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Role of Polyamines in Fruit Development, Ripening, Chilling Injury, Shelf Life and Quality of Fruit Crops - A review

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SUMMARY

The plant growth regulators are the organic chemical compounds, other than nutrients and vitamins, which modify or regulate physiological processes in an appreciable measure in the plant when used in small concentration. They are known to influence fruit set, retention, yield and quality of fruit crops. Fruit trees are considered high-value crops and even small modifications in production efficiency, product quality or enhanced cosmetic appeal have the potential to significantly increase product value. Application of plant growth regulators results in better output as it improves the internal physiology of developing fruits to improve fruit set, reduce fruit drop and to amend various physiological disorders in order to improve quality and yield.

INTRODUCTION

Polyamies (PA) are the second generation plant growth regulators. They are organic polycations having variable hydrocarbon chains and two or more primary amino groups. These are widespread in living organisms, found in high concentration in actively proliferating cells and involved in diverse physiological responses. There are three major forms of polyamines i.e., putrescine (PUT), spermidine (SPD) and spermine (SPM). PA's are distributed in all vegetative and reproductive plant organs (Abbasi *et al*., 2017). They 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). Role of polyamines in fruit crops are proliferation of cell division, differentiation, improving fruit set, fruit retention, fruit quality, shelf life and abiotic stress resistance.

Polyamines in plants

Putrescine(PUT)**,** Spermidine (SPD)**,** Spermine (SPM)**,** Cadaverine, Homospermidine, Caldopentamine**,** Canavalmine, Aminobutyl canavalmine, Aminopropyl Canavalmine, 1,3-diaminopropane**,** Norspermidine (caldine)**,** Norspermine (thermine). 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. 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).

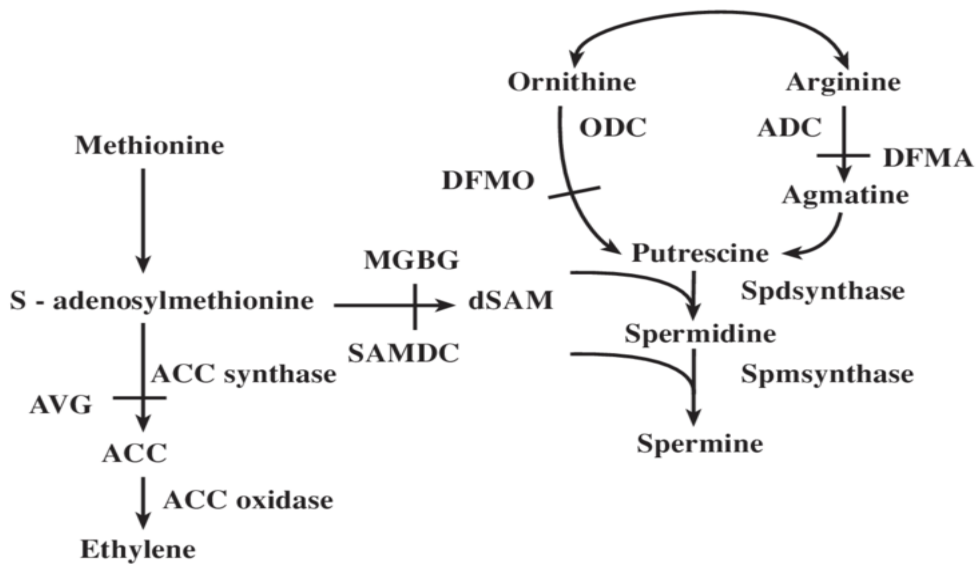
Distribution in plants

PA's are distributed in all vegetative and reproductive plant organs such as roots, stems, leaves, flowers (pollen, stamens, pistils), seeds (embryo and endosperm), seedlings, tubers, meristem, xylem, phloem, parenchyma tissues.

Forms of polyamines

In cells polyamines are present in vacuole, mitochondria and chloroplast. They are found in a wide range of organisms from bacteria to plants and animals. They occur in both free as well as conjugated forms and titres, depending on external conditions such as light and temperature. . It is also known that polyamine titres increase during seed germination (Puga-Hermida *et al*., 2003) and root and shoot formation. The conjugated polyamines are known to be associated with the physiology of flowering in higher plants (Tang *et al*., 2004). Free polyamines covalently combine with a small molecular substance, such as a phenolic compound. The phenolic compound may be hydroxy cinnamic acid, coumaric acid, caffeic acid, or ferulic acid. Free polyamines covalently bind to bio macromolecules, such as proteins, nucleic acids, uronic acids, or lignin by ionic and hydrogen bonds to form bound PAs.

