

Review Article

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Role of Polyamines on Post-Harvest Fruit Quality and Storability

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ABSTRACT

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As most of the fruits are highly perishable, short shelf life remains one of the major impediments in the market and to increasing international trade, despite several research efforts in the past to extend its storage life. A suitable method for shelf life extension, which avoids detrimental effects on quality of fruit, would be beneficial for both the consumer and the producer. One such strategy is use of postharvest treatments with polyamines. Polyamines (PAs) are biological compounds of low molecular weight with aliphatic nitrogen groups that are ubiquitous in living organisms, both animals and plants. The most common PAs are putrescine (Put), spermidine (Spd) and spermine (Spm). Polyamines (Spm, Spd, Put) and ethylene production are interrelated, since they share a common precursor (SAM). Therefore, there is a possibility that polyamines may regulate the process of fruit ripening and storage. The present paper reviews the effect of exogenous polyamine application on improving the shelf life and quality of fruits during storage.

Introduction

Polyamines (PAs) are small aliphatic amines that are ubiquitous in all plant cells. Polyamines interact with negatively charged macromolecules such as DNA, RNA, proteins, and phospholipids in such a way that they are involved in the regulation of the physical and chemical properties of membrane structure and functions of nucleic

acids and modulation of enzyme activities (Galston and Sawhney 1990). In higher plants, PAs are mainly present in their free form. Putrescine (Put), spermidine (Spd), and spermine (Spm) are the main PAs in plants, and they are involved in many biochemical and physiological processes such as cell division, cell elongation, flowering, fruit set and development, fruit ripening, and senescence (Evans and Malmberg, 1989;

Galston and Kaur-Sawhney, 1990; Bouchereau *et al.*, 1999). Many of these processes have direct implications on various aspects of postharvest biology of fruit crops including quality, storage life, senescence, chilling and other stresses and disease development (Valero *et al.*, 2002)

The activities of PA metabolic enzymes and PAs contents change throughout the stages of plant growth. In whole plants, endogenous PAs and PA synthetase activity were found to be highest in the meristem and growing cells, and lowest in senescent tissues. As senescence occurs, the chlorophyll content gradually decreases, and the activities of ADC (arginine decarboxylase) and ODC (arginine decarboxylase) decrease, while the activities of PAO (polyamine oxidase) and hydrolases, such as ribonuclease and protease increase rapidly.

All of these changes can be inhibited by the application of exogenous PAs (Duan, 2000; Cai, 2009, Chen *et al.*, 2019). However, one of the main aspects of the relationship between polyamines and fruit are those related to fruit ripening. Generally, there is an inverse relationship between the content of endogenous polyamines and ethylene production which is attributed to the fact that both share the common precursor S-adenosyl methionine (SAM) in their biosynthesis pathway (Valero and Serrano, 2010).

Polyamine biosynthesis and regulation

The biosynthesis and catabolism of the PAs are strictly controlled processes. In the case of plants, two pathways lead to Put formation from arginine. One involves the transformation from arginine to ornithine, which is catalyzed by the enzyme arginase. Then, ornithine is transformed to Put catalyzed by ornithine decarboxylase (ODC). The other route involves decarboxylation of

arginine by arginine decarboxylase (ADC) to form agmatine and then agmatine is first converted by agmatine iminohydrolase to N-carbamoylputrescine which is finally converted to Put by N-carbamoylputrescine amidohydrolase. The existence of two alternative routes (ADC/ODC) for the synthesis of Put could be explained by the differential compartmentalization of the two enzymes (ADC is chloroplast-localized and ODC is generally considered to be cytoplasmic), resulting in the specific regulation of different plant processes. The enzymes ADC and ODC can be inhibited by the reversible inhibitors DL- α -difluoromethylarginine (DFMA) and DL- α -difluoromethylornithine (DFMO), respectively. Decarboxylated S adenosyl-methionine (DCSAM), which is formed from S adenosylmethionine (SAM) by the enzyme SAM decarboxylase (SAM-DC), can be used as an aminopropyl donor in the conversion of Put to Spd and from Spd to Spm by two reactions catalyzed by two separate and distinct enzymes, Spd synthase and Spm synthase, respectively. It has been demonstrated that Put and Spd levels inhibit ODC mRNA translation. Methylglyoxal-bis-guanylhydrazone (MGBG) and cyclohexylamine are irreversible inhibitors of SAM-DC and Spd synthase activities, respectively. SAM is an important metabolic crossroad since it is also a precursor of ethylene via ACC, in a reaction catalyzed by ACC synthase and finally, ACC is converted to ethylene by ACC oxidase. Furthermore, in some plants, the methyl moiety of SAM can be transferred to Put via Put-N-methyl-transferase, to form Nmethyl- Put, which serves as a precursor of nicotine and other alkaloids. As in the case of any plant growth regulators, the intracellular free PA pool does not only depend on its synthesis but also on several other processes including degradation, conjugation, and transport (Valero and Serrano, 2010).

