Mineral uptake and biochemical responses of hydroponically grown *Rosa hybrid* cv. Dulce Vita to polyamines

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Abstract

Among plant growth regulators, polyamines (PA) have a major role in diverse plant physiological responses throughout vegetative and reproductive phases and senescence. The present study was conducted to investigate the impact of polyamine on different physiological and biochemical aspects of hydroponically grown rose (cv. Dulce Vita) plants. Putrescine (Put) (1, 2, and 3 mM), Spermidine (Spd) (0.5, 1, and 1.5 mM), and Spermine (Spm) (1, 2, and 4 mM) were sprayed on rose plants during growth and subsequently, different aspects of vegetative growth, flower quality, mineral uptake, and some biochemical responses of the plants were studied. Foliar application of Spd at 1.5 mM concentration caused the highest flower stem length and flower bud size. Vase life was affected by PA application as Spd had the greatest beneficial outcome. Absorption and accumulation of the studied macro- and micro-nutrient contents of leaves were also influenced by PA treatment. ACC synthase and chlorophyllase activity in leaves of cut flowers harvested from PA-treated plants was affected, where 4 mM Spm treatment lead to the minimum levels of these compounds. Although malondialdehyde production in leaves of Dolce Vita rose increased during postharvest life as flowers aged, the increment was retarded by PA application.

Keywords: ACC synthase, chlorophyllase, malondialdehyde, postharvest, vase life

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Introduction

With an annual trade worth of about 800 million euros, roses are one of the most important dicot species throughout the world (Anonymous 2018). Roses are one of the most diverse and extensively cultured plants through the northern hemisphere in terms of growing habit, flower color, and shape (Gaurav et al., 2021). Roses are mostly produced for their ornamental value within the ornamental industry as cut flowers, pot plants, and bedding

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plant; moreover, roses and their products have numerous applications in various industries such as beverage, cosmetics, food, and pharmaceutics (Zlesak, 2007). As an ornamental plant, quality and visual charm features such as freshness, size, color, and longevity of flowers besides the length and diameter of flower stem are the major factors that can fulfil consumers' satisfaction and boost its economic value in marketing and trade (Hosseini Farahi et al., 2019). Therefore, improving the quality of the flowers by any method is highly important and a priority in pre- and post-harvest studies.

External polyamine (PA) applications have revealed promising positive effects on quantity and quality of different ornamental plants ((Lin et al., 2021; Rezvanypour et al., 2015). PAs are important metabolites that play positive roles in various biological stages and mechanisms such as cell division, *in vitro* embryo induction, stem formation, root induction, vascular differentiation, flower induction, flower development, senescence, and fruit ripening (Nandy et al., 2022). Interestingly, PAs can retard senescence by inhibiting protease activity and ethylene synthesis as well as delaying chlorophyll degradation. Moreover, in various biological systems PAs are also involved in carbohydrate biosynthesis (Killiny and Nehela, 2020).

The beneficial effect of PA involvement in several physiological activities has fostered research on ornamental plants, particularly using putrescine (Put). Some researchers observed that pre-harvest treatment of *Gladiolus callianthus* by Put increased several vegetative and reproductive (flowering) parameters(Sankaran et al., 2022). In their study, foliar application of 200 mg L^{-1} Put improved gladiolus height, weight (dry and fresh), number of leaves, produced cormlets and their weight (dry and fresh), flower stalk length, and florets. Plants' metabolites were also affected as they had the highest quantity of chlorophyll (*a* and *b*) and carotenoids pigments, total phenol, soluble solids, and nutrients (such as N, P, K). Similarly, foliar application of Put in *Matthiola incana* increased leaf number, plant height, and weight (dry and fresh) during vegetative growth (El-Ghait et al., 2022). In the same way, development and growth in *Catharanthus roseus* were also improved under Put treatment (Alhaithloul et al., 2019). In carnation, researches reported that Put had positive effects on endogenous hormones, antioxidant activity, and chemical composition(Mustafavi et al., 2018).

Similar reports have also been published for other cut flowers. In *Chrysanthemum indicum*, putrescine application increased flowering period, cut flower yield, flower stalk length, and fresh and dry weights (Sedaghathoor et al., 2020). They also observed that Put treatment increased carbohydrate contents (such as starch) and photosynthetic pigments (chlorophylls and carotenoids). Besides, pre-harvest application of Put increased vase life of cut *Chrysanthemum* (up to 2 folds) by preventing internal ethylene biosynthesis. Karimi et al. (KARIMI et al., 2017)reported similar results for *Dianthus caryophyllus* flowers. Application of Put on Dahlia plants, increased vegetative features such as leaf number, stem number, stem diameter, and plant weight (fresh and dry) (Kasem et al., 2023).

Treatment of roses with other polyamines has resulted in similar findings. For example, application of Spermine (Spm) reduced membrane permeability of petals and leaves, ethylene biosynthesis, and also malondialdehyde contents in petals of cut rose (Ghorbani et al., 2018). Improved flowering and increased qualitative characteristics of gladiolus spike have also been reported under Spm treatment (Hosseini Farahi and Aboutalebi Jahromi, 2018). In cut carnation, Spermidine (Spd) delayed senescence by decreasing ethylene biosynthesis (Karimi et al., 2017).

In order to improve the physiological properties of a commercially important and extensively cultured rose cultivar and consequently its cut flower quality, 'Dulce Vita' rose plants were treated with different PAs and the impacts of PAs on various physiological and biochemical aspects of plant and cut flower were studied.

