


Mini Review

# Gibberellin and polyamines in plant growth, development, and postharvest senescence of ornamental plants – a review

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## Abstract

The polyamines, putrescine, spermidine and spermine, are low-molecular weight substances, synthesized in eucariot cells from their immediate precursor, ornithine. The polyamines are found in fruits and vegetables, foods of animal origin and fermented food products. As plant growth regulators, are believed to be involved in several physiological processes. Gibberellins are plant hormones that regulate growth and influence various developmental processes and are derived via the ent-gibberellane skeleton. Gibberellins are synthesized by the terpenoid pathway in plastids and then modified in the endoplasmic reticulum and cytosol until they reach their biologically-active form. Here, we show the importance gibberellin and polyamines functions in plant growth, development, and postharvest senescence of various ornamental plants. Studies initiated on the application of the polyamines and gibberellins in ornamental plants should improve our knowledge in the future.

**Key-words:** Floriculture, Quality characteristics, Plant hormone, Biosynthesis

## Introduction

The application of phyto regulators remains a technique of regulation of effective growth, and a quick elimination is not possible because it is still necessary to obtain quality in various crop productions. New trends requiring implementation of phyto regulators should adapt to this change of horticultural management respectful with the environment, adaptation through three main aspects: a) the development of new less polluting products; b) the improvement of our knowledge in the implementation and use of phyto regulators; c) optimize with early techniques of regulation (Martínez López, 2010).

Cut flower senescence is genetically programmed and mediated via hormonal and

developmental signaling therefore, vase life of cut flowers would probably be prolonged by reversing the detrimental effects of the senescence-signaling hormones (Musembi et al., 2013) and/or interrupting the developmental memory (Musembi et al., 2012). Natural leaf senescence is influenced by various external (e.g. nutrient deficiency or shading) and internal (e.g. plant hormone level) factors (Gans, 2004). In fact, certain phyto regulators have been previously shown to either promote or retard leaf senescence (Cottrell et al., 2010).

Examples of senescence-promoting plant regulators include ethylene, abscisic acid, jasmonate, methyl jasmonate, salicylic acid and brassinosteroids; conversely, cytokinins, auxins, gibberellins, and

polyamines are senescence-retarding agents (Gans, 2004; Schippers et al., 2007).

Gibberellins affect plant growth when applied exogenously, alone or associated with other plant growth regulators such as auxins and cytokines which affect stem growth through cell elongation and division (Davies, 2004). Polyamines are positively charged aliphatic amines that are ubiquitous in living organisms. The universal occurrence of polyamines (putrescine, spermidine and spermine) in plant organs suggests that they perform important functions in plant growth regulation (Champa et al., 2014).

We will start our rationale with a literature review on the effects of gibberellin and polyamines functions in plant growth, development and postharvest senescence of various ornamental plants.

### Gibberellin

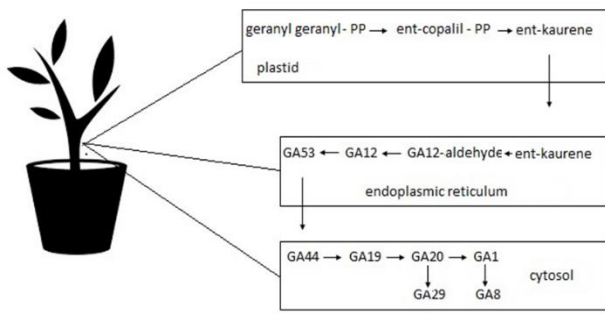
Gibberellins commonly known as gibberellic acids first came to the attention of western scientists in 1950s, they had been discovered much earlier in Japan. In 1950s scientists of Tokyo University isolated and characterized 3 different gibberellins from gibberellin A sample, naming them gibberellin A1, gibberellin A2 and gibberellin A3. The numbering system used for gibberellins in the past 50 years builds on this initial nomenclature of gibberellins A1 (GA<sub>1</sub>), GA<sub>2</sub>, and GA<sub>3</sub> (Gupta and Chakrabarty, 2012). This topic was reviewed previously by Yamaguchi (2008) and Hedden and Thomas (2012). GAs are formed primarily from the methylerythritol phosphate pathway 2002, by which the hydrocarbon intermediate ent-kaurene is produced from GGPP (trans-geranylgeranyl diphosphate) in proplastids. It has been generally assumed that ent-kaurene synthesis competes with that of other GGPP-derived metabolites for a common pool of GGPP. However, the finding that loss of geranyl diphosphate synthase in tomato and *Arabidopsis thaliana* (hereafter referred to as *Arabidopsis*) reduces GA content without affecting the levels of carotenoids and chlorophylls suggests that ent-kaurene is produced from a separate pool of GGPP, via a GGPS (GGPP synthase) that, in contrast with the GGPS isozymes involved in pigment synthesis, has a requirement for GPP as substrate (van Schie et al., 2007).

