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Role of Polyamines and Their Effect on Photosynthesis in Plants

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ABSTRACT

Polyamines are special nitrogenous compounds derived from amino acids and like sources. They are synthesized in all types of living organisms and play a crucial role in regulating various types of physiological phenomenon. They exhibit a key role from seedling stage up to senescence in multiple parts of plants and also help defend various stress factors that influence the plant life cycle. Photosynthesis is a crucial physiological mechanism that makes plants a food source for the whole planet. Polyamines are found synthesized in thylakoids of plant chloroplast and help in defending the stress influence on the rate of photosynthetic. The exogenous application or in-vivo synthesis of various polyamines in the plant help in defending various stress factors in plants. The monitoring of concentration of polyamines can be used as a best tool to identify the stress tolerance ability of a plant towards any ecological stress factor.

Keywords: polyamines; photosynthesis; thylakoid membrane.

Abbrevations:-Transglutaminase-TGase; Aspartate decarboxylase-ADC

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INTRODUCTION

Polyamines (PAs) are nitrogenous compounds of low molecular weight abundantly available in all life forms [1]. In plants, polyamines such as spermidine (Spd), spermine (Spm) and their diamine form putrescine (Put) are found largely. They are derived from aliphatic hydrocarbons substituted with two or more amino groups. PAs display wide range of role in regulating plants and photosynthetic organisms at fundamental processes, such as membrane stabilization, enzyme activity modulation, replication and gene expression, growth and development, senescence, and adaptation to abiotic and biotic stress factors [2]. They are found in the free form or as conjugated with compounds like phenolic acids, proteins and nucleic acids [3]. PAs are the best plant growth regulators, their physiological role and mechanism of action in plants is complex and yet to be disclosed.

Plant cell organelles like chloroplasts and photosynthetic sub-complexes like thylakoids, light harvesting complex-II (LHCII complex), photosystem-II (PS-II) complex and thylakoid membranes are enriched with three major polyamines. Especially Spm was abundantly available in PS-II core complex and the reaction center of PS-II [4,5]. PAs exhibit a protective role in the photosynthetic apparatus of plants in response to various abiotic stresses. From several years the role of polyamines in the maintenance of the photochemical efficiency of plants has become much of research interest in plant and Agriculture researchers. An increase in conjugated Put content stabilizes the thylakoid membrane, thus helps in enhancing the resistance of tobacco plants towards UV-B radiation [6]. Low temperature stress reduces the content of Put in thylakoids and Put/Spm ratio in LHCII of *Phaseolus vulgaris* L., and hence leads to a drift in photosynthetic electron transport rate causing inactivation of the PS-II reaction center [7]. Put is found in the development of photosynthetic apparatus having high concentration of reaction center with a small functional antenna that leads to enhanced photochemical quenching of absorbed light [4]. PAs biosynthesis is under the control of light whereas the biosynthesis of Spm and Put, their ratios are identified to be regulated according to photo adaptations of the photosynthetic apparatus in plants. Studies illustrate that various changes in polyamines ratio and concentration in the sub-cellular organelles are involved in protective role of photosynthetic apparatus during stress conditions.

After the identification of the above said alterations several investigators started to monitor the importance of polyamines and their exogenous applications on plants for protection against various environmental stress factors. Thorough investigation has demonstrated the interference of exogenously applied polyamines in defending the environmental stress towards photosynthetic apparatus in the intact chloroplast apparatus [8] and their protective role against adverse effects of environmental stress factors [5]. However, the effect of polyamines depends on the level of stress acting and the type or/and amount of exogenous polyamine applied on the plant.

EFFECT OF POLYAMINES ON PHOTOSYNTHESIS

Improvement in the photosynthetic capacity is observed with exogenous polyamines application on a salt-stressed cucumber plant, also they are found to be involved in elevating the photochemical efficiency of PS-II [9]. Investigations with addition of Put, Spd and Spm to low salt stressed thylakoids showed, Spd as a potent polyamine in restoration of maximum photochemical efficiency [Fv/Fm].But at higher amount it may lead to decline in the photochemical efficiency [10]. It was also found that exogenously used Spd samples on *Physcia semipinnata* when exposed to UV-A radiation, had higher chlorophyll-a quantity and PS-II activity than in Spm and Put added samples [11]. Analysis of PS-II particles in the presence of Put, Spd and Spm solutions under the dark conditions showed that Spd interacts directly with thylakoid membranes, and was effective against the loss of LHCII in detached leaves, thus leaves containing Spd are more stable and protected against degradation during senescence phenomenon [12].Several studies explain high activities of polyamine biosynthetic enzymes and Transglutaminase (EC 2.3.2.13) [TGase] in chloroplast sub-organelle, synthesizing the covalently bound polyamines with proteins [13-15]. These bound proteins are found to be involved in regulating photosynthesis in response to stress conditions [16].

