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REVIEW

POLYAMINES – POSSIBILITIES FOR APPLICATION TO INCREASE PLANT TOLERANCE AND ADAPTATION CAPACITY TO STRESS

Todorova D.*[*]*, Z. Katerova, V. Alexieva, I. Sergiev

Institute of Plant Physiology and Genetics, Bulgarian Academy of Sciences, Acad. G. Bonchev Str., Bldg. 21, 1113 Sofia, Bulgaria

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Summary: Polyamines are plant growth regulators distributed among all plant species. The major polyamines are diamine putrescine, triamine spermidine and tetraamine spermine. Polyamines are involved in a number of growth and developmental processes, as well as in plant responses to a variety of unfavorable factors. Polyamines can stabilize cell constituents and protect macromolecules from free radicals generated by adverse stress agents. Endogenous polyamines could contribute to plant stress tolerance as part of defense mechanisms or adaptation programs that help plant organism to cope with the negative stress consequences. The current review is focused on the latest investigations regarding the possibilities for exogenous polyamine application to increase plant tolerance and adaptation capacity to diverse abiotic impacts including mineral nutrient deficiency, salinity, water stress, heavy metal toxicity, low and high temperature stresses, UV irradiation, ozone, air pollutants and herbicides as well as to biotic stress factors such as infections with fungal, bacterial and viral pathogens and attacks by herbivorous insects.

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Abbreviations: AscPOA – ascorbate peroxidase; CAT – catalase; PAs – polyamines; PSII – photosystem II; SOD – superoxide dismutase; Spd – spermidine; Spm – spermine; Put – putrescine.

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[*]Corresponding author: dessita@bio21.bas.bg

1. Plant stress and polyamines

Abiotic and biotic stresses cause alterations in the normal physiological processes of all plant organisms, including the economically important crops. Independently of the type of stress, an increased production of reactive oxygen species (ROS) occurs in plants that alter their normal physiological functions, decrease the biosynthetic capacity of plant organisms, and cause damages which may lead to plant death (Ahmad et al., 2008; Gill and Tuteja, 2010b; Potters et al., 2010). The major targets of deleterious ROS action are the cellular macromolecules such as phospholipids, proteins, and nucleic acids. Plant organisms possess a complex antioxidant protective system which, in addition to its role to detoxify the excess of ROS generated during the normal functioning, is actively engaged to cope with destructive effects of the unfavorable environmental conditions.

A significant number of studies provided evidence that endogenous PAs also contribute to plant stress tolerance as a part of defense mechanisms or adaptation programs that help plants to mitigate the negative stress consequences of variety of abiotic stresses. Polyamines are organic nitrogen-containing compounds with low-molecular weight and straight-chain C_3–C_{15} aliphatic structure which includes at least two primary amino groups and one or more internal imino groups (Edreva, 1996; Groppa and Benavides, 2008; Gill and Tuteja, 2010a). The triamine spermidine (Spd), tetraamine spermine (Spm), and their precursor the diamine putrescine (Put) are the major polyamines (PA) widespread in all plant species.

Putrescine

$H_2N(CH_2)_4NH_2$

Spermidine

$H_2N(CH_2)_3NH(CH_2)_4NH_2$

Spermine

$H_2N(CH_2)_3NH(CH_2)_4NH(CH_2)_3NH_2$

Under physiological pH conditions PAs are positively charged and are able to interact with other negatively charged organic molecules like phenolic acids, proteins, phospholipids or nucleic acids. Thus, PAs in higher plants are present in free, soluble conjugated and insoluble bound forms. The interaction with macromolecules and cell constituents permits PAs to contribute to a number of important growth and developmental processes in plants. Additionally, PAs act in concert with light and phytohormones and are considered as plant endogenous growth regulators with hormone-like features. Endogenous PAs possess free radical scavenging properties and antioxidant activity and may confer plant tolerance to different biotic and abiotic stresses (Groppa and Benavides, 2008; Gill and Tuteja, 2010a; Fariduddin et al., 2013) like mineral nutrient deficiency (Wimalasekera et al., 2011; Takahashi et al., 2012), drought, salinity and osmotic stress (Todorova et al., 2008; Alcázar et al., 2011a; Alcazar et al., 2011b; Orsini et al., 2011; Hussain et al., 2011; Wang et al., 2011; Alet et al., 2012), heavy metal toxicity (Kuthanova et al., 2004), low and high temperature stress (Todorova et al., 2003; Todorova et al., 2007; Szalai et al., 2009; Kocsy et al., 2011), herbicides (Cuevas et al., 2004), UV-irradiance (Radyukina et al., 2010; Kondo et al., 2011; Katerova and Todorova 2009, 2011, 2012,), and ozone stress (Iriti and Faoro, 2009), as well as biotic stresses like fungal (Pal et al., 2011), viral (Edreva et al., 2007; Kusano et al., 2008; Bassard et al., 2010), and bacterial infection (Moschou et al., 2009; Gonzalez et al,. 2011). The investigations clearly demonstrate that endogenous PAs play a pivotal role in conferring plant stress tolerance and adaptation potential.

