Chapter 8

POLYAMINES AND COTTON FLOWERING

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INTRODUCTION

Cotton production is plagued by various biotic and abiotic stresses. Even though cotton originates from areas that are characterized by adverse environmental conditions, the cotton crop is still vulnerable to stresses particularly during the reproductive stage. Environmental stress during floral development is a major reason for the disparity between actual and potential yields in crops with valuable reproductive structures (Boyer, 1982; Oosterhuis, 2002; Castiglioni, *et al.*, 2008). In cotton, even moderate stresses can result in reproductive failure in a multitude of ways, such as by disabling pollen vectors, or by causing sterility, asynchrony in pollen and ovule production, or even abortion of reproductive structures (Chiariello and Gulmon, 1991). The physiological functions that occur during flowering have been well documented (Mauney and Stewart, 1986; Stewart *et al.*, 2010). However, information is limited about the metabolic functions in the cotton flower and how these are affected by adverse conditions. Despite some recent reports on the effects of high temperature stress on metabolism in the cotton flower (Burke and Wanjura, 2010; Snider *et al.*, 2010, 2011a, 2011b, 2011c) and a number of older publications on hormone affects and interactions in cotton fruiting forms (Guinn, 1981, Guinn and Brummett, 1988), the overall picture is still not clear. Polyamines were first accepted as plant growth regulators at the International Conference of Plant Growth Substances in 1982 (Davies, 1987). However, controversial opinions exists as to whether PAs qualify to be classified as hormones, due to their abundance in plants, and the much higher concentrations that are required to induce biological responses. Most of the published work on hormones in cotton deals with ethylene, abscisic acid and auxin, with little known about the role and importance of the “new” phytohormones such as polyamines. This review covers the role of polyamines in reproductive development and what is known in cotton.

POLYAMINES

Polyamines (PAs) are low-molecular-weight organic polycations with two or more primary amino groups (NH_2), and are ubiquitous in bacteria, plants and animals. They were discovered as early as 1678, when three-sided crystals from human semen were first described (van Leeuwenhoek, 1678), but their correct chemical composition and structure were only determined in the 1920’s (Galston and Kaur-Sawhney, 1990).

Diamine putrescine (PUT) and its derivatives, triamine spermidine (SPD), and tetramine spermine (SPM) are the most common polyamines in plants. Spermine is found specifically in flowering plants, while its isomer thermospermine is present in all plants (Minguet *et al.*, 2008). PUT derives either directly from ornithine or indirectly from arginine through ornithine decarboxylase (ODC) or arginine decarboxylase (ADC), respectively (Adiga and Prasad, 1985; Kao, 1997). Exceptions exist in the biosynthetic pathways with arabidopsis (*Arabidopsis thaliana*) using only the arginine-ADC pathway. In general, the activities of ADC and ODC enzymes appear to regulate overall PUT biosynthesis in plants (Bagni and Tassoni, 2001) with ADC being associated with tissues undergoing cell expansion and ODC with tissues growing by cell division. The triamine SPD and tetramine SPM are synthesized from PUT and SPD, respectively, with addition of one aminopropyl moiety (Palavan-Ünsal, 1995). The aminopropyl group, decarboxylated S-adenosylmethionine (dcSAM), is produced from S-adenosylmethionine (SAM) mediated by S-adenosylmethionine decarboxylase (SAMDC) (Bagni and Tassoni, 2001). Polyamines are degraded by diamine oxidases (DAO) or polyamine oxidases (PAO) (Bagni and Tassoni, 2001). DAOs occur in high levels in dicots and catalyze the oxidation of PUT to 4-aminobutanal, hydrogen peroxide (H_2O_2) and ammonia (Cona *et al.*, 2006). PAOs on the other hand, are found at high levels in monocots (Sebela *et al.*, 2001) and they are either involved in terminal catabolism of SPD and SPM to 4-aminobutanal, H_2O_2 and 1,3-diaminopropane (Cona *et al.*, 2006) or participate in back-conversion of SPM to SPD with simultaneous production of H_2O_2 (Moschou *et al.*, 2008).

