THINK INDIA Journal

ISSN:0971-1260

Vol-22-Issue-16-August-2019

Abiotic Stress Response of Polyamines In Plants And It's Mode of Action

Harish. B. Jadhav, Madhuri Girdhar, Nidhi Mehta, Anand Mohan*

School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab

Corresponding Author: Dr. Anand Mohan, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab, India anandmohan77@gmail.com

Abstract

Abiotic and biotic stresses are the major parameters affecting plants growth and yield. In the current scenario of crops and other plants as important sources of food grains, vegetables, fruits for the ever burgeoning population of world, it becomes important to chalk out the impact of varying stresses. There is an urgent need to analyze these stress factors so as to ensure the feeding of the entire future world population, and to develop new techniques and strategies so as to come up with sustainable agriculture. Without knowing the background details of a problem it is not possible to find a solution hence detailed study on plants and their response to various stress would help to find some new dependable solutions. Among various compounds involved in stress tolerance one such small organic compound which are cationic in nature have gained attention in the past and they are known as Polyamines (PAs). These PAs play a wide variety of roles in plant life among which we will be focusing only on abiotic stress although they are also known to show biotic stress response also. The concentrations of PAs in plants vary with respect to time, environmental conditions and under stress situation. Their biosynthesis, transport and catabolism play very crucial role in plant stress response. Different PAs act on different type of stresses and stress specific in nature. PAs are very important for heat, cold, drought, ozone, radiation, salt etc stress tolerance in plants. This article will be elaborating about some of the important PAs and their role in plant stress response.

Abbreviations

PAs	Polyamine
Put	Putrescine
Spd	Spermidine
Spm	Spermine
CuAO	Copper binding diamine oxidases
DAO	Diamine oxidases
PAO	Polyamine oxidases
ADC	Arginine decarboxylase

ISSN:0971-1260

Vol-22-Issue-16-August-2019

ROS Reactive oxygen species

SAMDC S-Adenosylmethionine decarboxylase

Introduction

All the living organisms are either directly or indirectly depend upon plants their survival. Although at present there is enough of the food available to feed the entire population but the rapidly increasing world's population is giving signs that there is a need to develop new techniques to increase the crop yield. Plants experience a wide variety of stresses in their life cycle. They may be biotic stresses like weeds, birds, nematodes, micro organisms, etc or abiotic stresses like salt stress, cold stress, heat stress, drought stress, radiation stress etc. In order to come up with effective strategies it is important to study the plant's behaviour under stress conditions and how they react to the stress, what mechanism they follow to overcome those stressful situations.

PAs are one of the most important organic compounds that are cationic in nature and contain two or more amino groups. Put, spd and spm are the most extensively available PAs in plants. Arginine decarboxylase (ADC) is the enzyme that is responsible for decarboxylation of arginine to produce Put similarly enzyme ornithine decarboxylase (ODC) acts on ornithine and upon its decarboxylation produces put. The enzyme spd synthase converts put to spd subsequently spm synthase converts spd to spm. PAs may either be present in free or in conjugated form. The conjugated forms of PAs are found to be associated with nucleic acids, proteins and with many other molecules. CuAO/DAO and PAO have important role in controlling growth and in providing tolerance to stress conditions to plants [1][2]. PAO has also shown its effect on Programmed Cell Death [3] [1], tolerance to osmotic stress [4] [2] and many other stress related tolerance. The genes that encodes those enzymes which are responsible for synthesis of PA can be overexpressed in different plants in order to get higher folds of tolerance towards both biotic and abiotic stress as reviewed by [5] [6]. In this review article we will be focusing on different types of PAs and their role in plants to initiate the mechanism involving tolerance against various types of stress.

Role of polyamines in response to salt stress

One of the most common salt that induces stress on plants is NaCl and many other salts are also found to be affecting the plant's normal metabolism and normal state of development. Different plants show different range of tolerance towards the salt stress. Na^+ competes with K^+ and disables the K^+ to bind to specific site of enzyme there by inhibiting the enzymatic activity. Transgenic rice with transformed ADC gene of the oat showed enhanced activity of the expressed ADC enzyme and the accumulation of put in the transformed rice was estimated to be more than non transformed one along with the former showing increased yield when they were subjected to NaCl stress [7]. The rice cultivar which was sensitive to salt tolerance had higher content of put accumulated where as the rice cultivar that showed tolerance

ISSN:0971-1260

Vol-22-Issue-16-August-2019

towards salt stress had higher amount of spm and spd accumulated in it [8]. After observing different levels of PA that were accumulated in varying amount in the shoot, it was inferred that the salt sensitivity of a particular rice cultivar was due to their ability to accumulate different PAs like the spd and spm content was less as compared to that of put, which was accumulated at a higher concentration [9]. As observed by [10], the put was found to be accumulated at a higher level of concentration in plasma membrane of their root in the rice cultivar that was salt sensitive whereas the rice cultivar which were salt tolerant had increased amount of spm and spd in the plasma membranes of their root. There are many evidences of PAs accumulating in a wide range of plants in response to salt stress. The accumulation of spm and spd benefited the rice plants in preventing the efflux of amino acids as well as electrolytes from shoot and root system of those plants which signified that they are crucial for response to the salt stress [11]. The harmful effects of salt stress were controlled by spd and spm when they were applied externally by nullifying the effects of salt stress and thereby increasing the photosynthetic efficiency as well as reactive oxygen metabolism to support plant's normal growth and development[12][13]. According to [14] ABA along with PAs can work efficiently in providing tolerance to salt stress as it was observed in the seedlings of grape.

