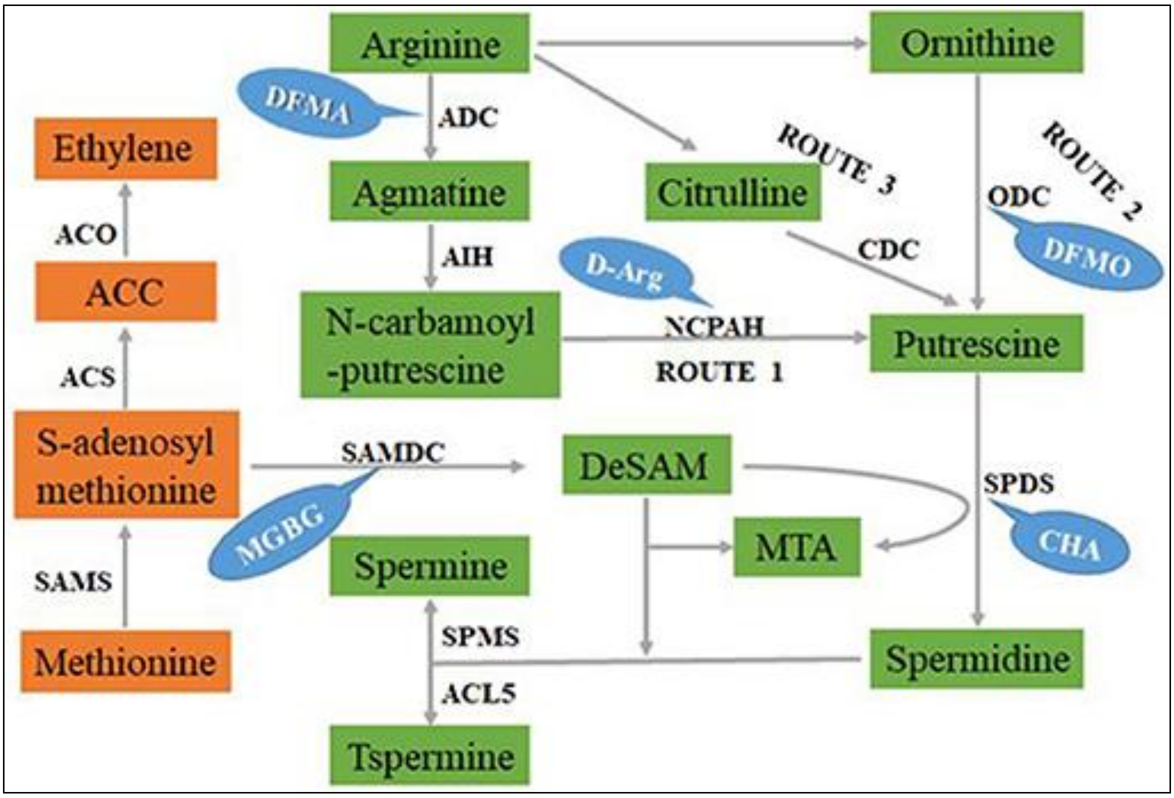

Fig 1: The pathway of Polyamines biosynthesis in plants. The orange part is the ethylene synthesis pathway, and the green art is the polyamine synthesis pathway (there are three routes of putresine synthesis route 1, route 2 and route 3, and the blue part isthe corresponding enzyme inhibitor. Photo extracted from Chen *et al*. (2019)

Putrescine and abiotic stress tolerance in plants

There are many studies which concluded that overall polyamine metabolism enhanced in response to variety of abiotic stresses- chemical or physical. Minocha *et al*. (2014) [41] summarised the various roles of polyamines in tolerance and /or amelioration of stress in plants. These include: (i) assisting as compatible solutes along with Proline, glycine betaine and GABA; (ii) interactions with macromolecules alike DNA, RNA, transcriptional and translational complexes, and cellular and organellar membranes to stabilize them; (iii) purpose as directly scavenging oxygen and hydroxyl radicals and promoting the production of antioxidant enzymes and metabolites; (iv) playing as signal molecules in the ABA-regulated stress response pathway and through the production of H_2O_2; (v) regulators of several ion channels; (vi) role in metabolic regulation of ammonia toxicity, nitric oxide (NO) production, and equilibrating organic N metabolism in the cell and, finally (vii) participation in programmed cell death.

There are four types of studies (Minocha *et al*. 2014) [41] that make a strong case in favor of the importance of PAs in plant stress response These include: (i) up-regulation of PA biosynthesis in plants via transgene expression generally increases their tolerance to a variety of stresses such as freezing (Altabella *et al*. 2009) [9], drought (Alcázar *et al*. 2010b) or both (Alet *et al*. 2011) [8] (ii) increased PA accumulation in plants under stress conditions is followed by raise in the activity of PA biosynthetic enzymes and the expression of their genes (iii) mutants of PA biosynthetic genes generally have less tolerance of abiotic stress (Kasinathan and Wingler 2004; Urano *et al*. 2004; Cuevas *et al*. 2008) [29, 64, 15] (iv) although exogenous supply of PAs makes the plants tolerant to stress, inhibition of their biosynthesis makes them more prone to stress damage.