This would require that GAs and the GGPP-derived pigments were produced in different tissues and was consistent with ent-kaurene synthesis in

leaves occurring in immature chloroplasts associated with the vasculature (Silverstone et al., 1997). Ent-Kaurene is relatively volatile and has been found to exchange with the external environment, prompting the suggestion that it may function as a mediator of plant-plant communication (Otsuka et al., 2004). However, since regulation of GA biosynthesis occurs mainly at later stages of the pathway (Fleet et al., 2003), exogenous ent-kaurene is unlikely to have a major influence on GA content and the resulting growth. The conversion of ent-kaurene into the bioactive forms involves the action of membrane-associated P450s (cytochrome P450 monooxygenases) and soluble ODDs (2-oxoglutarate-dependent dioxygenases). The formation of GA<sub>12</sub>, which is considered the common precursor for all GAs in plants (Hedden and Phillips, 2000), requires six oxidative steps catalysed by two monooxygenases, KO (ent-kaurene oxidase) and KAO (ent-kaurenoic acid oxidase). Ent-kaurene oxidase belongs to the CYP701A P450 clade and KAO to the CYP88A (Mizutani and Ohta, 2010). These enzymes are localized in the endoplasmic reticulum and, in the case of KO, also in the plastid envelope (Helliwell et al., 2001). In higher plants, GA<sub>12</sub> lies at a branch-point in the pathway, undergoing hydroxylation on C-13 and/or C-20. The nature of the enzymatic activity responsible for 13-hydroxylation, by which GA<sub>12</sub> is converted into GA<sub>53</sub>, is unclear. Both P450 and ODD 13-hydroxylase activities have been detected (reviewed in Sponsel and Hedden (2004)), and it has been recently reported that rice contains two P450s that convert GA<sub>12</sub> into GA<sub>53</sub> (Magome et al., 2010). Interestingly, the enzymes present in *Arabidopsis* (CYP714A) and *Stevia rebaudiana* (CYP716D) is? 13-hydroxylate ent-kaurenoic acid rather than GA<sub>12</sub> (Yamaguchi, 2008; Brandle and Richman, 2008). The final step in the formation of the biologically active hormones is the 3β-hydroxylation of GA<sub>9</sub> and GA<sub>20</sub> to GA<sub>4</sub> and GA<sub>1</sub> respectively, catalysed by the ODD GA<sub>3</sub>ox (GA 3-oxidase). The Fig. 1 shows the gibberellin biosynthesis pathway that ultimately produces GA<sub>1</sub>, the biologically active form of gibberellin.

In shoots of dicotyledonous species this reaction tends to be highly regiospecific, with a single product being produced (Lester et al., 1997), whereas in several monocotyledons, in addition to GA<sub>1</sub>, GA<sub>3</sub> is formed from GA<sub>20</sub> via the intermediate GA<sub>5</sub> by the

action of a single GA<sub>3</sub>ox (Spray et al., 1996; Appleford et al., 2006).