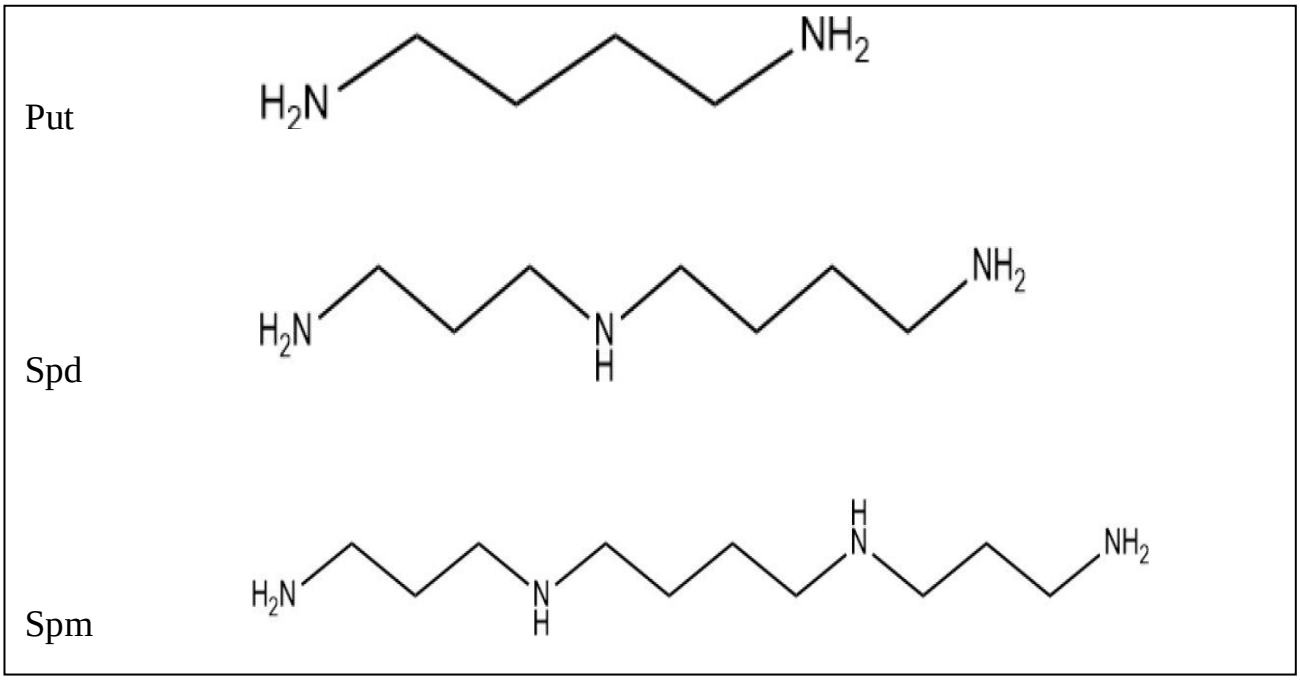

Figure. 1 Structure of Polyamines from plants adapted from [15]

Polyamines response to water stress

Drought stress is also a matter of concern because it has major contributing role in agricultural yield loss. Conventional plant breeding and modern GE techniques may provide some beneficial results in overcoming drought stress among which GE has gained a widespread

ISSN:0971-1260

Vol-22-Issue-16-August-2019

importance in recent fast moving world. PAs can regulate the opening and closing of stomatal aperture there by controlling the rate of transpiration in plants [16], where PAs can manage the pore size of the plasma membrane present in the guard cells as well as have control over K^+ channels. Arabidopsis undergoes stomatal closure in response to drought conditions and shows higher level of put when ADC2 was used for overexpression in order to tolerate low water stress [17]. Another example which proves the function of PAs in controlling the water stress response is, as observed by workers [18], where the exogenous treatment of spm to Citrus reticulate which was dehydrated responded by closing its stomatal aperture thereby reducing the amount of water to be lost, leakage of electrolytes in lesser amount and exhibiting little wilting as compared to those plants that were not treated with spm. Seed germination in case of alfalfa that was subjected to exogenous put applications under drought conditions induced by applications of PEG of varying concentrations was found to be increased and there was positive influence of put on overall dry as well as fresh weight of shoot and root and showed healthy growth of hypocotyls with increased length [19]. Researchers further showed that among the three major PAs found in plants drought resistance in case of apple was strongly influenced under the response initiated by spm [20] and the same was observed by other workers [21] where spm had major influence on drought tolerance in cherry tomato. H_2O_2 was found to be involved in certain signalling pathways which were produced as a result of oxidation of PAs where the pathway would provide tolerance towards drought stress in plants [22].