The importance of the problem, as well as the impact of plant stress on the physiological processes and productivity has drawn the attention of a number of investigators to study the possibilities for overcoming the stress consequences by using different substrates with various chemical nature and physiological action. Applied at low doses, they can activate cellular metabolism and increase the physiological activity of plants to mitigate the negative effects of a stressor. In the present review, the possibilities of exogenous PAs to increase plant tolerance and adaptation capacity to stress are discussed.

2. Possibilities for PAs application to alleviate stress injuries

Various metabolic pathways are targets of different stress factors (natural and anthropogenic). Generation of free radicals as a consequence of the stress action is the common physiological response of affected plants. An oxidative attack on membranes leads to fatty acid peroxidation, phospholipid deesterification and subsequent phospholipid degradation (Senaratna et al., 1988). The overproduction of ROS may also cause protein denaturation (Thomashow, 1999; Langridge et al., 2006).

Polyamines are considered to act as free radical scavengers which protect plants against oxidative stress, Spm and Spd being frequently reported to be more effective in this respect than Put (Zheleva et al., 1994; Kurepa et al., 1998; Belle et al., 2004; Velikova et al., 2000; Groppa et al., 2001; Nasrin et al. 2012). In addition to their direct properties as free radical scavengers, PAs have also been reported to stabilize biological membranes, thus maintaining their structural integrity under stress conditions (Velikova et al., 1998; Ndayiragije and Lutts, 2006).

2.1. Abiotic stress

2.1.1. Mineral nutrient deficiency

Since macro- and micronutrients are of paramount importance for normal plant growth and development, the insufficient mineral nutrition affects all physiological processes in plants. Tachimoto et al. (1992) showed that the growth of cultures of *Lemna paucicostala* 6746 and *Lemna gibba* G3 under potassium deficiency was recovered to some extent when Put was added to the nutrient medium. Spermine treatment (10^{-5} M) substantially stimulated pollen tube growth and pollen germination in *Helianthus annuus* plants grown at deficiency of boron. Both physiological processes were forced within the first 15 min after Spm addition to the germination medium for the incubation of pollen (Çetin et al. 2000). The possible mode of action of PAs during the development and germination of pollen grains describing the relation between mineral requirements and pollen germination hypothesizes that Spm might be able to interact and bind by its basic groups to the pollen membrane constituents. The authors concluded that the cation bridges necessary for membrane integrity were reformed by Spm supply under boron deficiency conditions.