Put has been found to be associated with plant response to abiotic stress for over six decades. Richards and Coleman (1952) reported the elevated presence of Put in barley plants upon potassium starvation. This was attributed to the decarboxylation of Arg, thus implicating ADC. Since then, many reports have appeared on the association of the ADC pathway with abiotic stress in plants.

The accumulation of Put during drought stress is thought to be primarily the result of increased ADC activity that may be assured by transcript levels and/or enzyme activity in Arabidopsis (Alca´zar *et al*. 2006b; Urano *et al*. 2003) [2, 63], rice (Yang *et al*. 2007) [73] and other species. In Arabidopsis ADC1 and ADC2 were predominately induced by at least one type of abiotic stress (salt, drought, and cold) and ABA treatment (Alcázar *et al*. 2011) [4]. In addition *Poncirus trifoliate* and *Prunus persica* (Peach) ADC were also induced by multiple abiotic stresses (Liu *et al*. 2009; Wang *et al*. 2011a, b) [36, 69, 70]. All these data suggested a putative connection between Put metabolism fluxes and plant abiotic stress responses.

Do *et al*. (2013) [18] reported that levels of Put and Spd decreased significantly under drought stress, while Spm piled up; make it the most abundant PA under drought stress in rice. The accumulation of PAs due to abiotic stress reported in other studies conducted in rice i.e., drought (Yang *et al*. 2007) [73], cold (Akiyama and Jin, 2007) [1] in wheat under osmotic (Liu *et al*. 2004) in apple callus under chilling, salt and dehydration (Hao *et al*. 2005). Put accumulates in Arabidopsis plants within 12 h after exposure to 4◦C, and this level is enhanced or sustained for at least 84 h (Cuevas *et al*. 2008) [15].

Transgenic plants overexpressing ADC having abiotic stress tolerance

Modification of the Put level by transgenic approach and study of the role of Put in response to several stresses has been analyzed. Manipulation of the Put level in several plants such as tobacco may lead to ameliorated plant tolerance against multiple environmental stresses. Different levels of mRNA accumulation of oat ADC, improved ADC activity and accumulation of PAs at different levels were observed in tobacco (Masgrau *et al*. 1997) [39], rice (Capell *et al*. 1998; Roy and Wu, 2001) [14, 52], eggplant (*Solanum melongena*) (Prabhavathi and Rajam, 2007) [49], and wheat (*Triticum aestivum)* (Bassie *et al*. 2008) [11]. Transgenic plants were generated by expressing the ADC gene of datura (*Datura stramoniun*) and oats under the control of different constitutive (maize ubiquitin 1) and inducible (ABA and tetracycline) promoters, transgenic plants showed tolerance to salt and drought with an increased accumulation of Put, Spd, and Spm (Roy and Wu. 2001; Capell *et al*. 2004; Bassie *et al*. 2008) [52, 13, 11]. The accumulation of Put as well as enhanced tolerance to salt, dehydration, freezing stress was observed in transgenic *A. thaliana*. (Alet *et al*. 2011) [8]. Overexpression of ADC of *Poncirus trifoliata* (PtADC) in *A. thaliana* showed increased synthesis of Put and enhanced tolerance to high drought, osmotic and cold stress. (Wang *et al*. 2011b) [70]. PtADC in transgenic tobacco and tomato confers enhanced tolerance to dehydration and drought (Wang *et al*. 2011a) [69].

Conclusion

Various abiotic stressors as a consequence of climate change and global warming are devastatingly affecting the plant productivity worldwide. On the other hand the demand for food is expected to increasing as a result of burgeoning population growth and rising incomes. Therefore, it is utmost need to develop stress-tolerant varieties to cope with this upcoming problem of climate change and food security. In this context PAs will lay a mighty important role as it leads to play a vital role in regulation of various cellular processes including growth, development and stress tolerance in plants might have general implications. However, in plants the role of PAs metabolism and is regulatory role in imparting abiotic stress tolerance is just at the initial stage and effort are still required to decipher in detail the molecular mechanism of protective role of Put in abiotic stress tolerance. It is required to identify the genes which are upregulated or downregulated by putrescine leading to stress tolerance in plants. High throughput analysis such as microarray, transcriptomics, metabolomics, reverse genetics approaches will also be inculcated to understand the involvement of PAs biosynthetic pathways in abiotic stress tolerance. Isolation and assessment of regulation of the enzymes of PAs biosynthetic pathways will also be of immense help in our better understanding of the mechanism of stress tolerance. Furthermore, the external application of PAs as can also be exploited for increasing tolerance to salinity, cold, drought, heavy metal, osmotic stress and various abiotic stressors.

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