Response of polyamines for temperature stress

The anthropogenic activities has led to global warming and irregular patterns of climate change which has direct adverse affects on plants, animals as well as all other living organisms also. Plants start to accumulate PAs as they sense temperature stress. The plasma membrane of cell has got the phospholipids which have the tendency to allow the binding of PAs to them and when there is binding of PAs to desired site on phospholipids the cell undergoing, cytolysis due to cold stress can be stopped thus providing cold tolerance to plants [23]. It was observed that the spm that was treated externally induced the accumulation of both spd and spm internally but not allowing the put content to increase and thus lowered the damage that would have been caused by chlling stress [24] [25]. As the chickpea was subjected to chilling stress it was observed that there was increase in concentration of put [26]. Cold tolerance can be enhanced by providing spd along with the growth medium as it was done in cucumber by workers [27]. The tomato that was made to over-express SAMDC resulted in spd and spm accumulation at higher concentrations and along with this the enzymes that showed antioxidant activity were synthesized and the oxidative degradation of the lipids present in the membrane was prevented when there was stress due to higher temperature [28]. According to workers [29] the increase in concentration of spm, spd and N-spd were linked to increased proline synthesis during heat stress as observed in tobacco plant and it was seen that as there was increase in the production of proline, it stimulated the accumulation of conjugated and free PAs. PAs have the ability to increase the photosynthetic

ISSN:0971-1260

Vol-22-Issue-16-August-2019

efficiency in plans during heat stress as well as having the capacity to enhance the antioxidative properties and maintain osmotic balance inside the cells [30].

Response of polyamines for heavy metal stress and mineral deficiency

The presence of heavy metals and absence of macro and micro nutrients will overall affect the plant growth, development and yield. Providing right amount of nutrition to plants is essential for their normal growth and development. In K deficient conditions there was increase in significant amount of put and ADC activity [31]. As deficiency of K can be known by their put levels in the same way boron deficiency can also be known as it was seen by researchers [32] in tobacco plants whose leaves were found to be accumulating conjugated put and roots accumulated free put. It was observed in grapevine that PA concentration was altered in those conditions where N and Mg were present in limiting conditions [33]. The metabolic activity of PA production was found to be regulated by concentrations of Cu^{2+} and Cd^{2+} as estimated in the wheat and sunflower leaves, where the amount of put was found to be increased and amount of put in sunflower leaves was found to be decreased [34]. The functioning of SOD and GR is hampered by these two above mentioned metals which can be prevented by treating with appropriate concentrations of spm and spd before the commencement of these metal stresses [35].

Response of polyamines during oxidative stress

Oxidative stress may be due to any factors that results in decreasing the plant's ability to fight against the free radicals and show its antioxidant property. The superoxide free radicals can be detoxified by PAs like put, spm, spd [36]. Due to oxidative stress there will be increase in the amount of ROS which results in damage of plants DNA, proteins and lipids. Researchers showed that the oxidative stress can be tolerated by the plants if there is pretreatment of PAs before the occurrence of stress [37] as they have confirmed that in the leaves of maize by pre treating them with put and spm. A supporting example for relation between PAs and enhancing the antioxidant property of plant was given by workers where they showed that application of spd exogenously enhanced the production of spm and spd internally where as reducing the content of put in cucumber root, when the plant was encountered with low oxygen stress which somewhat indicated that there was a relationship between PAs and their ability to stimulate the antioxidant activity [38] [39]. Along with enhancing the antioxidant property there were some other benefits which were observed to be associated with PAs such as better regulation of ROS scavenging, decreased amount of lipid degradation in the membranes. Although PAs are resoponsible for production of H_2O_2 which acts as a signalling molecule to induce the plants defense mechanisms but still this H_2O_2 that can lead to cellular damage [40].

Polyamines response towards mechanical stress

Mechanical stress that may be due to biotic or abiotic factors influences the PAs to induce response in plants. There was increase in the levels of free put and enhanced ADC2 expression in *Arabidopsis* as it was subjected to treatment of methyl jasmonate along with providing wounding which was a mechanical stress [41]. According to workers PAO, CuAO had the ability to heal the wound in plants [42]. There was deposition of suberin and lignin

ISSN:0971-1260

Vol-22-Issue-16-August-2019

around the place where they was injury in maize and this deposition was found to be increased as a result of increased biosynthesis of H_2O_2 with the aid of PAO thus signifying that PAO has a positive influence on wound healing [43].

Table 1. Abiotic stress response of Polyamines in different plants and the its outcome, modified [15]

Type of stress	**Type of Plant**	**Type of PA**	**Effect of PA**	**Result**	**Reference**
0.15M NaCl	*Panax ginseng*	0.00001 M, 0.0001M, 0.001M Spd	Decrease in amount of of chlorophyll degradation, accumulation of spd and spm in higher content, increased activity of enzymes that perform scavenging	Increased tolerance to salt stress	[44]
Oxidative stress	Seedlings of *Cerasus humilis*	0.0002M spm or spd	Increased antioxidative property, higher amount of spm, spd, put accumulation, activities of the enzymes SAMDC, ADC and ODC	oxidative damage was found to be stopped that was caused as result of drought	[45]
0.08M Calcium nitrate	Muskmelon	0.05M GABA	The amount of put was decreased but that of spm and spd got increased,PAO , SAMDC, ODC, ADC, DAO enzymatic activity was enhanced	Seedlings of muskmelon showed higher levels of tolerance towards calcium nitrate stress	[46]
0.001M $CuCl_2$ or $CdCl_2$	Sunflower and wheat	0.0001M PAs	Helped in normal development and prevented the effects of those metals stress on plant	Increased amount of tolerance towards stress caused by the heavy metals	[47]
Water stress	*Thymus vulgaris* L.	0.02g/L of p put	Lowered amount of injury to cells, increased activity of enzymes showing antioxidant functions, increased dry Matter and increased water content of the leaf	There were no harmful effects of drought stress on plants	[48]

