REVIEW PAPER

Application of polyamines in horticulture: A review

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Abstract

Polyamines are ubiquitous organic compounds in plants that are involved in various physiological functions; they play key role in the regulation of ion channels and molecule transportation in the cell membrane. Being positively charged, polyamines can bind to macromolecules such as DNA, RNA and proteins, hence stabilize them against free radicals activity. Their importance with respect to plant growth and development is already established especially their role against stresses is of prime concerns to the scientists. It is revealed by various scientists that exogenous application of polyamines protects the plants from stress by expressing various stress relevant genes. Polyamines also play direct defensive role during stress by eliciting cell death at the sight of pathogen entry. A lot of work has been done on various aspects of fruits, vegetables and ornamental crops using exogenous polyamines. Present paper is developed to gather all possible published research from reliable resources in a logical sequence especially related to horticulture, so the researchers and other stake holders related to this field can get the benefit.

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Introduction

What are polyamines?

Polyamines are organic polycations having variable hydrocarbon chains and two or more primary amino groups. They have varying number of amines ranging from diamine putrescine, triamine spermidine to tetraamine spermine. These are widespread in living organisms, found in high concentration in actively proliferating cells. Polyamines are responsible for many fundamental processes which include transcription, RNA modification, and synthesis of protein and the modulation of enzyme activities (Takashashi and Kakehi, 2010).

There are three major forms of polyamines i.e. putrescine, spermidine and spermine. Amongst them putrescine is classified as diamine while the other two are considered as higher polyamines. This classification is based on the strength of the amines which increase gradually from putrescine to spermidine and spermine. These are found in all the living organisms and are responsible for different functions. The biological functioning of all of them is similar. These occur in different forms i.e. free living, conjugated and titers (Tang et al., 2004).

The increase in the activity of the titers was found during the process of sprouting, seed germination and during root and shoot formation (Galston and Flores, 1991; Mengoli et al., 1992). While the conjugated form is considered to be associated with flowering (Solcum et al., 1984; Martin–Tanguy, 2001).

Biosynthesis, transport, degradation and congjugation of polyamines in plants

In plants, putrescine is synthesized by the decarboxylation of arginine or ornithine catalyzed by arginine decarboxylase or ornithine decarboxylase respectively. The following addition of two aminopropyl groups to putrescine (put) in two reactions catalyzed by spermidine (spd) synthase and spermine (spm) synthase lead to the formation of spermidine and spermine, respectively. The aminopropyl moieties arise from the decarboxylation of S-Adenosylmethionine by the enzyme S-adenosylmethionine decarboxylase (Groppa and Benavides, 2008).

Free polyamines level in plant cells depends not only on their synthesis but also on their transport, degradation and conjugation. Putrescine degradation is catalyzed by diamine oxidase, a copper containing enzyme that oxidizes the diamine at the primary amino group whereas spermidine and spermine are oxidized at their secondary amino groups by a flavin – containing polyamine oxidase (Flores and Filner, 1985). Polyamines can be conjugated to small molecules like proteins, antibiotics and phenolic acids, mostly hydroxycinnamic acid (Martin-Tanguy, 2001).

Role of polyamines in plants

In plants polyamines are responsible for the performance of wide range of functions like growth and development because of its effect on cell division and differentiation, flowering, growth, development and fruit ripening (Khan et al., 2008).

These polyamines are reported to have the regulatory effect on promoting the productivity of the plants (Gharib and Ahmed, 2005). They are found to be anti-senescent agents and effective for delaying softening in several fruits, as they help in the integrity of cell membrane (Khan et al., 2007). They are also considered as one of the carbon and nitrogen reserves, new class of growth regulators which act as second hormonal messenger (Nahed et al., 2009) and help in the synthesis of protein and RNA (Kim and Jin, 2006).

Polyamines readily bind to the negatively charged phospholipids' head groups or other anionic sites at membranes thus affecting the stability and permeability of such membranes. They are also involved in the buffering mechanism to maintain cellular pH and ion homeostasis (Pand et al., 2007).

Fate of polyamines in plants

Different studies clearly indicate the relationship between polyamines and plant development.

Generally the polyamines level is high during the start of development as compared to the lateral stages. However, this depends upon the plant species and the major polyamine content found in the plant (Liu *et al.*, 2006). Active cell divisions at the early stages of growth require elevated level of PAs. While the decaline at the end of the developmental stage act as a signal for the onset of senescence and death of the plant or part of the plant. However, opposite results have also been shown in fruits like tomato and citrus (Saftner and Baldi, 1990).

Several studies have been made to understand the concentration of polyamines in plants during growth, development and senescence in both, climacteric and non climacteric fruits.

Table 1. Effect of exogenous application of polyamines on growth, quality and shelf life of fruits.

Crop	BN	PAs	Inferences	References
Apple (Golden Delicious McIntosh and Hi Early)	*Malus domestica*	PUT, SPD, SPM	Effected fruit set of apple delayed the fruit ripening and extend shelf life	Costan and Bagni 1983; Costa *et al.*, 1986; Kramer *et al.*, 1991; Wang *et al.*, 1993
Apricot (Canino, auricio)	*Prunus armenica* L.	PUT, SPM	Improved trees productivity, lowered the chilling injury incidence and enhanced the antioxidant enzyme activities. Delayed color changes, suppressed ethylene production	Ali *et al.*, 2010; Saba *et al.*, 2012; Martinez-Romero *et al.,* 2002
Blueberry	Vaccinium asheri Reade	PUT, SPM	Enhanced quality and storability	Basiouny, 1996
Dates (Zaghloul and Bargee)	*Phoeix dactylifera L.*	PUT	resulted in significantly lower tissue softening or breakdown as compared to the control; improved quality, storability and marketability	Al-Obeed, 2010
Grape (Emperatriz, Fantasy, Thompson Seedless, Flame seedless	*Vitis vinifera*	PUT	Had a role in embryo development and inhibited abscission; Preharvest foliar sprays improved yield, quality and shelf life, improved color and anthocynine development	Ponce *et al.*, 2002; Aziz *et al.*, 2001; Farag, *et al.*, 1998; Marzouk and Kassem, 2011
Jujube	*Ziziphus jujuba* Mill.	PUT	Improved productivity, fruit quality and profitability of jujube trees.	Kassem, *et al.*, 2011
Lemons cv. Verna	*Citrus limon* L. Burm	PUT	Influenced endogenous polyamines, firmness, and abscisic acid	Valero *et al.*, 1998
Mango (Haden, Kent, Glenn and Kensington Pride)	*Mangifera indica* L.		Regulation of fruit set and retention in Improved shelf life and quality	Singh and Singh 1995; Singh and Janes, 2000; Malik and Singh, 2005, 2006
Nectarine Stark Red Gold	*Prunus persica* L Batch	PUT, SPD	Reduced ethylene production, higher fruit TA and lower dry weight , SSC and modulated the ripening	Bergoli *et al.,* 2006; Torrigiani *et al., 2004*
Oranges 'Navel' 'Trifoliate	*Citrus sinensis* L.	PUT, SPD	Preharvest foliar application extended harvest season and enhanced the shelf life; Enhanced the growth by up taking the nutrient elements by the roots	Marzouk and Kassem, 2011; Qing-Sheng and Zou, 2009
Peach (Babygold-6)	*Prunus persica* L	PUT, SPD, SPM	Improved storability Reduced ethylene production, respiration rate and susceptibility to mechanical damage; with higher fruit firmness	Bregoli *et al.*, 2002; Martinez- Romero *et al.*, 2000
Pear (Comice and Housui)	*Pyrus communis* L	PUT	Influenced ovule senescence, fertilization time and fruit set Extends effective pollination period Positively affected fruit set	Crisosto *et al.*, 1988, 1992; Franco-Mora, 2005
Plum (Japanese, Golden Japan, Black Diamond, Black Star, Santa Rosa, Angelino)	*Prunus silicina* Lindl.	PUT	Inhibited ethylene production with delayed fruit softening Delayed changes related to ripening and extended the storage (0 ± 1 ∘C) life for up to 6 weeks.	Khan and Singh, 2008, 2010; Khan *et al,* 2007, 2008; Serrano *et al.,* 2003; Perez-Vicente *et al.*, 2002
Pomegranate (Mollar de Elche, Rabbab and Mridula)	*Punica granatum* L.	SPD, PUT	maintained functional properties in pomegranate arils during storage: were effective on maintaining the concentration of ascorbic acid, total phenolic compounds, , total anthocyanins and total antioxidant activity (TAA) during storage; alleviated the affect of salinity and effected positively on growth relevant parameters of the seedlings; enhanced shelf life by alleviating chilling injury;	Mirdehghan *et al.*, 2007a, 2007b ; Amri *et al.*, 2011; Barman *et al.*, 2011a, 2011b
Tea Crabapple	*Malus hupehensis Rehd*	SPM, SPD	Alleviated lipid peroxidation induced by cadmium chloride stress	Zhao and Yang , 2008

Liu *et al.* (2006) studied the concentration of free polyamines during the growth and development of peach fruit. There was continued decrease in the contents of free polyamines from fruit set to ripening suggesting antagonistic effect of polyamines and senescence, explaining the indirect role of polyamines on growth and development, as these are considered the nutritional sink for the plant growth and development.

No major changes were observed in endogenous spermine and spermidine in pepper while Spermidine in case of tomato fruits during development. However, Put in bell pepper fruit and Spm in tomato fruit increased very early until about 30-38 days from fruit set and reached a minimum level at maturity and ripening. Tomato fruit showed a consistent increase in putrescine concentration (Yahia *et al.*, 2001).

Table 2. Effect of exogenous application of polyamines on growth, quality and shelf life of vegetables.

Crop	BN	PAs	Influences	References
Cucumber 'Changchun mici' and 'Beijing jietou'	*Cucumis sativus* L.	PUT, SPD	Enhance chilling tolerance through modulating antioxidative system	Zhang *et al.*, 2009
Globe artichoke	*Cynara Scolymus* L.	PUT	Improved growth, productivity and Quality	El-Abagy *et al.*, 2010
Melon	*Cucumis melo*	PUT, SPD, SPM	Delayed senescence by enhancing the activity of antioxidant enzymes and promoted a longer marketable life	Lester, 2000
Radish	*Raphanus sativus* L.		Acted as Antioxidant Protectors against Paraquat Damage in Cotyledons	Kim and Jin, 2006
Tomato	*Lycopersicon esculentum* M.	SPD, SPM	Improved pollen germination and tube growth in vitro under high temperature stress; effective in amelioration of NaCl stress stimulation and inhibition of pollen germination and pollen tube growth in vitro	Song *et al.*, 1999; Slathia *et al.*, 2012
zucchini squash	*Cucurbita pepo* L.		Reduced polygalacturonase activity and chilling injury incidence	Martinez-Tellez *et al.*, 2002

Role in plant growth and development
Polyamines are known to improve growth and development of plants because of their effects on cell division and differentiation. Such findings were confirmed in bean plants (Altman *et al.*, 1982). Abd El-Wahed *et al.*, (2005) found that Spd significantly enhanced plant height, number of branches, and shoot fresh and dry weight/plant during vegetative and flowering stages in chamomile plants. Moreover, putrescine has a regulatory role in promoting productivity of many plants such as sweet pepper (Talaat, 2003), tomato (Cohen *et al.*, 1982) and pea plants (Gharib and Hanafy, 2005).