In the recent days, the role of PAs in structure and function of the cell organelles like thylakoids [photosynthetic apparatus] are widely investigated. As a response to various stress factors PAs and their related-metabolic enzymes act as positive regulators in plant photosynthesis [17]. However, the specific protective mechanisms exhibited by polyamines in protecting photochemical efficiency of stressed-plants remains a question till today to large group of researchers. Thus, we need to understand the regulatory role of PAs in photosynthetic processes using advanced molecular biology and proteomic approaches to thoroughly understand them.

STOMATAL OPENING/ CLOSURE:

Stomata are surrounded by two guard cells and are responsible for gas exchange between plants and the atmosphere [18]. Stomata play a key role in sensing abiotic stresses like drought, heat, chilling and salinity conditions in the atmosphere [19]. Stomata regulated by PAs are closely correlated with the photosynthetic process and increases the amount of CO_2 available for carbon fixation by RUBISCO enzymes (E.C-4.1.1.39). However, the roles of polyamines in regulating stomatal functioning and its correlation with environmental stress conditions, its specific mechanisms are still unclear.

Natural polyamines, such as cadaverine (Cad) and putrescine (Put), spermidine (Spd), spermine (Spm) at a given concentration, strongly inhibit opening of stomata. According to Liu *et al.*,[20] 1mM Spd and Spm completely prevent light-induced stomatal opening, whereas Cad and Put inhibited opening by 88% to 63%, respectively. Polyamines significantly reduces the stomatal aperture, Spd and Spm are found to be more effective than that of Put at 1 mM. Çavuşoğlu *et al.,*[21] showed that pre-treatment with polyamine could decrease stomata number and length in the upper surface under saline conditions by reducing the transpiration.

In the Spm-pretreated *Citrus reticulata* samples were observed with smaller stomatal aperture size than in the control at a given point of time, during the whole experiment [22].

Many environmental factors regulates stomatal aperture by modulating the ion channel activity in guard cells [23]. Change in guard cell turgor helps to instigate the stomatal movements that control number of ion channels and pumps [24]-[25]. As an important player in stomatal regulation, I Kin is an indirect target of polyamine action. A number of studies illustrated the activity of I Kin-inhibiting processes or factors that often inhibit stomatal opening [26]. Liu and co workers [20] using patch-clamp analysis demonstrated that intracellular application of polyamines inhibited the inward KI current across the plasma membrane of *Vicia faba* guard cells and modulated stomatal movement. Changes in free Ca^{2+} ions in the cytoplasm of guard cells are involved in stomatal aperture/closure. In the Spm-deficient mutant Arabidopsis seems to be impaired in Ca^{2+} homeostasis, which affects the stomatal movement, and this inhibited effect was restored by application of exogenous Spd in the mutant plants [27]. It has also been reported that polyamine-induced ROS scavenging is an essential effect and stimulated stomatal closure (lower water loss) upon dehydration, which may function collectively to enhance dehydration tolerance in plants [28]-[29]. The above mentioned findings suggest that polyamines target KAT1-like inward K1 channels in guard cells, modulate stomatal movements and provides a link between stress conditions, polyamine levels, and stomatal regulation.

PHOTOSYNTHETIC PIGMENT

Chlorophyll (Chl) is an important molecule that plays an important role in photosynthesis for the plant growth process, such as light absorption, in combination with protein complexes, for the transfer of energy into carbohydrate [30]. A variety of reports indicate that changes in chlorophyll content of plants may decrease in response to environmental factors or leaf senescence [31]-[32].

Aliphatic polyamines (PAs) are involved in the delay or loss of chlorophyll and lead to an increased efficiency of light capture resulting in the improvement of net photosynthetic rate, but the molecular mechanism is not clarified. Positive effects of exogenous supplied polyamines on the content of Chla and total Chl in leaves were observed during various stresses, but there were distinct differences in the effect of three main polyamines. Unal et al. [11] explained that Chla content was significantly increased in *Physcia semipinnata* by exogenously addition of polyamines during exposure to UV-A radiation, and exogenously Spd added samples had higher Chla content than Spm and Put added sample during the same stress. Spd delayed the loss of Chl more than Spd or Put in detached wheat leaves during dark incubation this imply the importance of valency of organic cations [33]. The above said phenomenon is in agreement with those of Aldesuquy et al. [34] who reported similarly using detached wheat leaves infected with the yellow rust *Puccinia striiformis*. Among the various exogenous supplied PAs, Spm has been shown to regulate the in vivo amount of proto-chlorophyllide (PChlide) and Chl both in darkness and in light in contrast with Put and Spd [35]. Similarly Beigbeder and co workers [36] suggested that the intracellular level of Put was decreased by the usage of 1, 4-diamino-2-

