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A Review: Polyamines and Photosynthesis

Sheng Shu, Shi-Rong Guo and Ling-Yun Yuan
College of Horticulture, Nanjing Agricultural University, Key Laboratory of Southern Vegetable Crop Genetic Improvement, Ministry of Agriculture, Nanjing China

1. Introduction

Polyamines (PAs) are low molecular weight ubiquitous nitrogenous compounds found in all living organisms (Kaur-Sawhney et al., 2003). In higher plants, the most common polyamines are spermidine (Spd), spermine (Spm) and their diamine obligate precursor putrescine (Put). They are formed by aliphatic hydrocarbons substituted with two or more amino groups (Figure.1). Because of the polycationic nature at physiological pH, PAs are present in the free form or as conjugates bound to phenolic acids and other low molecular weight compounds or to proteins and nucleic acids (Childs et al., 2003). Like hormones, PAs displaying high biological activity are involved in a wide array of fundamental processes in plants, such as replication and gene expression, growth and development, senescence, membrane stabilization, enzyme activity modulation and adaptation to abiotic and biotic stresses (Galston et al., 1997; Bais and Ravishankar, 2002; Zapata et al., 2008). Although, according to these reports, PAs seem to be important growth regulators, their precise physiological function and mechanism of action still remain unclear.

It has been shown that chloroplasts and photosynthetic subcomplexes including thylakoids, LHCII complex and PSII membranes are enriched with three major polyamines, while PSII core and the reaction center of PSII are exclusively rich in Spm (Kotzabasis et al., 1993; Navakoudis et al., 2003). The potential role of polyamines in maintaining the photochemical efficiency of plants has become a research focus. These studies mainly focused on the effect PAs exert a positive role in the photosynthesis of plants in response to various environmental stresses. In green alga, it was shown that the bound Put content of the thylakoid membrane was increased in environments with high CO_2 concentrations, which caused an increase in reaction center density and led to an increased photosynthetic rate (Logothetis et al., 2004). An increase in conjugated Put content can stabilize the thylakoid membrane, thus enhancing resistance of tobacco plants to ozone pollution (Navakoudis et al., 2003) and UV-B radiation (Lütz et al., 2005). Low temperature stress reduced the content of Put as well as the Put/Spm ratio in thylakoids and the light-harvesting complexes LHCII in *Phaseolus vulgaris* L., leading to a decrease in photosynthetic electron transport rate and inactivation of the PSII reaction center (Sfakianaki et al., 2006). Put is also involved in the induction of a photosynthetic apparatus owning high concentration of reaction center with a small functional antenna that leads to enhance photochemical quenching of the absorbed light energy (Kotzabasis et al., 1999). PAs biosynthesis is controlled by light and the Spm/Put ratio is correlated to the structure and function of the photosynthetic apparatus

during photoadaptation. These studies indicated that changes of endogenous polyamines might be involved in an important protective role in the photosynthetic apparatus.

A lot of researches started to pay attention to the effects of application of exogenous polyamines on photosynthesis under various stresses. It has been demonstrated that exogenously applied polyamines can rapidly enter the intact chloroplast (He et al., 2002) and play a role in protecting the photosynthetic apparatus from adverse effects of environmental stresses (Navakoudis et al., 2003). However, the effect of polyamines on the photosynthetic efficiency of stressed plants depends on the stress level and the type of exogenous polyamines. Exogenous polyamines improved the photosynthetic capacity of salt-stressed cucumber plants by increasing the level of the photochemical efficiency of PSII (Zhang et al., 2009). In green alga *Scenedesmus obliquus* cultures, exogenously added Put was used to adjust the increase in the functional size of the antenna and the reduction in the density of active photosystem II reaction centers, so that to confer some kind of tolerance to the photosynthetic apparatus against enhanced NaCl-salinity and permit cell growth even in NaCl concentrations that under natural conditions would be toxic (Demetriou et al., 2007). Investigations into restoration of the maximum photochemical efficiency (Fv/Fm) by adding Put, Spd and Spm to low salt thylakoid showed that Spd are the most efficient ones in Fv/Fm restoration, but higher amounts of Spm and/or Spd reverse the effect and lead to a decline of the Fv/Fm (Ioannidis and Kotzabasis, 2007). When *Physcia semipinnata* was exposed to UV-A radiation, it was also found that exogenously Spd added samples had higher Chl a content and photosystem II activity than Spm and Put added samples (Unal et al., 2008). In addition, analysis of PSII particles isolated from leaf fragments floated in the presence of Put, Spd and Spm solutions under the dark conditions was conducted. It was observed that Spd could interact directly with thylakoid membranes, which was effective in the retardation of the loss of LHCII observed in water-treated detached leaves, so that they become more stable to degradation during senescence (Legocka and Zajchert, 1999).

Several studies have shown that chloroplasts contain high activities of polyamine biosynthetic enzymes and transglutaminase (TGase) catalyzing the covalent binding of polyamines to proteins (Del Duca et al., 1994; Andreadakis and Kotzabasis, 1996; Della Mea et al., 2004) (Table 1). These enzymes are also involved in regulation of photosynthesis in response to stress conditions (Wang et al., 2010). Arginine decarboxylase (ADC) has been shown to be mainly localised in the chloroplasts of leaves and nuclei of roots (Borrell et al., 1995). It was established that spinach ADC was associated with LHC of photosystem II (Legocka and Zaichert, 1999). PAs synthesised in chloroplasts evidently stabilized photosynthetic complexes of thylakoid membranes under stress conditions (Borrell et al., 1995). An evidence is supported by salt treatment induced a decreased chlorophyll content and photosynthetic efficiency in the lower arginine decarboxylase activity of mutant plants, which leads to reduced salt tolerance in Arabidopsis thaliana (Kasinathan and Wingler, 2004). 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 (Del Duca et al., 1994). In *Dunaliella salina* whole cells, TGase seems to play a role in the acclimimation to high salt concentrations under light condition, and the content of chlorophylla and b of chloroplast were enhanced, the amount of 68kD and 55kDa polypeptides was particularly high in algae already acclimated cells (Dondini et al., 2001). Recently, Ortigosa et al. (2009) showed that the over-expression of maize plastidial transglutaminas (chlTGZ) in the young leaves of tobacco

chloroplasts seemed to induce an imbalance between capture and utilization of light in photosynthesis. Although these changes were accompanied by thylakoid scattering, membrane degradation and reduction of thylakoid interconnections, transplastomic plants could be maintained and reproduced in vitro.

At present, the roles of PAs in the structure and functions of the photosynthetic apparatus are widely investigated. Most of researchers consider the PAs and their related-metabolic enzymes be positive regulators of plant photosynthesis in response to various environmental stresses. However, the specific mechanism of polyamine on the protection of photochemical efficiency of stressed-plants remains until today largely unknown. Thus, we need use advanced molecular biology and proteomic approaches to further understanding the role of PAs in the regulation of photosynthetic processes.
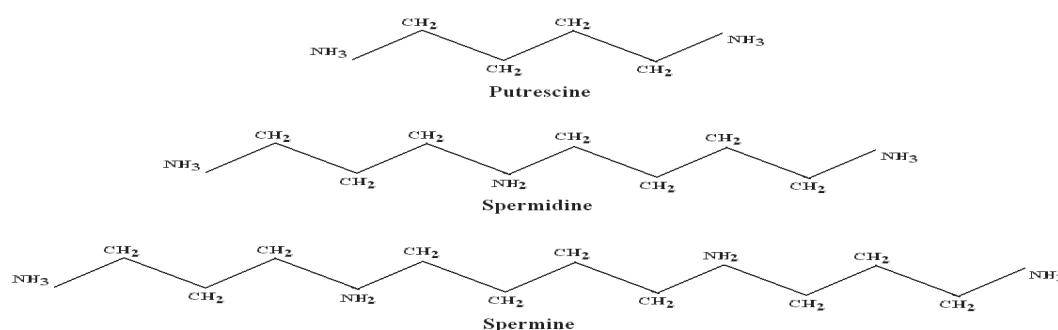

Fig. 1. The chemical structure of three major polyamines

2. Effect of polyamines on photosynthesis

2.1 Stomatal opening/ closure

Stomatal is defined by two guard cells and is responsible for gas exchange between plants and the atmosphere (Mansfield et al., 1990). Stomatal plays a key role in signal transduction, sensing and adaptive responses to abiotic stresses like drought, heat, chilling and high salinity (Hetherington and Woodward, 2003). Polyamines regulated stomatal closely correlated with the improvement of photosynthesis, which could be caused by the greater amount of CO_2 available for its fixation by photosynthetic enzymes. However, most of the roles of polyamines in regulating stomatal research are focused on environmental stress conditions, and the specific mechanisms are still unclear.

All natural polyamines, including cadaverine (Cad) and putrescine (Put), spermidine (Spd), spermine (Spm) at a given concentration, strongly inhibited opening of stomata. Liu et al. (2000) found that 1 mM Spd and Spm completely prevented light-induced stomatal opening, whereas Cad and Put inhibited this opening by 88% and 63%, respectively. Although all polyamines significantly reduced the stomatal aperture, Spd and Spm appeared to be more effective than Put at 1 mM. Çavuşoğlu et al. (2007) showed that polyamine-pretreaments 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 in smaller stomatal aperture size than the control at a given time point or during the whole experiment (Shi et al., 2010).

Many environmental factors regulated stomatal aperture through modulation of ion channel activity in guard cells (MacRobbie, 1997). Changes in guard cell turgor that instigate stomatal movements are controlled by a number of ion channels and pumps (Raschke et al.,

1988; Ward et al., 1995). As an important player in stomatal regulation, the I Kin is an indirect target of polyamine action. A number of studies have shown that I Kin-inhibiting processes or factors often inhibit stomatal opening (Assmann, 1993). Liu et al. (2000) using patch-clamp analysis demonstrated that intracellular application of polyamines inhibited the inward K1 current across the plasma membrane of Vicia faba guard cells and modulated stomatal movement. Changes of free Ca^{2+} 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 that this inhibited effect was restored by application of exogenous Spd in the mutant plants (Yamaguchi et al., 2007). In addition, it has 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 (Pei et al., 2000; Bright et al., 2006). These findings suggest that polyamines target KAT1-like inward K1 channels in guard cells and modulate stomatal movements, providing a link between stress conditions, polyamine levels, and stomatal regulation.