It is an admitted fact that plant growth is supported by the organic carbon source which can alter the growth rate while its direction is regulated by plant growth regulators (Jimenez-Cervantes, *et al.*, 1998). The growth promoting effect of polyamines is considered because of their contribution to cellular carbon and nitrogen to the plants, secondly they are cationic molecules, positively charged under intracellular pH, which is helpful in plant growth and development. According to some researchers the increment effect of polyamine on growth rate is because they help in the uptake of minerals like N, P and K from soil as well (Shawky, 2003).

Table 3. Effect of exogenous application of polyamines on growth, quality and shelf life of medicinal plants.

Crop	BN	PAs	Inferences	References
Black Cumin	*Nigella sativa* L.	PUT	Significantly increased growth and yield parameters under heat stress	Talaat *et al.*, 2005
Chamomile	*Chamomilla recutita* L.	SPD	Had stimulatory effect on growth, flowering, biochemical constituents and essential oil contents	Abd El-Wahed and El Din, 2004.
Flax	*Linum usitatissimum*	PUT	Physiologically effected the growth and quality of flax plant and seed	El-Lethy *et al.*, 2010
Periwinkle	*Catharanthus roseus*	PUT	Photosynthetic pigments (chlorophyll a, chlorophyll b and carotenoids), soluble and total insoluble sugars, total proteins , total alkaloids in the leaves , endogenous GA3, IAA, cytokinins and ABA were increased	Talaat *et al.*, 2005
Sweet Basil	*Ocimum basilicum* L.	PUT	Significantly improved the physical and chemicals parameters including yield and oil contents	Talaat and Balbaa, 2010

The role of polyamines in plant growth and development has been studied by several researchers. Increased vegetative growth of gladiolus plant was observed by exogenous application of putrescine during the vegetative stage (Nahed *et al.*, 2009). Similar effects of polyamines were confirmed by Shawky (2003) who found the increase in the growth and leaf nutrients uptake in pepper. Putrescine treatment significantly increased the shoot and root biomass of trifoliate orange seedlings (Wu *et al.*, 2010). Putrescine has also been found to be a substitute for inorganic nitrogen for the growth of in vitro explants from dormant tubers of Helianthus tuberosum (Evans and Malmberg, 1989). Exogenous application of PUT and SPD enhanced the growth of oranges by helping in the uptake of nutrient elements from the roots (Qing-Sheng and Zou, 2009).

Table 4. Effect of exogenous application of polyamines on growth, quality and shelf life of ornamentals.

Crop	BN	Pas	Inferences	References
Chrysanthemum	*Chrysanthemum indicum* L.	PUT	Positively affected flower characters and photosynthetic pigments	Mahros *et al.*, 2011
Dahlia	*Dahlia pinnata*	PUT	Foliar sprays improved growth, flowering and photosynthetic pigments	Mahgoub *et al.*, 2011
Gladiolus	*Gladiolus grandflorum* L	PUT	Improved growth , flowering and chemical constituents	Nahed *et al.*, 2009
Periwinkle	*Catharanthus roseus* L	SPD	Incorporation into the nutrient medium stimulated pollen-tube growth in vitro in.	Prakash *et al.*, 1988

Role of Polyamines in flowering, fruit setting and fruit retention

Yield of the crop is directly related to the fruit set after pollination. Poor fruit set either by heavy post-bloom and preharvest drop, seldom produce economic crop (Callan, 1977; Lombard and Richardson, 1982; Lombard *et al.*, 1971). Low level of self fruit fullness because of the short effective pollination period (EPP) as in 'Comice' pear could also be the reason for the little fruit set (Williams, 1966). When flower clusters of apple were sprayed with polyamines, pistil longevity was prolonged and fruit set was improved (Wang *et al.*, 1996).
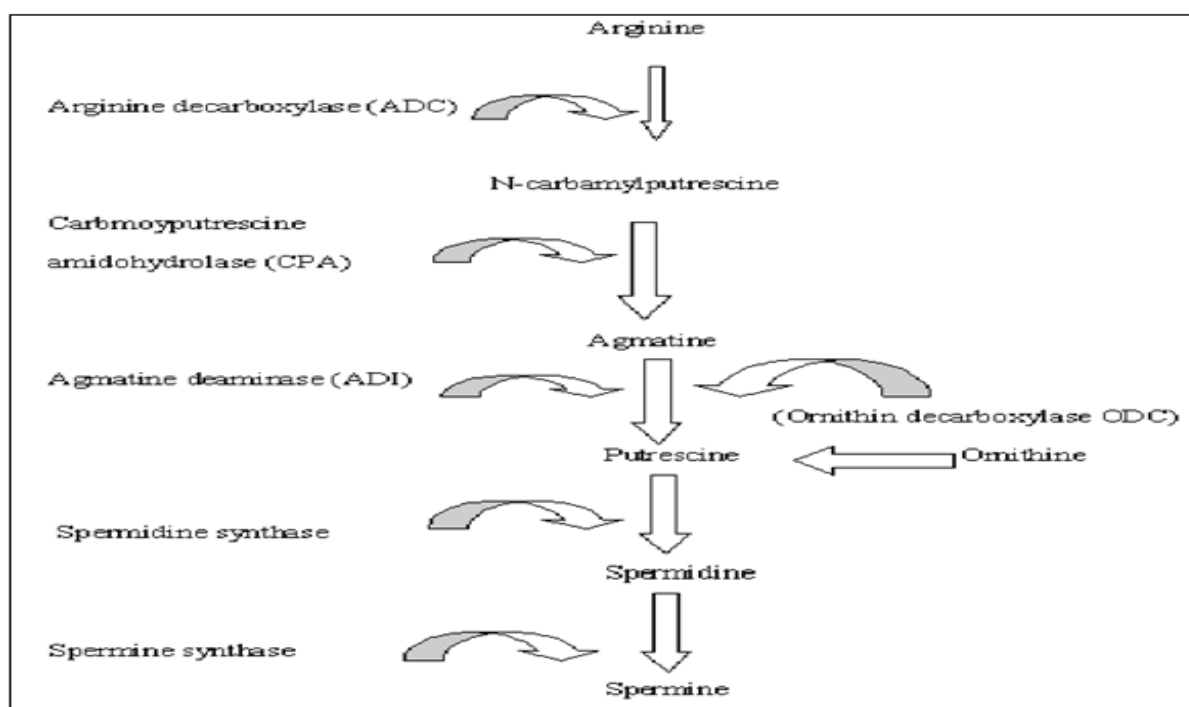

Fig. 1. Polyamine biosynthetic pathway (Kaur-Sawhney *et al.*, 2003).

Moreover, ethylene was evolved from pollinated flowers than from non-pollinated flowers. This observation suggests a possible role of ethylene in fertilization. Nichols *et al.* (1983) found an increase in l-aminocyclopropane-l-carboxylic acid (ACC), an ethylene precursor, in hand-pollinated styles of carnation flowers.

Putrescine applied at anthesis did not reduce the levels of ethylene evolved from flowers during the bloom period, although it extended ovule longevity and increased fruit set and yield (Crisosto *et al.*, 1988). Moreover putrescine increased effective pollination period (EPP) in the 'Comice' pear by improving the nitrogen and boron contents of leaves and flowers which play a vital role in increasing EPP (Ewart and Kliewer, 1977). Increase in the leaf nutrient contents including nitrogen by the application of polyamines have also been found in various other horticulture plants including gladiolus, pepper and trifoliate orange seedlings (Nahed, *et al.*, 2009; Shawky, 2003; Wu *et al.*, 2010).

Heavy fruit drop because of the development of abscion layer, is an important factor contributing to low fruit yield in fruit like mango as sometimes only 0.1% of set fruit reach maturity (Chadha, 1993). Because of the antiscenesce nature, polyamines have been reported to reduce the fruit drop by maximizing the fruit retention and increasing the yield in many fruits including mango (Singh and Singh, 1995; Singh and Janes; 2000; Malik and Singh, 2003; Malik and Singh, 2006), apple (Costa *et al.*, 1986), olive (Rugini and Mencuccini, 1985), litchi (Stern and Gazit, 2000) and grapes (Ponce *et al.*, 2002; Aziz *et al.*, 2001; Farag, *et al.*, 1998; Marzouk and Kaser 2011).
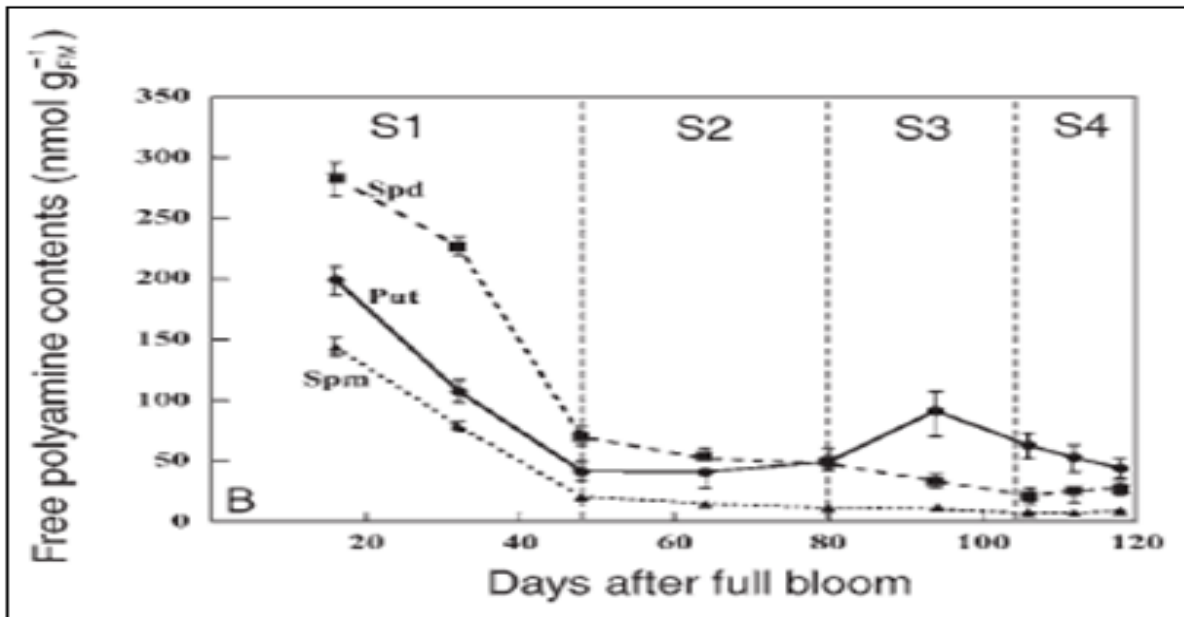
Fig. 2. Free Polyamine contents during growth and development of peach fruit (Liu *et al.,* 2006).

