REVIEW ARTICLE Agricultural Reviews, Volume Issue : ()

Role of Polyamines in Regulating Abiotic Stress Tolerance in Agricultural Crops: A Review

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10.18805/ag.R-2242

ABSTRACT

At present plants had to face adverse climatic fluctuations which are often detrimental for their growth in order to cope up with this situation, they develop certain adaptive tactics like synthesis of new proteins, micro RNAs, compatible solutes/ osmolites and radical release to avoid its adverse effects. Of these study on compatible solutes such as polyamines (PAs) gained popularity among researchers. In plant, they are involved in a wide variety of regulatory and cellular processes under normal conditions. During these stresses they acts by activating biosynthesis of signaling molecules like NO, H_2O_2; affects abscisic acid synthesis; Ca^{2+} homeostasis; ion channel signaling or even apoptosis in severe conditions. Over expression of PAs is reported in various stresses due to the presence of stress-responsive elements in the promoters of PA biosynthetic genes. This review paper, summarizes the effect of polyamines in boosting plants growth during abiotic stress and its mechanisms of action.

Key words: Abiotic stress, Polyamines, Putrescine, Spermidine, Spermine.

Plants live in an erratic environment, which are often inappropriate for their growth and development. About two thirds of plant's yield potential is decreased due to various environmental stresses while world's population is raising rapidly which may leads to severe food scarcity. Hence, crops with augmented vigor and resistance to various environmental stress should be developed to feed the rising population demands.

Plants develop different adaptive tactics to counteract with these adverse conditions at physiological, biochemical and molecular levels (Kumaraswamy *et al.,* 2016). Currently molecular level response is extensively studied which includes synthesis of new proteins, micro RNAs, compatible solutes and radical release (Hussain *et al.,* 2011). Genes induced during stress conditions protects cells by producing two important stress proteins called heat shock proteins (maintains conformation of proteins and prevent its aggregation) and antioxidant enzymes (reduce oxidative damage). In case of gene expression the sequence specific post-transcriptional regulators microRNAs (miRNAs) responds to different stresses during plant growth. Compatible solutes/osmolites protects cell's water potential, act as chaperones which stabilizes membrane proteins or ROSscavengers. Nowadays studies on the role of osmolites has gained severe importance due to its role in protecting against different kinds of stresses (Jogawat, 2019). These osmolites are classified into (i) amino acids (e.g. proline) (ii) polyols (e.g. mannitol, trehalose) (iii) quaternary amines (e.g. glycine betaine, polyamines). Among them polyamines (PAs) a type of quaternary amine stand as one of the most effective component against environmental stress.

Polyamines (PAs) are organic compounds containing aliphatic amine group present in almost all living organisms. PAs concentration in plants varies depending on species, organ or tissue and at different developmental stage.In plant cell they are present in all organelles including the nucleus, regulating different fundamental processes and induce stress responses (Bouchereau *et al.,* 1999).Plants stress stimulates either production or oxidation of polyamines. Thus, the genetic engineering of genes of enzymes in PAs metabolism or applying it exogenously to plants may provide better stress tolerance.

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How to cite this article: Lakshmi, G., Beena, R. (2021). Role of Polyamines in Regulating Abiotic Stress Tolerance in Agricultural Crops: A Review. Agricultural Reviews. DOI: 10.18805/ag.R-2242.

Submitted: 19-04-2021 **Accepted:** 22-11-2021 **Online:** 24-12-2021

Methodology

Review work was conducted at Department of Plant Physiology, College of Agriculture, Vellayani, Kerala. During 2020-2021, nearly ten months were spent collecting literature and writing manuscript. A total of 150 scientific papers were screened, of which 47 of them being used to prepare this manuscript. Various data bases were used to search for research papers, including the ARCC journals, Google scholar, Research Gate and Scopus.

Polyamines

Polyamines (PAs) are small organic cation present all living organisms. In plants, PAs commonly occur as: putrescine (Put), spermidine (Spd) and spermine (Spm), thermospermine (Tspm) and cadaverine (Cad) in free or soluble conjugated or insoluble bound forms. Because of their cationic nature, they bind freely with negative charged DNA, RNA or proteins through electrostatic linkages results in stabilization or destabilization (Fig 1). Polyamines are also involved in various developmental processes like survival of plant embryos, translation in eukaryotes, cell signaling, membrane stabilization; cell proliferation, apoptosis and cell death. Large amount of polyamines accumulation reduces ammonia toxicity in acell bycutting off extra nitrogen (N).