2.2 Photosynthetic pigment

Chlorophyll (Chl) is a molecule substance that plays an important role in photosynthesis for the plant growth process, such as light absorption, and combination with protein complex, transfer the energy into carbohydrate (Meskauskiene et al., 2001). A variety of reports indicate that changes in chlorophyll levels of plants may decrease in response to environmental factors or leaf senescence (Sfichi-Duke et al., 2008; Munzi et al., 2009). Aliphatic polyamines (PAs) are involved in the delay 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 for various stresses, but there were distinct differences in the effect of three main polyamines. Unal et al. (2008) found that Chla content was significantly increased in *Physcia semipinnata* by exogenously added polyamines during exposure to UV-A radiation, and exogenously Spd added samples had higher Chla content than Spm and Put added samples. Spd delayed the loss of Chl more than Spd or Put in detached wheat leaves during dark incubation implying the importance of valency of organic cations (Subhan and Murthy, 2001). The result is in agreement with those of Aldesuquy et al. (2000) who reported that using detached wheat leaves infected with the yellow rust *Puccinia striiformis*. Among of exogenous supplied polyamines, in contrast with Put and Spd, Spm has been shown to regulate the in vivo amount of protochlorophyllide (PChlide) and Chl both in darkness and in light (Beigbeder and Kotzabasis, 1994). Beigbeder et al. (1995) suggested that the intracellular level of Put was decreased by the use of 1, 4-diamino-2-butanone inhibitor (1,4DB) dramatically increasing the PChlide levels with parallel reduction of chlorophyll. Many workers have reported retention of chlorophyll induced by exogenously supplied polyamines during the normal developmental senescence of leaves. Cheng and Kao (1983) demonstrated that Spd and Spm were effective in retarding loss of chlorophyll from detached leaves of rice, wheat and soybean. They describe the effect of locally applied polyamines as being similar to that of cytokinins. In plants of *Heliotropium* sp., leaf senescence is associated with low endogenous concentrations of polyamines (Birecka et al., 1984). One of the mechanisms by which PAs modulate chlorophyll

stabilisation could be due to their modification of chlorophyll-bound proteins, catalysed by TGase. In senescing leaves, foliar spray with 0.2 mM Spm treatment prevented degradation of Chla and Chlb, and increased TGase activity, producing more PA-protein conjugates. Spm was translocated to chloroplasts and bound mainly onto fractions enriched in PSII, whose light-harvesting complexes (LHC) sub-fractions contained TGase (Serafini-Fracassini et al., 2010).

2.3 CO_2 assimilation

CO_2 assimilation is the process of carbohydrates formation which utilized the ATP and NADPH produced by light. The capacity of CO_2 assimilation is connected with the plant growth, biomass and productivity. However, the effect of polyamines on CO_2 assimilation has been investigated very rarely and only a few information concerning the relationship between PAs and carbon assimilation.

Iqbal and Ashraf (2005) analyzed the influence of pre-sowing seed treatment with PAs on growth and photosynthetic capacity in two spring wheat (*Triticum aestivum* L.) cultivars MH-97(salt intolerant) and Inqlab-91(salt tolerant). The results showed that different priming agent did not affect the net CO_2 assimilation rate. The role of three PAs [putrescine (Put), spermidine (Spd) and spermine (Spm)] in improving drought tolerance in fine grain aromatic rice (*Oryza Sativa* L.) has been appraised by Farooq et al. (2009). Three of them were used each at 10 μM as seed priming (by soaking seeds in solution) and foliar spray. Drought stress significantly reduced maximum leaf CO_2 assimilation rate, while application of PAs significantly improved the leaf CO_2 assimilation rate but decreased Gs and transpiration rate (Tr) under drought stress. The resultes suggested that PAs enhanced drought tolerance in rice was due to improved CO_2 assimilation by Rubisco in producing photosyntheate and their partitioning in dry matter yield. Huang et al. (2010) found 0.1 mM CA treatment decreased P_N, but it did not affect the photosynthetic apparatus, which suggest that the decline is at least partially attributed to a lowered RuBPC activity. However, the exogenous application of 1 mM Spd partially restored RuBPC activity in leaves, the key enzyme of carbon reduction cycle (dark reaction), and thus improving the photosynthetic rate. Chen et al. (2010) reported that exogenous Spd application decreased the carbohydrate accumulation in leaves and total sugar, sucrose content in roots under salt stress, thus reduced negative feedback inhibition to photosynthesis caused by carbohydrate accumulation. Exogenous application of Spd can alleviate the damage caused by hypoxia stress and enhance the conversion and use of carbohydrate in roots, which can promote the formation of new metabolic balance seedlings attributed to tolerance of hypoxia stress (Zhou et al., 2007)

2.4 Chloroplast ultrastructure

It is necessary to maintain structural integrity and orderliness of chloroplast that plays a role in conversion of light energy for photosynthesis (Li et al., 2009). 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 (Kirchhoff et al., 2007). The membrane has no homogenous structure, but is subdivided into two domains: the strictly stacked grana thylakoids and the unstacked stroma lamellae (Kirchhoff et al., 2003). The structure of thylakoids is a major factor that affects functionality and performance of the photosynthetic apparatus (Ioannidis et al., 2009). It was reported

that some stresses led to the decrease in the photochemical efficiency and electron transport activity might be associated with the changes of the structure of photosynthetic apparatus (Parida et al., 2003).

Several studies have showed that polyamines are involved in stabilization the structure and function of photosynthetic apparatus in response to unfavourable environment factors (Demetriou et al., 2007). Under Nacl stress, Put as organic cations dramatically enhanced lipid accumulation in the chloroplasts and prevented the membrane degradation in the granal and stromal thylakoids by interacting with the negatively charged membrane sites (Tiburcio et al., 1994). The increase in the number of plastoglobules in the chloroplasts affected by Put can result from the redirection of cell metabolism towards the products of higher reduction potential (Paramonova et al., 2003). In our study, we observed that Put can alleviate the degradation of thylakoid membrane proteins induced by salt stress, and thus making a normal stacking order in the adjacent grana thylakoids (data not published). 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 (Li et al., 2009).

However, few earlier studies showed that high concentrations of polyamines may destroy the structure of chloroplasts which depended on different light conditions. Spd treatment with chloroplast for about 10 s displayed the envelope and the typical dense network of the thylakoid lamellae interspersed with numerous areas of stacked grana (Pjon et al., 1990). After 72 h, the chloroplast envelopes of spermidine-treated leaf disks incubated in the dark and under light conditions, the chloroplast envelope was destroyed by polyamine treatment, but there were distinct differences in the appearance of the chloroplast ultrastructures of dark and light-incubated leaves (Cohen et al., 1979).

2.5 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 subcompartment in which the primary reactions of photosynthesis occur. These reactions are organized in the four major multisubunit protein complexes, photosystem I (PSI), PSII, the ATP-synthase complex and cytochrome b6/f complex (Hippler et al., 2001).

Polyamines such as putrescine, spermidine, spermine, and methylamine interact with protein (H-bonding) through polypeptide C=O, C-N and N-H groups with major perturbations of protein secondary structure as the concentration of amines was raised. It has been shown the chloroplasts and various photosynthetic subcomplexes including thylakoids, LHCII complex and PSII membranes are enriched with polyamines, especially are exclusively rich in PSII core and the reaction center of PSII (Kotzabasis et al. 1993; Navakoudis et al. 2003). Several studies have reported the interaction of polyamines with proteins of photosynthetic apparatus under various environmental factors. However, the action site of polyamines at photosynthetic proteins may vary with polyamine concentration and stress levels. In the alga *S. obliquus* the bound polyamines were found to be associated with both the oligomers and the monomers of LHCII, as well as with the CPs (Kotzabasis et al., 1993). However, the distribution does not reflect a constant pattern: in LHCII

subcomplexes Put and Spm levels fluctuated depending on the light adaptational status of the photosynthetic apparatus. Put and Spm are bound to the photosynthetic complexes, mainly to the LHCII oligomeric and monomeric forms (Navakoudis et al., 2007). It is well documented that the LHCII protein is abundant in thylakoids and its surface is negatively charged (Standfuss et al., 2005). Kirchhoff et al. (2007) have recently shown that incubation of thylakoids under unstacking conditions leads to intermixing and randomization of the protein complexes, accompanied by disconnection of LHCII trimers from PSII and a decreased connectivity between PSIIα centers. Interestingly, exogenously added polyamines can reverse those damaging effects. Thus, there was strong indication that polyamines possessed a pivotal role in photosynthesis.

Chloroplasts also contain high activities of several polyamine biosynthetic enzymes (Borrell et al.1995; Andreadakis and Kotzabasis 1996) and transglutaminase (TGase) catalyzing the covalent binding of polyamines to proteins (Del-Duca et al., 1994; Dondini et al., 2001; Della-Mea et al., 2004). Polyamines can covalently bind with thylakoid membrane proteins under the TGase form of protein- glutamyl-polyamine or protein-glutamyl-polyamines-glutamyl-protein (Dondini et al., 2003), such as D1, D2 protein and cytochrome b6/f, together with the involvement of polyamine, could be important for stabilisation of molecular complexes in the thylakoid membranes of osmotically stressed oat leaves (Besford et al., 1993). 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 (Sobieszczuk-Nowicka et al., 2009).

However, high concentration of polyamines added to submembrane fractions of photosynthetic apparatus causes a strong inhibition of PSII activity (Hamdani et al., 2010). FTIR spectroscopy analysis Spd and Spm at higher cation concentrations (5 and 10 mM), the result showed that the polyamine significant alterations of the thylakoid protein secondary structure with a decrease of the α-helical domains from 47% (uncomplexed PSII) up to 37% (cation complexes) and an increase in the β-sheet structure from 18% up to 29% (Bograh et al., 1997). So far, this specific inhibition mechanism of polyamines is not clear, but it is likely that the proteins were affected by these polycations re either extrinsic polypeptides associated with the oxygen evolving complex or portions of integral polypeptides protruding at the surface of the PSII membranes (Beauchemin et al., 2007).

3. Polyamines and stress photosynthesis

3.1 Salinity

Salt stress causes an initial water-deficit and ion-specific stresses resulting from changes in K^+/Na^+ ratios. Thus, it leads to an increased Na^+ and Cl^- concentrations that decrease plant growth and productivity by disrupting physiological processes, especially photosynthesis (Shu et al., 2010). Salt stress affects photosynthetic efficiency of plant through stomatal limitation and non-stomatal limitations, such as stomatal closure (Meloni et al., 2003), chlorophyll content loss (Sudhir and Murthy, 2004), inhibition of Rubisco activity (Brugnoli and Björkman, 1992; Ziska et al., 1990), and degradation of membrane proteins in photosynthetic apparatus (Khan and Ungar, 1997).