Reponse of PAs to other types of stress

ISSN:0971-1260

Vol-22-Issue-16-August-2019

PAs have role in response to UV radiation which is a known stress to plants. The amount of conjugated PAs was estimated to be higher and the levels of free PAs was estimated to be lowered when *Phaseolus vulgaris* was subjected to UV-B stress [49]. When the same type of radiation stress was provided to tobacco there was accumulation of higher amount of put, but prolonged exposure to that radiation resulted in lowering the levels of PA [50]. Although other examples are also present but still by considering these two examples it signifies that there is some relation between radiation stress recognition and to initiate response against it by the PAs in the plants. As the ozone is directly hitting the plants it is affecting the plants normal growth and development, inefficient photosynthesis, damage to foliar regions and ultimately leading to senescence of plant [51]. The leaves of barley plant showed enhanced activity of ADC when the leaves were treated with ozone. Researchers showed in vitro that spm, spd and put with levels between 0.01M to 0.05M were able to control the formation of superoxide free radicals [52]. Arabidopsis had gained the ability to detoxify the effect caused by paraquat when it was treated with PAs [53] which signified that the PAs may be stimulating the antioxidant properties of the plants. Salt tolerance can be achieved in tobacco by overexpressing CuAO (genes coding for diamine oxidase) [54] and the result of ZmPAO (maize polyamine oxidase) overexpression in tobacco plant would result in better healing of the wound [55]. Researchers showed that acid resistance in plants was found to be enhanced when the plant was treated with put under acid stress conditions and it was able to stabilize the membrane [56]. There will be increase in the content of PAs when the plants encounter biotic stress like when a pathogen enters a plant cell there will be activation of PA oxidase which results in accumulation of H_2O_2 that will inhibit the further entry of pathogens into the plant cell [57].

Protection of plants by Polyamines

PAs play many vital roles in plants like they regulate plants growth, development, cell differentiation, PCD, providing response when plants encounter biotic and abiotic stress and many other functions will be regulated by PAs. They protect biopolymers, proteins, membranes and lipids due to their ability to interact with the sites where there will be negative charge on the molecules with whom they interact. Whenever the plants encounter stress the degradation of nucleic acids and proteins is protected and stabilised by PAs. A diamine put has very crucial role in initiating the response to plant stress and it also serves as a precursor molecule for spd and spm synthesis [58]. Under stressful conditions there will be reduction in chlorophyll content and increase in biopolymer degrading enzymes which ultimately causes the plant cell to undergo senescence, but the presence of spm and spd will prevent the cell form undergoing senescence [59]. Researchers found that by giving osmotic stress to oat plants and treating them with spd showed that spd protected Rubisco, cytochrome, and D1, D2 proteins of the thylakoid and also helped in stabilizing their structure [60]. On expressing *Saccharomyces cerevisiae* SAMDC (S-adenosylmethionine decarboxylase) in tomato plant and upon providing the plant with prolonged chilling treatment and then subjecting to mild warming increased the spm and spd content in the fruit along with which a pathogenesis related protein PR1b1 was also found to be accumulated [61] and thus it was inferred that the accumulation of protein was due to PAs thus providing a link between PAs and their role in cold stress response. ADC1 expression is specifically increased when there is cold stress [62] (Hummel et al. 2004) whereas ADC2 expression is generally expressed in higher amount during abiotic stresses [63][64][65] [66] [67]. When the plant experiences only salt stress then

ISSN:0971-1260

Vol-22-Issue-16-August-2019

it is observed that the plants accumulates more amount of SAMDC2 and when the plants experiences cold stress then SAMDC1 and SAMDC2 both are observed to be accumulating in higher amount [68]. In response to salt stress the increased activity of CuAO results in increased concentration of GABA [69] or may trigger the synthesis of ROS in the apoplast [70] [71] due to PA oxidation in larger amount where PAs aims at protecting the plant under stress induced by salt. The external treatment of put decreases the damage to chlorophyll and protects the thylakoid membrane during stress conditions and the activity of PSII was found to be enhanced [72][73][74]. The function of PAs in ROS scavenging can be understood by [75] work where the oxidative damage to DNA was found to be inhibited due to presence of spm in *Mesembryanthemum crystallinum*.