2.1.2. Salinity stress

Soil salinity is one of the main environmental factors that affect crop production in at least 20% of the irrigated agricultural land worldwide (Sudhur and Murthy, 2004). Salt stress causes initial water-deficit and ion-specific stresses resulting from changes in the K^+/Na^+ ratio. Thus, it leads to increased Na^+ and Cl^- concentrations that decrease plant growth and productivity by disrupting physiological processes (Shu et al., 2012). It has been demonstrated by several authors that foliar application of PAs may improve plant response to NaCl (Krishnamutry, 1991; Lutts et al., 1996; Tang and Newton, 2005; Zhang et. al., 2009a). Rahdari and Hoseini (2013) found that Spd and Put reduced the detrimental effects of salinity stress in wheat seedlings by decreasing the rate of chlorophyll and protein destruction in NaCl-stressed plants. Shu et. al. (2012) announced that exogenous application of Spd improved the photosynthetic capacity of salt stressed cucumber seedlings. According to the authors, the positive effect of exogenous Spd on photosynthesis may involve regulation of endogenous PA levels and stabilization of xanthophyll components that protect LHCII reaction centers against salinity induced oxidative damage. According to Nasrin et al. (2012), exogenous Spm exerted its protective effect on salt-stressed chamomile plants through NO-pathway since methylene blue, a known blocker of cyclic guanosine monophosphate signaling pathway, reduced the alleviating effect of Spd. Chattopadhayay et al. (2002) investigated the effects of exogenous Spm and Spd on physiological and biochemical characteristics of 12-day-old rice seedlings (salt-sensitive and salt-tolerant) subjected to salt stress. Application of Spd and Spm at physiological concentrations prevented salinity stress-induced leakage of electrolytes and amino acids from roots and shoots. To different degrees, they also prevented chlorophyll loss and inhibition of photochemical reactions of photosynthesis. The inhibitory effect of salinity and its reversal by exogenous PAs were more pronounced in salt sensitive rice plants. Zhao et al. (2007) found that Spd improved the K^+/Na^+ homeostasis in salt-stressed barley seedlings by restricting Na^+ influx into roots and preventing K^+ loss from shoots. Verma and Mishra (2005) also reported that Put reversed the salinity-induced reduction of seedling growth and biomass accumulation and increased $O_2^{\cdot -}$, H_2O_2 levels, MDA content and electrolyte leakage in leaf tissues of *Brassica juncea*. Duan et al. (2008) announced that exogenous Spd enhanced short-term salinity tolerance in *Cucumis sativus* roots. The ability of Spd to ameliorate the adverse effects of salinity in citrus rootstock Troyer citrange seedlings were shown in the work of Anjum (2011). Addition of Spd (0.1 or 0.5 mM) to the saline nutrient solution and its weekly sprays (1 or 5 mM) on NaCl-stressed plants increased leaf number, chlorophyll content, the F_v/F_m ratio, net photosynthetic rate, N content, as well as total Spd and Spm contents. On the other hand, this treatment reduced Na^+ content of the plants. Amri et al. (2011) also confirmed the protective effect of foliar applied Spd and Put on salt stressed pomegranate grown under greenhouse conditions. Recently Slathia et al. (2012, 2013) presented that co-application of 24-epibrassinolide and Put was more beneficial for NaCl stress mitigation in tomato (*Lycopersicon esculentum* L.) plants than the individual treatments. These findings have a huge agricultural importance with focus on NaCl stress amelioration using bio-friendly and cost effective strategies.

However, Ndayiragije and Lutts (2006) demonstrated that exogenous Spm or Spd added to the nutrient solution did not show a protective effect in the presence of salt in salt-sensitive rice cultivar. Moreover, in the PA-treated plants exposed to NaCl a strong increase in malondialdehyde content was induced which suggested a decrease in cell membrane stability. The increase in malondialdehyde amount was higher for Spm and Spd than for Put. The authors accepted the hypothesis of De Agazio and Zacchini (2001) who have proposed that exogenous Spm and Spd are oxidized by an apoplastic PA oxidase in maize roots, and the resulting H_2O_2 would then induce an oxidative stress acting on membranes and leading to MDA production. Nevertheless, Shi et al. (2013a) have shown that the pretreatment with exogenous PAs conferred increased salt- as well as drought-tolerances in bermudagrass. They performed comparative proteomic analysis of PA-mediated responses and identified 36 commonly regulated proteins by at least two types of PAs in bermudagrass, including 12 proteins with increased level, 20 proteins with decreased level and other 4 specifically expressed proteins. Additionally, proteins involved in electron transport and energy pathways were largely enriched along with nucleoside diphosphate kinase (NDPK) and three antioxidant enzymes which were extensively regulated by PAs. Accumulation of osmolytes was also observed after exogenous PA application, which is consistent with other proteomics results that several proteins implicated in carbon fixation pathway were mediated generally by PA pretreatment. The authors proposed that PAs could activate multiple pathways that enhance bermudagrass adaption to salt and drought stresses (Shi et al. 2013a). Their findings could be appropriate for genetically engineering of grasses and crops in order to improve stress tolerance.