It has been suggested that exogenous application of polyamines can to some extent alleviate salinity-induced decline in photosynthetic efficiency, but this effect strongly depended both on PAs concentrations or types and stress levels (Duan et al., 2008). The maximum quantum efficiency of PSII (Fv/Fm) measured in leaves of salt-stressed cucumber seedlings was not

Species	Types of polyamine-related enzyme	Stress reponse	Measured photosynthetic parameters	Author
Helianthus tuberosus	TGase	Ca and light stimulate	Chlorophyll-a/b antenna complex (LHCII, CP24, CP26 and CP29);large subunit of ribulose-l,5-bisphosphate, carboxylase/oxygenase.	Del-Duca et al. (1994)
Avena sativa	ADC	Osmotic stress	ADC activity in the thylakoids membrane	Borrell et al. (1995)
Dunaliella salina	TGase	Salt stress	Thylakoid photosynthetic complexes and Rubisco	Dondini et al. (2001)
Spinacia oleracea	SAMDC	Chilling	Photoinhibition	He et al.(2002)
Helianthus tuberosus	TGase	Light condition	Light-harvesting complex II thylakoid activity	Della-Mea et al. (2004)
Arabidopsis thaliana	ADC	Salt stress	Chl contents photosynthetic efficiency	Kasinathan, and Wingler (2004)
Barley	TGase	Senescence	Thylakoid fraction	Sobieszczuk-Nowicka et al. (2009)
Zea mays	TGase	Natural condition	Chloroplast transformation; Grana stacking; PSII and PSI	Ioannidis et al. (2009)
Arabidopsis	ADC	Drought	Transpiration rate stomata conductance and aperture	Alcázar et al. (2010)
Nicotiana tabacum	TGase	Oxidative stress	Thylakoid remodelling chloroplast ultrastructure	Ortigosa et al. (2010)
Poncirus trifoliata	ADC	Multiple stresses	Chl contents stomatal density	Wang et al. (2011)

Table 1. High activities of arginine decarboxylase (ADC), adenosylmethionine decarboxylase (SAMDC) and trantaminase (TGase) are involed in regulation of photosynthesis in response to environmental stress. SAMDC is an enzyme that catalyzes the conversion of S-adenosyl methionine to S-adenosylmethioninamine. ADC is an important enzyme responsible for putrscine synthesis. TGase is present in the chloroplasts of higher plants and its activity is modulated by the presence of light.

much influenced by 1mM Spd application, although Spd could ameliorate plant growth and increase net photosynthetic rate (P_N), stomatal conductance (Gs), intercellular CO_2 concentration (Ci), actual efficiency of photosystem II (ΦPSⅡ) and the coefficient of photochemical quenching (qP) of cucumber seedlings subjected to salinity (Li et al., 2007). 10

mM Put also alleviated the reduction of salt stress on P_N. However, Put had no effect on Gs and transpiration rate (Tr), and aggravated the reduction of salt stress on Ci. The result suggested that Put strongly affects photosynthetic apparatus involving in enhancement of photochemical quenching rather than regulation of stomatal closure or opening (Zhang et al., 2009). It was also found that exogenous Put improved the photoadaptability of Scenedesmus by altering the content of LHCII monomers and oligomers and PSI and PSII core proteins in the thylakoid membranes (Navakoudis et al., 2007). In green alga Scenedesmus under high salinity, exogenously applied Put effectively decreased the functional size of the antenna and increased the density of active PSII reaction centers, thereby reducing the salt-induced increase in excitation pressure that may cause oxidative damage to the photosynthetic apparatus (Demetriou et al., 2007). Application of Put, Spd and Spm through the root was also effective in alleviating the salt damage to PSI and PSII activities (Chattopadhayay et al., 2002). However, the effects of polyamines on the salt damage to the structure and functions of the photosynthetic apparatus of higher plants remain until today largely unknown.

Several publications have reported that changes of endogenous polyamine level and forms are involved in regulating the photochemical efficiency of salt-stressed plants, and polyamines metabolism-related enzymes are closely correlated with photosynthesis. Exogenous polyamines increased bound Spd contents in chloroplasts to enhance the photosynthetic capacities of corn suffering salt stress (Liu et al., 2006). Exogenously supplied Put in the salt stressed of green alga cultures was shown to increase the Put/Spm ratio in thylakoids and lead to a decrease of the functional antenna size, both by decreasing the size of LHCII and increasing the quantum yield of PSII primary photochemistry, so that the damaging effects induced by salinity are diminished (Demetriou et al., 2007). In our study, applications of 8 mM Put to salt-stressed plant leaves increased content of endogenous polyamines in the thylakoid membranes and overcame the damaging effects of salt stress on the structure and function of the photosynthetic apparatus, which was associated with an improvement in the actual PSII efficiency (data unpublished).

3.2 Drought stress

Drought is the major abiotic stress factor limiting crop productivity in the worldwide (Wang et al., 2003; Sharp et al., 2004). Under drought stress, plants rapidly close stomata with decrease in leaf water potential, thus leading to a significant inhibition of photosynthesis (Zlatev & Yordanov, 2004). To cope with drought, plants initiate a reprogramming of transcriptional, post-transcriptional and metabolite processes that restricts water loss. Several studies have reported that exogenous PAs application is involved in improving drought tolerance against the perturbation of biochemical processes (Yang et al., 2007; Alcázar et al., 2010), but mechanisms of their action during exogenous application in modulating physiological phenomena especially in photosynthesis is not fully understood (Bae et al., 2008). Both net photosynthetic net (P_N) and water use efficiency (WUE) in leaves of rice subjected to drought stress for 7 days were significantly improved by spraying of plants with 10 μM Put, Spd and Spm solutions, while amongst the PAs, Spm was the most effective (Farooq et al., 2009). Drought resistance of two different tomato cultivars, application of 0.1mM exogenous Spd increased the P_N, Gs and Tr in the tomato seedling leaves of the two tomato cultivars and decreased Ci by preventing stoma closure and stimulating CO_2 uptake during the later period under drought stress (Zhang et al., 2010).

They also observed that the mitigative effects of exogenous Spd on photosynthesis in drought-sensitive cultivars were greater than those in high drought-resistant cultivars. In addition, exogenous Spm to pines under drought caused a decline in transpiration rates, enhanced photosynthesis and promoted osmotic adjustment, which would help to maintain turgor (Anisul et al., 2003; Pang et al., 2007). Base on the above studies, we proposed a model describing the role of PAs on photosynthesis during drought-stress: PAs may modulate the activities of certain ion channels at the plasma membrane and stimulate stomatal closure, which would help to enhance photosynthetic efficiency under drought.

3.3 Temperature stress

Temperature is an important ecological factor for plant growth and development, when the temperature is too high or too low, plant growth will stop (Berry and Raison, 1981). It has been demonstrated that high temperature or low temperature adversely affects plant growth and survival, but the impact of temperature stress on the photosynthetic apparatus is considered to be of particular significance because photosynthesis is often inhibited before other cell functions are impaired (Haldimann and Feller, 2004). Extensive research over the last years has focused on the organization and structure of photosynthetic complexes in response to high temperature or low temperature stress (Santamaria and Vierssen, 1997). There are at least three major stress-sensitive sites in the photosynthetic machinery, the PSII, the ATPase and the carbon assimilation process (Allakhverdiev et al., 2008; Mathur et al., 2011).

Heat-shock often induced changes in polyamine content which can be ascribed as protective responses aimed at structural integrity of membrane and cell walls (Edreva et al., 1998), and tolerant plants are able to increase total spermidine and spermine pools under heat stress (Bouchereau et al., 1999). Increased contents of polyamines can stabilize the structure of thylakoid membranes and prevent chlorophyll loss, playing an important role in the protective response of plants to heat stress. Because of the polycationic nature at a physiological pH, polyamines can bind strongly to cellular constituents such as nucleic acids, proteins and membranes (Childs et al., 2003). Several reports have indicated the involvement of polyamines in regulating heat stress-induced the inhibition of photosynthetic efficiency. Exogenous application of 4 mM Spd improved the plant heat-resistance in two tomato cultivars, and especially in tolerant cultivars have higher ability to hardening and higher resistance to thermal damage of the pigment-protein complexes structure and the activity of PSII than sensitive cultivars (Murkowski, 2001). At filling stage of rice, high temperature stress caused a decline in photosynthetic capacity, chlorophyll content and RuBPc activity of two different resistance cultivars. However this effect was more severe in heat-sensitive variety than in heat-resistant variety, because it is closely related to the heat-resistant cultivars have a high content of endogenous polyamines, especially Put accumulation (Huang et al., 1999). In vivo and in vitro experiment showed that exogenous Spm was effective in alleviating heat damage to the photosynthetic apparatus of cucumber, suggesting that protein complexes in thylakoids were made more stable to heat due to their binding to Spm (Li et al., 2003).

In addition, published data showed that PAs levels increased the tolerance degree of the photosynthetic apparatus to low temperatures in different plant species (Hummel et al., 2004), comparison within species has revealed that cold-tolerant varieties/lines show higher endogenous PA contents in response to low temperature than non-tolerant ones (Zhang et

al., 2009). He et al. (2002) reported that Spd-pretreated cucumber plants had a high Spd content in both leaves and thylakoid membranes during chilling. They also found Spd pretreatment no effect of stomatal conductance in chilled leaves, but alleviated the decline of the maximum efficiency of PSII photochemistry (Fv/Fm), photosynthetic electron transport activity of thylakoids and activity of enzymes in carbon metabolism. Szalai et al. (1997) observed a marked increase of Put and Spd contents together with a significant decline of Fv/Fm in maize leaves during chilling at 5℃. Based on these results, we conclude that the increase of polyamine contents might be important in plant defense to the photosynthetic apparatus against the low-temperature photoinhibition. Biochemical and physico-chemical measurements showed that the response of the photosynthetic apparatus to low temperature is affected by the changes occurring in the pattern of LHCII-associated Put and Spm which adjust the size of LHCII. The decrease of Put/Spm ratio, mainly due to the reduction in the quantity of LHCII-associated Put led to an increase of the LHCII, especially of the oligomeric forms (Sfakianaki et al., 2006), which is consistent with a data obtained for spinach showed that the low temperature induced a decrease in the Put associated to the thylakoid membranes (He et al., 2002). These results suggest the Put/Spm ratio in the structure of the photosynthetic apparatus associated with the photosynthetic efficiency and the maximal photosynthetic rate, although the mechanism by which polyamines contribute to the increasing tolerance to low temperatures is not yet understood.