Conclusion

The biotic and abiotic stress if neglected will cause severe damage to crop and ultimately the plant may not be able to survive with such harsh conditions. There are some stresses which we can avoid but there are some stresses that are not under the control of our hands and for such stresses the development of stress tolerant crops or coming up with new conventional strategies are required. To develop any strategy it is necessary to know the detailed background of that problem so that we can come up with a better solution. Supporting to that statement PAs have been well understood and known to play a very crucial and promising role in initiating a stress response and providing tolerance towards stress in plant's life. Hence by using PAs we can go for conventional or trans/cis genic approaches to control the synthesis and catabolism of PAs in different plants as needed to provide tolerance to different stress conditions in plants.

The problem of biotic and abiotic stress have been affecting the crop yield since wayback but the research is still going on to make the plant tolerant towards that particular stress that a plant is facing. Although many conventional and biotechnological approaches have ensured that the future agriculture is free from danger but still those techniques that would bring a revolutionary change in the field of stress biolgy are in demand.

References

[1] A. Cona, G. Rea, R. Angelini, and R. Federico, P. Tavladoraki, "Functions of amine oxidases in plant development and defence," Trends Plant Sci, vol. 11, pp. 80–88, 2006.

[2] PN. Moschou, KA. Paschalidis, and KA. Roubelakis-Angelakis, "Plant polyamine catabolism. Plant Signal," Behav, vol. 3, pp. 1061–1066, 2008.

[3] KA. Paschalidis, and KA. Roubelakis-Angelakis, "Spatial and temporal distribution of polyamine levels and polyamine anabolism in different organs/tissues of the tobacco plant. Correlations with age, cell division/expansion, and differentiation," Plant Physiol, vol. 138, pp. 142–152, 2005.

ISSN:0971-1260

Vol-22-Issue-16-August-2019

[4] A. Aziz, J. Martin-Tanguy, and LF. Larher, "Plasticity of polyamine metabolism associated with high osmotic stress in rape leaf discs and with ethylene treatment," Plant Growth Regul, vol. 21, pp. 153–163, 1997.

[5] R. Alca´zar, T. Altabella, F. Marco, C. Bortolotti, M. Reymond, C. Koncz, P. Carrasco, and A. Tiburcio, "Polyamines: molecules with regulatory functions in plant abiotic stress tolerance," Planta, vol. 231, pp. 1237–1249, 2010.

[6] SS. Hussain, M. Ali, M. Ahmad, and KH. Siddique, "Polyamines: natural and engineered abiotic and biotic stress tolerance in plants," Biotechnol Adv, vol. 29(3), pp. 300–311, 2011.

[7] M. Roy,and R. Wu, "Arginine decarboxylase transgene expression and analysis of environmental stress tolerance in transgenic rice," Plant Sci, vol. 160, pp. 869–875, 2001.

[8] R. Basu, and B. Ghosh, "Polyamines in various rice genotypes with respect to NaCl salinity," Physiol Plant, vol. 82, pp. 575–581, 1991.

[9]Krishnamurthy, and Bhagwat, "Polyamines as modulators of salt tolerance in rice cultivars," Plant Physiol, vol. 91, pp. 500–504, 1989.

[10] P. Roy, K. Niyogi, DN. SenGupta, and B. Ghosh, "Spermidine treatment to rice seedlings recovers salinity stress-induced damage of plasma membrane and PM-bound H + -ATPase in salttolerant and salt-sensitive rice cultivars,"Plant Sci, vol. 168, pp. 583–591, 2005.

[11] MK. Chattopadhayay, BS. Tiwari, G. Chattopadhayay, A. Bose, DN. Sengupta, and B. Ghosh, "Protective role of exogenous polyamines on salinity-stressed rice (Oryza sativa) plants," Physiol Plant, vol. 116, pp. 192–199, 2002.

[12] D. Meng, L. Hou, and S. Yang, "Exogenous polyamines alleviating salt stress on peanuts (Arachis hypogaea) grown in pots," Chin. J. Plant Ecol, vol. 39, pp. 1209–1215, 2015.

[13] F. Baniasadi, VR. Saffari, and AAM. Moud, "Physiological and growth responses of Calendula officinalis L. plants to the interaction effects of polyamines and salt stress," Sci. Horticult, vol. 234, pp. 312–317, 2018.

[14] L. Sun, S. Yu and F. Zhao, "Effects of salt stress on polyamines and hormone metabolism in Grape seedlings," Xinjiang Agric. Sci, vol. 55, pp. 66–73, 2018.

[15] D. Chen, Q. Shao, L. Yin, A. Younis, and B. Zheng, Polyamine Function in Plants: Metabolism, Regulation on Development, and Roles in Abiotic Stress Responses. Front. Plant Sci, vol. 9, pp. 1945, 2019.

[16] K. Liu, H. Fu, Q. Bei, and E. Al, "Inward potassium channel in guard cells as a target for polyamine regulation of stomatal movements," Plant Physiol, vol. 124, pp. 1315–1325, 2000.

ISSN:0971-1260

Vol-22-Issue-16-August-2019

[17] R. Alcázar, J. Planas, T. Saxena, X. Zarza, C. Bortolotti, JC. Cuevas M. Bitrian, AF. Tiburcio, and T. Altabella, "Putrescine accumulation confers drought tolerance in transgenic Arabidopsis plants overexpressing the homologous Arginine decarboxylase 2 gene," Plant Physiol Biochem, vol. 48, pp. 547–552, 2010.