butanone inhibitor (1,4DB) dramatically increasing the PChlide levels with parallel reduction of total chlorophyll. Many workers have reported retention of chlorophyll during exogenous supplementation of polyamines during the normal developmental senescence of leaves.

Cheng and Kao [37] demonstrated that Spd and Spm were effective in retarding loss of chlorophyll from detached leaves of rice, wheat and soybean. They described the effect of locally applied polyamines as being similar to that of cytokinins. In *Heliotropium sp.,* leaf senescence is associated with low endogenous concentrations of polyamines [38]. One of the mechanisms by which PAs modulate chlorophyll stabilization was identified to be due to modification of chlorophyll-bound proteins, catalyses by TGase. Leaves with senescence condition, after foliar spray of 0.2 mM Spm prevented degradation of Chl-a & Chl-b, and increased TGase activity, producing more PA-conjugates of protein. Spm was found translocated to chloroplast organelles and bound mainly onto enriched PS-II fractions, whose light-harvesting complexes (LHC) sub-fractions contained TGase [39].

CHLOROPLAST ULTRASTRUCTURE

It is necessary to maintain structural integrity and orderliness of chloroplast organelle that plays a key role in conversion of light energy as carbohydrates during photosynthesis [40]. The chloroplasts are usually 5-10 micrometer long and consist of circular DNA molecules. In higher plants, the photosynthetic machinery is mainly localized in thylakoid membranes of the chloroplasts [41]. The membrane has no homogenous structure, but is subdivided into two domains: the strictly stacked grana thylakoids and the unstacked stroma lamellae [42]. The structure of thylakoids is a major factor that affects functionality and performance of the photosynthetic apparatus [43]. It was reported that some stress factors leads to the decrease in the photochemical efficiency and electron transport activity may be associated with the alterations in structure of photosynthetic apparatus [44].

Several studies have showed that polyamines are involved in stabilization of structure and function of photosynthetic apparatus in response to unfavourable environmental stress factors [45]. Under Na Cl stress, Put as organic cation dramatically enhanced lipid accumulation in the chloroplasts and prevented the membrane degradation in the grana and stroma thylakoids by interacting with the negatively charged membrane sites [46]. In our study, we observed that Put can alleviate the degradation of thylakoid membrane proteins induced by salt stress, UV-B stress, high light Stress and thus making a normal stacking order in the adjacent grana thylakoids in maize and wheat primary leaves [47]. In addition, exogenous Spd have been reported to protect the structure of chloroplasts by keeping an orderly arrangement of the thylakoids membrane and also have an ability to maintain a higher photosynthetic efficiency of *Nymphoides peltatum* under Cadmium stress [40].

However, few previous studies showed that high concentrations of polyamines may destroy the structure of photosynthetic apparatus which depended on different light conditions. Spd treatment with chloroplast for about 10 seconds to 12 hours displayed the envelope and the typical dense network of the thylakoid lamellae interspersed with numerous

areas of stacked grana [48]. Incubation of chloroplast envelopes (membranes) with spermidine-incubated in the dark and light conditions, for 72 hours shows damage in the chloroplast envelope by polyamine treatment, but there were distinct differences in the appearance of the chloroplast ultra-structures of dark and light-incubated leaves [49].

THYLAKOID MEMBRANE PROTEIN COMPLEXES

Photosynthetic apparatus in higher plants is a membrane bound protein complex composed of chlorophyll and carotenoid pigments that function in the conversion of light energy to chemical energy. It has been suggested that a large number of these proteins are related to photosynthesis. The thylakoid membranes within the chloroplast are the sub compartments in which the primary reactions of photosynthesis occur. These reactions are organized in the four major multisubunit protein complexes, photosystem I (PS-I), photosystem II (PS-II), the ATP-synthase complex and cytochrome b6f complex (Cytb6f) [50].