**Fig. 1.** The simplified biosynthetic pathway of gibberellin that ultimately produces GA<sub>1</sub>.

Physiologically, a major function of gibberellins in higher plants can be generalized as stimulating organ growth through enhancement of cell elongation and, in some cases, cell division. In addition, gibberellins promote certain developmental switches, such as between seed dormancy and germination, juvenile and adult growth phases, and vegetative and reproductive development. In this last case, gibberellins may promote the vegetative or reproductive state, depending on species (Hedden and Thomas, 2012).

Treatments with gibberellin can trigger flowering in some plants, in others the effect can be the opposite (Mutasa-Göttgens and Hedden, 2009). It is well documented that gibberellic acid (GA) can boost growth, vigor and flowering of various ornamental. Bose et al. (2003) conducted an experiment to study the effects of GA<sub>3</sub> in flowering and quality characteristics of gladiolus cv. 'Erovision'. Corms were soaked in solutions of 0 (control), 50 and 100 ppm GA<sub>3</sub> for 1 hour and were planted 5 days later at 49 corms/m<sup>2</sup>; GA<sub>3</sub> at 100 ppm shortened the time from planting to harvest and increased flowering percentage, spike length, the number of flowers per spike and diameter of flower stems. Hashemabadi and Zarchini (2010) observed the effect of GA<sub>3</sub> on growth and flowering of *Rosa hybrida* cv. Poison and found that 200 mg L<sup>-1</sup> at pre-harvest stage improved stalk length, fresh weight and yield. The growth rate of *Ficus benjamina*, *Schefflera arboricola* and *Dizigotheeca elegantissima* can be stimulated through increasing synthesis of photosynthetic pigments by applications of GA<sub>3</sub> (Sardoei et al., 2014). Schroeter-Zakrzewska and Janowska (2007) stated that application of GA<sub>3</sub> increased the number

of buds and flowers in *Impatiens walleriana*, but had not impact on the time of flowering. In the research presented, concentration of GA<sub>3</sub> did not affect the quality of plants. In *Ajania pacifica* exogenous application of GA<sub>3</sub> at concentrations, time and number of treatments investigated only slightly affected the growth and development (Zalewska and Antkowiak, 2013). They stated that the plant response to GA<sub>3</sub> treatment, which appears to be different from other ornamental species. In *Chrysanthemum* 'Yoko Ono' and 'Faroe', irrespective of the time and dose of GA<sub>3</sub>, no changes in plant length were observed (Vieira et al., 2011a, b). However, Schmidt et al. (2003) reported increase of shoots' elongation by almost 17% in *Chrysanthemum* 'Viking'. Zalewska et al. (2008) reported a significant effect of GA<sub>3</sub> on the length of shoots of flowering plants in cascade-like cultivars of chrysanthemum. In a study carried out on three tulip cultivars including 'Lacourtine', 'Yokohama' and 'Red Favourite', Shakarami et al. (2013) reported that GA<sub>3</sub> significantly reduced stem length, first internode length and duration of precocity period. Based on the results gibberellic acid at 250 and 500 ppm can be an effective agent in tulip's precocity. Arun et al. (2000) evaluated the effects of different levels of GA<sub>3</sub> on growth and flowering of rose "First red" and found that GA<sub>3</sub> could improve plant and flower neck height, as well flowering stalk. The results were that all treatments increased bud length, flower diameter and produced the most cut flowers in unit area. Kumar and Singh (2003) showed that spraying 100 and 200 mg L<sup>-1</sup> GA<sub>3</sub> increased flower weight in carnation 'Red corso'. Barzegar Fallah (2006) applied 0, 10, 25 and 50 mg L<sup>-1</sup> GA<sub>3</sub> on *Aquilegia × hybrida* and observed that the highest yield was obtained in 10 mg L<sup>-1</sup> GA<sub>3</sub>, while 50 mg L<sup>-1</sup> GA<sub>3</sub> caused diminishing of cut flowers. Also, Bhattacharjee and Singh (1995) showed that 300 mg L<sup>-1</sup> GA<sub>3</sub> decreased yield of rose 'Raktagandha' up to 11-20%. In current study, 300 mg L<sup>-1</sup> GA<sub>3</sub> reduced yield of cut rose 'Poison'. Hashemabadi and Mohammad Zarchini (2010) examined the effect of different GA<sub>3</sub> levels (150, 200, 250 and 300 mg L<sup>-1</sup>) on cut rose (*Rosa hybrida* 'Poison') and showed that the highest record of flower yield was obtained by application of 200 mg L<sup>-1</sup> GA<sub>3</sub>, with 192 cut flowers per year per m<sup>2</sup>. Sumanasiri et al (2014) investigated the role of GA<sub>3</sub> (0, 50, 100, or 200 mg L<sup>-1</sup>) in controlling vegetative growth and flowering of *Henckelia humboldtianus*