Polyamines occur in free forms, conjugated with phenolic acids or bound to other low molecular weight compounds or macromolecules (Galston and Kaur-Sawhney, 1990). Their high concentrations that range from micromolar to millimolar levels in the plant cells allow them to function as minerals without being toxic (Galston and Kaur-Sawhney, 1990). Free polyamines have been quantified in a variety of plants such as olives (*Olea europea* L.) (Pritsa and Vogiatzis, 2004), tomatoes (*Lycopersicum esculendum* L.) (Fos *et al.* 2003), peas (*Pisum sativum* L.) (Carbonell and Navarro, 1989), and Arabidopsis (Todorova *et al.* 2007). Only free PAs have been reported to be translocated throughout the plant in the phloem and the xylem sap mainly as PUT (Antognoni *et al.*, 1998). Short distance PA translocation is mediated by specific transporters (Antognoni *et al.*, 1993; Tachihara *et al.*, 2005), while long distance transport is both basipetal and acropetal despite their polycation nature (Friedman *et al.*, 1986; Rabiti *et al.*, 1989; Caffaro *et al.*, 1993). Polyamine uptake has been reported to be either active or passive (Kerschbaum *et al.*, 2003). Additionally, different rates of PA transport have been reported between leaves of different ages, with the younger leaves exporting PAs substantially slower than the older leaves (Antognoni *et al.*, 1998).

The importance of PAs in plants is due to their participation in a multitude of plant metabolism functions, including photosynthesis, enzyme activation and maintenance, cell proliferation, division and differentiation, morphogenesis and embryogenesis as well as organogenesis (Evans and Malmberg, 1989; Galston *et al.*, 1997; Kakkar *et al.*, 2000). In addition, PAs are involved in the correct conformation of nucleic acids, gene expression and translation, mediating hormone action, modulation of cell signaling, membrane stabilization and ion channel regulation, as well as heat shock protein and macromolecular synthesis. Besides all the aforementioned functions, PAs also act as second messengers in leaf senescence and apoptosis and more importantly for biotic and abiotic stresses (Kumar *et al.*, 1997; Walden *et al.*, 1997; Malmberg *et al.*, 1998; Bouchereau *et al.*, 1999; Liu *et al.*, 2000; Konigshofer and Lechner, 2002; Alcazar *et al.*, 2006b; Groppa and Benavides, 2007; Ioannidis and Kotzabasis, 2007; Kusano *et al.*, 2008).

Despite the extensive research on other crops, limited information for polyamine exists for cotton (*Gossypium hirsutum* L.) with the only reports being on the distribution of polyamines in the cotton plant (Bibi *et al.*, 2011), polyamine content just prior to rapid fiber elongation (Davidonis, 1995), the effect of heat stress on PAs (Bibi *et al.*, 2010), and the occurrences of uncommon polyamines (norspermidine, norspermine, pentamine, and hexamine) (Kuehn, *et al.*, 1990).

POLYAMINE DISTRIBUTION IN THE PLANT

Both the type and quantity of polyamines have been reported to vary within the plant. Kakkar and Rai (1993) reported that PAs and their titers were different in meristems and vegetative parts. Urano *et al.* (2003) reported that PA biosynthesis showed different profiles during plant development in arabidopsis as well as in response to environmental conditions. Increased concentrations of free and conjugated PAs have been reported to occur in the shoot apex and the flowering parts of many plants. The response appears to be time specific, with arabidopsis rosettes and bolts containing small quantities of SPD that increase dramatically in flowers. However, root and leaf PA concentrations appear to be unaffected from flower initiation or flower development (Li and Wang, 2004). Roots in general accumulate lower concentrations of PAs compared to the flowering parts of the plant, with leguminous plants being the only exception since the nodules accumulate 5 to10 times higher concentrations compared to other organs (Fujihara *et al.*, 1994). Differences in PA concentrations have been noticed between photosynthetic and non-photosynthetic tissues (Lefevre *et al.*, 2001) as well as within floral organs with flowers of Nicotiana species containing higher concentrations of PAs in their stamens compared to the pistils (Pedrizet and Prevost, 1981; Martin-Tanguy, 1997).

In cotton, PA concentrations of the leaf have been observed to be significantly lower compared to the ovary, while the ovary and the style have been reported to contain similar levels of Pas with the exception of PUT that occurs in considerably higher concentrations in the ovary than the style (Loka *et al.*, in press). Additionally, Bibi *et al.* (2011) showed that the concentration of PUT, SPD and SPM in the ovules of first-position white flowers varied up the main-stem of the cotton plant. PUT concentration decreased acropetally along the main-stem of the cotton plant with the highest concentration observed at the 7th node and the lowest at the 13th node. SPD concentration decreased below and above the 9th node, with the 9th node showing the highest amount of SPD and the 13th node the lowest in both years of the study. Similarly, the SPM concentration decreased below and above the 9th node. The highest amounts of PAs were observed at the 7th and the 9th node of cotton, and this may be associated with the majority of the yield distribution coming from these nodal positions. Genotypic differences were also observed in ovarian polyamine content (Bibi *et al.*, 2011).