❖ Distribution pattern of polyamines in plants.

Polyamines are omnipresent in nature, present almost all living cells and involved in a number of cellular processes.In higher plants, PAs are found as Put, Spd, Spm, thermospermine (Tspm) and cadaverine (Cad). Under certain conditions, in some plants other forms of PAs like caldopentamine and caldohexamineare also found. Polyamines occur as both free bases (mostly) and bounded form. In bounded form the free polyamines are covalently attached to macromolecules such as proteins, nucleic acids, phenolic compounds, uronic acids etc.(Duan *et al.* 2008). In plants, the bound polyamines found between phenolic compounds such as coumaric acid, hydroxycinnamic acid, ferulic acid, or caffeicacid, which act as secondary metabolites and involves in allergic reactions and morphogenesis in plants (Bagni and Tassoni, 2001).

Polyamines shows organ and tissue specific distribution in plants. For example, leaves contain three times high concentration of putrescine (Put) than spermine and spermidine. While other organs contains abundant amount of Spd (Masson *et al*., 2017). Inside cells different PAs show distinct localization patterns. In carrot cells, cell wall is rich in spermidine while cytoplasm abundant with putrescine (Chen *et al.,* 2006). In general, greater the polyamine content and metabolism results in more vigorous plant growth (Zhao *et al*., 2004).

History

In 1678 Antonie van Leeuwenhoek discovered some crystalline substance on several days old human semen (Fig 2). About 100 years later in 1791 Vauquelin reported that the crystals were phosphate derivatives of an unknown newcompound.Schreiner in 1878 identified the new compound as anorganic base. Ladenburg and Abel called this organic base as “spermine” in 1888. Von Roehl advocated the use of spermine incurring various diseases. Ciamician and Ravenna (1911), demonstrated that *Datura stramonium* contains putrescine. Rosenheim (1924) chemically synthesize putrescine (Put) $[NH_2(CH_2)_4NH_2]$, spermine(Spm)$[NH_2(CH_2)_3NH(CH_2)_4NH(CH_2)_3NH_2]$ and spermidine (Spd) $[NH_2(CH_2)_3NH(CH_2)_4NH$. Herbst and Snell (1948) found putrescine in orange juice while Richards and Coleman (1952) reported the accumulation of putrescine potassium-deficient barley leaves serves as the first evidence for the role of polyamines in abiotic stress. Currently researches are conducted to estimate the polyamine levels in response to different stresses (Bachrach, 2010).

Polyamine biosynthesis

The primary precursor for polyaminesbiosynthesis is arginine or ornithine (in case of animals). The initial step is the decarboxylation of ornithine and arginine by the enzymes ornithine decarboxylase (ODC; EC 4.1.1.17) and arginine decarboxylase (ADC; EC 4.1.1.9) (Ali *et al.,* 2020). Decarboxylation of ornithine directly yields putrescine. Putrescine production from arginine require two other enzymes namely agmatineimino hydrolase (AIH; EC 3.5.3.12) and N-carbamoyl putrescine amidohydrolase (CPA; EC 3.5.1.53). The addition of aminopropyl group from decarboxylated *S*-adenosylmethionine (dcSAM) to putrescine by the catalyzed by spermidine synthase (SPDS; EC 2.5.1.16) produce spermidine which further adds another aminopropyl group to form spermine catalyzed by spermine synthase (SPMS; EC 2.5.1.22) (Fig 3).

Synthesis of decarboxylatedS-adenosyl methionine (dcSAM)

Methionine act as the precursor for *S*-adenosyl-methionine catalyzed by *S*-adenosyl methionine synthetase or methionine adenosyl transferase (MAT; EC 2.5.1.6) which further gets converted to decarboxylated *S*-adenosyl methionine (dcSAM) by action of *S*-adenosyl methionine decarboxylase (AdoMetDC; EC 4.1.4.50) (Lasanajak *et al*., 2014).