Effect of exogenously applied polyamines on post-harvest quality and storability of fruits

Given the opposite effects of PAs and ethylene on retarding or accelerating fruit ripening and senescence, respectively, as commented in the previous section, a great deal of research has been focused on the effect of pre- or postharvest PA treatments on fruit quality parameters related to the ripening process. In this sense several experiments have shown that preharvest treatments with PAs during the fruit growing season can decrease ethylene production and delay the ripening process in a wide range of fruit species. However, most of the research about the effect of PAs on fruit ripening has been performed with postharvest treatments and their effects are similar to those of preharvest treatments, thus there is a delay in the postharvest ripening process leading to maintenance of fruit quality attributes. This review comprehensively covers the effect of exogenously applied PAs on maintaining the shelf life of different fruits under postharvest storage conditions.

Apricot

Apricot fruits treated with putrescine (1mM) were subjected to mechanical damaged with a 25 N force and stored at 10°C. Putrescine treatment improved the shelf life of undamaged and the damaged fruits by reducing weight loss, colour change, ethylene evolution and respiration rates and reduced the bruised zones caused by mechanical damaged (Martinez *et al.*, 2002).

Fruits of two Iranian apricot cultivars ('Lasgerdi' and 'Shahrodi') were immersed in different concentrations of putrescine (1, 2, 3 and 4 mM) and in distilled water (control) for 5 min and stored at 4°C (95% relative humidity). Putrescine @ 4 mM reduced the

weight loss and maintained the firmness. Fruits treated with putrescine had lowest total soluble solids, pH and maturity index while the fruit firmness, titratable acidity, ascorbic acid, total phenolics and antioxidant activity were high. The quality of apricot fruits was improved by the use of putrescine due to its effect on delaying the ripening processes (Davarynejad *et al.*, 2013).

Postharvest application of putrescine or spermidine @1mM in two apricot cultivars 'Bagheri' and 'Asgarabadi' reduced the ethylene production and maintained the firmness and colour of the fruit. Chilling injury incidence was lower in spermidine treated than that of putrescine treated fruits (Koushesh *et al.*, 2012). Similarly, post harvest application of putrescine in apricot 'Tokhm-sefid' resulted in reduction of ethylene production, SSC, pH and increase in TA and fruit flesh firmness thus extending the storability (Khosroshahi and Ashari, 2007)

Banana

The effect of exogenous application of polyamines at varied concentrations viz. PUT (1 mM, 3 mM and 6 mM) and SPM (1 µM, 5 µM and 10 µM) in improving the quality and storability of banana fruits cv. Grand Naine was examined by Archana and Suresh, 2019.

Among the treatments 5 µM spermine was found to be more effective in reducing the physiological loss in weight (4.06%), fruit softening (991.18g), colour change, delaying the biochemical changes by decreasing the conversion of starch (3.61%) into sugars (16.53%), and in reducing the consumption of organic acids which was witnessed by low respiration rate (123.84 ml CO₂ /kg/h), highest value for ascorbic acid (13.69 mg/100g) and titratable acidity (0.396%) while maintaining good organoleptic qualities.

The effect of putrescine on quality and postharvest life of *Musa acuminata* L. during storage was studied by Hosseini *et al.*, (2016). Fruits were dipped in putrescine solution at different concentrations (0.5, 1 and 2 mM for 30 min) and distilled water as 'control'. Putrescine application maintained firmness, higher levels of TA, ascorbic acid and reduced the loss of weight, sensory acceptability and decay incidence compared to control. Archana *et al.*, (2015) reported that exogenous application of putrescine @1mM for 30 min in banana fruits cv. Grand Naine reduced the respiration rate, delayed the loss of firmness, peel colour changes and accumulation of total soluble solids content.

Mango

"Samar Bahisht Chausa" mangos were treated with different concentrations (0.0, 0.1, 1.0 or 2.0 mM) of putrescine and were made to ripen at $32 \pm 2^\circ\text{C}$ for seven days or stored at $11 \pm 1^\circ\text{C}$ up to 28 days. PUT @ 2.0 mM inhibited ethylene production and suppressed the activities of cell wall enzymes (exo-polygalacturonase, endo-polygalacturonase, endo-1,4- β -d-glucanase) while resulting in higher phenolics, activity of antioxidative enzymes (CAT, POX and SOD) and maintained better fruit quality during ripening and cold storage (Razzaq *et al.*, 2014).