2.1.3. Water stress

Drought is the major abiotic stress factor limiting crop productivity worldwide (Wang et al., 2003; Sharp et al., 2004; Shu et al., 2012). Several studies have shown that exogenous PA application leads to improved drought tolerance against the perturbation of biochemical processes (Yang et al., 2007; Alcázar et al., 2011b). Application of 0.1mM Spd increased drought resistance of two different tomato cultivars, the mitigating effects of exogenous Spd in the drought-sensitive cultivars being greater than those in the drought-resistant cultivars (Zhang et al., 2010). Exogenous Spm application to pines under drought caused a decline in transpiration rates, enhanced photosynthesis and promoted osmotic adjustment, which would facilitate turgor maintenance (Anisul et al., 2003; Pang et al., 2007). Gupta and Gupta (2011) studied the field efficacy of exogenously applied Put in wheat under water-stress conditions. Put (at concentrations of 0.01, 0.1 and 1.0 mM) was applied as seed treatment, as one or two foliar sprays. All treatments enhanced plant height, leaf area, grain number, grain weight, grain yield and biological yield under normal as well as under water stress conditions. Todorov et al. (2000) investigated the effects of some synthetic amines on PEG-stressed maize plants and found their protective role in relation to growth, pigments, relative water content, transpiration rate, proline, malondialdehyde and H_2O_2 levels, peroxidase and catalase activities. In an earlier study Todorov et al. (1998) compared the protective action of ABA, Put and the phenylurea cytokinin 4PU-30 in the same model system and found that the three compounds regardless of their different chemical structure and plant growth regulating activity alleviated to some extent injuries provoked by drought stress. Farooq et al. (2009) evaluated the role of PAs in improving drought tolerance in fine grain aromatic rice (*Oryza sativa* L.). Put, Spm and Spd were used at 10 µM each as seed priming and foliar spray. Expectedly, the drought stress (by bringing the soil moisture down to 50% of field capacity by halting water supply) severely reduced the rice fresh and dry weights, while exogenous PAs improved net photosynthesis, water use efficiency, leaf water status, production of free proline, anthocyanins and soluble phenolics and improved membrane properties. The authors claimed that PA-improved drought tolerance in terms of dry matter yield and net photosynthesis was associated with the maintenance of leaf water status and improved water use efficiency. Among the antioxidants, catalase activity was negatively related to H_2O_2 and membrane permeability, which indicated alleviation of oxidative damage on cellular membranes by PA application. Foliar application was more effective than seed priming, and among the PAs, Spm was the most effective in improving drought tolerance. Drought stress hampered rice performance principally by disrupting the plant-water relations and structure of biological membranes. Recently, Shi et al. (2013b) have stated that Spm pretreatment confers dehydration tolerance of citrus *in vitro* plants *via* modulation of antioxidative capacity and stomatal response.

Flooding, excessive irrigation and soil compaction lead to oxygen deficiency in the plant root zone, thus causing hypoxia stress. Hypoxia is an important environmental factor that inhibits plant growth and yield (Shu et al., 2012). Exogenous PAs were found to alleviate hypoxia-induced injuries in cucumber plants (Wang et al., 2005). Yiu et al. (2009) reported that exogenous Put decreased the flooding-induced oxidative damages in *Allium fistulosum* by increasing the antioxidant capacity. All these findings suggest that PAs are able to decrease the severity of oxidative stress by moderating the free radical scavenging system.

2.1.4. Heavy metals

Heavy metals are directly implicated in the generation of oxidative stress. Cadmium is one of the major industrial pollutants showing phytotoxicity even at low concentrations. Copper is an essential element for plants, but it is strongly phytotoxic at high concentrations. Both metals induced oxidative damages in sunflower leaf discs, as evidenced by an increment in lipid peroxidation and a decrease in antioxidant enzymes (ascorbate peroxidase, gluthatione reductase and superoxide dismuthase).