INTERACTION OF POLYAMINES WITH OTHER METABOLIC FACTORS

Polyamines participate in a number of metabolic and hormonal pathways that regulate plant growth and development as well as plant responses under conditions of environmental stress.

Polyamines and Ethylene

Ethylene and polyamine (SPD and SPM) biosynthesis pathways share the common precursor S-adenosylmethionine. However, their plant responses appear to be different if not occasionally antagonistic, i.e., PAs are considered to be plant growth promoters whereas ethylene is mostly associated with plant growth inhibition and senescence. Opposite opinions exist on the interdependence of the two biosynthetic pathways. However, utilization of the precursor SAM by the plants for either production of ethylene or polyamines, appears to be dependent on the type of tissue, the developmental stage as well as the growing conditions. Specifically, polyamine levels and synthesis rates are high in tissues that undergo cell division compared to the non-dividing or senescing tissues (Kushad and Dumbroff, 1991). Ethylene synthesis, on the other hand, increases significantly in older tissues whereas it is very limited in meristematic tissues. Research has indicated that preventing the conversion of SAM into ethylene can dramatically increase polyamine synthesis; however, in young tissues, where ethylene enhances growth, polyamine levels have been reported to increase. Conversely, in cases where ethylene acts as a growth inhibitor, for example under adverse conditions or senescence, polyamine responses vary. For example, PUT has been shown to increase in accordance with ethylene, while SPD and SPM remain unaffected (McDonald and Kushad, 1986; Corey and Barker, 1989; Gomez-Jimenez *et al.*, 2010). In experiments with exogenous application of polyamines, ethylene biosynthesis is inhibited (Suttle, 1981; Apelbaum *et al.*, 1981) however, the opposite has also been observed. In general, ethylene and polyamine functions may appear to be opposite (Kumar *et al.*, 1996; Pang *et al.*, 2006), however their responses are dependent on the species, the type of tissue as well as the experimental conditions (Gomez-Jimenez *et al.*, 2010; Quinet *et al.*, 2010). There does not appear to be any published research on the interaction of PAs and ethylene in cotton.

Polyamines and Abscisic Acid

Abscisic acid (ABA) has been reported to control PA levels in plants by affecting their synthesis, degradation, transfer and conjugation with other molecules under conditions of stress (Liu *et al.*, 2005; Nieves *et al.*, 2001). In maize (*Zea mays* L.), low concentrations of ABA due to chemical inhibition resulted in low PA levels (Liu *et al.*, 2005). Inhibition of ABA synthesis in wheat (*Triticum aestivum* L.) resulted in lower PUT concentrations due to decreased ADC activity (Lee *et al.*, 1997). Similar results were observed in arabidopsis (Cuevas *et al.*, 2008), however, Kim *et al.* (2002) reported that ABA and PAs had no interdependent action in leaves of cold-stressed tomato. Bueno and Matilla (1992) observed that exogenous application of ABA increased PA levels in isolated embryonic axes of chickpea (*Cicer ariennum* L.) seeds. Nieves *et al.* (2001) reported similar results in sugarcane (*Beta vulgaris*). In contrast, ABA application to cucumber cotyledons (Suresh *et al.*, 1978) resulted in decreased PA levels and a similar pattern was observed in rice (*Oryza sativa* L.) embryos (Choudhuri and Ghosh, 1982). As with ethylene, there have been no published results of PAs and ABA interactions in cotton.

Polyamines and Gibberellins

Gibberellins appear to regulate PA biosynthesis. Dai *et al.* (1982) observed that exogenous application of GA_3 resulted in significant increases in PUT and SPM concentrations in internodes of dwarf peas, while Kaur-Sawnhey *et al.* (1986) reported that only ADC activity increased, whereas application of PA inhibitors resulted in reduced length of internodes. Enhancement of GA_3 induced elongation has also been observed in lettuce hypocotyls (Cho, 1983). Increases in PUT levels, but not in SPD and SPM, were reported in seedless berries as well after application of GA_3 (Shinozaki *et al.*, 1998). Increases in PUT, SPD and SPM were reported by Smith *et al.* (1985) in dwarf peas. In addition, Kyriakidis *et al.* (1983) reported that application of GA_3 caused ODC activity to increase in barley seeds (*Hordeum vulgare*) and indicated that PAs and especially SPD were regulating GA_3 action and α-amylase formation. To the contrary, Lin (1984) reported that GA_3 application had no effect on polyamine levels in aleurone layer cells in barley seeds. As with ethylene and abscisic acid, there does not appear to be any reported research on interactions between GAs and PAs in cotton.