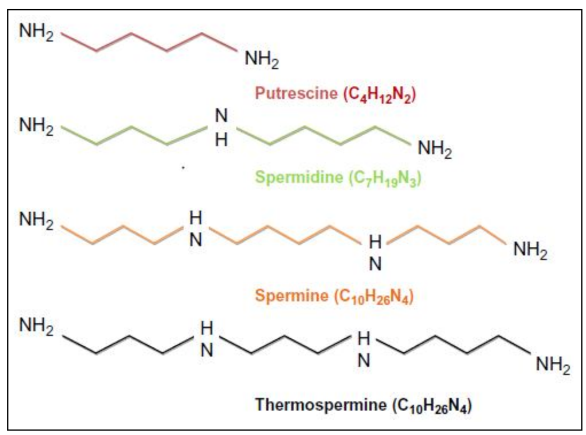

Fig 1: structure of polyamines.
(Singh *et.* al, 2018)

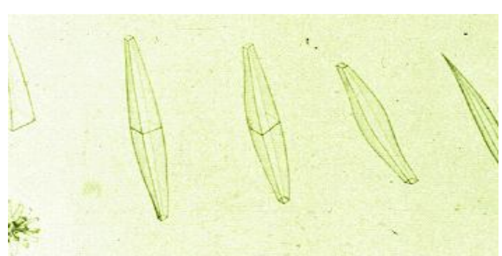

Fig 2: *Spermine phosphate crystals observed by A.van Leeuwenhoek (1678)* (Bachrach, 2010).

Inhibitors of polyamine biosynthesis

Difluoromethylarginine (DFMA) and difluorome thylornithine (DFMO) act as irreversible competitive inhibitors for arginine decarboxylase (ADC) andornithine decarboxylase (ODC), respectively.

Genes regulating polyamines biosynthesis

All genes encoding polyamines biosynthetic enzymes were identified and isolated from Arabidopsis and different plant species (Ge *et al.*, 2006). In Arabidopsis, there are six enzymes responsible for PA biosynthesis encoding 10 genes, they are: ADC-encoding genes (ADC1 and ADC2), SPDS (SPDS1 and SPDS2), SAMDC (SAMDC1, SAMDC2, SAMDC3, SAMDC4). Spm synthase, thermospermine synthase, agmatine iminohydrolase and N-carbamoyl putrescine amidohydrolase are represented in a single gene.

Polyamines catabolism

Amine oxidases are mainly involved in polyamine catabolism, which include diamine oxidase (DAO) and PA oxidase (PAO). In diamine oxidase (Cu^{2+} containing) having pyridoxal phosphate coenzyme, converts putrescine H_2O_2, ammonia and 4-aminobutanal. The newly formed 4-aminobutanal gets converted to pyrroline (PYRR), which further under the action of pyrroline dehydrogenase (PYRR-DH) converted into ^”-aminobutyric acid (GABA). After few reactions GABA gets converted into succinate, which gets incorporated into Krebs cycle. (Cona *et al.*, 2006) (Fig 4).

PA oxidase (PAO) having coenzyme flavin adenine dinucleotide (FAD) attached by non-covalent bonds is found at a high concentration in monocot plants while DAO at dicots (Masson *et al.*, 2017).

Multiple polyamine oxidase (PAO) families were observed in many plants (Liu *et al.*, 2014; Masson *et al.*, 2017).

(i) PAOs catalyze the production of metabolic end-products.

For *e.g.:* In wheat Spd or Spm gets oxidized by PAO to form 4-aminobutanal, 3- aminopropyl-4-aminobutanal,1,3-diaminopropane (Dap) and H_2O_2 (Cona *et al.*, 2006; Liu *et al.*, 2014).

(ii) PAOs catalyzing PA back-conversion pathway (PBCP), the polyamines get reversed to its precursors (Liu *et al.*, 2014; Takahashi *et al.*, 2018).

For *e.g.*: In Arabidopsis, the conversion of spermine to spermidine is mediated by PAO1 and PAO4 while PAO2 and PAO3 mediated conversion of spermidine form spermine and then to putrescine (Moschou *et al.*, 2008).