(Ceylon Rock Primrose) and conclude that all treatments increased peduncle length, plant height and petiole length providing a better appearance as a potted plant compared to the untreated plants. The action of GA<sub>3</sub> on the growth and flower yield of anthurium cv. Apalai was investigated by Lima et al. (2014). The authors conclude that application at 150, 300 and 450 mg L<sup>-1</sup> promoted an increase in the leaf area. However, there was no increase in the number of inflorescences produced or their quality. Tulip bulbs treated with 100 mg L<sup>-1</sup> GA<sub>3</sub> sprouted in significantly less number of days, exhibited higher sprouting percentage, more plant height, leaf area, leaf chlorophyll, photosynthesis rate, flower stalk length, stalk diameter, and fresh and dry stalk weight (Ramzan et al., 2014). Carvalho-Zanão et al. (2016) studied the production of gladiolus submitted to gibberellic acid in a protected environment and observed that high concentrations of GA<sub>3</sub> are not recommended for the production of flower spikes and corms of the 'White Friendship' gladiolus cultivar.

Postharvest senescence is a major limitation to the marketing of many species of cut flowers and considerable effort has been devoted to develop postharvest treatments to extend the marketing period (Bowyer and Wills, 2003). The use of gibberellins as flower preservatives is still limited since few flowers respond with positive effects and also the cost of the substances are higher than the other commercial compounds regularly applied to cut flowers (Finger et al., 2016). However, the efficacy of GA was indicated in the studies by Janowska and Schroeter-Zakrzewska (2010) and Janowska et al. (2013). These studies showed that GA<sub>3</sub> extends the post-harvest longevity of *Limonium latifolium* leaves. The leaves of *Arum italicum* also responded to GA (Janowska and Schroeter-Zakrzewska, 2008; Janowska, 2010). In studies conducted by Janowska and Jerzy (2003), GA had a favourable influence on the cut leaves of *Zantedeschia* with colourful spathes. In the cultivars 'Florex Gold' and 'Black Magic', leaves conditioned in GA at a concentration of 300 mg dm<sup>-3</sup> maintained their decorative values for the longest period of time. Brackmann et al. (2005) studied the effects of GA<sub>3</sub> on three varieties of chrysanthemums and noted the promotion of senescence of both leaves and flowers. The application of GA<sub>3</sub> in the field did not reduce or retard the senescence process in chrysanthemum 'Faroe' (Vieira et al., 2010). Eason (2002) reported that treatment of GA, a component of certain