Stomatal movements

Stomata are responsible for the exchange of gases between plant and the environment. Changes in guard cell turgor that instigate opening and closing of stomatal aperture are controlled by number of factors through modulation of ion channel activity and pumps (Ward *et al.*, 1995). Potassium ions play an important role in the regulation of stomatal opening and closing. A number of studies have shown that inward K^+ channel-inhibiting processes or factors often inhibit stomatal opening. Such factors include ABA, Ca^{2+} levels and polyamines (Liu *et al.*, 2000).

Like ABA, polyamines, have a role in stomatal regulation, having different mechanism, whereas ABA elicit turgor loss by activating anion channels and outward K^+ channels (Pei *et al.*, 1997). On the contrary, polyamines do not affect inward K^+ or anion channels, suggesting thereby possibility of some other polyamine targets in addition to inward K^+ channels in guard cells for induction of stomatal closure. Stomatal regulation is one of the most studied mechanisms of plant responses to stresses. Many of the stress factors are known to elevate polyamines. Electrophysiological and molecular studies in animal systems have demonstrated the role of polyamines in modulation of ion channels by direct binding to the channel protein or membrane component (Johnson,

1996). Studies of Brüggemann *et al.* (1998) showed that in higher plants, polyamines block fast activating vacuolar cation channels. Among the ion channels in the guard cells, the inward K^+ channels are an important player in stomatal regulation and factors/processes blocking inward K^+ channels inhibiting stomatal opening. Studies of Liu *et al.* (2000) in *Vicia faba* leaves revealed involvement of polyamines in regulation of voltage-dependent inward K^+ channels in plasma membrane of guard cells. Whole-cell patch clamp analysis showed that intracellular applications of all natural polyamines including spermidine, spermine, cadaverine and putrescine induced closure of stomata by inhibiting the inward K^+ current across the plasma membrane of guard cells. Further, identification of target channel at molecular level revealed that spermidine induced closure of stomata, occurred due to inhibition of inward K^+ current carried by KATI channel. Single channel recording analysis indicated that regulation of K^+ channels by polyamines requires unknown cytoplasmic factors (Liu *et al.*, 2000). In an effort to identify the target channel at molecular level, they suggested that polyamines target KATI-like inward K^+ channels in guard cells to modulate stomatal movements hence provide a link between stress conditions, polyamine levels and regulation of stomatal movements.
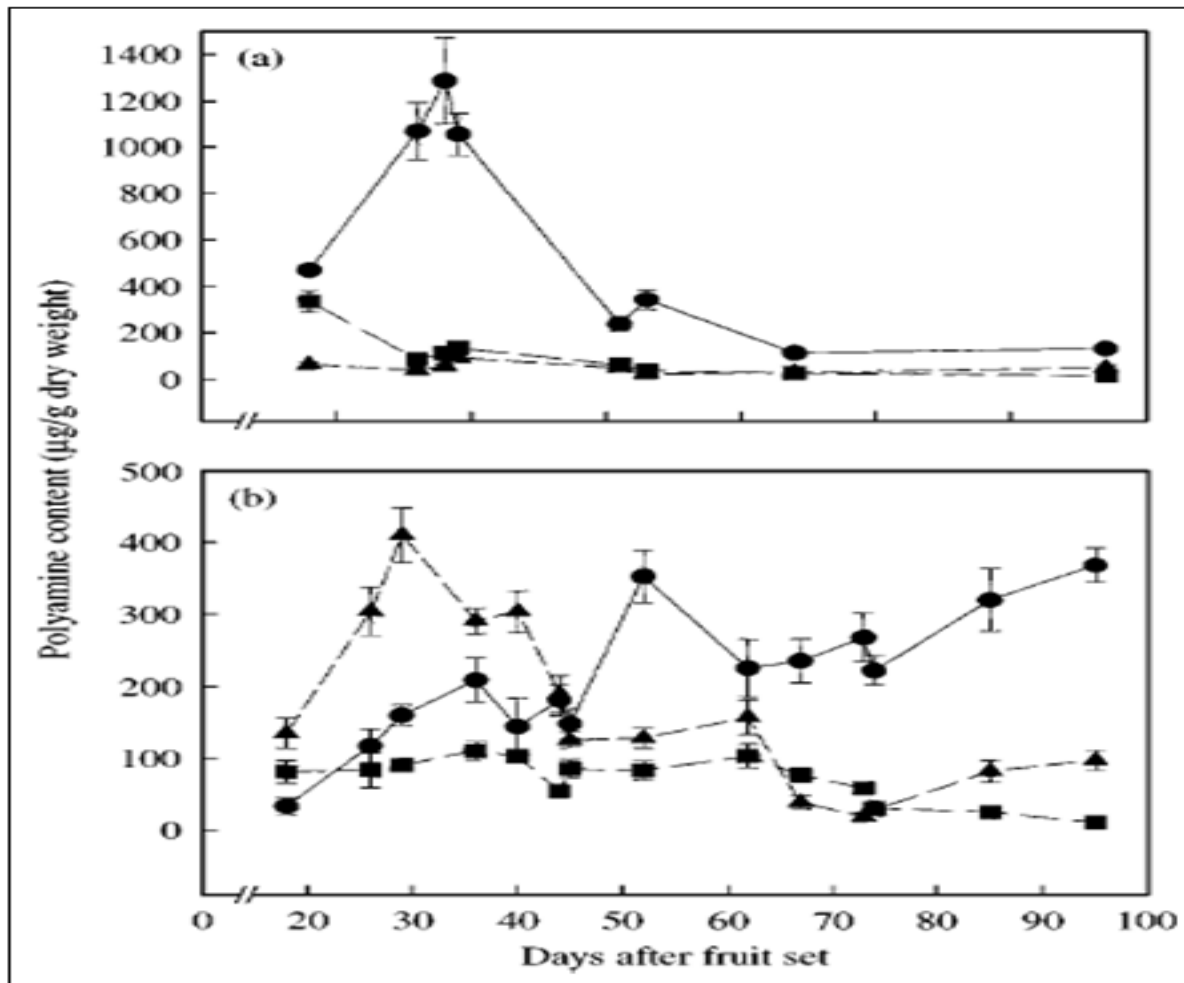
Fig. 3. Changes in the polyamines during development, maturation and senescence of bell pepper (a) and tomato (b) fruit. Putrescine (; Spermidine ; Spermine (Yahia *et al.*, 2001).

Role of polyamines in shelf life extension and anti-senescence agent

Senescence is a highly ordered and genetically regulated process, which can be viewed at cell, tissue, organ or whole plant level. The process is largely an oxidative, mainly characterized by cessation of photosynthesis, disintegration of organelle structures, loss of chlorophyll, proteins, and a dramatic increase in lipid oxidation, breakdown of cell wall components and disruption of cell membranes leading to loss of cell/tissue structure (Buchanan-Wollaston, 1997). Senescence, though a terminal developmental stage in the life cycle of a plant, can also be accelerated by an array of both abiotic and biotic factors (Smart, 1994). Sharp increase in the ethylene production is the key feature of climacteric fruits after physiological maturity like mango, banana, apple, peach, plum and apricot. During climacteric fruit ripening, a burst in

ethylene production occurs in concomitant with increased activities of 1-aminocyclopropane-1-carboxylic acid synthase (ACS) and 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) enzymes (Lelievre *et al.*, 1997), while the enzymatic changes that lead softening of the fruits are also associated with the fruit ripening. Major enzymes taking part in the softening of the fruits are polyestrase and endo, exo polygalacturonase (Huber, 1983).

As ethylene is a senesce promoting hormone and promotes fruit ripening. The researchers are interested to slow down the production of ethylene especially in the climacteric fruits to prolong the shelf life and maintain the quality for the longer period of time. Both polyamine and ethylene has the same precursor i.e. S-adenosyl methionine (SAM) so

biosynthesis of polyamines inhibit ethylene biosynthesis by competing for the common precursor (Pandey *et al.*, 2000), as both of them have opposite effect on the fruit ripening and senescence Many observations indicated that polyamines could inhibit the synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC), the precursor of ethylene, thus reducing ethylene production. Polyamines also inhibited auxin-induced ethylene production and conversion of methionine and ACC to Ethylene (Li *et al.*, 2004).

The inhibition of ethylene is reported in many horticultural crops including tomatoes by application of exogenous polyamines (Suttle, 1981). In cut carnation petals, Spm reduced ACC content, ethylene production, the activities and transcript amounts of ACC synthase and ACC oxidase (Lee *et al.* 1997). Ahmad *et al.*, (2007) reported that pre storage application of polyamines retarded fruit softening and ethylene production by lowering the activities of both the fruit softening and ethylene producing enzymes i.e. ACC, ACS. ACO exo-PG, endo-PG, PE, EGase during low temperature storage, thus improving the shelf life of the fruit. Similar effect of polyamines on reducing the production of ethylene was reported earlier in apricot (Martinez–Romero *et al.*, 2001), kiwi fruit (Petkou *et al.*, 2004), mango (Malik and Singh, 2005), peach (Bergoli *et al.,* 2002) and plum (Perez- Vicente *et al.,* 2001; Serrano *et al.*, 2003). Exogenously applied polyamines maintained the quality of blueberry for the longer period of time compared to control and heat treatment. (Fouad, 1996).

The antisenescence behavior of polyamines is not universal, as several counter examples have been reported where polyamines did not seem to retard senescence. The increased flower longevity and retarded senescence in cut carnation with aminotriazole was the result of inhibition of climacteric peak of ethylene production, but the treatment had no effect on levels of polyamines (Serrano *et al.*, 1991). Also, the addition of 10mM putrescine and spermine to culture solutions of cut carnations failed to increase flower longevity (Downs

and Lovell, 1986). On the contrary, an increase in endogenous level of free putrescine was observed in carnation flowers during senescence, while no variation in content of free polyamines was observed in climacteric and non-climacteric carnation flowers at pre-climacteric stage. Studies of Botha and Whitehead (1992) on petunia flowers showed that initial decline in polyamines during pre-climacteric stages was not accompanied by concomitant increase in ethylene production. This can be due to the fact that synthesis of ACC by ACC synthase is rate limiting step and not the availability of SAM in the pathway of ethylene production during pre-climacteric stage. This is further supported by the use of D-arginine and MGBG (Methylglyoxal-bis-guanylhydrazone), inhibitors of putrescine synthesis, respectively, which did not result in stimulation of ethylene synthesis during pre-climacteric phase of petunia flowers. However, the degree of relationship between polyamines and ethylene at both physiological and biochemical levels still remains unresolved.