In *Brachypodium distachyon*, PAO 2 catalyze the conversion of spermine to spermidine and then to putrescine, withSpd as the preferred substrate.

Polyamine metabolism is linked to many other biosynthetic pathways related to stress response. The H_2O_2 formed as byproduct of polyamine metabolism takes part in signal transduction process as a response to biotic and produced by PA oxidation functions in the signal transduction during stress responses (Mellidou *et al.*, 2017) and also influence abscisic acid (ABA) induced closing of stomata (Cona *et al.*, 2006). By some unknown mechanisms polyamines are involved in nitric oxide (NO) formation (Yamasaki and Cohen 2006) which act as signaling molecule (Agurla *et al.*, 2018) in response to abiotic stress (Tun *et al.* 2006). In response to dehydration stress, the concentration the intermediates in polyamine metabolism: ^”-aminobutyric acid (GABA) agmatine (Urano *et al.* 2009) and putrescine

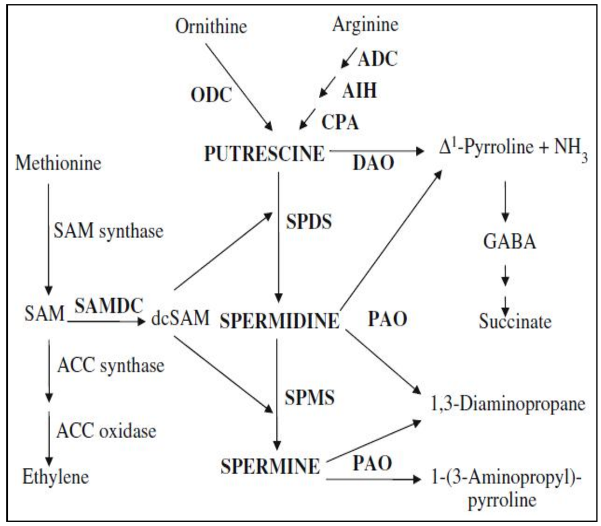

Fig 3: Polyamine biosynthesis and catabolism in plants.

ACC: 1-amino-cyclopropane-1-carboxylic-acid

ADC: arginine decarboxylase

AIH: agmatineiminohydrolase

CPA: N-carbamoylputrescineamidohydrolase

DAO: diamine oxidase

dcSAM: decarboxylated S-adenosylmethionine

GABA: c-aminobutyric acid

ODC: ornithine decarboxylase

PAO: polyamine oxidase

SAM: Sadenosylmethionine

SAMDC: S-adenosylmethionine decarboxylase

SPDS: spermidine synthase,

SPMS: spermine synthase(Alca´zar*et.* al, 2006)

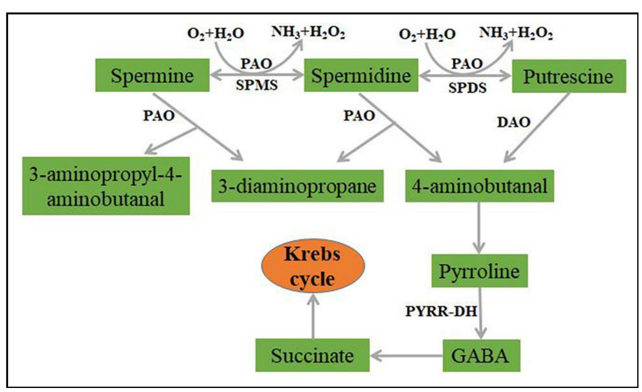

Fig 4: *polyamine catabolism in plants.*
(Chen *et al,* 2019.)

increases (Alcázar *et al.* 2006), which suggests a metabolic connection between these routes in response to stress. Also during salt stress the concentration of osmolites such as proline increases with respect to polyamine catabolism because they share arginine/ornithine as a common precursor (Urano *et al.* 2005). In conclusion, the polyamine metabolism is connected to several important hormonal and metabolic pathways involved in development, stress responses, nitrogen assimilation and respiratory metabolism.In plants, polyamines furtherfunctions and itsunderlying mechanisms can be examined by studying the relation between polyamine metabolism, plant hormones and the signaling molecules.

❖ Expression of polyamine biosynthetic genes in response to abiotic stress.