Postharvest application of 2 mM spermidine improved the firmness and delayed the deterioration of mango cv. Langra, by suppressing the ethylene production, delaying the chlorophyll decomposition and colour change and through maintaining higher antioxidant and phenolic contents. It also decreased the fungal contamination and increased the shelf life and quality of mango (Zahedi *et al.*, 2019). Fruits of 'Nam Dok Mai No.4' mango were dipped in different concentrations of putrescine (1, 2 and 4mmol/L) and then stored at 14°C . Putrescine

@ 2mmol/L reduced the weight losses, improved superoxide dismutase, catalase, guaiacol peroxidase, ascorbate peroxidase and glutathione reductase activities and total antioxidant content. So, putrescine was found to be effective in prolonging the shelf life (Bussarin and Kanogwan, 2018)

Mango fruits were treated with different concentrations (0, 0.01, 0.5, 1 mM) of polyamines (SPM, SPD and PUT) and stored at 13°C (RH $85 \pm 5\%$). Application of low concentration of SPM (0.5 mM) and higher concentration of PUT (1 mM) or SPD (1 mM) in mango cv. Kensington Pride were found effective in reducing weight loss. SPM was more effective in retarding fruit softening during storage, while PUT was effective in improving fruit quality of ripe fruit. Application of polyamines improved shelf life of mango by retarding fruit softening and colour development during storage and maintained fruit firmness at the ripe stage with increased ascorbic acid content (Malik *et al.*, 2006).

The effect of putrescine at varied concentrations (0.0, 1.0, 2.0 or 3.0 mM) on storage life and quality of mango fruits cv. Langra was studied by Jawandha *et al.*, (2012). PUT (2.0 mM) was found to be best concentration which led to reduction in loss of physiological weight and percentage of spoilage and highest palatability rating and provided the good blend of TSS and acidity under storage.

Fruits of mango cv. Dashehari were dipped in putrescine (0.5 and 1 mM), spermine (0.5 and 1 mM) and spermidine (0.5 and 1mM) for 10 minutes and stored under room and refrigerated conditions. Fruits treated with putrescine (1.0 mM) resulted in the lowest physiological loss in weight while spoilage was significantly reduced to 3.3 percent in mango fruits treated with 0.5mM putrescine

compared to 13.3 percent in control after 28 days of storage under refrigerated condition. After four weeks of refrigerated storage chilling injury index was the lowest (0.86) in mango fruits treated with 1mM putrescine whereas it was highest (4.0) in control. Storage life was extended to 4 weeks in mango fruits treated with 1 mM putrescine compared to 2 weeks in control under refrigerated condition (Anju *et al.*, 2014).

The comparative effectiveness of polyamines (PUT, SPD and SPM) was assessed by Chakraborty *et al.*, (2016) in mango cv. Alphonso at concentrations of 0.1 mM and 0.5 mM. Fruits dipped in 0.5 mM SPM solution registered least changes in physiochemical properties of mango fruit during the entire storage period. The effectiveness of polyamines to maintain the physiochemical properties of mango were found in the following order SPM > SPD ≥ PUT for most the parameters.

Grape

Bunches of grapes cv. Flame Seedless were dipped in putrescine and spermidine at different concentrations of 0.0, 0.5, 1.0 and 1.5 mM and stored at 3–4 °C and 90–95% RH. Putrescine and spermidine at the lowest dose (0.5 mM) was found to be effective in maintaining the berry firmness, peel colour (L^* , C^* , h°) and stabilized anthocyanins as well as suppressing the pectin methylesterase activity and reducing the rate of electrolyte leakage. The polyamines also retarded the degradation of TSS and TA while maintaining higher total phenol content and reduced decay incidence (Champa *et al.*, 2014).

Application of 1 mM PUT and 1% Chitosan maintained quality of fresh table grapes (*Vitis vinifera*) cultivar “Shahroudi” by reducing the weight loss, decay incidence, browning, berry shattering and cracking. Berries treated with

polyamines (1 and 2 mM) exhibited higher total phenolic content, catechin, total quercetin and antioxidant activity and lower quercetin 3-galactoside (Shiri *et al.*, 2012)

Pre-harvest foliar spray of putrescine and spermidine (0, 1, 2 mM) reduced the rate of softening, fungal infection and weight loss during the storage period. The treated fruits showed higher phenolic content, antioxidant activity and anthocyanins (Mirdehghan and Rahimi, 2016).