Role of polyamines in abiotic and biotic stress
Major abiotic stress contributors are extreme temperatures, drought, salinity, frost, high intensity of sunshine and pollutants. While biotic stress contributors are the pathogens. Physiological processes of the horticultural crops are altered by the stress whether it is biotic or abiotic, hence, plant is damaged and the productivity is decreased which results in the economic losses.

It is established fact that all types of stresses produce the reactive oxygen species in the biological system which is highly toxic to the system and causes the oxidative stress (Alexieva *et al.*, 2003). Polyamines are well known to be relevant with different biotic and abiotic stresses (Tang *et al.*, 2004). A stress, therefore, affects the normal metabolic process in negative way. The extent of the consequences of the stress depends upon the time period to which the plants species remain exposed to the stress. The researchers have observed the role of polyamines reducing the damage done by different stresses, as they are reported to be radical scavengers (Kim and

Jin 2006). On the other hand some researchers argue that the counteraction of the cell with the stresses is due to the boost in the antioxidant defense systems by the application of polyamines (Velikova *et al.,* 2000).

Role of polyamines in eliminating the chilling injury
Application of polyamines can be used to inhibit the symptoms of chilling injury in the fruits and vegetables if the dozes are to be standardized in the near future, to enhance the marketable life and quality of the horticultural perishable commodities.

Increase in the membrane permeability is caused by the deleterious effects of chilling injury as it involves the modification of the membrane phase transition i.e. from a liquid- crystalline to a solid-gel state of the membrane lipids and proteins. This increases the ions and electrolyte leakage (Stanley, 1991; G´omez-Galindo *et al.,* 2004). Chilling Injury not only deteriorates the shape of the produce but also affects the quality very badly. The problem of chilling injury is very common in horticultural produce like banana, mango, peach and pomegranate in low temperature storage (Mirdehghan *et al.,* 2007), while polyamines induce cold acclimation, which results in the maintenance of the membrane integrity and fluidity. The imbalance that is created during the stress causes acidification of the cytoplasm with serious consequences on the metabolic regulation and the homeostasis of living cells (Flores *et al.,* 1985; Smith, 1984).

The association of polyamines with various stresses has been reported earlier (Mc-Donald and Kushad, 1986; Richard and Coleman 1952; Smith, 1982; Young and Galston 1983). Many theories have been reported for the accumulation of polyamines induced by stress (Flores *et al.,* 1985).

Studies on citrus resulted towards increase in phospholipids and other polar compounds during citrus cold hardiness (Yelenosky, 1985). This could be attributed to the increase in polyamines titers. Another hypothesis suggests that increase in polyamines during stress may have a direct role in

maintaining cell membrane thermostability against changes in fluidity and solute leakage (Smith, 1982). Application of 1 to 10 mM Put or Spm protected isolated protoplasts against lysis and reduced macromolecules breakdown (Altman *et al.,* 1977; Galston and Kaur-Sawhney, 1980). According to some studies the accumulation of polyamines has maintained the integrity of cell membrane (Guye *et al.,* 1986; Smith, 1982; Smith, 1971). A study was conducted to determine the polyamine levels in three citrus cultivars during low temperature acclimation. It was noted that citrus trees responded to low temperature acclimation with a uniform and substantial increase in polyamines (Kushad and Yelenosky, 1987).

Exogenous application of polyamines has been reported to reduce the symptoms of chilling injury during storage in various horticultural commodities. Post harvest dips of polyamines have been used to reduce the chilling injury in Zucchini squash (Kramer and Wang, 1989) and cucumber (Zhang *et al.,* 2009). Nair and Singh (2004) obtained the similar results when they applied the polyamines exogenously to the mango fruit. Pomegranate fruit treated with polyamines and stored at 2 °C developed lesser chilling injury symptoms as compared to control (Mirdehghan *et al.,* 2007). Thus some data appeared, which make it possible to consider polyamines not only as ROS scavengers but also as activates of the expression of the genes encoding antioxidant enzymes like CAT, SOD and POD (Hiraga *et al.* 2000; Aronova *et al.,* 2005).

In addition, during chilling injury, changes are also reported in the cell membrane lipid, resulting in the increase in permeability and leakage of ions (Stanley 1991, Gomez-Galindo *et al.,* 2004). All these changes were reduced significantly when the pomegranate fruit treated with polyamines kept in the storage conditions (Mirdehghan. *et al.* 2007). Martinez Romero *et al.,* (1999) reported polyamines as physiological markers of mechanical stress in lemon when exogenous polyamines were applied. However, the mechanism by which polyamine counteract the

stress effects are still unclear. The researchers argue the following possibilities.

Polyamines directly act as free radical scavengers (Drolet et al.., 1986, Bors et al.., 1989; Velikova et al.. 2000).

As they are polycationic in nature, they might interact with membrane, giving the stability to membrane in different stresses (Besford et al., 1993; Borrell et al.. 1997).

Heat Stress

High temperature stress is one of the key cause of lower yield and adaptability of the crops all around the world, especially when the crop is at its critical stage of growth and development (Mc Williams, 1980; Chen et al., 1982; Paulsen, 1994; Maestri et al., 2002). Even short term exposure to high temperatures ranging from 45 to 50 °C tempts noticeable alteration in the physiological processes of the plants (Bauer and Senger, 1979).

Synthesis of heat shock proteins (HSPs) is one of the responsive mechanisms adopted by the plant to shield the harmful effect of high temperature stress. Konigshofer and Lechner (2002) suggested that polyamines (PAs) might directly affect the synthesis of heat shock proteins at synthesis level or by affecting cell membrane properties.

The intensity of conjugated and free PAs, as well as PAO and ADC activities, were superior in the callus of tolerant agronomic crops under non stressed state. Moreover, infrequent PAs, norspermine and norspermidien, were perceived in tolerant one, which amplified under high temperature stress (Roy and Ghosh, 1996). Similar findings were reported by Konigshofer and Lechner (2002) working on tobacco. SAMDC (S-adenosyl-l-methionine decarboxylase) is one of the major regulatory enzymes in the synthesis of PAs. Transgenic tomato plants having SAMDC produced 1.7 to 2.4 time higher spermine and spermidine than non transgenic under heat stress. Enhanced antioxidant enzyme activity and the

protection of membrane lipid per oxidation were also observed in these plants. These findings revealed that improving PA biosynthesis in plants can be inductive for the resistance against high temperature stress (Cheng et al., 2009).

Heat resistance of two tomato cultivars was improved by the application of 4 mM spermidine, which also improved pollen growth and tube germination under high temperature stress (Song et al., 1999; Murkowski, 2001). Foliar application of spermidine (SPD) improved the activity of antioxidant enzymes of cucumber seedlings hence alleviated the effects of high temperature (Tian, et al., 2012).

Atmospheric Pollutant

Common atmospheric pollutants like SO_2 caused an increase in bound and free polyamines as observed in pea plants. This might be because of the release of H^+ ions, because sulfur dioxide absorption into cells forms acids (Priebe et al., 1978). Furthermore, beans treated with cadmium chloride ($CdCl_2$) had increased PUT contents (Weinstein et al., 1986). Furthermore, treating crabapple with SPM and SPD under cadmium chloride stress resulted in alleviated lipid per oxidation.

Ozone (O_3) is another most important constituent of air pollution which adversely effects the growth, development and ultimately the yield of the crop. Exogenous application of polyamines alleviated the deleterious effects of ozone in the tomato plants (Ormrod and Beckerson, 1986; Bors et al., 1989).

Foliar application of polyamines protected cucumber from the effect of UV radiation (Kramer et al., 1991) and paraquat damage in Radish by invoking the antioxidants protector enzymes i.e. SOD and APX (Kim and Jin 2006). These findings suggest that polyamines can be helpful in finding the solution of the environmental pollutants which are one of the major hindrances in the crop production now a day.

Drought and Salinity Stress

Drought causes adverse effects on plant growth and

productivity (Parida and Das, 2005). Means of irrigation are one of the major factors for successful plant production in dry zones. Not only lack of water, but also the bad quality of irrigation water, due to the presence of disproportionate ion concentrations another big issue of dry areas. High salt concentration in the irrigated water is problem in more than one third of the irrigated land worldwide (Postel, 1993). Among crop species, horticultural commodities are regarded as very sensitive to drought and soil salinity. An electric conductivity (EC) of 4 mS cm^{-1} (corresponding to 40 mM NaCl or 0.27% salt) of the saturation extract is regarded as critical in orchards. It is noteworthy that irrigation water for fruit trees should not exceed 2 mS cm^{-1}.

Shevyakova (1981) noted a remarkable buildup of putrescine (Put) and cadaverine (Cad) in bean and pea plants grown in high salt conditions. In contrary to findings of Shevyakova (1981) Smith (1973) and Anderson and Martin (1973) found PA (Put and Spd) metabolism did not change with the exposure to salinity changes. A similar trend was observed in *Vicia faba* (Fabaceae, Magnoliophyta) (Priebe and Jager 1978). Conversely, Tattini *et al.* (1993) recorded a spectacular reduction in putrescine contents of roots of olive plants supplied with increasing salinity. In tomato plants polyamines application was effective in amelioration of NaCl stress.

To check the association of the ADC (arginine decarboxylase) pathway in salinity stress response, putrescine biosynthetic gene expression, the polyamine titre and enzyme activities were examined in apple (*Malus sylvestris* L.) Mill. var. *domestica* (Borkh.) Mansf. *In vitro* callus under salt stress. Salt stress (200 mM NaCl) caused an increase in free putrescine content. Accumulation of putrescine was in accordance with induction of ADC activity and expression of the apple *ADC* gene (*MdADC*). All of these findings indicated that the ADC pathway was tightly involved in the salt stress response. Accumulation of putrescine under salt stress, suggests a possible physiological role of putrescine in alleviating stress damage (Liu *et al.*, 2006).

Disease control

The protection of fruit from invasion of fungal pathogens is largely due to activation of a highly coordinated biochemical and structural defense system that helps ward off the spread of pathogens (Lawton *et al.*, 1996; Schroder *et al.*, 1992). Chitinase and β-1,3- glucanase hydrolyze polymers of fungal cell walls, are thought to be involved in plant defense mechanisms against fungal infection (Collinge *et al.*, 1993; Schlumbaum *et al.*, 1986). *Phenylalanine ammonia-lyase* (PAL) is a key enzyme in the first step of the phenylpropanoid pathway, which is related to the plant defense system (Dixon and Paiva, 1995). POD activity produces the oxidative power for cross-linking of proteins and phenylpropanoid radicals resulting in reinforcement of cell walls against attempted fungal penetration (Huckelhoven *et al.*, 1999; Kristensen *et al.*, 1999).