3.4 UV radiation stress

An important consequence of stratospheric ozone depletion is the increased transmission of solar ultraviolet radiation (UV) to the Earth's lower atmosphere and surface. Effects of enhanced UV radiation (200-320 nm) on plants have been studied on plant morphology, growth and development, and physiology aspects, which have potential adverse effects on agricultural production and natural plant ecosystems (Caldwell et al., 1998; Madronich et al., 1998; An et al., 2000; Zhang et al., 2003; Bjorn et al., 1996). UV radiation may also induce the formation of reactive oxygen species (ROS) in plants, leading to the damage of photosynthetic apparatus, lipid peroxidation and the changes of PAs levels. The potential role of polyamines in maintaining the photochemical efficiency of plants in response to UV stress has become a research focus.

In the leaves of six genotypes of silver birch (Betula pendula Roth) seedlings, PAs analyses showed that the concentrations of Put were increased and Spd decreased with elevated temperature. Therefore, there was a change in polyamine accumulation towards more conjugated forms. It has been suggested that the conformation of antenna proteins is regulated by polyamines, affecting the efficiency of light harvesting. The changes in Put and Spm metabolism implied that the moderately elevated temperature increased photosynthetic antenna size in silve birch leaves (Tegelberg et al., 2008). The functional and biochemiacal aspects of the photosynthetic apparatus in response to UV-B radiation were examined in unicellular oxygenic algae *Scenedesmus obliquus*, which is the first comparative characterization of the photosynthetic responses exhibited by the Wt (wild type) and Wt-lhc (a chlorophyll b-less mutant) mutant to UV-B irradiation with emphasis on the response of polyamines and xanthophylls (Sfichi-Duke et al., 2008). The results showed that light stress led to an 204% increased of Spm (which could positively regulate antenna size) and a threefold decrease in Put/Spm ratio. The attachment of Spm to thylakoids could be of structural or functional importance. Along with xanthophylls, polyamines at the LHCII level

are more sensitive to UV-B stress than xanthophylls and their responsiveness is abolished in Chl b-less mutants. The tobacco cultivars Bel B and Bel W3 were employed to describe possible protective functions of polyamines against UV-B radiation in sun light simulators (GSF/Munich) with natural diurnal fluctuations of simulated UV-B (Lütz et al., 2005). The results indicated that an increase of PAs, especially of Put level, in thylakoid membranes upon elevated UV-B exposure comprises one of the primary protective mechanisms in the photosynthetic apparatus of the tobacco variety Bel B against UV-B radiation. In addition, the sensitivity to UV-B of Bel W3 (sensitive to ozone) is attributed to its incapability to enhance Put level in thylakoid membranes. After prolongation of UV-B exposure, when endogenous plant balances are being gradually restored, due to secondary responses, (e.g., biosynthesis of carotenoids and of additional flavonoids) and the plant is adapting to the altered environmental conditions, the the PAs level is being reduced. Unal et al.(2007) repoted that under exposure to UV-A for 24 and 48h, the photosynthetic quantum yield ratio of Physcia semipinnata decreased, while that of 1mM polyamine treated were not influenced. It was also found that exogenously added Spd had higher Chla content than Spm and Put added samples. By exposure of the samples with polyamines before the UV-A treatment for 48h, MDA contents was found lower than control group and other groups. These data supported that polyamines, especially Spd and Spm, would play a role in protecting Chl a content, protein content and decreasing lipid peioxidation. This is in agreement with the report of Kramer et al. (1991) whose found membrane lipid may be a target of UV-B damage and polyamine accumulation in response to UV-B radiation stress is consistent with similar reaponses to other environmental stressors. Smith et al. (2001) investigated the influence of UV-B radiation on the UV-B sensitive legume *Phaseolus vulgaris* L. "Top Crop" over a two-week period. Total free polyamines showed marked decreases in response to UV-B radiation, primarily due to a decrease in Put, which was correlated with UV-B induced chlorophyll loss. Kramer et al. (1992) reported that photosynthetically active radiation (PAR) had a large effect on polyamine levels in leaves, with higher levels of Put and Spd observed at 600 than at 300 μmol m^{-2} s^{-1} in both cultivars (UV-B-sensitive and–insensitive cultivars). The results indicated that the inhibition of UV-B stress by high PAR may involve polyamine accumulation.

The sensitivity of the photosynthetic apparatus to UV-B irradiation was studied in cultures of unicellular green alga *Scenedesmus obliquus* incubated in low light (LL) and high light (HL) conditions, treated or not with exogenous polyamines. UV-B radiation induces a decrease in the thylakoid-associated Put and an increase in Spm, so that the reduction of Put/Spm ratio leads to the increase of light-harvesting complex II (LHCII) size per active reaction center and, consequently, the amplification of UV-B effects of the photosynthetic apparatus. The separation of oligomeric and monomeric froms of LHCII from isolated thylakoids showed that UV-B induces an increase in the oligomeric forms of LHCII, which was more intense in LL than in HL. By manipulating the LHCII size with exogenous polyamines, the sensitivity degree of the photosynthetic apparatus to UV-B changed significantly. Specifically, the addition of Put decreased highly the sensitivity of LL culture to UV-B because of the inhibitory effect of Put on the LHCII size increasing, wheres the addition of Spm enhanced the UV-B injury induced in HL culture because of the increasing of LHCII size (Sfichi et al., 2004). Zacchini et al. (2004) reported that the put content in tobacco was enhanced, compared with control, in upper layers of calli 6 h after UV-C high dose stress and decreased 24 and 48 h after irradiation, though remained statistically higher than control.

No differences between control and UV-irradiated calli were detected in lower layers. Spermidine and spermine were not affected by UV treatment.

3.5 Hypoxia stress

In natural conditions, flooding, excessive irrigation and soil compaction extremely lead to oxygen deficiency in the root-zone of plant, thus causing to hypoxia stress (Drew, 1997). Hypoxia stress is one of an important environmental factor inhibits plant growth and yield (Avijie et al., 2002). Previous several studies have been shown that suitable concentration of exogenous polyamines could alleviate hypoxia stress-induced physiological damage and improve photochemical efficiency of plants (Vigne and Frelin, 2008). Zhou et al. (2006) demonstrated application of exogenous polyamines to some extent increased net photosynthetic rate (P_N) and water use efficiency (WUE) in cucumber leaves. Shi et al. (2009) also observed that exogenous Put alleviated the reduction of P_N, Gs, Ci of cucumber subjected to root-zone hypoxia through enhancing the actual and maximal nitrate reductase activities. Application of exogenous 0.05 mM Spd added to the hypoxia nutrient solutions significantly suppressed the accumulation and insoluble bound Put in roots and leaves of cucumber seedlings, which was associated with a decreased in dissipation energy (NPQ) and xanthophylls de-epoxidation state (DEPS) during hypoxia stress, while Spd enhanced maximal photochemical efficiency (Fv/Fm), PSII photochemistry rate (ΦPSII) and P_N (Jia, 2009). These results implied that exogenous polyamines increased photosynthetic capacity might be involved in regulating changes of endogenous polyamine contents in the chloroplasts, thus enhancement of root-zone hypoxia tolerance.

3.6 Oxidative stress

Oxidative stress has been postulated, years ago, to be a causal factor in responses to environmental stresses (Velikova et al., 2000; Patil et al., 2007). The basic tenet of this hypothesis is that the stress-associated decline in the functional capacity of biological systems is primarily due to the accumulation of irreparable oxidative molecular damage (Sohal et al., 1995). Adverse environmental stresses induced a decrease in photosynthetic activity which often associated with the oxidative stress (Krause, 1994). It has been shown that plant could overcome the effect of the oxidative stress and sustain photosynthetic efficiency that may be related to the scavenging of stress-induced toxic oxygen species, such as hydrogen peroxide (H_2O_2), hydroxyl radical (OH$\cdot$) and superoxide radical ($O_2\cdot^-$) (Sopory et al., 1990).

Polyamines (PAs) are regarded as a new class of growth substances and are also well known for their positive effects on the photosynthetic efficiency under various stress conditions due to their acid neutralizing and antioxidant properties, as well as to their membrane and cell wall stabilizing abilities (He et al., 2002; Mapelli et al., 2008; Zhao and Yang, 2008). Exogenous application of spermidine (Spd) could alleviate salt-induced membrane injury of chloroplast by increasing the active oxygen scavenging ability. The activities of superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR), the contents of ascorbic acid (AsA), Car and glutathione reduced form (GSH), and the ratios of GSH/GSSG in chloroplasts were increased, which increased the salinity tolerance of the photosynthetic apparatus in cucumber seedlings (Duan et al., 2008a; Duan et al., 2009b). Pretreatment with Spd markedly reduced lipid peroxidation and membrane relative permeability in wheat leaves under water stress (Duan et al., 2006). They found that Spd

also improved the transcription of PSII genes and translation of the corresponding proteins, which sustains a higher activity in PSII during water stress. Yiu et al. (2009) showed that 2 mM putrescine (Put) pre-treatment confers flooding tolerance to the photosynthetic efficiency of welsh onion plants, probably through inducing the activities of various anti-oxidative systems. It has been shown that lipid peroxidation levels were significantly decreased by PAs treated with Physcia semipinnata during the exposure to UV-A (Unal et al., 2008). Among the three polyamines, Spm-treated samples had lower concentration of MDA and higher in the amount of chlorophyll a levels than spd-and put-treated samples. These results indicate that polyamines may protect photosystem II from oxidative stress.