The exogenous applications of Putrescine @ 2Mm along with Salicylic acid @ 4mM two times in grape; when berry reached about 4-6 mm in diameter and at veraison stage reduced cluster weight loss, maintained berry firmness, stabilized berries anthocyanine, reduced juice acidity, berry softening, berries decay and rachis browning during cold storage at 0-2°C and 90-95 % RH. It suppressed other ripening related changes as Pectin methylesterase activity. Thus, this treatment can be used commercially maintain quality during cold storage and extend the shelf life of "Flame seedless" grape with acceptable fruit quality (Bassiony *et al.*, 2018).

Pomegranate

Application of 2% calcium chloride in combination with 2mM spermidine significantly reduced chilling injury, browning, water loss, electrolyte and K^+ leakage and improved the titrable acidity in pomegranate (Ramezani and Rahemi, 2010)

Combined application of PUT along with carnauba wax enhanced the shelf life of pomegranate fruits by reducing the chilling injury, respiration and ethylene release rate. They maintained the fruit quality by mitigating discoloration, strengthening the firmness of fruit peel without any weight loss

(Barman *et al.*, 2011). Similarly 2mM putrescine and 1:10 carnauba wax (carnauba wax : water) retained higher anthocyanins, antioxidant, ascorbic acid, tannin and sensory qualities in pomegranate (Barman *et al.*, 2014).

Mirdehghan *et al.*, (2007a) reported that exogenous application of Put or Spd under pressure-infiltration or immersion induced acclimation of pomegranate to low temperature, and in turn protect the fruit from chilling by increasing the levels of endogenous Put and Spd. In addition, the polyamine treatment by reducing the loss of weight and retarded the maturation process by reducing softening and the increasing the ratio SSC/acidity.

Thus, storability and shelf-life could be extended in pomegranate stored at low temperatures that usually develop CI. Pressure-infiltration of polyamines seems to be the best tool to increase the endogenous polyamines, although immersion also imparted beneficial effects which could be attributed to the waxy nature of pomegranate skin. Similarly, in a study by Mirdehghan *et al.*, (2007b) pomegranate fruits treated with putrescine (Put) or spermidine (Spd) at 1 mM were found to be effective in maintaining higher concentration of ascorbic acid, total phenolic compounds, and total anthocyanins in arils.

Plum

Four plum cultivars (“Santa Rosa”, “Black Star”, “Black Diamond” and “Golden Japan”) when exogenously treated with PUT (1 mM) followed by their storage at 20 °C resulted in enhancement of shelf life and improved quality attributes of fruits with higher fruit and flesh firmness, lower soluble solids concentration and titratable acidity evolution, reduced weight loss and delayed colour

changes (Serrano *et al.*, 2003). Khan *et al.*, (2008) reported that pre-harvest spray application of PUT @ 2.0 mmol L⁻¹, one week before anticipated commercial harvest was effective in delaying the fruit ripening process with acceptable fruit quality during ripening at ambient temperature or to extend the storage life at 0 ± 1 °C of plum up to 6 weeks with minimum losses of fruit quality.

Pre- and post-harvest application of PUT (0.1, 1.0 or 2.0 mM) to “Angelino” plums resulted in delayed fruit ripening under storage (0 ± 1 °C, 90 ± 5% RH) by reducing the ethylene production and activities of fruit softening enzyme (exopolygalacturonase, endopolygalacturonase, pectin esterase and endo-1,4-β-D-glucanase) in skin and pulp tissues during storage (Khan *et al.*, 2007).

The effect of putrescine during the postharvest storage period of mechanically damaged “Blackstar” plums was investigated by Vicente *et al.*, (2002). Putrescine (1mM) reduced the mechanical damage and flesh deformation. The accumulation of cell wall conjugated PUT and SPD was observed in plums for two weeks under storage. Enhanced levels of bounded PAs contributed to the high level of firmness. Besides this, during initial seven days of storage, damaged control plums showed higher levels of free SPD and were considered a physiological marker for stress induced by mechanical damage.

Citrus

Raeisi *et al.*, (2013) investigated the effect of spermidine at various concentrations (0, 1 and 1.5 mM) on Valencia orange var. olinda. They found that spermidine @1.5 mM was effective in reducing the chilling injury and improving the quality of fruits.

Valero *et al.*, (1998) reported that vacuum infiltration with 1mM putrescine was more

effective than that with calcium to retard the senescence process of the lemon fruit at the early ripening stage, which induced increased fruit firmness and lowered weight loss. Both treatments delayed the colour change, which could be related to the lower levels of ABA during storage. Post-harvest application of putrescine and calcium (at 1 mM) in lemon maintained higher firmness values and more resistance to peel rupture during storage at 15 °C. Treated lemons showed also less deformation when the compression force (50 N) was applied to induce mechanical damage (Martinez *et al.*, 1999).