Researchers have also suggested that β-1, 3-glucanase, PAL and POD are related to induced resistance in plants (Hammerschmidt *et al.*, 1982; Pellegrini *et al.*, 1994; Mohammadi and Kazemi, 2002; Qin *et al.*, 2003).

Increase in the activity of enzymes like POD and PPO was noted in the bean plant by Haggag (2005) when polyamines or their precursors were applied to the leaves of plants. The increase in the activity of these enzymes is related to the increase in the resistance against the disease causing organisms (Kumar and Balasubramanian, 2000).

Free and conjugated phenols as well as pathogen related proteins (PR) were enhanced followed by polyamines treatment. In fact, synthesis of phenols is important in many forms of resistance (Garriz *et al.*, 2003). The activity of pathogens related protein is another phenomenon by which the plants develop resistance against the viral and fungal infections. Expression of phytopathogenesis-related protein (PR) gene resulted in the reduced viral infection (Hiraga *et al.,* 2000). Hiraga *et al.* (2000) proposed a hypothesis that polyamines might have a role in resistance of plants against infection by activating PR

gene. But no work on this aspect on horticultural crops was observed during the review of literature.

The spread of disease depends upon the plants response in interacting with the pathogens (Walters, 2000; Walters, 2003; Cowely and Walters, 2002).

Polyamines conjugated to phenolic compounds, hydroxycinnamic acid amides (HCAAs), have been shown to accumulate in incompatible interactions between plants and a variety of pathogens, while changes in the diamine catabolic enzyme, diamine oxidase suggest a role for this enzyme in the production of hydrogen peroxidase during plant defense responses (Walters, 2003).

The increase in the activity of ethylene during pathogen infection lowers the concentration of polyamines which also describes the possible role of the polyamines in the control of viral and fungal infection (Jose *et al.*, 1991).

Biotic stress is a vastly open field for the scientists as no or very little literature is available explaining the role of polyamines in controlling the disease and infection in horticultural commodities. It is the demand of the day to work on this aspect to reduce the pre and post harvest losses due to diseases which are very high in developing countries.

Future prospects

Human interference has changed the natural climate, causing certain type of enhanced biotic and abiotic stresses and other adverse affects on the plants which have to feed the increasing population of the world. The role of polyamines has been studied by different scientists to solve agricultural issues but still a lot of research is needed to understand the proper phenomenon of the action of polyamines. Secondly, a few reports are there which show the effect of polyamines on inducing the resistance in agronomic crops against the pathogens and diseases, but a very little or no work is done in horticultural plants regarding this aspect. So there is great need of time to do the work in this direction, and to know the proper

mechanism of polyamines involved in inducing resistance against diseases and pathogens.

References

Abd-El-Wahed MSA, Karima M, Gamal-El-Din M. 2005. Effect of putrescine and atonik on growth and some biochemical constituents as well as essential oil composition of chamomile plant (*Chamomilla recutita* L., Rausch.). Journal of agriculture science. Mansoura University **30,** 869-882.

Abd-El-Wahed MSA, Gamal El-Din KM. 2004. Stimulation effect of spermidine and stigma sterol on growth, flowering, biochemical constituents and essential oil of chamomile plant (*Chamomill recutita* L., Rausch). Bulgarian Journal of Plant Physiology **30,** 48-60.

Ahmad SK, Sing Z, Abbasi NA. 2007. Pre storage putrescine application suppresses ethylene biosynthesis and retards fruits softening during low temperature storage in 'Angeline' plum. Postharvest Biology and Technology **46,** 36-46.

Alexieva V, Ivanov S, Sergiev I, Karanov E. 2003. Interaction between stresses. Bulgarian Journal of Plant Physiology Special Issue. 1-17.

Ali EAM, Sarrwy SMA, Hassan HSA. 2010. Improving canino apricot trees productivity by foliar spraying with polyamines. Journal of applied science research **6,** 1359-1365.

Al-Obeed RS. 2010. Improving fruit quality, marketability and storagability of Barhee date palm. World Applied Science Journal **9(6),** 630-637. http://dx.doi.org/10.1080/09637480120091982

Altman A, Kaur-Sawhney R, Galston AW. 1977. Stabilization of oat protoplast through polyamine-mediated inhibition of senescence. Plant Physiology **60,** 570-57.

Altman A, Friedman R, Amir D, Levin N. 1982.

Polyamine effects and metabolism in plants under stress conditions. In: Wareing, P.F. (ed.), Plant Growth Substances, Academic Press, London 483-494 p.

Amri E, Mirzaei M, Moradi M, Zare K. 2011. The effects of spermidine and putrescine polyamines on growth of pomegranate (*Punica granatum* L. cv 'Rabbab') in salinity circumstance. International Journal of Plant Physiology and Biochemistry **3,** 43-49.

Anderson JN, Martin RO. 1973. Identification of cadaverine in *Pisum sativum*. Phytochemistry **12,** 443–6.

Aronova EE, Shevyakova NI, Sresenko, LA, Kuznesov VIV. 2005. Cadaverine-induced induction of superoxide dismutase gene expression in *Mesmbryanthemum crystallinum L*. Doklady of Biological Science **403,** 1-3.

Autar K, Subhash M, Minocha C, Minocha R, Avtar K. 2010. Polyamines and cellular metabolism in plants: transgenic approaches reveal different responses to diamine putrescine versus higher polyamines spermidine and spermine. Amino Acids **38,** 405–413.
http://dx.doi.org/10.1007/s00726-009-0399-4.

Aziz A, Brun O, Audran JC. 2001. Involvement of polyamines in the control of fruitlet physiological abscission in grapevine (*Vitis vinifera*). Physiology Plantarum **113,** 50-58.

Barman K, Asrey R, Pal RK. 2011a. Putrescine and carnauba wax pretreatments alleviate chilling injury, enhance shelf life and preserve pomegranate fruit quality during cold storage. Journal of Food Science and Technology **51(1),** 111-117.
http://dx.doi.org/10.1007/s13197-011-0483-0.

Barman K, Asrey R, Pal RK. 2011b. Influence of putrescine and carnauba wax on functional and sensory quality of pomegranate (*Punica granatum* L.)

fruits during storage. Journal of Food Science and Technology **51,** 111-117.
http://dx.doi.org/10.1007/s13197-011-0483-0

Basiouny FM. 1996. Blueberry fruit quality and storability influenced by postharvest application of polyamines and heat treatments. Proceedings of Florida State Horticulture Society **109,** 269-272.

Bauer H, Senger M. 1979. Photosynthesis of ivy leaves (*Hedera lelix* L.) after heat stress. 11. Activities of RuBP carboxylase, Hill reaction and chloroplast ultra structure. Journal of Plant Physiology **95,** 359-369.

Berry JA, Bjorkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. Annual Reviews of Plant Physiology **31,** 491-543.
http://dx.doi.10.1146/annualreview.pp.31.060180.002423

Besford RT, Richardson CM, Campos JL, Tiburcio AF. 1993. Effects of polyamines on stabilization of molecular complexes in thylakoid membranes of osmotically – stressed oat leaves. Plantarum **189,** 201-206.

Borrell A, Carbonell L, Farras, R, Puig-Parellada P, Tiburcio AF. 1997. Polyamines inhibit lipid peroxidation in senescing oat leaves. Physiology Plantarum **99,** 385-390.
http://dx.doi.org/10.1111/j.1399-3054.1997.tb00551.x

Bors W, Langebartels C, Michel C, Sandermann H. 1989. Polyamines as radical scavengers and protectants against ozone damage. Phytochemistry **28,** 1589-1595.
http://dx.doi.org/10.1016/S0031-9422(00)97805-1

Botha ML, Whitehead CS. 1992. The effect of polyamines on ethylene synthesis during normal and pollination induced senescence of *Petunia hybrida* L. flower. Plantarum **188,** 478-483.

Bregoli AM, Scaramagli S, Costa G, Sabatini E, Ziosi V, Bionsim S, Torrigiani P. 2002. Peach (*Prunus persica*) fruit ripening: aminoethoxyvinylglycine (AVG) and exogenous polyamines affect ethylene emission and flesh firmness. Physiology Plantarum **114,** 472-481. http://dx.doi.org/1034/j.1399-3054.2002.1140317.x

Brüggemann UI, Pottosin II, Schönknecht G. 1998. Cytoplasmic polyamines block the fast-activating vacuolar cation channel. Plant Journal **16,** 101-105.

http://dx.doi.org/10.1046/j.1365313x.1998.00274.x

Buchanan-Wollastonsd V. 1997. The molecular biology of leaf senescence. Journal of Experimental Botany **48,** 181-199.

Callan NW. 1977. Effect of boron sprays on fruit set, fruit quality, boron distribution, and floral morphology of 'Italian' prune (*Prunus Domestica* L.). PhD, Oregon State University Corvallis. (Dissertation Abstract International. 77-15366).

Chadha KL. 1993. Fruit drop in mango. In: Chadha, K.L., Pareek, O.P. (Eds.), Advances in Horticulture, vol. 3. Malhotra Publishing House, New Delhi. 1131–1166.

Chen HH, Shen ZY, Li PH. 1982. Adaptability of crop plants to high temperature stress. Crop Science **22,** 719-725.

http://dx.doi.org/10.2135/cropsci1982.0011183X002200040006x

Cheng L, Zou Y, Ding S, Zhang J, Yu X, Cao J, Lu G. 2009. Polyamine accumulation in transgenic tomato enhances the tolerance to high temperature stress. Journal of integrated plant biology. **51,** 489-99.

http://dx.doi.org/10.1111/j.17447909.2009.00816.x.

Cohen E, Arad S, Heimer YM, Mizrahi Y. 1982.

Participation of ornithine decarboxylase in early stages of tomato fruit development. Plant Physiology**. 70,** 540-543.
http://dx.doi.org/10.1104/pp.70.2.54.0

Collinge DB, Kragh KM, Mikkelsen JD, Nielsen KK, Rasmussen U, Vad K. 1993. Plant chitinases. Plant Journal. 3, 31-40.
http://dx.doi.org/10.1046/j.1365-313X.1993.t01-1-00999.x

Costa G, Biasi R, Bagni N. 1986. Effect of putrescine on fruiting performance of apple (cv. Hi Early). Acta Horticulturae. **179,** 355-361.

Costa G, Bagni N. 1983. Effects of polyamines on fruit set of apple. Horticulture Science **18,** 50-61.