Polyamines and Cytokinins

Polyamine biosynthesis has been reported to be regulated by cytokinins (Galston, 1983; Bouchereau *et al.*, 1999). Additionally, PAs have been observed to block cytokinin-action (Romanov *et al.*, 2002). Romanov *et al.* (2004) reported that exogenous application of PAs to Arabidopsis plants resulted in blocking cytokinin activity and the efficiency of the PAs depended on their concentrations, with SPM being the most efficient at all concentrations. Similar interactions between cytokinins and PAs have been reported in Amaranthus seedlings (Feray *et al.*, 1992), but the opposite was reported in beet root cells (Naik *et al.*, 1980). Levels of PUT and cytokinins were observed to increase in embryogenic cell cultures of celery (*Apium graveolous* L.) at embryogenesis, while application of PA biosynthesis inhibitors resulted in restriction of cell division (Danin *et al.*, 1993). No apparent reports exist of cytokinins and PAs in cotton.

Polyamines and Nitric Oxide

Nitric oxide (NO), a reactive gaseous molecule, has been shown to act as a signal in plant responses to biotic and abiotic stresses (Delledonne *et al.*, 2001), as well in regulation of a variety of plant growth and developmental processes such as germination and flowering, fruit ripening, and senescence (Hung and Kao 2003; Pagnussat *et al.*, 2004*)*. The amino acid arginine is the common precursor for both polyamine and nitric oxide pathways (Yamasaki and Cohen, 2006). Recent evidence has indicated that PAs are involved in NO production in plants (Tun *et al.*, 2006; Groppa *et al.*, 2008; Arasimowicz-Jelonek *et al.*, 2009), and exogenous application of PAs to arabidopsis seedlings was observed to enhance NO production (Tun *et al.*, 2006). Similar results were reported by Manjunantha *et al.* (2010) in banana fruits (*Musa acuminate* L.) and by Silveira *et al.* (2006) in Brazilian pine (*Araucaria angustifolia*) after application of PUT, while application of either SPD or SPM had the opposite results (Silveira *et al.*, 2006). In conclusion, PAs have an effect on NO production although the exact mechanism involved is yet to be elucidated. The relationship between PA and NO has not been quantified for cotton.

Polyamines and Hydrogen Peroxide

Polyamines are involved in antioxidant metabolism through their function as free radical scavengers, and they also participate in generation of hydrogen peroxide (H_2O_2) through their catabolism by DAOs or PAOs. Hydrogen peroxide, a reactive oxygen species at high concentrations leads to plant cell death, and in lower concentrations serves as a signaling molecule inducing tolerance to biotic and abiotic stresses due to its high permeability across membranes and relatively long life (Quan *et al.*, 2008). Additionally, H_2O_2 is involved in vascular development of plants through lignin polymerization (De Marco and Roubelakis-Angelakis, 1996). Previous research has indicated that increased levels of PAs resulted in decreased production of H_2O_2 and lipid peroxidation (Nayyar and Chander; 2004; Verma and Mishra, 2005).The relationship between PA and H_2O_2 has not been documented for cotton.

POLYAMINES AND REPRODUCTIVE DEVELOPMENT

A relationship between PAs and reproductive development has long been established due to the significant increase in their concentrations as plants transition from their vegetative to reproductive stage of growth (Kakkar and Rai, 1993). Kloareg *et al.* (1986) indicated that PAs are indispensable to plants at the time of flowering and early fruit development. In support of this observation, experiments with PA-deficient mutants or mutants with unbalanced PA metabolism resulted in abnormal growth and flowering patterns as well as delayed flowering (Galston *et al.*, 1997; Kakkar and Sawhney, 2002; Hanzawa *et al.*, 2002; Alcazar *et al.*, 2005). Polyamines have been implicated in flower induction (Evans and Malmberg, 1989; Faust and Wang, 1992; Bagni *et al.*, 1993;Bouchereau *et al.*, 1999; Kakkar and Sawhney, 2002), flower initiation (Kaur-Sawhney *et al.* 1988), pollination (Falasca *et al*,. 2010), fruit growth and ripening (Kakkar and Rai, 1993). Sexual differentiation of tissues appears to be dependent on PA biosynthesis and catabolism, as well as their free or conjugated forms (Martin-Tanguy, 1997).