In Arabidopsis, expression of genes encoding ADC (ADC1 and ADC2) has been observed in response to various environmental stresses. In cold stress stimulatesADC 1 and SAMDC genes while ADC 2 gene expressed in dehydration, high salinity and K+ deficiencies. Spermidine and spermine production increases in dehydration stress by inducing SPMS and SPDS genes.

Over expression of PAs reported in various stresses like drought, salinity, extreme temperatures, oxidative stress and metal toxicity (Bartels and Sunkar, 2005) (Minocha *et al.*, 2014) is due to the presence of stress-responsive, drought-responsive (DRE), low-temperature-responsive and ABA-responsive elements (ABRE and/or ABRE-related motifs) in the promoters of PA biosynthetic genes (Chen *et al.*, 2006).

In cells during stressed conditions, polyamine content is regulated by catabolism by amine oxidase such as (Cona *et al.*, 2006), diamine oxidase (DAO) and polyamine oxidase (PAO). For *e.g.* in rice, due to the action of PAO high concentration of spermine and spermidine is observed until 3 days after inducing drought stress and drops after 6 days (Capell *et al.,* 2004). Abscisic acid dependent expression of polyamine biosynthetic genes (ADC2, SPDS1 and SPMS) under drought stress because the drought responsive (DRE) and ABA responsive elements (ABRE or its related motifs) are present in the promoters a single gene (Peréz-Amador *et al.*, 2002).

❖ Polyamine mediated signaling molecules produced in response to stress:

Polyamines maintains redox homeostasis of Reactive Oxygen Species (ROS) (Alcázar *et al.,* 2020). H_2O_2 produced as a result of polyamine catabolism act as a signal molecule, mediates many cellular processes like closure of stomata, influence ion channels and activate stress mediated MAPK cascade. Spermidine activates NADPH-oxidase thus stimulates the production of superoxideanion (Oÿ$_2^{-}$) and superoxide dismutase converts it to H_2O_2 (Fig 5).

Polyamines also induce the production of Nitric Oxide (NO), a gaseous intra and intercellular messenger inducing several stress responses.

In citrus plants, several PA regulated S-nitrosylated proteins such as Fe-superoxide-dismutase, dehydroascorbate reductase and monodehydroascorbate reductase were identified in response to stress. NO also act as an signaling molecule in different plant hormone (abscisic acid, auxin, cytokinin and ethylene) biosynthetic pathways. Polyamines depolarize the membrane by indirectly regulating ion channel. At hyperpolarized state the opening of voltage gated Ca^{2+} causes which leads to high cytoplasmic calcium ion concentration, thereby causing stress responses like stomatal movements and regulation of ion channels (Fig 5).

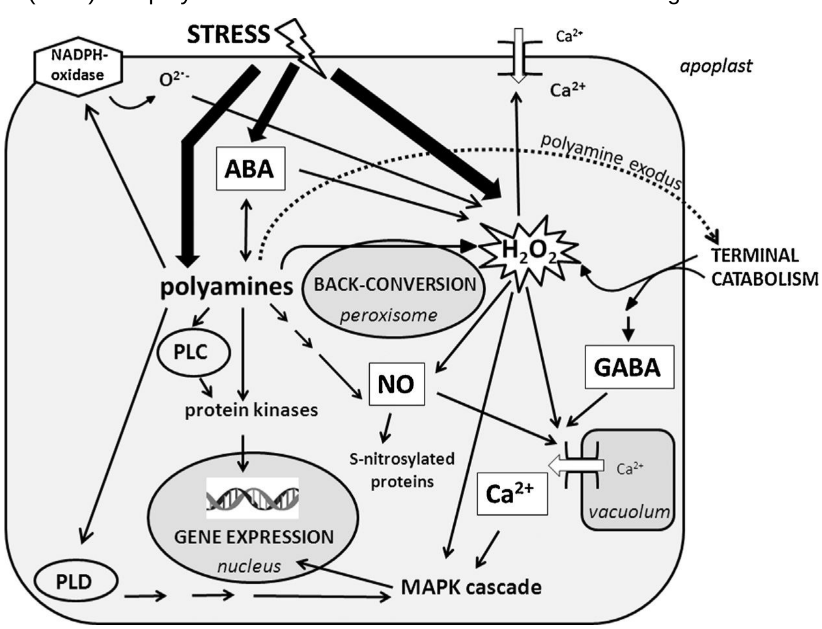

Fig 5: *Signaling routes mediated by polyamines.*

ABA, abscisic acid; GABA, ^"-aminobutyric acid; PLC, phospholipase C; PLD, phospholipase D. (Pál *et al.* 2015).