Cowely T, Walters DR. 2002. Polyamine metabolism in barley reacting hypersensitively to the powdery mildew fungus *Blumeria graminis* spp. Plant Cell Environment **25,** 461-468.

Crisosto CH, Lombard PB, Sugar D. 1988. Putrescine influences ovule senescence, fertilization time and fruit set in 'Comice' pear. Journal of the American Society for Horticultural Science **113,** 708-712.

Crisosto C, Garner D, Sibbett S, Day K. 1992. Maturity studies on Asian pear. Central Valley Postharvest Newsletter **1,** 1-3.

Dixon RA, Paiva NL. 1995. Stress-induced phenylpropanoid metabolism. Plant Cell **7,** 1085-1097.
http://dx.doi.org/10.1105/tpc.7.7.1085

Downs CG, Lovell PH. 1986. The effect of spermidine and putrescine on the senescence of cut carnations. Plant Physiology **66,** 679-684.

Drolet G, Dumbroff EB, Legg RL, Thompson JE. 1986. Radical scavenging properties of polyamines. Phytochemistry **25,** 365-371.

http://dx.doi.org/10.1016/s0031-9422(00)85482-5

El-Abagy HMH, Rashid EM, Abdel-Mawgoud AMR, El-Greadly NHM. 2010. Physiological and biochemical effects of some bioregulators on growth, productivity and quality of artichoke (*Cynara scolymus* L.) plant. Research Journal of Agriculture and Biological Sciences **6,** 683-690.
http://dx.doi.org/10.1146/annurev.pp.40.060189.00 1315

El-Lethy SR, Ayad HS, Talaat IM. 2010. Physiological effect of some antioxidants on flax plant (*Linum usitatssimum* L.). World Journal of Agriculture. Sciences **6,** 622-629.

Evans PT, Malmberg RL. 1989. Do polyamines have roles in plant development? Annual Reviews of Plant Physiology Plant Molecular Biology. **40,** 235-269.
http://dx.doi.org/10.1146/annurev.pp.40.060189.00 1315

Ewart A, Kliewer WM. 1977. Effects of controlled day and night temperatures and nitrogen on fruit set, ovule fertility, and fruit composition of several wine grape cultivars. American Journal of Enology and Viticulture **28,** 88-95.

Farag KM, Kasem HA, Hussein A. 1998. Enhancing color formation of flame seedless grapes using safe compounds or low dose of ethephone. Emirates Journal of Agriculture Science **10,** 47-57.

Feirer RP, Wann SR, Einspahr DW. 1985. The effects of spermidine synthase on in vitro plant development. Plant Growth Regulations **3,** 319-327.
http://dx.doi.org/10.1007/BF00117589

Flores HE, Filner P. 1985. Polyamine catabolism in higher plants: characterization of pyrroline dehydrogenase. Plant Growth Regulators **3,** 277-291.
http://dx.doi.org/10.1007/BF00117586

Fouad MB. 1996. Blueberry fruit quality and storability influenced by postharvest application of polyamines and heat treatments. Proceedings of Florida State Horticulture Society **109,** 269-272.

Franco-Mora O, Tanabe K, Itai A, Tamura F, Itamura H. 2005. Relationship between endogenous free polyamine content and ethylene evolution during fruit growth and ripening of Japanese pear (*Pyrus pyrifolia* Nakai). Journal of Japanese Society for Horticulture Sciences **74,** 221–227.

Galston AW, Flores HE. 1991. Polyamines and plant morphogenesis, IN: Slocum R, Flores HE. (eds). The biochemistry and physiology of polyamines in plants. CRC Press, Boca Raton, Florid. 175-186 p.

Galston AW, Kaur-Sawhney R, 1980. Polyamines and plant cells. What's New in Plant Physiology **11,** 5-8.

Garriz A, Dalmasso M, Piecckenstain FL, Ruiz O. 2003. The putrescine analogue 1-aminooxy-3-aminopropane perturbs polyamine metabolism in the phytopathogenic fungus *Sclerotinia sclerotiorum*. Archives of Microbiology **180,**169-175.

Gharib AA, Ahmed AH. 2005. Response of pea plants (*Pisum sativum* L.) to foliar application of putrescine, glucose, foliar feed and silicon. Journal of Agriculture Sciences Mansoura University **30,** 7563-7579.
http://dx.doi.org/10.1007/s00203-003-0572-1

Gomez-Galindo F, Herppich W, Gekas V, Sjoholm I. 2004. Factors affecting quality and postharvest properties of vegetables. Integration of water relations and metabolism. Critical Reviews of Food Science and Nutrition **44,** 139-154.
http://dx.doi.org/10.1080/104086904904246.49

Groppa MD, Benavides MP. 2008. Polyamines and abiotic stress. Recent advances. Amino Acids **34,** 35-45.
http://dx.doi.org/10.1007/s00726-007-0501-8

Guye MG, Vigh L, Wilson JM. 1986. Polyamine titre in relation to chill sensitivity of Phaseolus sp. Journal of Experimental Botany **37,** 1036-1043. http://dx.doi.org/10.1093/jxb/37.7.1036

Haggag WM. 2005. Polyamines: induction and effect on rust disease control of bean. Plant Pathology Bulletin **14,** 89-102.

Hammerschmidt R, Nuckles EM, Kuc J. 1982. Association of enhanced peroxidase activity with induced systemic resistance of cucumber to *Colletotrichum lagenarium.* Physiology and Plant Pathology **20,** 73–82. http://dx.doi.org/10.1016/0048-4059(82)90025-X

Hiraga S, Ito H, Yamakawa H, Ohtsubo N, Seo S, Mitsuhara I, Matsui H, Homma M, Ohashi Y. 2000. An HR-induced tobacco peroxidase gene is responsive to spermine, but not to salicylate, methyl jasmonate, and ethephon. Molecular Plant-Microbe Interaction 13, 210- 216. http://dx.doi.org/10.1094/MPMI.2000.13.2.210

Huber DJ. 1983. The role of cell wall hydrolyase in fruit softening. Horticulture Reviews **5,** 169-219.

Hückelhoven R, Fodor J, Preis C, Kogel KH. 1999. Hypersensitive cell death and papilla formation in barley attacked by the powdery mildew fungus are associated with H_2O_2 but not with salicylic acid accumulation. Plant Physiology **119,** 1251–1260.

Hye-Sook K, Chang-duck J. 2006. Polyamines as antioxidant protectors against paraquat damage in Radish (*Raphanus Sativus* L.) cotyledons. Journal of Plant Biology **49,** 237-246. http://dx.doi.org/10.1007/bf03030539

Jiménez-Cervantes C, Martínez-Esparza M, Solano F, Lozano JA, García- Borron JC. 1998. Molecular interactions within the melanogenic complex: formation of heterodimers of tyrosinase and TRP1 from B16 mouse melanoma. Biochemistry Bio-physics Research Communication **253,** 761- 767.

Johnson TD. 1996. Modulation of channel function by polyamines. Trends in Biochemical Sciences **17,** 22-27. http://dx.doi.org/10.1016/0165-6147(96)81566-5

Jose MB, Carbonell J, Conejero V. 1991. Polyamines in plant infected by citrus exocortis viroid or treated with silver ions and ethephon. Plant Physiology **96,** 1053-1059.

Kassem HA, Al-Obeed RS, Ahmed MA, Omar AKH, 2011. Productivity, fruit quality and profitability of jujube trees improvement by Preharvest application of agro-chemicasl. Middle-East Journal of Scientific Research **9,** 628-637.

Kaur-Sawhney R, Shih L, Flores HE, Galston AW. 1982. Relation of polyamine synthesis and titer to aging and senescence in oat leaves. Plant Physiology **69,** 405-410. http://dx.doi.org/10.1104/pp.69.2.405

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

Khan AS, Singh Z, Abbasi NA, Swinny EE. 2008. Pre or post harvest application of putrescine and low temperature storage affect fruit ripening and quality of 'angeline' plum. Journal of Science Food and Agriculture **88,** 1686-1695.

Khan AS, Singh Z, Abbasi NA. 2007. Pre storage putrescine application suppresses ethylene biosynthesis and retards fruit softening during low temperature storage in 'Angeline' plum. Postharvest Biology and Technology **46,** 36-46.

Kim H, Jin C. 2006. Polyamines as antioxidant protectors against paraquat damage in radish (*Raphanus sativus* L.) cotyledons. Journal of Plant Biology **49,** 237-246. http://dx.doi.org/10.1007/BF03030539

Kramer GF, Norman HA, Krizek DT, Mirecki RM. 1991. Influence of UV-B radiation on polyamies, lipid peroxidation and membrane lipid in cucumber. Phytochemistry **30,** 2101-2108.

Kramer GF, Wang YC. 1989**.** Reduction of chilling injury in zucchini squash bytemperature management, Horticulture Science **24**, 995– 996.

Kristensen BK, Bloch H, Rasmussen SK, 1999. Barley coleoptile peroxidases. Purification, molecular cloning, and induction by pathogens. Plant Physiology **120,** 501-512.

Kumar ALR, Balasubramanian P. 2000. Induction of phenols in groundnut rust resistance. International Archives Newsletter **20,** 55-57.

Königshofer H, Lechner S. 2002. Are polyamines involved in the synthesis of heat-shock proteins in cell suspension cultures of tobacco and alfalfa in response to high-temperature stress. Plant Physiology and Biochemistry **40,** 51-59.

Kushad MM, Yelenosky G. 1987. Evaluation of polyamine and proline levels during low temperature acclimation of citrus. Plant Physiology **84,** 692-695. http://dx.doi.org/10.1104/pp.84.3.692.

Lawton K, Friedrich L, Hunt M, Weymann K, Delaney T, Kessmann H, Staub T, Ryals J. 1996. Benzothiadiazole induces disease resistance in Arabidopsis by activation of the systemic acquired resistance signal transduction pathway. Plant Journal **10,** 71–82.

Lee MM, Lee SH, Park KY. 1997. Effects of Spermine on Ethylene Biosynthesis in Cut Carnation (*Dianthus caryophyllus* L.) Flowers during Senescence. Journal of Plant Physiology **151,** 68–73.

Lelievre JM, Latche A, Jones B, Bouzayen M, Pech JC. 1997. Ethylene and fruit ripening. Physiology Plantarum **101,** 727-739.

Lester GE. 2000. Polyamines and their cellular anti-senescence properties in honey dew muskmelon fruit. Plant Science **160,** 105-112. http://dx.doi.org/10.1016/S0168-9452(00)00369.1

Li CZ, Wei XP, Li W, Wang GX. 2004. Relationship between Ethylene and Spermidine in the Leaves of *Glycyrrhiza uralensis* Seedlings under Root Osmotic Stress. Russian Journal of Plant Physiology **51,** 372–378.