preservative solutions has been found to delay the onset of tepal fading and wilting in *Sandersonia aurantiaca* flowers. Gibberellic acid (GA<sub>3</sub>) applied as a pulse treatment (500 mg·dm<sup>-3</sup>, 20 h) increased leaf longevity in oriental lily 'Helvetia' when used alone (Rabiza-Świder et al., 2012). Rabiza-Świder et al (2015) observed that gibberellic acid increased longevity of leaf in LA 'Richmond' in all three different "experimental variants", over three-fold relative to respective controls. The foliage on a complete shoot lasted the longest, i.e. over 60 days, but an increase in longevity due to GA<sub>3</sub> was even more pronounced in decapitated shoot. In *Alstroemeria* leaf, application of GA enhanced the longevity, chlorophyll content and superoxide dismutase (Nouri et al., 2012). Treatments with GA<sub>3</sub> (50 ml L<sup>-1</sup>) and sucrose (50 g L<sup>-1</sup>) were reported to improve the fresh weight, concentration of petal sugar, activities of SOD and decreased LOX activity which delayed petal senescence and enhanced vase life of gladioli (Singh et al., 2008). These treatments were ineffective in extending the vase life of cut scapes of *Iris germanica* despite being able to increase the antioxidant activity of SOD, CAT and APX (Ahmad and Tahir, 2016). Gerbera cut flowers held in GA<sub>3</sub> at concentration (2.5, 5.0 and 7.5 mg L<sup>-1</sup>) had significantly higher water content in flower heads and stems, reduced flower senescence and increased flower quality after 14 days of holding (Emongor, 2004). Imsabaia and van Doornb (2013) reported that, depending on the experiment, continuous treatment with 0.03–0.45 mM of GA<sub>3</sub> delayed petal blackening by 0.5–1.5 d (controls lasted 4 d), but in experiments during the hot/rainy season (May–September) GA<sub>3</sub> had no effect. Danaee et al. (2011) studied the effect of GA<sub>3</sub> on the postharvest quality and vase life of gerbera cut-flowers, observing that GA<sub>3</sub> 50 mg L<sup>-1</sup> was the most effective treatments on vase life, fresh weight, solution uptake, membrane stability and total soluble solids. Gibberellic acid applied at lower concentrations (25 mg L<sup>-1</sup> GA<sub>3</sub>) renders greater beneficial effects on vase life quality, membrane stability and antioxidant activities in gladiolus cut spike, and further higher application rates cause no improvement in the flower longevity (Saeed et al., 2014). Effect of GA<sub>3</sub> on senescence of cut gladiolus flowers was also reported by Costa et al. (2016). The authors observed that stems subjected to solution of 100 μM GA<sub>3</sub>, the average was 5.8 days, which corresponded to a percentage increase of 11.53% in

longevity when compared with stems in water (control). Saeed et al. (2014) reported that GA applied at lower concentrations renders greater beneficial effects on vase life quality, membrane stability and antioxidant activities in gladiolus cut spike and higher application rates cause no improvement in the flower longevity. Gibberellin treatments (pulsing or spraying) increased inflorescence longevity in Asiatic lily hybrids and GA<sub>4</sub>+ GA<sub>7</sub> at 100 mg·dm<sup>-3</sup> was more effective than GA<sub>3</sub>, either when applied alone or in combination with BA as the commercial preparation Promalin (Ranwala and Miller, 2002). The same was confirmed in LA ‘Richmond’ held in GA<sub>3</sub> water solution. In LO ‘Siberia’ and LA ‘Dream Land’, GA<sub>4</sub>+ GA<sub>7</sub> was more effective for longevity prolongation than GA<sub>3</sub> either when applied as water solution or in Promalin, either by dipping or spraying (Kim et al., 2005). In trials conducted by Ranwala and Miller (2002) on Asiatic hybrids, spray or pulse treatments with gibberellins prevented leaf chlorosis, GA<sub>4</sub>+ GA<sub>7</sub> being more effective than GA<sub>3</sub>. The effects of GA<sub>4</sub>+ GA<sub>7</sub> on the vase life and flower quality of Alstroemeria cut flowers in the holding solution at 2.5–10.0 mg L<sup>-1</sup> significantly delayed the onset of leaf senescence by around 7 days and significantly increased days to 50% petal fall by ca. 2 days (Mutui et al., 2006). Favero et al. (2017) reported that ‘Chiang Mai Pink’ stems with GA<sub>4</sub>+GA<sub>7</sub> + BA did not influence vase life nor water uptake. However, concentrations higher than 0.5 mg L<sup>-1</sup> increased fresh weight by approximately 10% compared to control treatment. Similar results were obtained by Bunya-atichart et al. (2004) with application of 50 and 100 mg L<sup>-1</sup> GA<sub>3</sub>. Gibberellic acid induces the water status improvement by increasing water absorption or reducing water loss through lowering the transpiration rate (Goszczyńska et al., 1990). There is also indication of GA<sub>3</sub> involvement in enhancing the hydrolysis of starches into sugars which contributes to improve the water balance status (Eason, 2002). Studies in the literature show that gibberellins may mediate the effect of other hormones and cold storage can induce modification of a plant’s lifetime, certainly by modifying cell metabolism (Valle et al., 1989; Nowak and Rudnick, 1990; Galston and Kaur-Sawhney, 1994; Meng et al., 2009). Vieira et al. (2010) studied the biochemical changes in postharvest chrysanthemum ‘Faroe’ submitted to different concentrations of GA<sub>3</sub> applied in the field and observed increase in the level of