Pretreatment with exogenously added PAs overcame to some extent the negative effects of the oxidative stress (Groppa et al., 2001). Zhao and Yang (2008) also reported that exogenous PAs alleviated the lipid peroxidation induced by Cd-stress in *Malus hupehensis*. Protective effects of Spm and Spd against Cu stress were observed by Wang et al. (2007) in the aquatic plant *Nymphides pellatum*. Polyamine treatment reversed Cu-induced effects not only in relation to proline, soluble protein and H_2O_2 content, but also by increasing the levels of endogenous Spm, Spd and the (Spd+Spm)/Put ratio. Xu et al. (2011) studied the effects of exogenous Spd on the reactive oxygen species levels and polyamine metabolism under Cu stress in *Alternanthera philoxeroides* (Mart.) Griseb leaves. Cu treatment induced a marked accumulation of Cu, enhanced contents of MDA, H_2O_2 and increased the generation rate of $O_2^{\cdot -}$. However, application of exogenous Spd effectively decreased H_2O_2 content and the generation rate of $O_2^{\cdot -}$, prevented Cu-induced lipid peroxidation and reduced Cu accumulation. The results indicated that the application of exogenous Spd could enhance the tolerance of *A. philoxeroides* to Cu stress by reducing the reactive oxygen level and balancing polyamine metabolism. Stoeva et al. (2005) announced a protective effect of diethylenetriamine (DETA) on oxidative processes provoked by As in maize plants. DETA, applied 24 h prior to the As treatment, decreased considerably the lipid peroxidation level and the peroxidase itself in maize plants.

Chromium (Cr, III or VI) is not required by plants for their normal plant metabolic activities, but the excess of Cr in agricultural soils causes oxidative stress to many crops. The easy penetration of Cr in the human food chain has made it a potent carcinogen. Anthropogenic release of Cr from leather, electroplating, chromic acid production and refractory steel industries constitutes the main sources of Cr pollution (Shanker et al., 2005; Linos et al., 2011). Choudhary et al. (2012) demonstrated that co-application of epibrassinolide and Spd is more effective in alleviation of Cr stress in radish than their individual treatments. Improved Cr-stress mitigation with their co-application involved physiological and molecular interactions in a synergistic and/or additive manner. Therefore, these findings provide a unique and eco-friendly strategy employing interplay of both compounds to overcome heavy metal stress, and abiotic stress in general, in radish. As it was shown above (Slathia et al., 2012, 2013), a similar combination was found to be highly effective in NaCl stress mitigation in tomato plants.

Ding et al. (2012) studied the influence of exogenous Spd on ADC, ODC, PAO activities and PAs, and proline contents in water hyacinth leaves under Hg stress. The authors found that Put content was augmented, while the contents of Spd and Spm and the (Spd+Spm)/Put ratio were reduced considerably with increasing Hg concentrations. Exogenous Spd (0.1mM) evidently reduced the augmentation of Put, amplified Spd and Spm content and the (Spd+Spm)/Put ratio as compared to the Hg treatment alone. This was accompanied by enhanced activities of ADC, ODC and PAO as well as increased proline content. The authors suggested that exogenously applied Spd could alleviate the negative effect of Hg on polyamine metabolism in water hyacinth leaves.