NO production induced by PAs activates H^+*-ATP-ase* while nitrosylation causes the inhibition of outward K^+ channels. Polyamines block vacuolar cation channels in the sequence: *Spermine > spermidine > putrescine.*

Mechanism of operation of PAs in response to abiotic stress

Polyamine act as compatible solute

Compatible solutes are the non-toxic, osmolite molecules, which protects the cells from osmotic stress. Polyamine shows properties like hydropholicity, protection of macromolecules, active oxygen scavengers, maintenance of cellular pH etc.also due to their cationic nature they stabilizes the negatively charged biomolecules like DNA under unfavorable conditions (Liu *et al.*, 2014).

Proline, produced during stressed condition act as osmolite, have common precursor with that of proline and responds to abiotic stress in a similar manner (Raghavendra *et al.*, 2017). But compatible solutes such as proline are produced at high concentration in response to stress compared to this the PA concentration is very small, hence the concept of polyamines as compatible solutes is still controversial.

Polyamines mediated antioxidant response

As a response to abiotic stress plant produce some toxic molecules which damages the cell membrane and macromolecules called Reactive oxygen species (ROS) which includeOÿ$_2^{-}$, H_2O_2 and OH". In order to fight with the detrimental effects caused by the ROS plants are equipped with different antioxidant enzymes such as superoxide dismutase (SOD), different peroxidases (POD), catalase (Cat) and glutathione reductase (GR) which scavenge the toxic ROS (Kumar *et al.*, 2013).

Polyamines act as an antioxidant enzyme activity, increasing ROS scavenging ability and lowers membrane lipid peroxidation (Parker *et al.*, 2019). In response to abiotic stress the polyamine catabolism (Liu *et al.*, 2014) induce the production of ROS by polyamine oxidase (Cona *et al.*, 2006). For e.g., In 15 days old chickpea plants which were subjected to a combination of drought and cold stress, have reduced level of H_2O_2 and malondialdehyde (MDA) content after the exogenous application of polyamines.

Polyamines also inhibit the hydroxyl ion mediated oxidative degradation of DNA. For e.g., In *M. crystallinum* the total DNA is damaged after incubating in an OH" generating system while the addition of spermine inhibits the DNA degradation. Polyamine conjugates also act as efficient scavengers of ROS radicals.

Production of polyamine mediated signal molecule against stress response

As discussed earlier polyamines induce the production of signaling molecules like H_2O_2, NO and abscisic acid in response to abiotic stress (Gill and Tuteja, 2010). H_2O_2, produced by PA catabolism act as a signal molecule which activates defensive response under stress conditions.In *Arabidopsis* after spermine and spermidine treatment the NO accumulation is reported. Further research is needed to understand the underlying mechanism behind interconnection of these three signaling molecules and polyamines.

Polyamine regulated ion channels

Polyamines are positively charged molecules which interact with ion channels and blocks it. The effect of polyamines in ion channels is in the order of charge: Spm^{+4}>Spd^{+3}>Put^{+2}. They blocks inward rectifying K^+ and Na^+ channel (Zhao *et al.*, 2004) but activates H^+-ATPase thus affects plasma membrane potential by intensify the interaction with 14-3-3 binding proteins. In *Vicia faba* guard cells spermine regulates KAT-1 like voltage K^+ channel thereby inhibiting stomatal opening while inducing its closure. Under salinity stress PAs reduce the efflux of K^+ induced by salinity through non-selective cation channels by blocking the route of Na^+ uptake.During drought stress, spermine deregulate Ca^{2+}channels results in increased cytoplasmic Ca^{2+}concentration causing the closing of stomata.