polyamines (Put, Spd and Spm). As the interactions between GA and other hormones involve components from the GA biosynthetic and response pathways, we quote introduce a few relevant players in these pathways. For a more comprehensive description of these pathways, see recent reviews (Hedden and Phillips, 2000; Lange and Lange, 2006; Razem et al., 2006).

## Polyamines

Research on polyamines (PAs) in plants laps a long way of about 50 years and many roles have been discovered for these aliphatic cations (Del Duca et al., 2014). As plant growth regulators, polyamines, putrescine (Put), spermidine (Spd), and spermine (Spm) are believed to be involved in several physiological processes including morphogenesis, cell division, vascular differentiation, shoot formation, flower initiation and development, and fruit growth and development (Evans and Malmberg, 1989; Galston and Kaur-Sawhney, 1990; Alcázar et al., 2006). In plants, Put is produced via the catalytic actions of ornithine decarboxylase and arginine decarboxylase in three steps. Put is then converted into Spd by Spd synthase, with the addition of an aminopropyl moiety donated by decarboxylated S-adenosylmethionine. This same compost is synthesized from methionine via two sequential reactions that are catalyzed by methionine adenosyltransferase and S-adenosylmethionine decarboxylase, respectively. Spd is then converted into Spm or thermospermine, again using S-adenosylmethionine as an aminopropyl donor, in a reaction catalyzed by Spm synthase and thermospermine synthase, respectively (Kusano et al., 2008; Vera-Sirera et al., 2010; Pegg and Casero, 2011; Gupta et al., 2013).

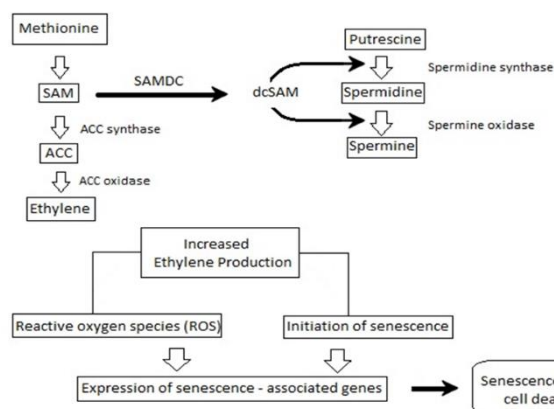
The application with PAs can also be observed in some ornamental plants, but the effect can be the opposite. The effect of foliar application of Put (50, 100 and 150 ppm), in addition to untreated plants as control on vegetative growth, on flowering and photosynthetic pigments of *Dahlia pinnata* L. were observed by Mahgoub et al. (2011). The authors related that the highest values (plant height, number of branches, number of leaves, fresh and dry weight of leaves, stem diameter and fresh and dry weight of stem) were obtained when plants were treated with 150 ppm and that the application increased yield of flower, flowers caracteres and chlorophyll contents