2.1.5. Low and high temperature stress

Low temperature injuries have been also linked to oxidative stress events. Zhang et al. (2009b) reported that exogenous PAs can protect cucumber plants against the deteriorating action of free radicals induced by low temperature. Todorova et al. (2012) studied the protective effect of Spm, Spd, Put, 1,3-DAP and its synthetic analogue diethylenetriamine (DETA) on winter wheat plants. The foliar application of PAs retarded the destruction of chlorophyll, and lessened fresh weight losses due to freezing stress. DETA was most effective in all experiments followed by Spm. The authors concluded that the application of PAs to wheat plants could be a promising approach for improving plant growth under unfavourable conditions, including freezing stress. Put reduced cold-induced electrolyte leakage from primary leaves of wild-type and an ABA-deficient mutant (flacca) of tomato (*Lycopersicon esculentum* Mill.) (Kim et al., 2002). Çakmak and Atici (2009) studied the effects of Put, low temperature and their combinations on the activities of apoplastic antioxidant enzymes in the leaves of winter and spring wheat cultivars. Under control conditions, Put treatments were found to increase more efficiently the antioxidant enzyme activities in winter wheat than in spring wheat. Unexpectedly, under cold conditions, Put treatments induced enzyme activities in spring wheat but generally reduced those in winter wheat leaves. The authors concluded that Put might act as an agent inducing primary changes in the apoplastic antioxidant system of wheat leaves during reactive oxygen species-mediated injury caused by low temperature stress. Zhang et al. (2009b) used cucumber one chilling-resistant cultivar and several sensitive ones to investigate the effects of exogenous PAs on protection against chilling injury. The authors found that pretreatment with Put and Spd diminished the increased electrolyte leakage and MDA content caused by chilling stress in the leaves of both cultivars. Put was shown to increase floral retention, pod set and seed yield in cold stressed chickpea (Nayyar, 2005). Mirdehghan et al. (2007) applied Put or Spd (1mM) under pressure-infiltration or immersion prior to cold storage in order to reduce chilling injury in pomegranate fruit stored at low temperature. Non-treated fruit developed rapidly chilling injury manifested with the following main symptoms: skin browning, increased electrolyte leakage and weight loss. The authors observed losses of firmness and colour but an increased respiration rate during storage. They stated that all these changes were significantly delayed by PA-treatments. The reduction in severity of chilling injury was found to correlate with enhanced levels of free endogenous Put and Spd in the skin, which might promote acclimation of pomegranate to cold temperature and a mechanism of protection against chilling injury, with a net increase in shelf-life. Martinez-Tellez et al. (2002) also showed that the application of Spm, Spd and Put significantly reduced the chilling injury, ion leakage, and polygalacturonase activity in zucchini squash fruits stored for 12 days at +2^{o}C. Jiang et al. (2012) investigated the effect of exogenously applied Put on two tomato cultivars differing in their sensitivity to suboptimal temperatures. Their results showed that Put effectively reduced the decline in net photosynthetic rate and chlorophyll content in leaves caused by the temperature stress in both cultivars and stimulated an increase in organic osmolytes (proline and soluble sugar) contents and root 2,3,5-triphenyltetrazolium chloride (TTC)-reducing activity. Saeidnejad et al. (2012) examined the possibility of Spm application to improve chilling tolerance of maize under stress conditions. The authors established that the negative effects of stress on fresh and dry weight, relative water content, electrolyte leakage, and antioxidant defense enzymes were mitigated by Spm treatment. Accordingly, Abavisani et al. (2013) found that Put application into root nutrient or by spraying of leaves of dragonhead improved antioxidative properties (such as anthocyanin, flavonoids, phenolic compounds and POD enzyme activity) of plants grown under low temperature.

Heat stress is an agricultural problem occurring in many areas in the world. Throughout plant ontogeny, enhanced expression of a variety of heat shock proteins, other stress-related proteins and production of reactive oxygen species (ROS) constitute the major plant responses to heat stress.

The role of PAs in heat-shock protection of soybean seedlings by application of exogenous Put, Spm, and Spd and their biosynthetic inhibitors involving CHA (cyclohexylamine) and DFMO (D, L α-diflouromethylornithine) was investigated (Amooaghaie and Moghym , 2011). Application of PAs as a pre-treatment at 28°C for 2 h prior to heat-shock (45°C for 2 h) enhanced the recovery growth of both roots and hypocotyls. Treatment with CHA and DFMO resulted in thermo sensitization, making seedlings vulnerable to heat-shock. Treatment with PAs plus inhibitors reduced the inhibitory effects and enhanced the growth recovery of seedlings. Application of PAs decreased electrolyte leakage and malondialdehyde from different tissue sections, suggesting protection of membrane integrity.

Bibi et al. (2007) succeeded to ameliorate high-temperature stress in cotton flowers through exogenous application of Put. Exogenous treatment increased the levels of endogenous Put in flowers and this was associated with increased seed set.

Tian et al. (2012) investigated whether the application of exogenous Spd could increase antioxidant activities, and thus elevate the heat tolerance of cucumber seedlings. After treatment with exogenous Spd, the activities of antioxidant enzymes (SOD, AscPOA, and CAT) were noticeably enhanced. The authors concluded that foliar spray with Spd effectively improved the total antioxidant ability of cucumber seedlings and, therefore, enhanced the tolerance of the plants to high temperature stress.

Cheng et al. (2012) investigated the effects of exogenous Spd and high temperature (HT) on transcriptional profiles of ripening tomato fruit. An Affymetrix tomato genome array was used to identify HT- or/and Spd-regulated genes. Many regulatory factors, ethylene-related genes, PA biosynthesis genes, hormone pathways genes, and oxidation/reduction genes exhibited regulation ability in response to Spd treatment. The authors concluded that Spd might alleviate the heat stress injury during tomato fruit ripening.

Recently, Sagor et al. (2013) reported that Spm protected *Arabidopsis* from heat stress-induced damage by increasing the expression of heat shock-related genes.