[18] J. Shi, XZ. Fu, T. Peng, XS. Huang, QJ. Fan, and JH. Liu, "Spermine pretreatment confers dehydration tolerance of citrus in vitro plants via modulation of antioxidative capacity and stomatal response," Tree Physiol, vol. 30, pp. 914–922, 2010.

[19] IM. Zeid, and ZA. Shedeed, "Response of alfalfa to putrescine treatment under drought stress," Biol. Plant, vol. 50, pp. 635–640, 2006.

[20] Y. Liu, Z. Zuo, and J. BHu, "Effects of exogenous polyamines on growth and drought resistance of Apple seedlings. J," Northwest Forestry Univ, vol 25, pp. 000039–000042, 2010.

[21] D. Montesinos-Pereira, Y. Barrameda-Medina, L. Romero, JM. Ruiz, and E. Sánchez-Rodríguez, "Genotype differences in the metabolism of proline and polyamines under moderate drought in tomato plants," Plant Biol, vol. 16, pp. 1050–1057, 2015.

[22] I. Toumi, PN. Moschou, KA. Paschalidis, B. Bouamama B, Salem-fnayou, AW. Ghorbel, A. Mliki, and KA. Roubelakis-Angelakis, "Abscisic acid signals reorientation of polyamine metabolism to orchestrate stress responses via the polyamine exodus pathway in grapevine. J," Plant Physiol, vol. 167, pp. 519–525, 2010.

[23] Y. Li, and J. He, "Advance in metabolism and response to stress of polyamines in plant," Acta Agric. Boreali Sinica, vol. 27, pp. 240–245, 2012.

[24] Y. Zhen, S. Li, and X. Su, "Polvamine changes and chilling injury in cold-stored Loquat fruits. J," Integr. Plant Biol, vol. 42, pp. 824–827, 2000.

[25] M. Roy, and R. Wu, "Arginine decarboxylase transgene expression and analysis of environmental stress tolerance in transgenic rice," Plant Sci, vol. 160, pp. 869–875, 2001.

[26] H. Nayyar, Putrescine increases floral retention, pod set and seed yield in cold stressed chickpea. J Agron Crop Sci, vol. 191, pp. 340–345, 2005.

[27] L. He, K. Nada, and S. Tachibana, "Effects of spd pretreatment through the roots on growth and photosynthesis of chilled cucumber plants (Cucumis sativus L.)," J Jpn Soc Hort Sci, vol. 71, pp. 490–498, 2002.

[28] L. Cheng, YJ. Zou, SL. Ding, JJ. Zhang, XL. Yu, JS. Cao, and G. Lu, "Polyamine accumulation in transgenic tomato enhances the tolerance to high temperature stress," J Integr Plant Biol, vol. 51, pp. 489–499, 2009.

ISSN:0971-1260

Vol-22-Issue-16-August-2019

[29] M. Cvikrová, L. Gemperlová, J. Dobrá, O. Martincová, IT. Prásil, J. Gubis and R. Vanková, "Effect of heat stress on polyamine metabolism in proline-over-producing tobacco plants," Plant Sci, vol. 182, pp. 49–58, 2012.

[30] J. Tian, "Physiological regulation function and proteomics research of exogenous spermidine on alleviating high temperature stressthe of cucumber seedlings," Nanjing Agric. Unive, pp. 7–21, 2012.

[31] MB. Watson, and RL. Malmberg, "Regulation of Arabidopsis thaliana (L.) Heynh arginine decarboxilase by potassium deficiency stress," Plant Physiol, vol. 111, pp. 1077–1083, 1996.

[32] JJ. Camacho-Cristóbal, JM. Maldonado, and A. Gonzláez-Fontes," Boron deficiency increases putrescine levels in tobacco plants," J Plant Physiol, vol. 162, pp. 921–928, 2005.

[33] PT. Evans, and RL. Malmberg, "Do polyamines have roles in plant development?," Annu Rev Plant Physiol Plant Mol Biol, vol. 40, pp. 235–269, 1989.

[34] MD. Groppa, MP. Benavides, and ML. Tomaro, "Polyamine metabolism in sunflower and wheat leaf discs under cadmium or copper stress," Plant Sci, vol. 164, pp. 293–299, 2003.

[35] ND. Groppa, ML. Tomaro, and MP. Benavides, "Polyamines as protectors against cadmium or copper-induced oxidative damage in sunflower leaf discs," Plant Sci, vol. 161, pp. 481–488, 2001.

[36] G. Drolet, EB. Dumbroff, RL. Legge, and JE. Thompson, "Radical scavenging properties of polyamines," Phytochemistry, vol. 25, pp. 367–371, 1986.

[37] N. Durmus, and A. Kadioglu," Spermine and putrescine enhance oxidative stress tolerance in maize leaves," Acta Physiol Plant, vol. 27, pp. 515–522, 2005.

[38] Y. Jia, S. Guo, and J. Li, "Effects of exogenous putrescine on polyamines and antioxidant system in cucumber seedlings under root-zone hypoxia Stress," Acta Bot. Boreali Occidentalia Sinica, vol 28, pp. 1654–1662, 2008.