Liu J, Nada K, Honda C, Kitashiba H, Wen X, Pang X, Moriguchi T. 2006. Polyamines biosynthesis of apple callus under salt stress: importance of arginine decarboxylase pathway in stress response. Journal of Experimental Botany. **57,** 2589-2599. http://dx.doi.org/10.1093/jxb/erl018

Liu J, Nada K, Honda C, Kitashiba H, Wen X, Pang X, Moriguchi T. 2006. Role of polyamines in peach fruit development and storage. Tree physiology **26,** 791-798.

Liu JH, Honda C, Moriguchi T. 2006. Involvement of polyamines in floral and fruit development. Japan Agricultural Research Quarterly. **40,** 51-58.

Liu K, Fu HF, Bei Q, Luan S. 2000. Inward potassium channel in guard cells as a target for polyamine regulation of stomatal movements. Plant Physiology **124,** 1315-1325.

Lombard PB, Richardson DG. 1982. Increased fruit set and cropping of 'Comice' pear trees with an ethylene inhibitor, aminoethoxyvinylglycine. Acta Horticulturae **124,**165-169.

Lombard PB, Williams RR, Thompson MM. 1971. Effective pollination –the facts of life behind uniform pear cropping. Proceedings of Oregon Horticulture Society **62,** 31-36.

Maestri E, Kluevan N, Perrotta C, Gulli M,

Nguyen HT, Marmiroli N. 2002. Molecular genetics of heat tolerance and heat shock proteins in cereals. Plant Molecular Biology **48,** 667-681.

Mahgoub MH, Abd El Aziz NG, Mazhar AMA. 2011. Response of dahlia piñata L. plant to foliar spray with putrescine and thiamine on growth, flowering and photosynthetic pigments. American-Eurasian Journal of Agriculture and Environmental Sciences **10,** 769-775.

Mahros KM, El-Saady MB, Mona HM, Afaf MH, Imran ME. 2011. Effect of putrescine and uniconazole treatments on flower characters and photosynthetic pigments of *Chraysanthemum indicum* L. plant. Journal of American Society for Horticulture Sciences **7,** 399-408.

Malik AU, Sing Z. 2005. Pre storage application of polyamines improves shelf life and fruit quality in magngo. Journal of Horticulture Sciences and Biotechnology **80,** 363-369.
http://dx.doi.org/10.1080/14620316.2005.11511945

Malik AU, Sing Z. 2006. Improved fruit retention, yield and fruit quality in mango with exogenous application of polyamines. Scientia Horticulturae **110,** 167-174.
http://dx.doi.10.1016/j.scienta.2006.06.028

Malik AU, Singh Z. 2003. Abscission of mango fruitlets as influenced by biosynthesis of polyamines. Journal of Horticulture Sciences and Biotechnology **78,** 721–727.
http://dx.doi.org/10.1080/14620316.2003.11511689

Martinez- Romero D, Valero D, Serrano M, Martinez-Sanchez F, Riquelme F. 1999. Effects fo post harvest putrescine and calcium treatments on reducing mechanical damage and polyamines and abscisic acid levels during lemon storage. Journal of Science Food and Agriculture **79,** 1589-1595.
http://dx.doi.org/10.1002/(SICI)10970010(199909)79:12

Martinez- Romero D, Valero D, Riquelme F, Zuzunaga M, Serrano M, Burlo F, A Carbonell. 2001. Infiltration of putrescine into apricot helps handling and storage. Acta Horticulturae **553,** 189-192.

Martin-Tanguy J. 2001. Metabolism and function of polyamines in plants: recent development (new approaches). Plant Growth Regulation **34,** 135–148.
http://dx.doi.10.1023/A:1013343106574

Martinez-Tellez MA, Ramos-clamont MG, Gardea AA, Vargas-Arispuro I. 2002. Effect of infiltrated polyamines on polygalaturonase activity and chilling inury responses in zucchini squash (*Cucurbita pepo* L.). Biochemistryistry. Biophysics Research Communication **295,** 98-101.

Marzouk HA, Kassem HA. 2011. Extending harvest season and enhancing the shelf life of navel oranges by Preharvest treatments with different bioregulators. American-Eurasian Journal of Agriculture and Environonmental Sciences **10,** 396-403.

Marzouk HA, Kassem HA. 2011. Improving yield, quality and shelf life of Thompson seedless grapevine by preharvest foliar applications. Scientia Horticulturae **130,** 425-430.
http://dx.doi.org/10.1016/j.scienta.2011.07.013

Mc Williams JR. 1980. Adaptation of plants to water and high temperature stress; summary and synthesis. In N.C. Turner and P. J. Kramer (eds). Adaptioatin of plantas to water and high temperature stress. Jhon Wiley, New York. 444-447 p.

Mcdonald RE, Kushad MM. 1986. Accumulation of putrescine during chilling injury of fruits. Plant Physiology **82,** 324-326.
http://dx.doi.org/10.1104/pp.82.1.324

Mengoli M, Chriqui D, Bangni N. 1992. Protein, free amino- acid and polyamine contents during

development of hairy root Nicotiana–tabacum plants. Plant Physiology **139,** 697-702.

Mirdehghan SH, Rahemi M, Serrano M. 2007b. The application of polyamines by pressure or immersion as a tool to maintain fuctional properties in stored pomegranate arils. Journal of Agriculture and Food Chemistry **55,** 755-760.
http://dx.doi.org/10.1021/jf062985v

Mirdehghan SH, Rahemi M, Castillo S, Martinez-Romero, Maria Serrano D, Valero D. 2007. Pre- storage application of polyamines by pressure immersion improves shelf life of pomegranate stored at chilling temperateure by increasing endogenous polyamine levels. Postharvest Biology and Technology **44,** 26-33.

Mohammadi M, Kazemi H. 2002. Changes in peroxidase and polyphenol activity in susceptible and resistant wheat heads inoculated with *Fusarium graminearum* and induced resistance. Plant Science **162,** 491–498.

Muhitch MJ, Fletcher JS. 1985. Influence of culture age and spermidine treatment on the accumulation of phenolic compounds in suspension cultures. Plant Physiology **78,** 25-29.

Murkowski A. 2001. Heat stress and spermidine: effect on chlorophyll fluorescence in tomato plants. Biology Plantarum **44,** 53-57.
http://dx.doi.org/ 10.1023/A:1017966203859.

Nahed GA, Lobana ST, Soad MMI. 2009. Some studies on the effect of putrescine, ascorbic acid and thiamine on growth, flowering and some chemical constituents of gladiolus plants nubaria. Ozean Journal of Applied Sciences **2,** 169-179.

Nair S, Singh Z. 2004. Chilling injury in mango fruit in relation to biosynthesis of free polyamines. Journal of Horticulture Sciences and Biotechnology **79,** 515-522.
http://dx.doi.org/10.1080/14620316.2004.1151179.8

Nichols R, Bufler G, Mor Y, Fujino DW, Reid MS. 1983. Changes in ethylene production and l-aminocyclopropane- 1-carboxylic acid content of pollinated carnation flowers. Journal of Plant Growth Regulation. **2,** l-8.

Ormrod DP, Becker son DW. 1986. Polyamines as antiozonants for tomato. Horticulture Science **21,** 1070-1071.

Pandey S, Ranade SA, Nagar PK, Kumar N. 2000. Role of polyamine and ethylene as modulators of plant senescence. Journal of Bioscience **25,** 291-299.
http://dx.doi.org/10.1007/BF027039.38

Parida AK, Das AB. 2005. Salt tolerance and salinity effects on plants. A Review. Ecotoxicology and Environmental Safety **60,** 324-349.
http://dx.doi.org/10.1016/j.ecoenv.2004.06.010

Prakash L, Dutt M, Prathapsenan G. 1988. NaCl alters contents of nucleic acid, protein, polyamine and the activity of agmatine deiminase during germination and seedling growth of rice (*Oryza sativa* L.). Australian Journal of Plant Physiology **15,** 260–7.

Paulsen GM. 1994. High temperature response of crop plants. In K. J. Boote, J. M. Bennett, T. R. Sinclair, and E. M. Paulsen (eds), Physiology and determination of crop yield. Amer. Soc. Agron. Madison 365-389 p.

Pei ZM, Kuchitsu K, Ward JM, Schwarz M, Schroeder JI. 1997. Differential abscisic acid regulation of guard cell slow anion channels in Arabidopsis wild type and abi I and abi Z mutants. Plant Cell **9,** 402-423.
http://dx.doi.org/10.1105/tpc.9.3.40.9

Pellegrini L, Rohfritsch O, Fritig B, Legrand M. 1994. Phenylalanine ammonia-lyase in tobacco. Plant Physiology **106,** 877–886.

Perez-vicente A, Martinez romero D, Carbonell A, Burlo F, Serrano M, Valero D, Riquelm F, Zuzunaga M. 2001. Role of exogenous putrescine on the metabolism of conjugated polyamines in mechnically damaged plum during storage. Acta Horticulturae **553,** 193-194.

Petkou IT, Prista TS, Sfakiotakis EM. 2004. Effect of polyamines on ethylene production, respiration and ripening of kiwifruit. Journal of Horticulture Science and Biotechnology **79,** 977-980.

Pilar GJ, Rodrigo M, Robaina RR. 1998. Influence of plant growth regulators, polyamines and glycerol interaction on growth and morphogenesis of carposporelings of Grateloupia cultured in vitro. Journal of Applied Phycology **10,** 95–100.

Ponce MT, Guinazu M, Tizio R. 2002. Effect of putrescine on embryo development in the stenosper mocarpic grape Cvs. Emperatriz and Fantasy. Vitis **41,** 53-54.

Postel S. 1993. Water in crisis. A guide to the world's fresh water resources, oxford university press, Newyork pp. 56-66.

Priebe A, Jager HJ. 1978. Effect of NaCl on the levels of putrescine and related polyamines in plants differing in salt tolerance. Plant Science. Letter **12,** 365–9.

Qin GZ, Tian SP, Xu Y, Ya KW. 2003. Enhancement of biocontrol efficacy of antagonistic yeasts by salicylic acid in sweet cherry fruit. Physiology Molecular Plant Pathology **62,** 147–154.

Qing-Sheng WU, Zou Y. 2009. The effect of dual application of arbuscular mycorrhizal fungi and polyamines upon growth and nutrient uptake on trifoliate orange (Poncirus trifoliate) Seedlings. Notulae Botanicae Horti Agrobotanici Cluj-Napoca **37,** 95-98.

Rao MV, Ormrod DP. 1995. Ozone Exposure decreases UBV sensitivity in a UVB-sensetive flavonoid mutant of Arabiodopsis. Photochemisty and Photobiology **61,** 71-78.

Richard FJ, Coleman RG. 1952. Occurrence of putrescine in potassium deficient barley. Nature **170,** 460.