Polyamines such as put, spd, spm, and their methylamines interact with protein by H-bonding with polypeptidal C=O, C-N and N-H groups, the major perturbations of protein secondary structure, as the concentration of amines was raised. It has been shown the chloroplasts and various photosynthetic sub-complexes including thylakoids, LHCII complex and PS-II membranes are enriched with polyamines, especially they are exclusively rich in PS-II core and the reaction center of PS-II [4, 5]. Several studies have reported the interaction of polyamines with proteins of photosynthetic apparatus under several environmental stress factors. However, the action site of polyamines in photosynthetic proteins may vary with polyamine concentration and stress levels. In the algae *S. obliquus* the bound polyamines were found to be associated with both the oligomeric and the monomeric LHCII complex, as well as with the CPs [4]. However, the distribution does not reflect a constant pattern: in LHCII sub-complexes Put and Spm levels fluctuated depending on the light adapting mechanism of the photosynthetic apparatus. Put and Spm are bound to photosynthetic complexes, mainly to the LHCII oligomeric and monomeric forms [51]. It is well documented that the LHCII protein is abundant in thylakoids and its surface is negatively charged [52]. Kirchhoff et al. [41] have shown that incubation of thylakoids under unstacking conditions leads to intermixing and randomization of the protein complexes, accompanied by disconnection of LHCII trimers from PS-II and a decreased connectivity between PS-II centers. Interestingly, exogenously added polyamines can reverse the damaging effects. Thus, there were strong indications that polyamines exhibit a pivotal role in maintenance of photosynthetic efficiency.

Chloroplast also contain high activities of several polyamine biosynthetic enzyme [53,14] transglutaminase (TGase) catalyzing the covalent binding of polyamines to proteins [13,54,15]. TGase is present in the chloroplasts of higher plants, where its activity is modulated by the presence of light. Its substrates are Rubisco and some antenna complexes of thylakoids, such as LHCII, CP29, CP26 and CP24 [13]. In *Dunaliella salina* whole cells, TGase seems to play a key role in the acclimatations to high salt concentrations under light condition, and the content of chlorophyll a and b of chloroplast were enhanced. Mainly the amount of 68kD and 55kDa polypeptides was particularly high in acclimated algae cells [54]. Ortigosa and his co-workers

[55] identified over expression of plastidal TGase in maize and tobacco (Chl TGZ) in the young leaves of chloroplasts causing an imbalance between capture and utilization of light in photosynthesis. These changes were accompanied by thylakoid scattering, membrane degradation and reduction of thylakoid interconnections.

Arginine decarboxylase (E.C 4.1.1.11) (ADC) another enzyme involved in polyamine biosynthesis is localized in the chloroplasts of leaves and root nuclei [53]. It was established that spinach ADC was associated with LHC of photosystem II [12]. Evidence state that ADC gene mutant plants of Arabidopsis thaliana show decreased chlorophyll content and photosynthetic efficiency with lower ADC activity causing reduced salt tolerance [56] in them. Polyamines can covalently bind with thylakoid membrane proteins under the TGase form of protein- glutamyl-polyamine or protein-glutamyl-polyamines-glutamyl protein [57], such as D1, D2 protein and Cytb6f, together with the involvement of polyamine, could be important for stabilization of molecular complexes in the thylakoid membranes with osmotically stressed oat leaves [58]. Immunodetection of TGase in thylakoid fraction revealed that formation of covalent bonds between PAs and proteins by TGase is involved in regulating the process of chloroplast senescence [59].

However, high concentration of polyamines added to sub-membrane fractions of photosynthetic apparatus causes a strong inhibition of PS-II activity [60]. FTIR spectroscopy analysis of Spd and Spm at higher cation concentrations ranging 5 and 10 mM, resulted significant alterations of the thylakoid protein secondary structure with a decrease of the α-helical domains from 47% (cation un complexed PS-II) up to 37% (cation complexed PS-II) and an increase in the β-sheet structure from 18% up to 29% [61]. So far, this specific inhibition mechanism of polyamines are unclear, but it is understood that the proteins were affected by these polycations are either extrinsic polypeptides associated with the oxygen evolving complex or portions of integral polypeptides protruding at the surface of the PS-II membranes [62].

From all the above discussion, biochemical and physico-chemical measurements explains that the ratios of Put/Spm act as a defendable regulatory mechanisms in response to various stress factors in photosynthetic apparatus of plants which limits the photosynthetic efficiency of plants. Based on the above several investigations, we conclude that the increase of polyamine contents might be an important mechanism in monitoring plant defense phenomenon at photosynthetic apparatus against the various environmental stress factors. The mechanism by which polyamines contribute to tolerance towards stress factors is not yet thoroughly understood. Thorough understanding may help in increasing the photosynthetic rate of various plants during changing climatic conditions and help in uplifting the plant productivity ultimately.

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