Biosynthesis



The PA biosynthetic pathway in plants has been thoroughly investigated and reviewed in detail (Martin-Tanguy, 2001). Briefly, PAs are synthesized from arginine and ornithine by arginine decarboxylase (ADC) and ornithine decarboxylase (ODC) as illustrated. The intermediate agmatine, synthesized from arginine, is converted to PUT, which is further transformed to SPD and SPM by successive transfers of aminopropyl groups from decarboxylated S-adenosylmethionine (dSAM) catalysed by specific SPD and SPM synthases. The aminopropyl groups are derived from methionine, which is first converted to S-adenosylmethionine (SAM), and then decarboxylated in a reaction catalyzed by SAM decarboxylase (SAMDC). The resulting decarboxylated SAM is utilized as an amino propyl donor. SAM is a common precursor for both PAs and ethylene, and SAMDC regulates both biosynthetic pathways as illustrated.

Fate of polyamines in plants

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. Active cell divisions at the early stages of growth require elevated level of PAs. While the decline 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 (Abbasi *et al*., 2017).

Role of polyamines in fruit crops

Polyamines are known to improve growth and development of plants because of their effects on cell division and differentiation. 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.

In fruit crops major roles are cell division, organogenesis, fruit set, fruit retention, fruit quality, shelf life, abiotic stress.

Role of polyamines on cell division

Basic requirements for cell division: carbon matrix, nutrients, energy source. 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 (Abbasi *et al*., 2017).

Role of polyamines on Organogenesis

In plants, organogenesis involve intense mitotic activity and are dependent on an array of endogenous physiological factors. Putrescine, spermidine and spermine involve in cell cycle activity, growth and differentiation. Their accumulation is associated with growing tissue activity and organogenesis.

Role of polyamines in flowering

Flower bud differentiation is a complex process of morphogenesis. It is triggered by various factors, such as photoperiod, vernalization, nutrition, and water status, and is accomplished by the interaction and coordination of hormones and PAs. Many studies have shown that exogenous PAs and PA synthesis inhibitors can affect flower bud differentiation. Exogenous PAs were shown to accelerate the process of flower bud differentiation, and high PA contents in apical buds were beneficial for the initiation and maintenance of flower bud differentiation. Endogenous PUT was found to be closely related to IAA and gibberellin (GA) contents, and high levels of PUT and SPD were not conducive to the accumulation of IAA and GA. The effects of exogenous PAs and PA synthesis inhibitors on GA were mainly observed at the inflorescence differentiation and floret differentiation stages. Effect of spermidine (0.05mM) treatment on the flowering rate (%) increased percentage of flowering in ‘Fuji’ apple than control (Qin *et al*., 2019).

Role of polyamines in Fruit set

Yield of the crop is directly related to the fruit set after pollination. Poor fruit set either by heavy PAs act as a nitrogen source and antisenescence agent. Increased nutrients in leaves and decreased flower abscission could increase fruit set after exogenous application of PAs. (Kamiab *et al*., 2020). Increased ovule longevity and fruit set were associated with increased foliar and fower N and B levels in Putrescine treated plants. PAs may act as a nitrogen source rather than a regulator of fruit set. Increased nutrients in leaves and decreased fruit abscission could increase fruit set after exogenous application of PAs. Saleem *et al*., (2008) studied the effect of exogenous application of polyamines on fruit set of sweet oranges *cv*. Blood Red. All the PA treatments improved the fruit set. The mixture of the three polyamines has shown negative effects on fruit quality, possibly due to some antagonism among the chemicals. Dutta *et al*. (2018) investigated the effects of polyamines on fruit retention, quality and shelf life of mango *cv*. Himsagar. The highest number of fruits/tree (168.00 fruits/tree), fruit weight (250.22 g) and yield (42.03 kg/tree) was recorded with putrescine (0.5mM) followed by spermidine (1.5mM) whereas, the lowest number of fruits/tree (134.65 fruits/tree), fruit weight (214.50 g) and yield (28.88 kg/tree) was observed in control.

Role of polyamines on Fruit retention

Fruit drop mainly due to inadequate pollination, inadequate nitrogen levels and natural abscission probably by hormonal imbalance. By application of polyamines all these factors can be regulated and fruit retention will be increased (Kakkar and Rai, 1993). Polyamines improved fruit retention, possibly by inhibiting ACC synthase and endogenous ethylene bio-synthesis which is known to trigger abscission.