The mechanistic details of PAs effects have not been clarified, although a proposed mechanism is based on PAs neutralizing harmful ROS in tissues or cells and inducing the reorganization of the photosynthetic apparatus. Several results have confirmed that the increase in intra-cellular polyamine content or polyamine metabolism related enzyme activity played an important role in photosynthesis of plants and in oxidative stress resistance (Dondini et al., 2001; Cochòn et al., 2007; Demetriou et al., 2007). Polyamines and especially the thylakoid-associated polyamines play a decisive role in protecting photosynthetic apparatus against oxidative stress. He et al. (2008) found that Put induced the changes of endogenous polyamines in the photosynthetic apparatus to some extent, might be involved in the reduction of H_2O_2 contents and membrane lipid peroxidation under salt stress. This result is supported by our experiments that Put reduced the number of plastoglobuli resulting from gradual thylakoid membrane degradation induced by salinity (Unpublished data). It has been suggested that transglutaminase (chlTGZ) plays an important functional role in the formation of grana stacks, probably due to antenna protein polyaminylation (Ioannidis et al., 2009). Recently, in the transplastomic tobacco young leaves, oxidative stress induced the over-expression of chlTGZ in the tobacco chloroplasts seems to be related to polyaminylation of antenna proteins and thylakoid remodelling, the extended effect of this over-expression seems to induce an imbalance between capture and utilization of light in photosynthesis, changes in the photosynthetic electron transport chain and increasing oxidative risk (Ortigosa et al., 2010).

Species	PAs type	PAs dosage /conce-ntration	Organ	Mode of PAs treatment	Stress	Measured photosynthetic parameters	Author
Oryza sativa Triticumae stivum	Spd Spm	10 mM 10 mM	Leaves	Incubation	Normal conditions	Chl content	Cheng and Kao (1983)
Dicotyledo-nous komatsuna	Spd	1 mM	Leaf discs	Incubation	Dark and light conditions	Chl content photosynthetic activity chloroplast ultrastructure	Pjon et al. (1990)
Scenedesmus obliquus	Spm	320 µM	Leaves	Foliar spraying	Natural condition	Protochlorophyllide chlorophyll	Beigbeder and Kotzabasis. (1994)

Species	PAs type	PAs dosage /conce-ntration	Organ	Mode of PAs treatment	Stress	Measured photosynthetic parameters	Author
Spinacea oleracea	Spd Spm	10 µM 0.1mM 1 mM 5 mM 10 mM	PSII	Incubation	Natural condition	FTIR, secondary structure of PSII	Bograh et al.(1997)
Triticum aestivum	Put Spd Spm	10 µM 0.1 mM 0.5 mM	Leaves	Foliar spraying	Yellow rust	Chl contents, chloroplast ultrastructure	Aldesuquy et al.(2000)
Vicia faba	Spd	0.1, 0.5, 1.0, 3.0, 6.0 mM	Leaves	Incubation	Normal conditions	Stomatal movements	Liu et al. (2000)
Lycopersicon esculentum	Spd	4 mM	Roots	Addition to Hoagland nutrient solution	Heat	Fv/Fm, Amax, Rfd	Murkowski (2001)
Triticum aestivum	Put Spd Spm	20 µM 20 µM 20 µM	Leaves	Incubation	Dark conditions	Chl contents PSI, PSII activities	Subhan et al. (2001)
Oryza sativa	Spd Spm	1.0 mM 1.0 mM	Leaves	Root medium	Salt	Total Chl content, PSI activity, PSII activity	Chattopa-dhayay et al. (2002)
Cucumis sativus	Spd	0.5 mM	Leaves	Incubation in the solution (pre-treatment)	Chilling	Chl contents Fv/Fm, qP, qN	He et al. (2002)
Pinus strobus	Spm	10ug/L	Roots	Soaking	Water	P_N, WUE, Tr	Iqbal et al. (2003)
Nicotiana tabacum	Put Spd Spm	1 mM 1 mM 1 mM	Plants	Whole plant spraying	Ozone	P_N, Fv/Fm, Chl contents, chloroplast structure	Navako-udis et al. (2003)
Mesembryan themum crystallinum	Put	1 mM	Plants	Spraying	Salt	Ultrastructure of leaf mesophyll	Paramo-nova et al. (2003)
Mesembryan themum crystallinum	Put	1 mM	Plants	Spraying	Salt	Ultrastructure of chloroplasts	Paramo-nova et al. (2004)

Species	PAs type	PAs dosage /conce- ntration	Organ	Mode of PAs treatment	Stress	Measured photosynthetic parameters	Author
Triticum aestivum	Put Spd Spm	2.5 mM 5 mM 2.5 mM	Seed	Soaking (pre- sowing)	Salt	P_N, Ci, Gs, Tr	Iqbal and Ashraf (2005)
Triticum aestivum	Spd	0.2 mM	PSII	Irrigating or spraying	Water stress	Chlcontents, PSII phothochemical activity	Duan et al. (2006)
Zea mays	Cad, Put Spd, Spm	1 mM 1 mM 1 mM 1 mM	Leaves	Foliar spraying	Salt	P_N, Fv/Fm	Liu et al. (2006)
Cucumis sativus	Put Spd Spm	1 mM 0.5 mM 0.5 mM	Leaves	Foliar spraying	Hypoxia	P_N, Gs, Tr, Ci	Zhou et al. (2006)
Spinacea oleracea	Spd Spm	Millim olar range	PSII	Incubation	Natural condition	Oxygen evolution activity, Fv/Fo,Chl fluorescence decay kinetics Thermoluminescen ce, OJIP	Beauche- mie et al. (2007)
Berley	Cad, Put Spd, Spm	10 μM 10 μM 10 μM	The whole plant	Spraying Whole plants	Salt	The stomata number, stomata index, stomata length, the epidermis cell number, stomata width	Çavuso- glu et al. (2007)
Scenedesmus obliquus	Put	100 mM	Isolated thyla- koids	Medium	Salt	Fluorescence induction, oxygen evolving activity, chlorophyll content	Demetriou et al. (2007)
Nicotiana tabacum	Put Spd Spm	1 mM 0.1 mM 0.05 mM	Leaf discs	Floated in the solutions	Normal conditions	Fv/Fm, PSIIα and PSIIβ photopho- sphorylation oxygen evolution	Ioannidis and Kotzabasis (2007)
Cucumis sativus	Spd	1 mM	Leaves	Foliar spraying	Salt	P_N, Ci, Gs Fv/Fm, qP,ΦPSⅡ	Li et al. (2007)
Green alga	Put	1 mM	Cell	Incubation	Normal conditions	JIP-test parameters LHCIIoligomeric monomeric forms	Navako- udis et al. (2007)

Species	PAs type	PAs dosage /conce-ntration	Organ	Mode of PAs treatment	Stress	Measured photosynthetic parameters	Author
Arabidopsis	Put Spd Spm	1 Mm 1 mM 1 mM	Plants	Addition to wet filter papers	Drought	Chl contents Stomatal status	Yamaguchi et al. (2007)
Cucumis sativus	Spd	0.5mM	Leaves	Foliar spraying	Hypoxia	P_N, Gs, Tr, Ci	Zhou (2007)
Cucumis sativus	Spd	0.1 mM	Roots	Addition to Hoagland nutrient solution	Salt	P_N, Fv/Fm	Duan et al. (2008)
Physcia semipinnata	Put Spd Spm	1 Mm 1 mM 1 mM	Lichen thalli	Incubation	UV-A	Chla content, Fv/Fm	Unal et al. (2008)
Cucumis sativus	Spd	0.1 mM	Roots	Addition to nutrient solution	Salt	P_N	Duan JJ (2009)
Cucumis sativus	Spd	0.1 mM	Roots	Addition to nutrient solution	Salt	P_N	Duan JJ (2009)
Cucumis sativus	Spd	0.1 mM	Roots	Addition to Hoagland nutrient solution	Salt	P_N	Duan JJ (2009)
Oryza sativa	Put Spd Spm	10 µM 10 µM 10 µM	Whole plants	Seed soaking	Drought	P_N,Gs, Tr, WUE,	Farooq et al. (2009)
Cucumis sativus	Spd	0.05 mM	Roots	Addition to Hoagland nutrient solution	Hypoxia	P_N, Ci, Gs, Tr Fv/Fm, qP, qN ΦPSII, AQY	Jia (2009)
Cucumis sativus	Put	0.5 mM	Roots	Addition to nutrient solution	Hypoxia	P_N, Ci, Gs, Tr Vcyt, Valt	Shi et al. (2009)

Species	PAs type	PAs dosage /conce-ntration	Organ	Mode of PAs treatment	Stress	Measured photosynthetic parameters	Author
Citrus	Spm	1 mM	Leaves	Foliar spraying (pre-treatment)	Dehydra-tion	Stomatal closure/ opening	Shi et al. (2010)
Welsh onion	Put	1,2, 3mM	Plants	Applied to the substrate surface	Flood	Chl contents Fv/Fm	Yiu et al. (2009)
Cucumis sativus	Put	10mM	Leaves	Foliar spraying	Salt	Chl contents, P_N ,Gs, Tr, Ci, qP Fv/Fm, ΦPSII, NPQ	Zhang et al. (2009)
Cowpea cultivar	Spd	1 mM	Leaves	Foliar spraying	Cinnamic acid	Fv/Fm, ΦPSⅡ Rubisco activity	Huang and Bie (2010)
Lactuca sativus	Spm	0.2∼2 mM	Leaves /Leaf discs	Spraying/ Incubation	Sene-scence	Chl contents light-harvesting complexes	Serafini-Fracassini et al. (2010.)
Cucumis sativus	Put	8 mM	Leaves	Foliar spraying	Salt	Fv/Fm, qP, NPQ ΦPSII, rETR	Shu et al. (2010)
Lycopersicon esculentum	Spd	0.1mM	Leaves	Foliar spraying	Drought	P_N, Gs, Tr, Ci	Zhang et al.(2010)
Cucumis Sativus	Spd	0.1mM	Roots	Addition to Hoagland nutrient solution	Salt	P_N, Gs, Ci, Tr, total soluble sugar, sucrose, starch	Chen (2011)

Table 2. Effects of exogenous polyamines (Cad, Put, Spd, Spm) on various photosynthetic parameters of plants in response to stress and non-stress conditions. Chl, chlorophyll; P_N, net photosynthetic rate; Ci, intercellular CO_2; Gs, stomatal conductance; Tr, transpiration rate; WUE, water use efficiency; Fv/Fm, maximum quantum efficiency of photosystem II; Amax, area above the fluorescence induction curve; Rfd, informs about the interaction and equilibrium between primary photosynthetic reactions and dark enzymatic reactions; qP, photochemical quenching; qN, non-photochemical quenching; PSI, photosystem I; PSII, photosystem II; ΦPSII, actual photochemical efficiency; AQY, apparent quantum efficiency; Vcyt, cytochrome; Valt, alternative respiration; Rubisco, ribulose-1,5-bisphospate carboxylase/oxygenase