more than the untreated one. Application of Put significantly promoted plant height, number of leaves, fresh and dry weight of leaves in *Mathiola incanna* plants (Youssef et al., 2004). Similar results were also found by Mahgoub et al. (2006) on *Dianthus caryophyllus*, El-Sayed and Iman (2009) on chrysanthemum plants, Talaat et al. (2005) on periwinkle plant and Abdel-Aziz et al. (2009) on gladiolus plants. They reported that Put was more effective on fresh and dry weight of plants. In addition, other aspects of the role of PAs in plants, related to PA transport, metabolism, stress tolerance, conjugated PAs, and senescence were reviewed in plants by various authors in a 2010 special issue of Plant Physiology and Biochemistry dedicated to PAs. Postharvest senescence is the main constraint in the commercialization of most of cut flowers and efforts have been made to discover and develop postharvest treatments to increase its shelf life (Bowyer, 2003). It has been reported that PAs have the stimulated effects on the preservation of lilies (Geng et al., 2009), gerbera (Bagni and Tassoni, 2006) and carnation (Luo et al., 2003; Bagni and Tassoni, 2006). In another study, *Chrysanthemum morifolium* cv. 'Bright Golden Ann' was treated with various concentrations of PAs in a preservative solution. According to the results of this experiment, all treatments significantly increased post-harvest life of cut flowers when compared to the control (Kamiah and Zamanibahramabadi, 2016). Dantuluri et al. (2008) reported that PAs significantly vase life of gladiolus flowers and also delayed senescence and improved vase life of cut spikes by improving membrane stability. Sivaprakasam et al. (2009) reported that Spm at 5  $\mu\text{M}$  delayed flower senescence in ethylene-insensitive gladiolus by three days, along with increased fresh weight, which was retained for a longer period and increased vase solution uptake as compared to control. Tassoni et al. (2006) observed that cut carnation flowers treated with 10 mM Spd exhibited a delay in senescence. Effect of PAs on vase life of rose cv Dolcvita were reported by Farahi et al. (2013). These authors observed that PAs have significantly increased vase life of rose when compared with untreated ones. The longest vase life was obtained by 0.5 mM Spd and 1mM Spm. Singh et al. (2005) also reported that PAs (Spm, Spd and Put) at 100 ppm concentration, in combination with sucrose, were effective in extending vase life of gladiolus. In carnation, the greatest delay of

senescence was observed with 10 mM Spd in the irrigation solution (10 mM Spd-V), while no significant effect was obtained by spraying this substance on flowers (Bagni and Tassoni, 2006). Tatte et al. (2015) investigated the influence of different PAs in spray form on post harvest life of rose var. Samurai. In this study, roses treated with 10 ppm Spm showed slower bud opening from day 1 to day 7 and enhanced vase life (8.03 days), followed by 10 ppm Spd (7.76 days) as compared to control (4.24 days). Application of Put increased vase life of cut chrysanthemum and alstroemeria flowers (Kandil et al., 2011; Soleimany-Fard et al., 2014). Pandey et al. (2000) reported that the effect of Put on the extending vase life of cut lisianthus flower might be due to suppressed water loss, inhibited ethylene action and decreased transpiration rate. However, a study conducted on carnation stems conditioned in solutions of PAs confirmed their effect on the extension of vase life, but only when flowers were treated with PAs at the bud stage (Upfold and Van Staden, 1991). Rubinowska et al. (2012) investigated the effect on postharvest quality of conditioning of Rosa 'Red Berlin' stems in solutions of PAs: Spd at a concentration of 1.5 and 3 mmol dm<sup>-3</sup>; Spm at a concentration of 1 and 2 mmol dm<sup>-3</sup>; and Put at 2 and 4 mmol dm<sup>-3</sup>. The authors reported that PAs did not significantly affect the longevity of Rosa 'Red Berlin'. Nada et al. (2004) also observed that cut flowers of Rose 'Noblesse' kept in Spd withered earlier than those in distilled water. Additionally, Rubinowska et al. (2012) confirmed no effect of Spm on prolonging the vase life of Weigela florida 'Variegata Nana'. Exogenous application of Spd has been found to transiently delay senescence of *Dianthus caryophyllus* and *Petunia hybrida* flowers which has been implicated to be due to the ability of free Spd to bind to the main intracellular constitutive molecules, such as DNA, and stabilizing their structures (Tassoni et al., 2006). The quality of flowers in potted plants of gerbera cv. "Kosak" was studied by Vieira et al. (2017). The results indicated significant effect of Put and Spm, but mean comparison showed that 2mMol L<sup>-1</sup> Spm caused the maximum quality of plant gerberas. In petal tissue, ethylene is responsible for inducing many of the biochemical processes leading to programmed cell death, including the activation of senescence-related gene transcription (Lawton et al., 1990; Shibuya, 2012). Ethylene appears from the precursor S-