[39] J. Wu, S. Shu, C. Li, J. Sun, and S. Guo, "Spermidine-mediated hydrogen peroxide signaling enhances the antioxidant capacity of salt-stressed cucumber roots," Plant Physiol. Biochem, vol. 128, pp. 152–162, 2018.

[40] R. Minocha, R. Majumdar, and SC. Minocha, "Polyamines and abiotic stress in plants: a complex relationship," Front Plant Sci, vol. 5, pp. 175, 2014.

[41] MA. Perez-Amador, J. León, PJ. Green, and J.Carbonell, "Induction of the arginine decarboxylase ADC2 gene provides evidence for the involvement of polyamines in the wound responses in Arabidopsis," Plant Physiol, vol. 130, pp. 1454–1463, 2002.

ISSN:0971-1260

Vol-22-Issue-16-August-2019

[42] R. Angelini, A. Cona, R. Federico, P. Fincato, P. Tavladoraki, and A. Tisi, "Plant amine oxidases "on the move," an update. Plant Physiol Biochem, vol. 48, pp. 560–564, 2010.

[43] R. Angelini, A. Tisi, G. Rea, MM. Chen, M. Botta, R. Federico and A. Cona, "Involvement of polyamine oxidase in wound healing," Plant Physiol, vol. 146, pp. 162–177, 2008.

[44] S. Parvin, OR. Lee, G. Sathiyaraj, and E. Al, "Spermidine alleviates the growth of saline-stressed ginseng seedlings through antioxidative defense system," Gene, vol 537, pp. 70–78, 2014.

[45] ZP. Yin, S. Li, J. Ren, and E. Al, "Role of spermidine and spermine in alleviation of drought-induced oxidative stress and photosynthetic inhibition in Chinese dwarf cherry (Cerasus humilis) seedlings," Plant Growth Regul, vol 74, pp. 209–218, 2014.

[46] X. Hu, Z. Xu, W. Xu, and E. Al, "Application of g-aminobutyric acid demonstrates a protective role of polyamine and GABA metabolism in muskmelon seedlings under Ca(NO3)2 stress," Plant Physiol. Biochem, vol. 92, pp. 1–10, 2015.

[47] MP. Benavides, MD. Groppa, L. Recalde, and SV. Verstraeten, "Effects of polyamines on cadmium- and copper-mediated alterations in wheat (Triticum aestivum L) and sunflower (Helianthus annuus L) seedling membrane fluidity," Arch. Biochem. Biophys, vol. 654, pp. 27–39, 2018.

[48] H. Mohammadi, M. Ghorbanpour, and M. Brestic,, "Exogenous putrescine changes redox regulations and essential oil constituents in field-grown Thymus vulgaris L. under well-watered and drought stress conditions," Ind. Crops Prod, vol. 122, pp. 119–132, 2018.

[49] J. Smith, D. Burrit, and P. Bannister, "Ultraviolet-B radiation leads to a reduction in free polyamines in Phaseolus vulgaris L," Plant Growth Regul, vol. 35, pp. 289–294

[50] C. Lutz, E. Navakoudis, HK. Seidlitz, and K. Kotzabasis, "Simulated solar irradiation with enhanced UV-B adjust plastid- and thylakoid-associated polyamine changes for UV-B protection," Biochim Biophys Acta, vol. 1710, pp. 24–33, 2005.

[51] C. Langebartels, K. Kerner, S. Leonardi, M. Schraudner, M. Trost, W. Heller, and HJr. Sandermann, "Biochemical plant responses to ozone. I. Differential induction of polyamine and ethylene biosynthesis in tobacco," Plant Physiol, vol. 95, pp. 882–889, 1991.

[52] G. Drolet, EB. Dumbroff, RL. Legge, and JE. Thompson, "Radical scavenging properties of polyamines," Phytochemistry, vol. 25, pp. 367–371, 1986.

[53] MP. Benavides, SM. Gallego, ME. Comba, and ML. Tomaro, "Relationship between polyamines and paraquat toxicity in sunflower leaf discs," Plant Growth Regul, vol. 31, pp. 215–224, 2000.

ISSN:0971-1260

Vol-22-Issue-16-August-2019

[54] PN. Moschou, KA. Paschalidis, and KA. Roubelakis-Angelakis, "Plant polyamine catabolism," Plant Signal. Behav, vol 3, pp. 1061–1066, 2008.

[55] R. Angelini, A. Tisi, G. Rea, MM. Chen, M. Botta, R. Federico, and A. Cona, "Involvement of polyamine oxidase in wound healing," Plant Physiol, vol. 146, pp. 162–177, 2008.

[56] R. Li, H. Shen, and M. Li, "Effects of acid stress on the contents of proline and putrescine in several forest trees," J. Nanjing Forestry Univ, vol. 9, pp. 88–93, 1995.

[57] RY. Yordanova, VS. Alexieva, and LP. Popova, "Influence of root oxygen deficiency on photosynthesis and antioxidant status in barley plants," Russian J. Plant Physiol, vol. 50, pp. 163–167, 2003.

[58] PH. Masson, T. Takahashi, and R. Angelini, "Editorial: Molecular Mechanisms Underlying Polyamine Functions in Plants," Front. Plant Sci, vol. 8, pp.14, 2017.