‘Lisbon’ lemons were vacuum infiltrated with putrescine or spermidine @ 1mM at 15°C with -33 kPa for 10 min prior to cold storage. Untreated and spermidine treated fruits developed the symptoms of chilling injury such as peel pitting, electrolyte leakage after 2 weeks of storage, whereas these changes were reduced in putrescine treated fruits up to 6 weeks. Both the polyamines were found to be effective in maintain the firmness upto 4 weeks, but putrescine was found to be superior than spermidine (Safizadeh, 2013).

Peach

Peaches treated with putrescine (1 mM) and GA₃ (100 mg L⁻¹) maintained higher fruit firmness during storage, and the respiration rate and ethylene emission were reduced compared with control peaches. In addition, the treatments were also effective in reducing the susceptibility of the fruits to be mechanically damaged (Martinez *et al.*, 2000).

Peach fruits treated with PUT (1 mM) alone or in combination with ultrasound (32 kHz at 60 W/L, 10 m) improved peach quality and storability by inhibiting the respiration rate, delaying the process of ripening and improving the firmness.

It also reduced symptoms of browning and leatheriness as compared to control fruits after three weeks under storage (Bal, 2013).

Other fruit crops

Kiwifruits immersed in different concentrations of spermine [(0.5, 1.0 and 1.5) mM] and spermidine [(1.0, 1.5 and 2.0) mM] showed reduced amount of ethylene evolution, polygalacturonase and lipoxygenase activities and lower respiration rate when compared to control. The doses of spermine at 1.5 mM and spermidine at 2.0 mM were found to be best in extending the shelf life of kiwifruits (Jhalegar *et al.*, 2012). Pressure infiltration of polyamines retarded fruit ripening, inhibited ethylene production and reduced respiration in kiwi fruit (Petkou *et al.*, 2004).

Jiang and Chen (1995) recommended polyamines for the retention of red colour in litchi at low temperature storage for 30 days. Polyamines such as putrescine, spermine or spermidine (1 mmol/l) in combination with fungicides were reported to reduce ethylene production, POD activity and also retain membrane integrity. Among the polyamines tested, spermine was the most effective.

Hosseini *et al.*, (2017) reported that pre-harvest application of 1 and 2 mM putrescine maintained the postharvest life of pear cv. Spadona by reducing weight loss, fruit softening, color changes as well as retarding the degradation rate of TSS, TA, pH, vitamin C, total phenol and total antioxidant in pear fruit during storage.

Moreover, the storage life and marketability of putrescine treated fruits were prolonged by decreasing decay incidence. Thus, pre-harvest application of putrescine can be an effective means for extending the postharvest life of pear cv. Spadona.

The immersion of strawberry cv. “Selva” in putrescine at different concentrations (0.3, 0.5, 1 or 2 mM) led to decreased ethylene production and improved the appearance of fruit by increasing the firmness when stored at 5 °C. Fruits immersed in putrescine @ 1 and 2mM had shelf life upto 12 and 14 days whereas the control fruits had 8 days of storage life (Khosroshahi *et al.*, 2007). Vacuum infiltration of polyamines improved the firmness of strawberry slices when stored at 1°C (Ponappa *et al.*, 1993)

Preharvest foliar spray of putrescine and spermidine (0, 1, 2 mM) to pistachio tree, ‘Kalleh Ghochi’ and ‘Fandoghi’ 20 to 35 days before harvest improved the pistachio storability by delaying the softening and decreasing the weight loss and fungal infection when stored at 1.5 ± 1°C and 90-95% relative humidity (Mirdehghan *et al.*, 2012).

Jamun is underutilized minor fruit, which is seasonal and highly perishable with short shelf life. To improve the storage period, the fruits were treated with 1 mM putrescine for 5 min. The treated fruits registered lower respiration rates and higher firmness, delayed the physiochemical and physiological changes in jamun fruits under ambient storage (Archana *et al.*, 2015).

These results provide an evidence for the numerous beneficial effects of the exogenous PA treatments, at pre- and postharvest time in delaying the postharvest ripening and senescence processes by extending the shelf life of fruits and enhancing the fruit quality attributes. Polyamines are also effective on increasing the activity of several antioxidant enzymes, such as SOD, CAT, POD, and APX. Nevertheless, the precise physiological and molecular mechanisms by which polyamines increase both antioxidant systems remain elusive and deserve further research.

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