Polyamine and apoptosis or programmed cell death (PCD)

Apart from positive effects polyamines also regulates PCD or apoptosis in plants. During PA metabolism by the action of diamine oxidases releases H_2O_2. At lower concentrations it acts as signaling molecule while at higher concentrations triggershypersensitive response (HR) which leads to apoptosis. For e.g., H_2O_2produced by PA catabolism induce apoptosis in Tobacco Mosaic Virus (TMV) infected tobacco plants (Della Mea *et al.*, 2004). PAs induce K^+ efflux by interacting with ion channels during HR reactions the K^+efflux lead to low K^+ thus activating metacaspases and nucleases promoting apoptosis.

Plant response to abiotic stresses

Extreme temperature stress

Extreme temperatures *i.e.*, cold and heat stress are the major abiotic stress causing threat to crops. In heat stressed conditions, PAs act compatible solutes, increases photosynthesis and antioxidant activity thus stabilizing membrane by reducing membrane lipid peroxidation. For *e.g.*, In Arabidopsis during heat stress, polyamine biosynthetic genes such as ADC2, SPMS and SAMDC2 are induced leads to the production of spermine along with putrescine and spermidine content. Spermine protects Arabidopsis from heat shock related genes thus renders heat resistance to it.

Low temperature is detrimental for plants it disrupts nutrient intake and in extreme conditions lead to cytolysis. In this case, polyamines interact with plasma membrane phospholipid and prevents cytolysis. In Arabidopsis, cold stress induces a abiotic stress responsive, zinc finger transcription factor, Z at 12 induces the expression of ADC1 and ADC2 genes lead to accumulation of putrescine.

Because the promoter of ADC 1 contain a cold, desiccation and salinity responsive C-repeat/Dehydration-Responsive Element (CRT/DRE). Putrescine accumulation leads to the activation of zeaxanthin, an intermediate precursor of abscisic acid synthesis present in plastids. Zeaxanthin mediates ABA accumulation and ABA-responsive elements (ABRE) expression results in the production of protective metabolites and proteins against cold stress (Fig 6).

Salinity, water and drought stress

Salinity reduces membrane integrity by disturbing ionic balance and impairs the function of the photosynthetic apparatus. PAs act as osmolite, scavenges reactive oxygen species and increase photosynthesis thus reduces the detrimental effects caused by salinity.Salinity resistant plants is characterized by over expression of ADC 2, spermidine and diamine oxidase. The H_2O_2 produced by the action DAO induce expression of defense genes. GABA, an intermediate product of polyamine catabolism induce defense mechanism against salt stress.

During drought stressed condition polyamines regulate the opening and closing of guard cells of stomata by controlling ion channels in the cell thereby reducing water loss.

In Arabidopsis, during drought stressed condition ADC2 gene get overexpressed leads to high level of putrescine results in the stomatal closure (Alca´zar *et al.* 2006) (Fig. 7).

In Arabidopsis under water stress, expression of SAMDC leads to the accumulation of spermine which further stimulate NCED3 (a key gene in ABA biosynthesis). ABA regulate the expression of polyamine biosynthetic genes(ADC2, SPDS and SPMS genes) under water stress by controlling K^+ channels of guard cells (Alca´zar *et al.,* 2006).

Mineral deficiency and heavy metal tolerance

During mineral deficiencies the polyamine homeostasis g*et al*tered. For *e.g.*, in sunflower and wheat, cadmium and copper toxicity leads to increased expression of ADC or ODC and amine oxidases resulting in altered level of polyamines in cell (Fig 8).