Ornithine decarboxylase is reported to be the main enzyme controlling PA concentrations and may be required for flower development (Burtin *et al.*, 1989; Aribaud *et al.*, 1994; Tarenghi and Martin-Tanguy, 1995). In support of that theory, application of ODC inhibitors during early fruit growth resulted in complete inhibition of flowering in tomato and potato (*Solanum tuberosum* L.) (Cohen *et al.*, 1982). However, in tobacco (*Nicotiana tabacum* L.), ODC inhibitors had no effect on flowering, while the opposite was observed with ADC inhibitors (Tiburcio *et al.*, 1988). In general, however, the ODC pathway is associated with meristematic tissues, while ADC is common in mature tissues (Flores, 1991). Additionally, use of SPD biosynthesis inhibitors resulted in flower abortion and abscission in tobacco (Burtin *et al.*, 1989). Inhibition of SPD biosynthesis has been reported to result in anther malformation and pollen sterility in a variety of crops (Martin-Tanguy, 1996). Similar results were reported in kiwi fruit (*Actinidia deliciosa* L.) (Falasca *et al.*, 2010), tobacco (Chibi *et al.*, 1994), apple (*Malus domestica* L.) (Bagni *et al.*, 1981) and tomato (Song *et al.*, 2002). Kakkar and Rai (1993) suggested that SPD concentrations could be used as potential markers for floral induction. In maize, PAs have been observed to be involved in normal and aborting kernels, through their involvement in early endosperm development (Liang and Lur, 2002). In addition, the PUT:SPD ratio appears to play an important role in plant regeneration capacity (Shoeb *et al.*, 2001). The levels of PUT against the levels of SPD +SPM have been associated with totipotency as well as with embryo development and germination (Papadakis *et al.*, 2005; Silveira *et al.*, 2006).

In addition to flowering, PAs have also been reported to participate in regulation of post-fertilization development (Galston, 1983; Slocum and Galston, 1985; Lin, 1984; Evans and Malmberg, 1989). Numerous reports on PAs and their role in stimulating fruit set and fruit development exist, i.e., in apple (Costa and Bagni, 1983; Biasi *et al.*, 1991), pear (*Pyrus communis* L.) (Crisosto *et al.*, 1986; Crisosto *et al.*, 1988), pepper (*Capsicum annuum* L.) (Serrano *et al.*, 1995), olive (Rugini and Mencuccini 1985), mango (*Mangifera indica* L.) (Singh and Singh, 1995), tomato (Antognoni *et al.*, 2002), and strawberry (*Fragaria amanassa* Dutch.) (Tarenghi and Martin-Tanguy, 1995). In cotton, there has only been limited research on PAs and reproductive development. Bibi *et al.* (2010) measured PA content in cotton ovaries as affected by heat stress, showing that SPD and SPM, but not PUT, were decreased with elevated temperatures, and successful seed fertilization was also significantly decreased by the high temperature (Bibi *et al.*, 2007). Similar results were reported by Loka and Oosterhuis (2011) for the effect of water deficit on PAs in cotton flowers. PUT concentrations of water-stressed ovaries remained at the same levels as the control, whereas both SPD and SPM concentrations significantly decreased under conditions of water-deficit stress.

POLYAMINES AND PLANT RESPONSE TO STRESS

The first observation of PA involvement in plant response under adverse conditions was reported in potassium deficient barley plants that over-accumulated PUT (Richards and Coleman, 1952). Further research revealed that the ADC pathway is more active compared to the ODC pathway under stress conditions (Smith and Richards, 1964; Flores and Galston, 1984). Since then, extended investigation in a number of plant species has shown that changes in PA production is a common plant response to a variety of abiotic stresses, including salinity, chilling, heat and drought as well as biotic stresses (Bouchereau *et al.*, 1999; Alcazar *et al.*, 2006b; Groppa and Benavides, 2007). Additionally, recent advances indicate that the ratio of PA catabolism to PA anabolism is an important factor in PA mediated stress tolerance (Moschou *et al.*, 2009).