Role of polyamines on fruit quality

PAs effect on Fruit Firmness

Pectic substances play an important role in providing firmness to fruits, which is one of the most important fruit quality parameters. The diverse set of enzymes plays a vital role in reducing or degrading the firmness during the ripening and thereby affecting postharvest quality of fruits. These degrading enzymes include polygalacturonase (PG), pectin methyl esterase (PME), pectin esterase (PE) and cellulase. They play an important role in softening the fruit. PG is the principal enzyme involved in the hydrolytic cleavage in pear, avocado and apples. Activities of cell wall degrading enzymes such as PE, PME and PG are suppressed by PAs leading to maintenance of firmness in fruits along with enhancement of shelf life. Therefore, role of PA in reducing the softening of fruit was reported due to the inhibitory effects of PAs on the enzymes (PG, PE and PME) involved in degradation of cell wall. Cationic nature of PAs and their interaction with negatively charged carboxylic group led to induction of firmness in fruits thereby improving the quality of fruits at postharvest stage. PUT treatment was effective on increasing fruit firmness in lemon, in 'Black Star', 'Santa Rosa', 'Golden Japan' and 'Black Diamond' plums, in 'Mauricio' apricot and 'Babygold 6' peach. Moreover, PUT treatment delayed the firmness loss during storage for all fruit (Valero *et al*., 2002). Pre-harvest foliar application of Put and Spd on grapevines maintained higher firmness at harvest and postharvest periods and also improved the fruit quality in terms of antioxidant activity, phenolics, anthocyanin and also controlling weight loss during cold storage (Mirdehghan and Rahimi, 2016).

PAs effect on colour change

PAs retarded chlorophyll breakdown and carotenoid biosynthesis. They delayed the colour change by reducing the hydrolytic activities acting on chloroplast thylakoid membranes during storage, which is an indicator of reduced senescence rate.

PAs effect on mechanical damage

Mechanical damage is considered as a type of stress that occurs during the harvest and post-harvest manipulation of fruits. This stress is accompanied by physiological and morphological changes that affect the fruit commodity, such as increased respiration and ethylene production rates, bruising, cell rupture, ion leakage, among others**.** Mechanically damaged fruit have shown modified PA concentrations. These results showed direct effects of the mechanical stress on the metabolism of PAs; consequently, an increase in PA concentration could act as a physiological marker of mechanical stress, one of the less known type of stresses in fruits (Valero *et al*., 2002).

PAs effect on chilling injury

A wide variety of horticultural commodities, including many economically important crops indigenous to tropical and subtropical countries are susceptible to chilling injury (CI) when they are exposed to low but non-freezing temperatures either before or after harvest. Exposing these chilling sensitive crops to non-freezing temperatures causes a variety of symptoms that include uneven and abnormal ripening, increased water loss, surface pitting and discolouration, internal browning, tissue breakdown, off-flavour, increased $C0_2$ and ethylene production. Acts as scavengers and also as activates of the expression of the genes encoding antioxidant enzymes like CAT, SOD and POD (Aronova *et al*., 2005). PAs are positively charged compounds which can interact electrostatically with negatively charged proteins and ion channels and involved in membrane integrity and fluidity. Application of putrescine or spermidine (1mM) reduced chilling injury in pomegranate (Mirdehghan, *et al*., 2012). In valenica orange putrescine (5mM) increased tolerance towards low temperature injury (Mohammad *et al*., 2014). Koushesh *et al*., 2012 inferred that, application of PUT or SPD (1mM) showed apricot fruits tolerance to chilling injury at 1^{o} c for 21 days.

PAs effect on shelf-life

The anti-ethylene nature of the PAs led them to act as shelf life enhancing amines by affecting the diverse physiological processes under the storage conditions and enhancing the shelf life of fruits. Application of putrescine (2mM) inhibited ethylene release, respiration rate, fruit softness in mango (Javandha *et al*., 2012). In kiwi fruit putrescine (1mM) reduced the ethylene evaluation (Pritsa *et al*., 2004). Romero *et al*., 2002 inferred that, application of PUT or SPD (1mM) showed Increased shelf life, reduced respiration rate, reduction in ethylene release in apricot. Exogenous application of polyamines increased the shelf life of mango at ambient room temperature. putrescine (0.5mM) was most effective in extending the shelf life of mango (9 days) as compared to control having 5 days (Dutta *et. al*., 2018)

CONCLUSION

Polyamines are helpful in horticulture by way of their positive effects on flowering, improving fruit set, fruit retention, fruit quality, reducing mechanical damage, enhancing shelf life of fruits and protecting the plants against stress conditions. The beneficial effects of exogenous PAs in fruits are numerous, but the commercial application is low.

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