Rugini E, Mencuccini M. 1985. Increased yield in the olive with putrescine treatment. Horticulture Science **20,** 102-103.

Roy M, Ghosh B. 1996. Polyamines, both common and uncommon, under heat stress in rice (*Oriza sativa*) callus. Physiology Plantarum **98,** 196-200. http://dx.doi.org/10.1111/j.13993054.1996.tb00692.x

Saba MK, Arzani K, Barzegar M. 2012. Postharvest polyamines application alleviates chilling injury and effects apricot storage ability. Journal of Agriculture and Food chemistry **60,** 8947-8953. http://dx.doi.org/10.1021/jf302088e

Saftner RA, Baldi BG. 1990. Polyamine levels and tomato fruit development: Possible interaction with ethylene. Plant Physiology **92,** 547-550.

Schlumbaum A, Mauch F, Vogeli U, Boller T. 1986. Plant chitinases are potent inhibitors of fungal growth. Nature **324,** 365–367.

Schroder M, Hahlbrock K, Kombrink E. 1992. Temporal and spatial patterns of β-1, 3-glucanase and chitinase induction in potato leaves infected by Phytophthora infestans. Plant Journal **2,** 161–172.

Serrano M, Martinez-Romero D, Guillen F, Valero D. 2003. Effect of exogenous putrescine on improving shelf life of four plum cultivars. Postharvest Biology and Technology **30,** 259-271.

Serrano M, Romojaro F, Casas JL, Acosta M. 1991. Ethylene and polyamine metabolism in climacteric and nonclimacteric carnation flowers. Horticulture Science **26,** 894-896.

Shawky NBT. 2003. Physiological studies on the effect of salinity, ascorbic acid and putrescine on sweet pepper plant. Ph. D. thesis, Fac. Agric., Cairo University, Egypt **21,** 1070-1071.

Singh Z, Janes J. 2000. Regulation of fruit set and retention in mango with exogenous application of polyamines and their biosynthesis inhibitors. Acta Horticulturae **509,** 675–680.

Shevyakova NI, Arutyunova NV, Stroganov BP. 1981. Distribution of arginine and putrescine metabolism in cotton leaves in the presence of excessive Na_2SO_4 Sov. Plant Physiology **28,** 594-600.

Singh Z, Singh L. 1995. Increased fruit set and retention in mango with exogenous application of polyamines. Journal of Horticulture Science **70,** 271–277.

Slathia S, Sharma A, Choudhary SP. 2012. Influence of exogenously applied epibrassinolide and putrescine on protein content, antioxidant enzymes and lipid peroxidation in Lycopersicon esculentum under salinity stress. Amererican Journal of Plant Sciences **3,** 714-720.
http://dx.doi.org/10.4236/ajps.2012.36086

Smart CM. 1994. Gene expression during leaf senescence. New Phytologist **126,** 419-448.

Smith TA. 1971. The occurrence, metabolism and function of amines in plants. Biological Reviews **46,** 201-241.
http://dx.doi.org/10.1111/j.1469-185X.1971.tb01182.x

Smith TA. 1973. Amine levels in mineral deficient *Hordeum vulgare* leaves. Phytochemisty **12,** 2093–100.

Smith TA. 1982. The Function and metabolism of polyamines in higher plants. In PF Wareing, ed, Plant Growth Substances. Academic Press, New York pp. 463-472.

Smith T.A. 1984. Putrescine and inorganic ions. Adv. Phytochemistry **18,** 7-54.

Solcum RD, Kaur-Sawhney R, Galston AW. 1984. The physiology and biochemistry of polyamines in plants. Archives of Biochemistry and Biophysics **235,** 283-303.

Stanley DW. 1991. Biological membrane deterioration and associated quality losses in food tissues. Crititical Reviews of Food Science and Nutrition **30,** 487-553.

Song J, Nada K, Tachibana S. 1999. Ameliorative effect of polyamines on the high temperature inhibition of in vitro pollen germination in tomato (*Lycopersicon esculentum* Mill.). Scintia Horticulturae **80,** 203–212.

Song J, Nada K, Tachibana S. 2001. The early increase of S-adenosylmethionine decarboxylase activity is essential for the normal germination and tube growth in tomato (*Lycopersicon esculentum* Mill.) pollen. Plant Science **161,** 507–515.

Song J, Nada K, Tachibana S. 1999. Ameliorative effect of polyamines on high temperature inhibition of in vitro pollen germination in Tomato (*Lycopersicon esculentum* Mill.). Scientia Horticulturae **80,** 203-212.

Stern RA, Gazit S. 2000. Reducing fruit drop in lychee with PGR sprays. In: Basra, A. (Ed.), Plant Growth Regulators in Agriculture stress. In J. L. Key, T. Kosuge, eds, Cellular and Molecular Biology of Plant Stress.AR Liss Inc, New York 93-114 p.

Stress, In J, Key L, Kosuge T. Cellular and Molecular Biology of Plant Stress. Alan R. Liss, Inc, New York 93-114 p.

Suttle JC. 1981. Effect of polyamines on ethylene production. Phytochemistry **20,** 1477-1480.

Takahashi T, Kakehi J. 2010. Polyamines:

ubiquitous polycations with unique roles in growth and stress responses. Annuals of Botany **105,** 1–6. http://dx.doi.org/10.1093/aob/mcp259

Tattini M, Heimler D, Traversi ML, Pieroni A. 1993. Polyamine analysis in salt stressed plants of olive (*Olea europea* L.). Journal of Horticulture Science **68,** 613-617. http://dx.doi.org/10.1080/00221589.1993.11516392

Talaat IM, Balbaa LK. 2010. Physiological response of sweet basil plants (Ocimum basilicum L.) to putrescine and trans-cinnamic acid. American-Eurasian Journal of Agriculture and Environmental Science **8,** 438-445.

Talaat I, Bekheta MA, Mahgoub MH. 2005. Physiological response of periwinkle plants (*Catharanthus roseurs* L.) to Tryptophan and Putrescine. International Journal of Agriculture and Biology **7,** 210-213.

Talaat NB, 2003. Physiological studies on the effect of salinity, ascorbic acid and putrescine on sweet pepper plant. Ph.D Thesis, Agric, Bot. Dept., Fac. Agric., Cairo University 286 p.

Tang W, Ronald JN, Outhavong V. 2004. Exogenously added polyamines recover browning tissues into normal callus cultures and improve plant regeneration in pine. Physiology Plantarum **122,** 386-395.

Tian J, Wang L, Yang Y, Sun J, Guo S. 2012. Exogenous spermidine alleviates the oxidative damage in cucumber seedlings subjected to high temperature. Journal of American Society for Horticulture Science **137,** 11-19.

Torrigiani P, Naria A, Bregoli, Ziosi V, Scaramagli S, Ciriaci T, Rasori A, Biondi S, Costa G. 2004. Pre-harvest polyamine and aminoethoxy vinyl glycine (AVG) applications modulate fruit ripening in Stark Red Gold nectarines (*Prunus persica* L. Batsch). Postharvest Biology and Technology **33,** 293–308. http://dx.doi.10.1016/j.postharvbio.2004.03.008

Valero D, Martinez-Romero D, Serrano M, Riquelme F. 1998. Influence of postharvest treatment with putrescine and calcium on endogenous polyamines, firmness, and abscisic acid in lemon (*Citrus limon* L. Burm cv. Verna). Journal of Agriculture and Food Chemistry **46,** 2102–2109. http://dx.doi.org/10.1021/jf970866x

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. http://dx.doi.org/10.1016/S0168-9452(99)00197-1

Walters DR. 2003. Polyamines and Plant Disease. Photochemistry **64,** 97-107. http://dx.doi.org/10.1016/S0031-9422(03)003297

Wang CY, Conway WS, Abbott JA, Kramer GF, Sams CE. 1993. Postharvest infiltration of polyamines and calcium influences ethylene production and texture changes in 'Golden Delicious' apples. Journal of American Society for Horticulture Science **118,** 801–806.

Wang S, Song C, Li L, Zhang Y, Wang SP, Song CB, Li LC, Zhang YM. 1996. Physiological function of polyamines during blossoming and fruit setting in apple. Acta Horticulturae **23,** 319–325.

Wang SY, Faust M. 1994. Changes of polyamine content during dormancy in flower buds of `Anna' apple. Journal of American Society for Horticulture Science **119,** 70-73.

Ward JM, Pei ZM, Schroeder JI. 1995. Roles of ion channels in initiation of signal transduction in higher plants. Plant Cell **7,** 833-844. http://dx.doi.org/10.1105/tpc.7.7.8.33

Wei T, Newton JRJ, Outhavong V. 2004. Exogenously added polyamines recover browning

tissues into normal callus cultures and improve plant regeneration in pine. Physiology Plantarum **122,** 386-395.

Weinstein LH, Kaur-Sawhney R, Rajam MV, Wettlaufer SH, Galston AW. 1986. Cadmium-induced accumulation of putrescine in oat and bean leaves. Plant Physiology **82,** 641–645.
 http://dx.doi.org/10.1104/pp.82.3.641

Williams RR. 1966. The effective pollination period for some apple and pear varieties. Annual Report Long Ashton Agriculture Horticulture Research Station 136-138.

Wu QS, Zou YN, He XH. 2010. Exogenous putrescine, not spermine or spermidine, enhances root mycorrhizal development and plant growth of trifoliate orange (*Poncirus trifoliata*) seedlings. International Journal of Agriculture and Biology **12,** 576–580.
http://dx.doi.org/10.2306/scienceasia15131874.2010.36.254

Xiao-Ming, Zhang PZY, wen XP, Ban Y., Moriguchi T. 2007. Polyamines, all purpose players in response to environmental stress in plants. Plant stress **1,** 173-188.

Yahia EM, Contreras-Padilla M, Gonzalez-Aguilar G. 2001. Ascorbic acid content in relation to ascorbic acid oxidase activity and polyamine contents in tomato and bell pepper fruits during development, maturation and senescence. Lebnsm.-Wiss.U.-Tecnology **34,** 452-457.

Yelenosky G. 1985. Cold hardiness in citrus. Horticulture Reviews **7,** 201-238.

Young ND, Galston AW. 1983. Putrescine and acid stress. Plant Physiology **71,** 767-771.
http://dx.doi.org/10.1104/pp.71.4.767

Zhang W, Jiang B, Li W, Song H, Yu Y, Chen J. 2009. Polyamines enhance chilling tolerance of cucumber (*Cucumis sativus* L.) through modulating antioxidative system. Scientia Horticulturae. **122,** 200-208.

Zhao H, Yang H. 2008. Exogenous polyamines alleviate the lipid peroxidation induced by cadmium chloride stress in Malus hupehensis Rehd. Scientia Horticulturae. **116,** 442-447·
http://dx.doi.10.1016/j.scienta.2008.02.017