Salinity

Polyamine responses to salinity have been reported to vary in different plant species as well as within a plant species (Russak *et al.*, 2010), but there are no reports for cotton. Significant increases in PUT and SPM have been reported in arabidopsis under conditions of salt stress (Urano *et al.*, 2003) and similar results were found in rice (Basu and Ghosh, 1991) and mung beans (*Vigna radiata*L.) (Friedman *et al.*, 1986). Krisnamurthy and Bhagwat (1984) reported that SPD and SPM levels of salt-tolerant rice cultivars were increased under conditions of high salinity while PUT concentrations decreased. Similar findings were reported in maize (Jimenez-Bremont *et al.*, 2007), in soybean (*Glycine max* L.) (Campestre *et al.*, 2011), and in a variety of vegetable crops (Zapata *et al.*, 2004). However, Prakasch *et al.* (1988) observed that PA concentrations in rice plants under water stress significantly decreased compared to the control, and similar results were also observed in tomato (Santa-Cruz *et al.*, 1997). Furthermore, in experiments with transgenic arabidopsis plants, Yamaguchi *et al.* (2007) observed that SPM-deficient mutants were significantly more salt-sensitive compared to control plants. Similarly, salt-resistant plant varieties were found to have increased concentrations of PAs under conditions of salt stress (Erdei *et al.*, 1996; Basu and Ghosh, 1991), whereas over-production of PUT was also reported to increase salt tolerance in rice (Roy and Wu, 2001; Quinet *et al.*, 2010) and tobacco (Kumria and Rajam, 2002; Waie and Rajam, 2003).

Cold Stress

Chilling treatment was reported to increase PUT accumulation in Arabidopsis (Urano *et al.*, 2003; Cuevas *et al.*, 2009) while SPD and SPM concentrations remained unaffected or slightly decreased. PUT accumulation under conditions of cold stress was also observed in alfalfa (*Medicago sativa*) and wheat (Nadeau *et al.*, 1987; Kovacs *et al.*, 2010), in citrus and lemon (*Citrus* sp.) (McDonald and Kushad, 1986; Kushad and Yelenosky, 1987), in cucumber (*Cucumis sativus*) (Shen *et al.*, 2000),as well as in beans (*Phaseolus* sp.) (Guye *et al.*, 1986), and in rice (Lee *et al.*, 1997). However, differential responses to cold stress were reported within wheat species with a winter wheat variety showing increased PUT and SPD concentrations under stress while in a spring variety only the SPD and SPM concentrations were increased (Szalai *et al.*, 2009). Further research with exogenous application of PUT on tomato resulted in decreased electrolyte leakage due to the cold treatment whereas the use of PUT synthesis inhibitors had the opposite effect (Kim *et al.*, 2002). Freezing tolerance due to increased accumulation of PAs was also reported in Arabidopsis (Kasukabe *et al.*, 2004; Altabella *et al.*, 2009). Low temperatures are not usually a problem in cotton production except in some areas during germination; however, no work has been published on PAs during cotton early season growth.

Heat Stress

The most frequent response of polyamines to heat stress is an increase in one or more PAs (Narçin-Ünsal, 1995). In experiments with rice callus Roy and Ghosh (1996) reported that levels of free and bound PAs were significantly higher in heat tolerant varieties compared to the heat sensitive. Additionally, over-production of SPD and SPM in transgenic tomato plants resulted in significantly more heat tolerant plants (Cheng *et al.*, 2009). In support of these observations, Song *et al.* (2002) reported that extreme temperatures significantly decreased SPD and SPM concentrations in tomato pollen, while PUT concentrations increased. In cotton the negative effect of high temperatures during reproductive development is known (Oosterhuis and Snider, 2011), but research on free PAs under high temperature stress is limited. Kuehn *et al.* (1990) reported on the occurrences of uncommon polyamines in cotton under heat stress. Bibi *et al.* (2007) documented a negative correlation of temperature and PAs, with polyamine content in cotton ovaries decreasing with increased canopy temperature. Subjecting the plants to high temperatures (38°C) compared to the optimum (30°C) significantly decreased SPD and SPM levels but not PUT (Bibi *et al.*, 2010). Successful seed fertilization was significantly decreased by the high temperature**,** and significantly increased by exogenous application of PUT (Bibi *et al.*, 2010). Information is lacking about the specific role of PAs in the leaf and pistil in the response of the cotton plant to high temperature, and the possible protective role of PAs in thermostability in the leaf and pistil.