[59] J. Legocka, and J. Zaichert, "Role of Spermidine in the Stabilization of Apoprotein of the Light-Harvesting Chlorophyll a/b–Protein Complex of Photosystem II during Leaf Senescence Process," Acta Physiol. Plant., 1999, vol. 21, pp. 127–137, 1999.

[60] RT. Besford, CM. Richardson, JL. Campos, and AF. Tiburcio, "Effect of Polyamines on Stabilization of Molecular Complexes of Thylakoid Membranes of Osmotically Stressed Oat Leaves," Planta, vol. 189, pp. 201–206, 1993.

[61] RK. Goyal, T. Fatima, M. Topuz, A. Bernadec, R. Sicher, AK. Handa and AK. Mattoo, "Pathogenesis-Related Protein 1b1 (PR1b1) Is a Major Tomato Fruit Protein Responsive to Chilling Temperature and Upregulated in High Polyamine Transgenic Genotypes," Front. Plant Sci, vol. 7, pp, 2016.

[62] I. Hummel, G. Gouesbet, El A. Amrani, A. Ainouche, and I. Couee, "Characterization of the two arginine decarboxylase (polyamine biosynthesis) paralogues of the endemic subantarctic cruciferous species Pringlea antiscorbutica and analysis of their differential expression during development and response to environmental stress," Gene, vol. 342, pp. 199–209, 2004.

[63] R. Alca´zar, F. Marco, JC. Cuevas, M. Patro´n, A. Ferrando, P. Carrasco, AF. Tiburcio, and T. Altabella, "Involvement of polyamines in plant response to abiotic stress," Biotechnol Lett, vol. 28, pp. 1867–1876, 2006.

[64] P. Armengaud, R. Breitling, and A. Amtmann, "The potassiumdependent transcriptome of Arabidopsis reveals a prominent role of jasmonic acid in nutrient signalling," Plant Physiol, vol. 136, pp. 2556– 2576, 2004.

[65] MA. Perez-Amador, J. León, PJ. Green, and J. Carbonell, "Induction of the arginine decarboxylase ADC2 gene provides evidence for the involvement of polyamines in the wound responses in Arabidopsis," Plant Physiol, vol. 130, pp. 1454–1463, 2002.

ISSN:0971-1260

Vol-22-Issue-16-August-2019

[66] I. Hummel, G. Gouesbet, El A. Amrani, A. Ainouche, and I. Couee, "Characterization of the two arginine decarboxylase (polyamine biosynthesis) paralogues of the endemic subantarctic cruciferous species Pringlea antiscorbutica and analysis of their differential expression during development and response to environmental stress," Gene, vol. 342, pp. 199–209, 2004.

[67]K. Urano, Y. Yoshiba, T. Nanjo, Y. Igarashi, M. Seki, F. Sekiguchi, K. Yamaguchi-Shinozaki, and K. Shinozaki, "Characterization of Arabidopsis genes involved in biosynthesis of polyamines in abiotic stress responses and developmental stages," Plant Cell Environ, vol. 26, pp. 1917–1926, 2003.

[68] C. Vergnolle, MN. Vaultier, L. Taconnat, JP. Renou, JC. Kader, A. Zachowski, and E. Ruelland, "The cold-induced early activation of phospholipase C and D pathways determines the response of two distinct clusters of genes," 2005.

[69] SG. Xing, YB. Jun, ZW. Hau, and LY. Liang, "Higher accumulation of gamma-aminobutyric acid induced by salt stress through stimulating the activity of diamine oxidases in Glycine max (L.) Merr.roots," Plant Physiol Biochem, vol. 45, pp. 560–566, 2007.

[70] MP. Campestre, CD. Bordenave, AC. Origone, AB. Menéndez, OA. Ruiz, AA. Rodríguez, and SJ. Maiale, "Polyamine catabolism is involved in response to salt stress in soybean hypocotyls," J Plant Physiol, vol. 168, pp. 1234–1240, 2011.

[71] AA. Rodrı´guez, SJ. Maiale, AB. Mene0ndez, and OA. Ruiz, "Polyamine oxidase activity contributes to sustain maize leaf elongationn under saline stress," J Exp Bot, vol. 60, pp. 4249–4262, 2009.

[72] AS. Cohen, RB. Popovic, and S. Zalik, " Effects of polyamines on chlorophyll and protein content, photochemical activity, and chloroplast ultrastructure of barley leaf discs during senescence," Plant Physiol, vol. 64, pp. 717–720, 1979.

[73] RB. Popovic, DJ. Kyle, AS. Cohen, and S. Zalik, "Stabilization of thylakoid membranes by spermine during stress induced senescence of barley leaf discs," Plant Physiol, vol. 64, pp. 721–726, 1979.

[74] RH. Zhang, J. Li, SR. Guo, and T. Tezuka, "Effects of exogenous putrescine on gas exchange characteristics and chlorophyll fluorescence of NaCl-stressed cucumber seedlings," Photosynth Res, vol. 100, pp. 155–162, 2009.

[75] Vl. Kuznetsov, and NI. Shevyakova, "Polyamines and stress tolerance of plants," Plant Stress, vol. 1, pp. 50–71, 2007.