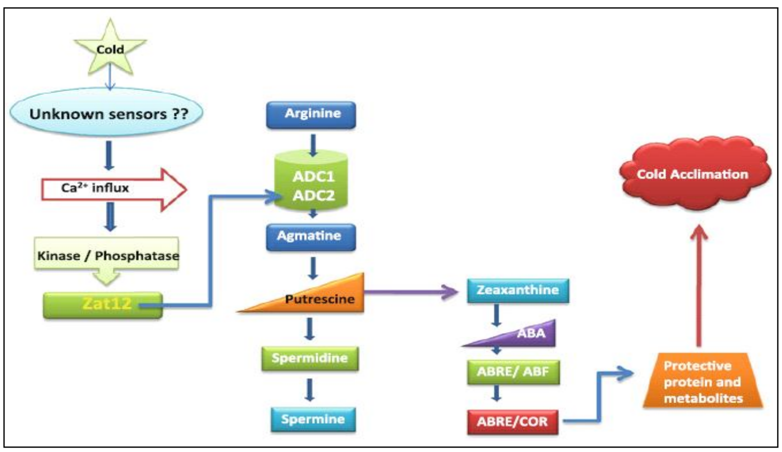

Fig 6: *Effect of cold stress on polyamine synthesis. Cold induces ZAT12, a zinc finger protein lead to activation of ADC and increased production of Put resulting in accumulation of ABA, protective proteins and metabolites.* (Gupta *et*. al 2013)

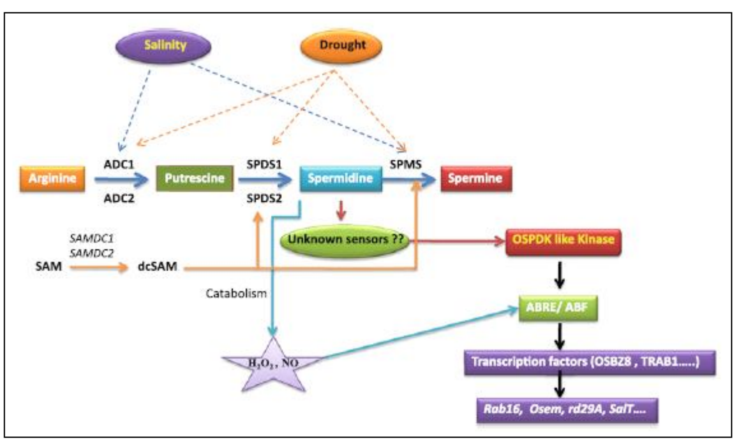

Fig 7: *Salt and drought stress leads to accumulation of polyamines especially spermidinestimulated by the expression of polyamine biosynthetic genes. Catabolism of PA produce H_2O_2upregulates several stress responsive elements resulting in stress tolerance.* (Gupta *et*. al 2013)

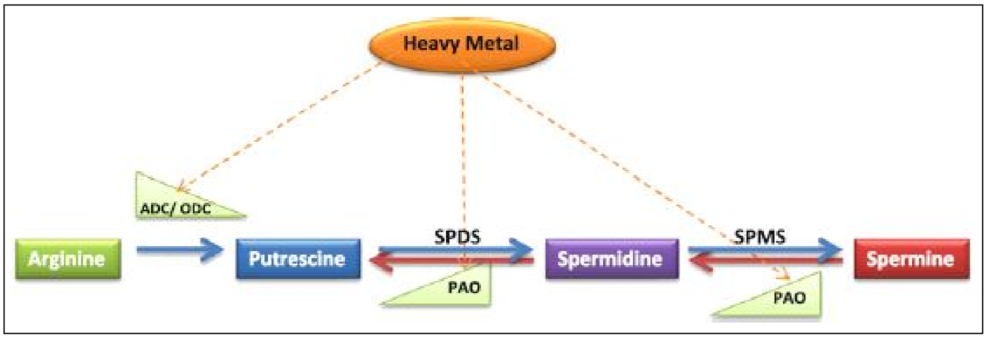

Fig 8: *Altered polyamine homeostasis caused by metal toxicity.* (Gupta *et al.,* 2013).

Mechanical stress

In mechanically stressed plants polyamines play an important role in wound healing. For *e.g.,* in wounded chickpeas and *Zea mays*, the H_2O_2produced by polyamine catabolism by amine oxidases stimulate lignin and suberin deposition around wounded area leading to wound healing.

CONCLUSION AND PERSPECTIVE

Polyamines are multifaceted molecules plays an important role in inducing stress responses against a wide variety of abiotic stresses. The molecular mechanism and mode of action behind the action of polyamines is still not fully understood. The use of these information regarding polyamines is currently restricted only to plant models like Arabidopsis and transfer of knowledge to crop species for maintaining their yield is an emerging challenge for the improvement of plant tolerance to abiotic stresses. In future¸ the exogenous application of polyamines can be exploited as a substitute for farm chemicals in order to withstand the adverse environmental stresses.

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