Water-deficit Stress

Polyamines have been reported to be involved in plant responses under limited water conditions either as signaling molecules due to their connection to ABA metabolism (Alcazar *et al.*, 2006a) or as protective agents against water stress (Capell *et al.*, 1998). In support of these observations, Alcazar *et al.* (2010) reported that transgenic Arabidopsis plants that over-accumulated PUT had increased drought tolerance compared to the control as well as reduced stomatal aperture. Similar results were observed in rice plants over-producing SPD and SPM by Capell *et al.* (1998) while after imposition of water stress on cell cultures of drought tolerant alfalfa, SPD and SPM concentrations increased while PUT levels decreased (Yamaguchi *et al.*, 2007). The opposite was observed in detached oat leaves under conditions of water stress with PUT significantly increasing while SPD and SPM showed a dramatic decrease (Flores and Galston, 1984). Furthermore, SPM-deficient arabidopsis plants were observed to be significantly more drought sensitive compared to the control (Yamaguchi *et al.*, 2007). Regarding cotton, experiments with cultivars differing in drought tolerance revealed that water-deficit stress resulted in significant increases in PUT, SPD, and SPM levels in both ovary and leaf of the drought-sensitive cultivar, whereas no significant effect was observed on PA concentrations of the drought-tolerant cultivar (Loka *et al.*, in press).

Biotic Stress

PAs have been reported to interact with fungal (Greenland and Lewis, 1984) and viral (Torrigiani *et al.*, 1997) pathogens as well as mycorrhizae (Walters, 2000). Apart from their role as signaling molecules that induce defensive mechanisms against the pathogen (Takahashi *et al.*, 2004), they also participate in resistance mechanisms against infections (Yamakawa *et al.*, 1998). Additionally, PAs provide the possibility of controlling fungal plant diseases by specific inhibition of their biosynthesis (Rajam and Galston, 1985; Walters, 2003) since experiments with certain PA biosynthesis inhibitors resulted in complete disruption of microcycleconidiation (Khurana *et al.*, 1996). Furthermore, polyamine catabolism pathways are also potentially able to regulate plant-pathogen interactions due to the concentrations of H_2O_2 and NO that are ultimately produced (Romero-Puertas *et al.*, 2004; Tun *et al.*, 2006; Walters, 2003). We are not aware of any published work on the involvement of PAs in biotic stress in cotton.

EXOGENOUS APPLICATION OF POLYAMINES

The documented importance of polyamines in reproductive development has directed many researchers to exogenously applying polyamines in an effort to enhance fruit development. Reports for mango (Singh and Janes, 2000) and apricot (*Prunus armeniaca* L.) (Alburquerque *et al.*, 2006) showed improved fruit retention and yield with exogenous PAs, while application of SPD and SPM alleviated high temperature inhibition of pollen germination and pollen tube growth in tomato (Song *et al.*, 2002). In apricot the exogenous application of PUT on flowers increased the percentage of functional ovules about 16 % (Alburquerque *et al.* 2006). Also, exogenous application of PUT has been shown to improve yield in litchi (*Litchi chinensis* L.) (Stern and Gazit, 2000), apple (Costa *et al.*, 1983), and olive (Rugini and Menciccini, 1985). Earlier, Galston and Kaur-Sawhney (1990) reported that the application of exogenous PAs to plants produced visible effects such as the prevention of senescence and the formation of embryos or floral primordial in certain otherwise vegetative tissue. According to Cohen *et al.* (1982) the development of pollinated tomato ovaries was prevented by inhibitors of ODC and could be counteracted by exogenous PUT application. Besford *et al.* (1993) showed that exogenously applied SPD and SPM prevented the destruction of chlorophyll, Rubisco and molecular complexes of thylakoids from occurring in osmotically stressed oat (*Avena sativa* L.) leaves, and Roberts *et al.* (1986) showed that exogenous PAs altered membrane fluidity in bean leaves. Various reports of exogenous polyamine application suggest a possible involvement of PAs in plant adaptation to several environmental stresses by preserving membrane functions and reversing growth inhibition as well as by decreasing ROS concentrations and increasing antioxidant enzyme activities (Ali, 2000; Iqbal and Ashraf, 2005a; Tang and Newton, 2005; Ndayiragiji and Lutts, 2006; Afzal *et al.*, 2009; Yiu et al, 2009; Zhang *et al.*, 2009). Farooq *et al.* (2008) reported that exogenous application of PAs increased drought tolerance in rice by improving leaf water status and decreasing membrane leakage. Similar results were reported by Rajasekaran and Blake (1999) who observed that application of SPD to drought stressed Jack pine (*Pinus banksana Lamb*.) seedlings reduced ethylene production and membrane leakage. Application of SPD was also reported to ameliorate chilling injury of rice seedlings (Tajima and Kabaki, 1981), while Shi *et al.* (2008) observed that PUT application significantly ameliorated salt stress in cucumber.