2.1.6. UV-irradiance

The deleterious effects of UV radiation on the growth, productivity and photosynthesis of higher plants have been extensively studied (for a review see Jenkins, 2009). Data suggest that ROS are involved in the damages caused by UV radiation. Hajiboland and Ebrahimi (2011) found that application of PAs (0.5 mM, 2 weeks) to the nutrient solution of tobacco plants mitigated the negative effects of UV-treatment (10 kJ $m^{-1}d^{-1}$). In addition, the authors discussed the significant role of proline in plant response to exogenous PAs and protection against UV radiation treatments. The authors suggested that exogenous PAs improved background protecting ability of photosynthetic membranes in UV-treated leaves via reduced H_2O_2 production and a rise of proline content.

Unal et al. (2008) indicated that external PAs might have some protective role on photosystem II (PSII) and membranes in *Physcia semipinnata* exposed to UV-A radiation and visible light. Samples treated with Spd had higher chlorophyll *a* content than samples treated with Spm and Put. The authors showed that samples with exogenous PAs decreased significantly lipid peroxidation levels as compared to UV-A-treated samples. Todorova et al. (2013) also showed that preliminary application of Spm protected pea plants against increased UV-C irradiation by maintaining normal plant growth, stabilizing cell membranes and activating non-enzymatic antioxidants.

2.1.7. Ozone and air pollutants

The most important air pollutants in terms of amount present in the atmosphere and harmful effects on plants are O_3, SO_2 and NO_x. SO_2 and NO_x are capable to form acidic compounds which are deposited as either dry or wet deposition (acid rain) (Hippeli and Elstner, 1996). Velikova et al. (1998, 2000) showed that acid rain strongly decreased photosynthetic rate, oxygen evolution, as well as PSII activity, induced lipid peroxidation and increased H_2O_2 level in bean plants. Pretreatment with Spd and Spm prevented these negative effects, the protection by Spm being more pronounced compared to Spd. The changes in the activity of antioxidant enzymes also contributed to their capability for detoxification of active oxygen species.

2.1.9. Herbicides

A lot of publications are focused on the protective effect of PAs against herbicide stress. One of the widely investigated herbicides is paraquat, a well known oxidative stress inducer through photosynthetically generated superoxide radicals (Calderbank, 1968). Spm, Spd and Put effectively counteracted the toxic effect of paraquat in *Arabidopsis* (wild type and late-flowering *gi-3* mutant) (Kurepa et al., 1998), rice (Chang and Kao, 1997) and sunflower leaf discs (Benavides et al., 2000).

Atrazine is a selective herbicide belonging to the group of PSII electron transport inhibitors, and its application provokes also oxidative damages in plants. Zheleva et al. (1994) demonstrated the protective action of exogenous PAs against atrazine. Pea plants treated with a combination of atrazine and Spm showed improved growth, gas exchange, chlorophyll content, and *de novo* protein synthesis than those treated with atrazine alone. Later, Sergiev et al. (2000) confirmed the antidote effect of Spm in the same model system by studying the changes in some antioxidant enzymes and proline content. Stoynova et al. (1999) investigated the protective effect of Spm against atrazine at the ultrastructural level. It was shown that atrazine accelerated cell senescence by lipid peroxidation and loss of unsaturated fatty acids from thylakoid membranes of pea plants. Spm stabilized the molecular composition of the membranes by preventing lipid peroxidation and protected thylakoid system and structural integrity of chloroplasts. Spm treatment also contributed to the process of neutralization of free radicals in the peroxisomes.