4. Conclusion

From the published literature, it can be deduced that PAs play an important role in wide spectrum of physiological processes such as cell division, dormancy breaking of tubers and

germination of seeds, stimulation, and development of flower buds and fruits, somatic embryogenesis, differentiation and plant morphogenesis, signal transduction and in the protection of the photosynthetic apparatus. Although considerable evidence indicates that PAs exhibits various positive effects on photosynthetic processes of plant in response to abiotic stresses (Table 2), their precise role in these specific processes is still far from being complete. So far, it seems that one of the modes of PAs action in the regulation of photosynthesis under environmental stresses is probably by reducing the production of free radicals, scavenging the free radicals and/or involved in activation of expression of genes encoding antioxidant enzymes. On the other hand, we can also speculate that conjugated PAs play an important role in the protection of related proteins in the photosynthetic apparatus. The mechanism of their action probably involves direct binding of PAs to the extrinsic proteins and the hydrophilic portions of intrinsic polypeptides of PSII through electrostatic interaction due to their poly-cationic properties, and the poly-cationic selectivity effect in decreasing order is $Spm^{4+} > Spd^{3+} > Put^{2+}$. This electrostatic interaction could provide some stability to the conformation of thylakoid proteins against various stresses and consequently help in maintaining the photosynthetic activity. In addition, the biological functions of PAs on photosynthesis may be also as a signal component to cascade with other growth regulator or hormone. In order to better elucidate the role of PAs in the photosynthesis of plants response to abiotic stress, application of advanced molecular biology and proteomic approaches will help elucidate the mechanisms of PAs in particular improvement of photochemical efficiency in plant processes involved in stress tolerance.

5. Acknowledgement

6. References

Alcázar, R.; Planas, J. Saxena, T. Zarza, X. Bortolotti, C. Cuevas, J. Bitrián, M. Tiburcio, AF. & Altabella, T. (2010). Putrescine accumulation confers drought tolerance in transgenic arabidopsis plants over-expressing the homologous *Arginine decarboxylase* 2 gene. *Plant Physiology and Biochemistry,* 48: 547–552.

Aldesuquy, HS.; Abdel-Fattah, GM. & Baka, ZA. (2000). Changes in chlorophyll, polyamines and chloroplast ultrastructure of puccinia striiformis induced 'green islands' on detached leaves of *Triticum aestivum. Plant Physiologyand Biochemistry,* 38: 613−620.

Allakhverdiev, S.; Kreslavski, V. Klimov, V. Los, D. Carpentier, R. & Mohanty, P. (2008). Heat stress: an overview of molecular responses in photosynthesis, *Photosynthesis Research,* 98: 541–550.

Andreadakis, A. & Kotzabasis, K. (1996). Changes in the biosynthesis and catabolism of polyamines in isolated plastids during chloroplast photodevelopment. *Journal of Photochemistry and Photobiology B: Biology,* 33: 163−170.

Anisul, IM.; Blake, TJ. Kocacinar, F. & Lada, R. (2003). Ambiol, spermine, and aminoethoxyvinylglycine prevent water stress and protect membranes in *Pius strobes* L.under droght. *Tresss,* 17: 278–284.

Assmann, SM. (1993). Signal transduction in guard cells. *Annual Review of Cell and Developmental Bioogyl,* 9: 345–375.

Avijie, D.; Uehimiya, H. & Das, A. (2002). Oxygen stress and adaptation of semi-aquatic plant: Rice (*Oryza sariva*). *Journal of Plant Research,* 115: 315–320.

Bae, HH.; Kim, SH. Kim, MS. Sicher, RC. Lary, D. Strem, MD. Natarajan, S. & Bailey, BA. (2008). The drought response of *Theobroma cacao* (cacao) and the regulation of genes involved in polyamine biosynthesis by drought and other stresses. *Plant Physiology and Biochemistry,* 46: 174–188.

Beauchemin, R.; Gauthier, A. Harnois, J. Boisvert, S. Govindachary, S. & Carpentier, R. (2007). Spermine and spermidine inhibition of photosystem II: Disassembly of the oxygen evolving complex and consequent perturbation in electron donation from Tyr_Z to $P680^+$ and the quinone acceptors Q_A^- to Q_B. *Biochimica et Biophysica Acta,* 1767: 905– 912.

Beigbeder, A. & Kotzabasis, K. (1994). The influence of exogenously supplied spermine on protochlorophyllide and chlorophyll biosynthesis. *Journal of Photochemistry and Photobiology B: Biology,* 23: 201–206.

Beigbeder, A.; Vavadakis, M. Navakoudis, E. & Kotzabasis, K. (1995). Influence of polyamine inhibitors on light-independent and light-dependent chlorophyll biosynthesis and on the photosynthetic rate. *Journal of Photochemistry and Photobiology B: Biology,* 28: 235-242.

Berry, JA. & Raison, JK. (1981). Responses of macrophytes to temperature. In: Lange, OL.; Nobcl, PS. Osmond, CB. Ziegler, H. (Eds.), Physiological Plant Ecology I. Responses to the Physical Environment. Springer-Verlag, New York, pp. 277–337.

Birecka, H.; Dinolfo, TE. Martin, WB. & Frohlich, MW. (1984). Polyamines and leaf senescence in pyrrolizidine-bearing heliotropium plants. *Phytochemistry,* 23: 991–997.

Bograh, A.; Gingras, Y. Tajmir-Riahi, HA. & Carpentier, R. (1997). The effects of spermine and spermidine on the structure of photosystem II proteins in relation to inhibition of electron transport. *Federation of European Biochemical Societies,* 402: 41–44.

Borrell, A.; Culianez-Macia, FA. Altabella, T. Besford, RT. Flores, D. & Tiburcio, AF. (1995). Arginine decarboxylase is localized in chloroplasts. *Plant Physiology,* 109: 771–776.

Bouchereau, A.; Azis, A. Larher, F. & Martin-Tanguy, J. (1999). Polyamines and environmental challenges: recent development. *Plant Science,* 103–125.

Bright, J.; Desikan, R. Hancock, JT. Weir, LS. & Neill, SJ. (2006). ABA-induced NO generation and stomatal closure in Arabidopsis are dependent on H_2O_2 synthesis. *The Plant Journal,* 45: 113–122.

Brugnoli, E. Björkman, O. (1992). Growth of cotton under continuous salinity stress: influence on allocation pattern, stomatal and non-stomatal components of photosynthesis and dissipation of excess light energy. *Planta,* 187: 335–347.

Çavuşoğlu, K.; Kılıç, S. & Kabar K. (2007). Effects of pretreatments of some growth regulators on the stomata movements of barley seedlings grown under saline (NaCl) conditions. *Plant, Soil and Environment,* 53: 524–528.

Chattopadhayay, MK.; Tiwari, BS. Chattopadhayay, G. Bose, A. Sengupta, DN. & Ghosh, B. (2002). Protective role of exogenous polyamines on salinity-stressed rice (*Oryza sativa*) plants. *Physiologia Plantarum*, 116: 192–199.

Chen, LF.; Lu, W. Sun, J. Guo, SR. Zhang, ZX. & Yang, YJ. (2011). Effects of exogenous spermidine on photosynthesis and carbohydrate accumulation in roots and leaves of cucumber (*Cucumis sativus* L.) seedlings under salt stress. *J Nanjing Agricul University,* 34(3): 31–36.

Cheng, SH. & Kao, CH. (1983). Localized effect of polyamines on chlorophyll loss. *Plant and Cell Physiology,* 24: 1465–1467.

Childs, AC.; Mehta, DJ. & Gerner, EW. (2003). Polyamine-dependent gene expression. *Cellular and Molecular Life Sciences,* 60: 1394–1406.

Cochòn, AC.; Della Penna, AB. Kristoff, G. Piol, MN. San Martín de Viale, LC. & Guerrero, NR. (2007). Differential effects of paraquat on oxidative stress parameters and polyamine levels in two freshwater invertebrates. *Ecotoxicology and Environmental Safety,* 68: 286–292.

Del-Duca, S.; Tidu, V. Bassi, R. Esposito, C. & Serafini-Fracassini, D. (1994). Identification of chlorophyll-a/b proteins as substrates of transglutaminase activity in isolated chloroplasts of Helianthus tuberosus L. *Planta,* 193: 283–289.

Della-Mea, M.; Di-Sandro, A. Dondini, L. Del-Duca, S. Vantini, F. Bergamini, C. Bassi, R. & Serafini-Fracassini, D. (2004). A zea mays 39 kDa thylakoid transglutaminase catalyses the modification by polyamines of light harvesting complex II by polyamines in a light-dependent way. *Planta,* 219: 754–764.

Demetriou, G.; Neonaki, C. Navakoudis, E. & Kotzabasis, K. (2007). Salt stress impact on the molecular structure and function of the photosynthetic apparatus-The protective role of polyamines. *Biochimica et Biophysica Acta,* 1767: 272–280.

Dondini, L.; Bonazzi, S. Del-Duca, S. Bregoli, AM. & Serafini-Fracassini, D. (2001). Acclimation of chloroplast transglutaminase to high NaCl concentration in a polyamine-deficient variant strain of *Dunaliella salina* and its wild type. *Journal of Plant Physiology,* 158: 185–197.

Drew, M. (1997). Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. *Annual. Review of Plant Physiology and Plant Molecular Biology,* 48: 223–250.

Duan, HG.; Shu, Y. Liu, DH. Qin, DH. Liang, HG. & Lin, HH. (2006). Effects of Exogenous spermidine on photosystem II of wheat seedlings under water stress. *Joumal of Integrative Plant Biology,* 48: 920–927.

Duan, JJ.; Guo, SR. Kang, YY. Zhou, GX. & Liu, XE. (2009). Effects of exogenous spermidine on active oxygen scavenging system and bound polyamine contents in chloroplasts of cucumber under salt stress. *Acta Ecologica Sinica,* 29: 0653–0661.

Duan, JJ.; Li, J. Guo, SR. & Kang, YY. (2008). Exogenous spermidine affects polyamine metabolism in salinity-stressed *Cucumis sativus* roots and enhances short-term salinity tolerance. *Journal of Plant Physiology,* 165: 1620–1635.