adenosylmethionine, which is common to the synthesis of the PAs, Spd, and Spm (Bouchereau et al., 1999). PAs inhibit ethylene production by regulating the activity of 1-aminocyclopane-1-carboxylic acid synthase and oxidase (Lee et al., 1997), while ethylene alters the formation of PAs by reducing the activity of arginine decarboxylase and SAM decarboxylase (Roustan et al., 1993). In other words, the ACC and ethylene syntheses might be largely dependent on PAs contents; the opposite might not be true, since PAs concentration is much higher than ACC and ethylene (Hatanaka et al., 1999). Ebrahimzadeh et al. (2013) reported that if a high concentration of PAs contributes to suppressing flower senescence, a long vase life cultivar would be expected to contain high PA concentration. Lee et al. (1997) observed that the application of Spm delayed the senescence of cut carnation flowers and reduced ethylene production, the endogenous 1-aminocyclopane-1-carboxylic acid content and the activity and transcript amounts of 1-aminocyclopane-1-carboxylic acid synthase, and oxidase in petals. However, also in carnation, Pandey et al. (2000) found that treatment with PA did not always increase flower longevity and may even result in an accelerated senescence. The floral, more specifically petal senescence, is accompanied by dramatic changes in cellular morphology, biochemical processes and gene expression (Rogers, 2012) (Fig. 2).



**Fig. 2.** Polyamine and ethylene pathways and their interrelationships (Waldem et al., 1977) and increasing ethylene production through key events regulating floral senescence in ethylene-sensitive species (Rogers, 2012).

This author reported that in some species, petal senescence is coordinated by the plant growth regulator (PGR), ethylene. In these species, a combination of increased ethylene production and

increased ethylene sensitivity act as a trigger for senescence initiation. This is modulated by other factors such as age-specific factors, external stress, and nutrient status. Together, these signals result in changes in gene expression and activation of senescence-related biochemical and cellular processes. During senescence, the levels of PAs are not constant showing peaks especially at its beginning, but thereafter PAs usually decrease (Galston and Kaur-Sawhney, 1990; Cohen, 1998). This pattern, however, depends on the type of senescence model, if induced by external factors or natural (Del Duca et al., 2014). Vieira et al. (2010) evaluated the changes in PAs content throughout the lifetime of leaves and inflorescences of chrysanthemum 'Faroe' kept at room temperature and cold storage. This study showed that the effect of cold storage on leaves and inflorescences promoted higher sprouting percentage concentrations of Spd and Spm appeared than Put. In leaves, there was a clear trend, i.e., sprouting percentage higher levels of Put in refrigerated samples. Several studies have shown that there is a decrease in the levels of PAs with senescence, attributed to the competition between ethylene and S-adenosylmethionine to form Spd and Spm (Bouchereau et al., 1999). Changes in the levels of PAs and ethylene have been reported during senescence in some plants, such as plums (De Dios et al., 2006). Studies also showed that degradation can occur by oxidases of PAs, generating  $H_2O_2$ , which is metabolized by peroxidase, inducing an increased activity of this enzyme (Bouchereau et al., 1999; Cona et al., 2006). The oxidation products cannot be converted back to PAs, and the role of PA oxidase in plant cell physiology may be a simple involvement with the terminal catabolism of PAs (Cervelli et al., 2000).

Aspects with limited information are highlighted for future research, extending our understanding on the importance of gibberellins and polyamines during growth and postharvest senescence and boosting future research with the aim to improve the qualitative and quantitative traits of crops.

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