2.2. Biotic stress

Biotic stress includes a number of plant-pathogen interactions as fungal, viral and bacterial infections, aphid and insect invasions and wounding, etc. (Öktem et al., 2008). Most of higher plants induce various defense responses which include suicide of the attacked host cells (hypersensitive response, HR); the production of antimicrobial secondary metabolites (phytoalexins); the production of pathogenesis-related (PR) proteins, and the production and oxidative cross-linking of cell wall polymers (Sudha and Ravishankar, 2002). Manipulation of plants by exogenous application of PAs might result in increased resistance to diseases and better growth of the infected plants. El Ghachtouli et al. (1995) reported that exogenous application of Put, cadaverine, Spd and Spm had positive effects on mycorrhizal infection of pea plants. The authors propose that polyamines favor the infection process of pea by *G. intraradices*. The external supply of PAs was shown to protect bean plants from rust disease provoked by *Uromyces appendiculatus* (Haggag, 2005). Mango fruit quality and quantity were increased by exogenous PAs (Malik and Singh, 2006). Application of thermospermine (unusual PA) was found to induce the defense genes in order to restrict CMV in *Arabidopsis thaliana* plants (Sagor et al., 2012). External application of PAs to micropropagated shoot tissues of clover phyllody phytoplasma-infected *Catharanthus roseus* plants was found to diminish the infection severity and deform the pathogen cells (Musetti et al., 1999). Yamakawa et al. (1998) found that exogenous application of Spm induced the expression of acidic *PR-1* gene and accumulation of acidic PR-2, PR-3 and PR-5 proteins in *Tobacco mosaic virus* (TMV)-infected *Nicotiana tabacum* leaves. Uehara et al. (2005) found that one Spm response element ZFT-1 (a Cys2/His2 type zing-finger transcription repressor) discovered in tobacco was induced by Spm application, not by Put or Spd. Furthermore, ZTF-1 was found to be over-expressed in tobacco plants more resistant to TMV. Takahashi et al. (2004b) established that hypersensitive response marker genes (*HSR203J, HSR201* and *HSR515*) were induced by Spm in Spm-signaling pathway of tobacco. The same authors identified another gene family *HIN1, HIN9* and *HIN18* (harpin-induced) which was Spm-responsive and controlled the TMV-induced HR (Takahashi et al., 2004a). The expression of *Arabidopsis thaliana* gene *HIN10* similar to tobacco *HIN1* was also controlled by Spm treatment and specifically accumulated during the HR caused by exposure to an avirulent *Cucumber mosaic virus* (CMV) strain (Zheng et al., 2004, 2005). Treatment with Spm (similarly to CMV-Y and CMV-B2 - strain infections) activated the expression of several transcription factor genes including *ZAT7, ZAT12, AtWRKY40* and *AtbZIP60* (Mitsuya et al., 2009). The first three genes encoded the proteins which contribute to H_2O_2 signalling in the host plant as part of its defense tools. The *AtbZIP60* gene encoded AtbZIP60 protein which plays a proven role in the unfolded protein response (UPR) in *Arabidopsis thaliana* that may function to control the expression of genes participating in protein folding and secretion. These results support the existence of a Spm-signaling pathway in *Arabidopsis thaliana* and its significant role in the defense mechanisms against CMV. Spermidine increased resistance responses in the pathosystem tobacco/TMV (Lazzarato et al., 2009). Both the hypersensitive response to TMV in a leaf disk model system and the systemic acquired resistance in whole plants were significantly affected. Moreover, this response was correlated with changes in the endogenous concentration of salicylic acid and in the transcript levels of PR-1a, PR-2, and arginine decarboxylase (ADC). Conjugated salicylic acid content and ADC transcripts were significantly increased locally and at the systemic level.

The volatile organic compounds (VOCs) can help host plants to respond effectively to a wide range of feeding attackers (Arimura et al., 2011). Exogenous application of Spm to Lima bean leaves induced the release of VOCs which are emitted in plants in response to herbivory (Ozawa et al., 2009).

3. Concluding remarks

Achieving global food security whilst reconciling demands of the environment is the greatest challenge faced by mankind. By 2050 we will need to feed 9 billion people and the demand for food is expected to increase as a result of the growing population. According to FAO, the world will need 70% more food by 2050. The importance of the problem to increase plant productivity, to improve quality and enhance sustainability could not be ignored anymore. The urgency to find a solution of this problem has led to a huge scientific advance. Since all types of stress limit plant growth and crop productivity, the efforts of scientists are focused on minimizing the negative stress consequences. Genetic manipulation of plants by conventional breeding to improve plant growth and yield under stress conditions (stress-tolerant plant varieties) is a sustainable solution of some of the problems caused by the global climate change. However, this approach is time-consuming and demands constant efforts. The use of growth regulators including PAs is a faster and pragmatic solution of such problems. Exogenous application of natural and synthetic PAs allows plants to improve their tolerance against a broad spectrum of stress factors, which in turn increases plant productivity, and extends the boundaries of crop cultivation.

For now, the large-scale agricultural application of PAs is rather limited. However, it seems that usage of exogenous PAs to cope with the negative consequences of different stresses is a promising approach to enhance plant tolerance and adaptation capacity to environmental stress.

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