Edreva, A.; Yordanov, I. Kardijeva, R. & Gesheva, E. Heat shock responses of bean plants: involvement of free radicals, antioxidants and free radical/active oxygen scavenging systems. *Biology of Plants,* 41: 185–191.

Farooq, M.; Wahid, A. & Lee, DJ. (2009). Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. *Acta Physiologiae Plantarum,* 31:937–945.

Haldimann, P. & Feller, U. (2004). Inhibition of photosynthesis by high temperature in oak (*Quercus pubescens*) leaves grown under natural conditions closely

correlates with a reversible heat-dependent reduction of the activation state of ribulose-1, 5-bisphosphate carboxylase/oxygenase. *Plant, Cell and Environment,* 27: 1169–1183.

Hamdani, S.; Yaakoubi, H. & Carpentier, R. (2010). Polyamines interaction with thylakoid proteins during stress. *Journal of Photochemistry and Photobiology B: Biology,* 11:1011−1344.

He, LX.; Ban, Y. Inoue, H. Matsuda, N. Liu, JH. & Moriguchi, T. (2008). Enhancement of spermidine content and antioxidant capacity in transgenic pear shoots overexpressing apple *spermidine synthase* in response to salinity and hyperosmosis. *Phytochemistry,* 69: 2133–2141.

He, LX.; Nada, K. Kasukabe, Y. & Tachibana, S. (2002). Enhanced susceptibility of photosynthesis to low-temperature photoinhibition due to interruption of chill-induced increase of S-adenosylmethionice decarboxylase activity in leaves of spinach (*Spinacia oleracea* L.). *Plant Cell Physiology,* 43: 196–206.

Hetherington, AM. & Woodward, FI. (2003). The role of stomata in sensing and driving environmental change. *Nature,* 424:21.

Hippler, M.; Klein, J. Fink, A. Allinger, T. & Hoerth, P. (2001). Towards functional proteomics of membrane protein complexes: analysis of thylakoid membranes from *chlamydomonas reinhardtii. The Plant Journal,* 28: 595−606.

Huang, XX. & Bie, ZL. (2010).Cinnamic acid-inhibited ribulose-1,5-bisphosphate carboxylase activity is mediated through decreased spermine and changes in the ratio of polyamines in cowpea. *Journal of Plant Physiology,* 167:47–53.

Huang, YJ.; Luo, YF. Huang, XZ. Rao, ZM. & Liu, YB. (1999). Varietal difference of heat tolerance at grain filling stage and its relationship to photosynthetic characteristics and endogenous polyamine of flag leaf in rice. *Chinese Journal of Rice Science,* 13: 205–210.

Hummel, A.; Amrani, EI. Gouesbet, G. Hennion, F. & Couée, I. (2004). Involvement of polyamines in the interacting effects of low temperature and mineral supply on *pringlea antiscorbutica* (kerguelen cabbage) seedlings. *Journal of Experimental Botany,* 55: 1125–1134.

Ioannidis, NE. & Kotzabasis, K. (2007). Effects of polyamines on the functionality of photosynthetic membrane in vivo and in vitro. *Biochimica et Biophysica Acta,* 1767: 1372–1382.

Ioannidis, NE.; Ortigosa, SM. Veramendi, J. Pintó-Marijuan, M. Fleck, I. Carvajal, P. Kotzabasis K. Santos, M. & Torné, JM. (2009). Remodeling of tobacco thylakoids by over-expression of maize plastidial transglutaminase. *Biochimica et Biophysica Acta-Bioenergetics,* 1787: 1215–1222.

Iqbal, M. & Ashraf, M. (2005). Changes in growth, photosynthetic capacity and ionic relation in spring wheat (*Triticum aestivum* L.) due to pre-sowing seed treatment with polyamines. *Plant Growth Regulation,* 46:19–30.

Jia, YX. (2009). Studies on physiological regulation function of exogenous spermidine on cucumber seedlings tolerance to hypoxia. [Degree]. Nanjing: *Nanjing Agricultural University,* 1–125.

Kasinathan, V. & Wingler, A. (2004). Effect of reduced arginine decarboxylase activity on salt tolerance and on polyamine formation during salt stress in Arabidopsis thaliana. *Physiologia Plantarum,* 121: 101–107.

Kaur-Sawhney, R.; Tiburcio, AF. Altabella, T. & Galston, AW. (2003). Polyamines in plants: An overview. *Journal of Cell and Molecular Biology,* 2: 1–12.

Khan, MA. Ungar, IA. (1997). Effect of thermoperiod on recovery of seed germination of halophytes from saline conditions. *America. Jourbal of Botany*, 84: 279–283.

Kirchhoff, H.; Haase, W. Haferkamp, S. Schoot, T. Borinski, M. Kubitscheck, U. & Rögner, M. (2007). Structural and functional self-organization of photosystem II in grana thylakoids. *Biochimica et Biophysica Acta-Bioenergetics*, 1767: 1180–1188.

Kirchhoff, H.; Hinz, HJ. & Rösgen, J. (2003). Aggregation and fluorescence quenching of chlorophyll a of the light-harvesting complex II from spinach in vitro. *Biochimica et Biophysica Acta-Bioenergetics*, 1606:105–116.

Kotzabasis, K.; Fotinou, C. Roubelakis-Angelaki, KA. & Ghanotakis, D. (1993). Polyamines in the photosynthetic apparatus. *Photosynthesis Research*, 38: 83–88.

Krause, GH. (1994). The role of oxygen in photoinhibition of photosynthesis. In C.H. Foyer and P.M. Mullineaux, (eds), Causes of photooxidative stress and amelioraton of defense systems in plants, CRC Press, Boca Raton, pp: 43–76.

Li, J.; Gao, XH. Guo, SR. Zhang, RH. & Wang, X. (2007). Effects of exogenous spermidine on photosynthesis of salt-stressed *cuellmis sativus* seedlings. *Chinese Journal of Ecology*, 26(10): 1595–1599.

Li, Y.; Shi, GX. Wang, HX. Zhao, J. & Yuan, QH. (2009). Exogenous spermidine can mitigate the poison of cadmium in nymphoides peltatum. *Chinese Bulletin of Botany*, 44: 571−577.

Li, ZJ.; Nada, K. & Tachibana, S. (2003). High-temperature-induced alteration of ABA and polyamine contents in leaves and its implication in thermal acclimation of photosynthesis in cucumber (Cucumis sativas L.). *Journal of the Japanese Society for Horticultural Science*, 72: 393–401.

Liu, J.; Zhou, YF. Zhang, WH. & Liu, YL. (2006). Effects of exogenous polyamines on chloroplast-bound polymine content and photosynthesis of corn suffering salt stress. *Acta Bot. Borea1.- Occident. Sin*, 26(2): 0254–0258.

Liu, K.; Fu, HH. Bei, QX & Luan, S. (2000). Inward potassium channel in guard cells as a target for polyamine regulation of stomatal movements. *Plant Physiology*, 124:1315–1325.

MacRobbie, EAC. (1997). Signaling in guard cells and regulation of ion channel activity. *Journal of Experimental. Botany*, 48: 515–528.

Mansfield, TA.; Hetherington, AM. & Atkinson, CJ. (1990). Some current aspects of stomatal physiology. *Annual Reviewof Plant Physiology and Plant Molecular Biology*, 41: 55–75

Mapelli, S.; Brambilla, IM. Radyukina, NL. Ivanov, YuV. Kartashov, AV. Reggiani, R. & Kuznetsov, VlV. (2008). Free and bound polyamines changes in different plants as a consequence of UV-B light irradiation. *General and Applied Plant physiology*, 34: 55–66.

Mathur, S.; Allakhverdiev, SI. & Jajoo, A. (2011). Analysis of high temperature stress on the dynamics of antenna size and reducing side heterogeneity of Photosystem II in wheat leaves (Triticum aestivum). *Biochimica et Biophysica Acta*, 1807: 22–29.

Meloni, DA. Oliva, MA. Martinez, CA. Cambraia, J. (2003). Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. *Environmental and Experimental Botany*, 49: 69–76.

Meskauskiene, R.; Nater, M. Goslings, D. Kessler, F. Camp, R. & Apel, K. (2001). A negative regulator of chlorophyll biosynthesis in arabidopsis thaliana. *PNAS*, 98:12826–12831.

Munzi, S.; Pirintsos, SA. & Loppi, S. (2009). Chlorophyll degradation and inhibition of polyamine biosynthesis in the lichen *xanthoria parietina* under nitrogen stress. *Ecotoxicology and Environmental Safety*, 72: 281–285.

Murkowski, A. (2001). Heat stress and spermidine: effect on chlorophyll fluorescence in tomato plants. *Biologia plantarum,* 44: 53–57.

Navakoudis, E.; Lütz, C. Langebartels, C. Lütz-Meindl, U. & Kotzabasis, K. (2003). Ozone impact on the photosynthetic apparatus and the protective role of polyamines. *Biochimica et Biophysica Acta-Bioenergetics,* 1621: 160–169.

Navakoudis, E.; Vrentzou, K. & Kotzabasis, K. (2007). A polyamine-and LHCII protease activity-based mechanism regulates the plasticity and adaptation status of the photosynthetic apparatus. *Biochimica et Biophysica Acta-Bioenergetics,* 1767: 261– 271.

Ortigosa, SM.; Díaz-Vivancos, P. Clemente-Moreno, MJ. Pintò-Marijuan, M. Fleck, I. Veramendi, J. Santos, M. Hernandez, J. & Torné, JM. (2010). Oxidative stress induced in tobacco leaves by chloroplast over-expression of maize plastidial transglutaminase. *Planta,* 232: 593–605.

Pang, XM.; Zhang, ZY. Wen, XP. Ban, Y. & Moriguchi, T. (2007). Polyamine, all-purpose players in response to environment stresses in plants. *Plant Stress,* 1(2): 173–188.

Paramonova, NV.; Shevyakova, NI. Shorina, MV. Stetsenko, LA. Rakitin, VY. & Kuznetsov, VIV. (2003). The effect of putrescine on the apoplast ultrastructure in the leaf mesophyll of mesembryanthemum crystallinum L. under salinity stress. *Russian Journal of Plant Physiology,* 50: 661–673.

Paramonova.; NV. Shevyakova, N I. & Kuznetsov, VIV. (2004). Ultrastructure of chloroplasts and their storage inclusions in the primary leaves of Mesembryanthemum crystallinum affected by putrescine and NaCl. *Russian Journal of Plant Physiology,* 51: 86–96.