In cotton, Bibi *et al.* (2007) reported that exogenous application of PUT to floral buds in controlled environment studies, 24 hours prior anthesis, increased the level of PUT in ovaries, but there was no effect on SPD and SPM concentrations. The increase in PA was associated with increased seed set. These authors also showed that increased temperatures decreased SPD concentrations in the pistil and seed set in cotton flowers, and exogenous application of PUT ameliorated the negative effect of high temperature on seed set.

The use of exogenous application of polyamines in row crops may not be a practical management practice due to the high cost of the material (and because it is still not in mass production (SPM=$180/5g, SPD=$118/5g, PUT= $55/25g). Nevertheless, an affordable alternative is to apply synthetic plant growth regulators. The plant growth regulator BM86 (active ingredient GA_{14}; Goëmar Laboratories, Saint-Malo, France) has been reported to regulate the synthesis of endogenic PAs. Broquedis *et al.* (1995) investigated the effect of GA_{14} on the composition of PAs in grapes (*Vitis vinifera* L.), and showed an increase in the accumulation of PAs particularly at the end of the first stage of fruit development. Treatment with GA_{14} increased the numbers, weight and growth of the fruit, and this was related to a significant increase in polyamine content in the flowers and in the fruit. It appears, therefore, that the BM86 stimulated the metabolism of PAs in the plant. Numerous anecdotal reports with horticultural plants have shown that BM86 acts to stimulate reproductive development of the plant. According to these reports (Anonymous, 2008), BM86 increased yield and oil production of olives, promoted uniform fertilization and fruit set in grapes and resulted in increased fruit size and total yield in citrus.

In cotton, (Rethwich *et al.*, 2006) associated BM86 application with increased yield, while Bibi *et al.* (2007) subsequently showed that application of BM86 at the first flower stage and two weeks later at 2.34 mL/ha had a positive effect on ovarian polyamine content of cotton. PUT and SPD concentrations one week after the first BM86 application and PUT concentration two week after the first BM86 application, were significantly increased compared to the untreated control. Additionally, higher seed set efficiency with the BM86 application was observed. Only small differences in ovarian polyamine content were detected among the genotypes tested, possibly due to the narrow genetic pool of the commercial cotton cultivars used. They concluded that application of BM86 could significantly increase cotton seed number by enhancing PAs biosynthesis, but cautioned that further research was needed.

SUMMARY

Polyamines are growth regulating compounds that occur widely in bacteria, plants and animals. They are involved in numerous plant metabolic activities and in plant response to stress. Polyamines are of particular importance in reproductive development and are considered indispensable to plants at the time of flowering and early fruit development, since they have been implicated in flower induction, flower initiation, pollination, fruit growth and ripening. Both the type and quantity of polyamines have been reported to vary within the plant, and during plant development, as well as in response to environmental conditions. In cotton, PA concentrations are generally higher in the ovary, and genotypic differences exist in ovarian polyamine content. Polyamines participate in a number of metabolic and hormonal pathways that regulate plant growth and development as well as plant responses under conditions of environmental stress, including salinity, chilling, heat, drought and biotic stresses. Despite the extensive research on other crops, limited information exists for cotton with the only reports being on the distribution of polyamines in the cotton plant, polyamine content just prior to rapid fiber elongation, the effect of heat stress on PAs, and the occurrences of uncommon polyamines. Exogenous application of PAs have been reported to enhance fruit retention, development, and yield in a number of horticultural crops, and improve plant adaptation to several environmental stresses. In cotton, exogenously applied putrescine increased the level of putrescine in ovaries, which was associated with increased seed set, and amelioration of the negative effect of high temperature on seed set. Understanding of the role of polyamines in cotton is limited, but given what we know in horticultural plants, it is obvious that as our understanding of the involvement of PAs in metabolic functions and in stress response increases, it would appear that research with cotton in this field will be a fruitful and rewarding endeavor.

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