Parida, AK.; Das, AB. & Mittra, B. (2003). Effects of NaCl stress on the structure, pigment complex composition, and photosynthetic activity of mangrove Bruguiera parviflora chloroplasts. *Photosynthetica,* 41: 191–200.

Patil, SB.; Kodliwadmath, MV. & Kodliwadmath, SM. (2007). Study of oxidative stress and enzymatic antioxidants in normal pregnancy. *Indian Journal of Clinical Biochemistry,* 22: 135–137.

Pei, ZM.; Kuchitsu, K. Ward, JM. Schwarz, M. & Schroeder, L. (1997). Differnential abscisic acid regulation of guard cell slow anion channels in arabidopsis wild-type and abi1 and abi2 mutants. *The Plant Cell, 9*:409–423.

Pjon, CJ.; Kim, SD. & Pak, JY. (1990). Effects of spermidine on chlorophyll content, photosynthetic activity and chloroplast ultrastructure in the dark and under light. *Bot. Mag. Tokyo,* 103: 43–48.

Raschke, K.; Hedrich, R. Reckmann, U. & Schroeder, JI. (1988). Exploring biophysical and biochemical components of the osmotic motor that drives stomatal movements. *Botanica Acta,* 101: 283–294.

Santamaria, L. & Vierssen, WV. (1997). Photosynthetic temperature responses of fresh-and brackish-water macrophytes: a review. *Aquatic Botany,* 58: 135–150.

Serafini-Fracassini, D.; Di Sandro, A. & Del Duca, S. (2010). Spermine delays leaf senescence in Lactuca sativa and prevents the decay of chloroplast photosystems. *Plant Physiology and Biochemistry,* 48:602–611.

Sfakianaki, M.; Sfichi, S. & Kotzabasis, K. (2006). The involvement of LHCII-associated polyamines in the response of the photosynthetic apparatus to low temperature. *Journal of Photochemistry and Photobiology B: Biology,* 84: 181–188.

Sfichi-Duke, L.; Ioannidis, NE. & Kotzabasis, K. (2008). Fast and reversible response of thylakoid-associated polyamines during and after UV-B stress: a comparative study of the wild type and a mutant lacking chlorophyll *b* of unicellular green alga *scenedesmus obliquus*. *Planta,* 228:341–353.

Sharp, RE.; Poroyko, V. Hejlek, LG. Spollen, WG. Springer, GK. Bohnert, HJ. & Nguyen, HT. (2004). Root growth maintenance during water deficits: physiology to functional genomics. *Journal of Experimental Botany,* 55: 2343–2351.

Shi, J.; Fu, XZ. Peng, T. Huang, XS. Fan, QJ & Liu, JH. (2010). Spermine pretreatment confers dehydration tolerance of citrus in vitro plants via modulation of antioxidative capacity and stomatal response. *Tree Physiology,* 30(7): 914–922.

Shi, K.; Gu, M. Yu, HJ. Jiang, YP. Zhou, YH. & Yu, JQ. (2009). Physiological mechanism of putrescine enhancement of root-zone hypoxia tolerance in cucumber plants. *Scientia Agricultura Sinica,* 42:1854–1858.

Shoal, RS.; Agarwal, A. Agarwal, S. & Orr, WC. (1995). Simultaneous overexpression of copper-and zinccontaining superoxide dismutase and catalase retards age-related oxidative damage and increases metabolic potential in *Drosophila melanogaster. The Journal of Biological Chemistry,* 270:15671–15674.

Shu, S.; Sun, J. Guo, SR. Li, J. Liu, CJ. Wang, CY. & Du, CX. (2010). Effects of exogenous putrescine on PSII photochemistry and ion distribution of cucumber seedlings under salt stress. *Acta Horticulturae Sinica,* 37: 1065–1072.

Sobieszczuk-Nowicka, E.; Wieczorek, P. & Legocka ▢J. (2009). Kinetin affects the level of chloroplast polyamines and transglutaminase activity during senescence of barley leaves. *Acta Biochimica Polonica,* 56: 255−259.

Sopory, SK.; Greenberg, BM. Mehta, RA. Edelman, M. Mattoo, AK. (1990). Free radical scavengers inhibit light dependent degradation of the 32-kDa photosystem II reaction center protein. *Z. Naturforsch. C,* 45: 412–417.

Standfuss, J.; Terwisschavan, AC. Lamborghini, M. & Kuehlbrandt, W. (2005). Mechanisms of photoprotection and nonphotochemical quenching in pea light-harvesting complex at 2.5Å resolution. *EMBO J,* 24: 919–928.

Subhan, D. & Murthy, SDS. (2001). Effect of polyamines on chlorophyll and protein contents, photochemical activity, and energy transfer in detached wheat leaves during dark incubation. *Biologia Plantarum,* 44: 529–533.

Sudhir, P. Murthy, SDS. (2004). Effects of salt stress on basic processes of photosynthesis. *Photosynthetica,* 42: 481–486.

Szalai, G.; Janda, T. Bartók, T. & Páldi, E. (1997). Role of light in changes in free amino acid and polyamine contents at chilling temperature in maize (*Zea mays*). *Plant Physiology,* 101: 434–438.

Tiburcio.; AF. Besford, RT. Capell, T. Borrell, A. Tes-tillano, PS. & Risueno, MC. (1994). Mechanisms of polyamine action during senescence responses induced by osmotic stress. *Journal of Experimental Botany,* 45: 1789–1800.

Unal, D.; Tuney, I. & Sukatar, A. (2008). The role of external polyamines on photosynthetic responses, lipid peroxidation, protein and chlorophyll a content under the UV-A (352nm) stress in *physcia semipinnata. Journal of Photochemistry and Photobiology B: Biology,* 90:64–68.

Velikova, V.; Yordanov, I. & Edreva, A. (2000). Oxidative stress and some antioxidant systems in acid rain-treated bean plants-protective role of exogenous polyamines. *Plant Science,* 151: 59–66.

Vigne, P. & Frelin, C. (2008). The role of polyamines in protein-dependent hypoxic tolerance of drosophila. *BMC Physiology,* 1–14.

Wang, W.; Vinocur, B. & Altman, A. (2003). Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta,* 218: 1–14.

Wang, J.; Sun, PP. Chen, CL. Wang, Y. Fu, XZ. & Liu, JH. (2011). An arginine decarboxylase gene *PtADC* from *Poncirus trifoliata* confers abiotic stress tolerance and promotes

primary root growth in Arabidopsis. *Journal of Experimental Botany,* doi:10.1093/jxb/erq463.

Ward, JM.; Pei, ZM. & Schroeder, JI. (1995). Roles of ion channels in initiation of signal transduction in higher plants. *Plant Cell,* 7: 833–844.

Yamaguchi, K.; Takahashi, KY. Berberich, T. Imai, A. Takahashi, T. Michael, AJ. & Kusano, T. (2007). A protective role for the polyamine spermine against drought stress in arabidopsis. *Biochemical and Biophysical Research Communications,* 352: 486–490.

Yang, JC.; Zhang, JH. Liu, K. Wang, ZQ. Liu, LJ. (2007). Involvement of polyamines in the drought resistance of rice. *Journal of Experimental Botany,* 58: 1545–1555.

Yiu, JC.; Juang, LD. Fang, DYT. Liu, CW. & Wu, SJ. (2009). Exogenous putrescine reduces flooding-induced oxidative damage by increasing the antioxidant properties of welsh onion. *Scientia Horticulturae,* 120: 306–314.

Zhang, CM.; Zou, ZR. Huang, Z. & Zhang, ZX. (2010). Effects of exogenous spermidine on photosynthesis of tomato seedlings under drought stress. *Agricultural Research in the Arid Areas,* 3: 182–187.

Zhang, RH.; Li, J. Guo, SR. & Tezuka, T. (2009). Effects of exogenous putrescine on gas-exchange characteristics and chlorophyll fluorescence of NaCl-stressed cucumber seedlings. *Photosynth Research,* 100: 155–162.

Zhang, WP.; Jiang, B. Li, WG. Song, H. Yu, YS. & Chen, JF. (2009). Polyamines enhance chilling tolerance of cucumber (*Cucumis sativus* L.) through modulating antioxidative system. *Scientia Horticulturae,* 122: 200–208.

Zhao, HZ. & Yang, HQ. (2008). Exogenous polyamines alleviate the lipid peroxidation induced by cadmium chloride stress in *Malus hupehensis* Rehd. *Scientia Horticulturae,* 116: 442–447.

Zhou, GX. (2007). Studies on effects of exogenous spermidine on photosynthesis and carbohydrate metabolism in cucumber seedlings under hypoxia stress.[Degree]. Nanjing: *Nanjing Agriculture University,* pp: 1–98.

Zhou, GX.; Guo, SR. & Wang, SP. (2006). Effects of exogenous polyamines on photosynthetic characteristics and membrane lipid peroxidation of cucumis sativas seedlings under hypoxia stress. *Chinese Bulletin of Botany,* 23: 341–347.

Ziska, LH.; Seemann, JR. & DeJong, TM. (1990). Salinity induced limitations on photosynthesis in *Prunus salicina*, a deciduous tree species. *Plant Physiology,* 93: 864–870.

Zlatev, ZS. & Yordanov, IT. (2004). Effects of soil drought on photosynthesis and chlorophyll fluorescence in bean plants. *Bulg. Journal of Plant Physiol,* 30: 3–18.
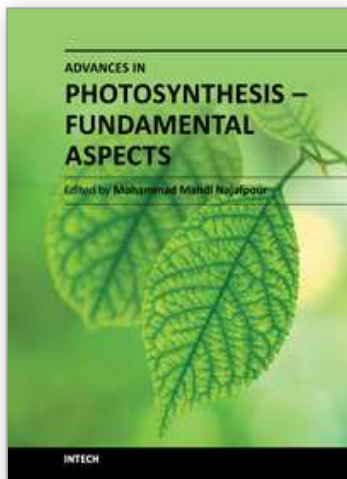
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Photosynthesis is one of the most important reactions on Earth. It is a scientific field that is the topic of many research groups. This book is aimed at providing the fundamental aspects of photosynthesis, and the results collected from different research groups. There are three sections in this book: light and photosynthesis, the path of carbon in photosynthesis, and special topics in photosynthesis. In each section important topics in the subject are discussed and (or) reviewed by experts in each book chapter.

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