Materials and Methods

Experiment set up

Rosa hybrid cv. 'Dulce Vita' rooted cuttings were obtained from a commercial local producer and cultured in plastic pots filled with coco peat: perlite mixture (50:50) in a hydroponic system. Established plants were fertigated with a nutrient solution containing ammonium nitrate (80 mg l^{-1}), Borax™ (disodium tetraborate) (1.5 mg L^{-1}), calcium nitrate (230 mg L^{-1}), Cu-EDTA (0.18 mg L^{-1}), Fe-EDTA 6% (23 mg L^{-1}), magnesium sulphate (40 mg L^{-1}), Mg-chelate (0.9 mg L^{-1}), monopotassium nitrate (140 mg L^{-1}), potassium nitrate (400 mg L^{-1}), sodium molybdate (0.5 mg L^{-1}), zinc sulphate chelate (0.9 mg L^{-1}) prepared with well water (Table 1). Fertigation was carried out on a daily basis, 5 times a day at 2-hour intervals and was conducted through an open drop irrigation system. Routine and usual cultural practices such as bending, pruning, and disease and pest management were carried out during growth period until plants flowered and samples were taken.

Treatment

Established rose plants were treated with Spermidine (Spd) (0.5, 1, and 1.5 mM), Putrescine (Put) (1, 2, and 3 mM), Spermine (Spm) (1, 2, and 4 mM), and sterilized distilled water (as control) for a period of one month. All applied treatments were prepared to have 4 ml L^{-1} Twin 20 ™. In order to ensure efficient treatment, foliar application of plants was conducted twice a day: early morning and late afternoon until runoff. Experiment was planned in a completely randomized design with 4 replications.

Morphological and chemical analyses

Vase life

Vase life was determined by assessing the appearance of symptoms such as bent neck, petal wilting and shedding, according to Jowkar et al. (2017).

Table 1
Tap water specification used for fertigation and treatment preparation

Ca^{+2}	Mg^{+}	Cl^{-}	$SO4^{-2}$ (m Eq L^{-1})	$CO3^{-2}$	$HCO3^{-2}$	EC x 10^6	pH
3.30	2.70	0.51	1.01	0.01	4.02	380	7.3

Leaf mineral content

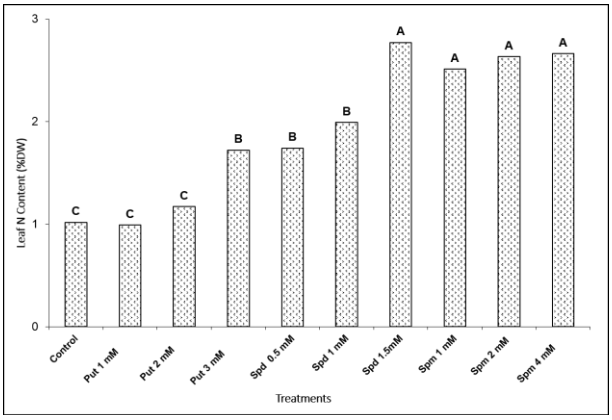
Leaves were sampled after assessing plant quality characteristics, to determine nutrient contents. After washing with 0.1 NHCl and rinsing with distilled water, leaves were dried in oven at 80 ℃ for 48 h. An aliquot of 0.2 g was then dried in oven at 250 ℃ for 30 min and then reduced to ashes at 550 ℃ for 4 h. Sample digestion was carried out with 4 ml hydrochloric acid, before determining Ca, Fe, Zn, and Cu contents by atomic-absorption spectrophotometry (GBC, Avanta, Australia) and K content by flame photometry (Jenway, Dunmow, UK) according to Roosta and Rezaei (Roosta and Rezaei, 2014). N content was measured using Kjeldahl method while P was measured by the colorimetric method as described by Emami (1996).

ACC synthase, chlorophyllase, and malondialdehyde activities

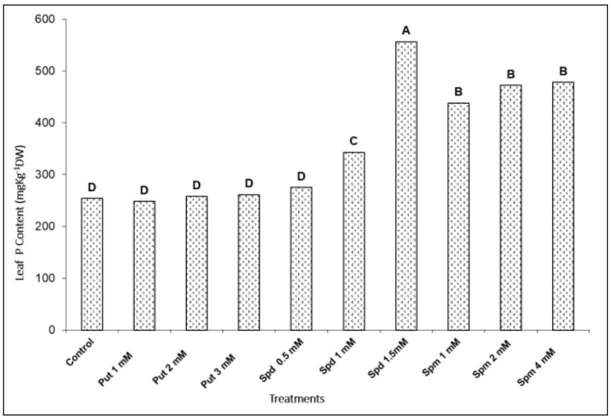
The ACC synthase activity was determined according to Jiang et al. (1994) method. The extraction buffer contained 3 ml of 50 mM Tris-HCL, 1 mM dithiothreitol (DDT), and 1 mM phenylmethylsulfonyl fluoride (PMSF at pH 8.2).

Chlorophyllase activity was measured according to Harpaz-Saad et al. (Harpaz-Saad et al., 2007)method. The extraction buffer contained 0.15% Triton X-100, 0.2 ml acetone, and phosphate buffer (pH 7) added to 0.2 ml of leaf extract solution. The activity of chlorophyllase enzyme in the lower phase was determined spectrophotometrically at 667 nm.

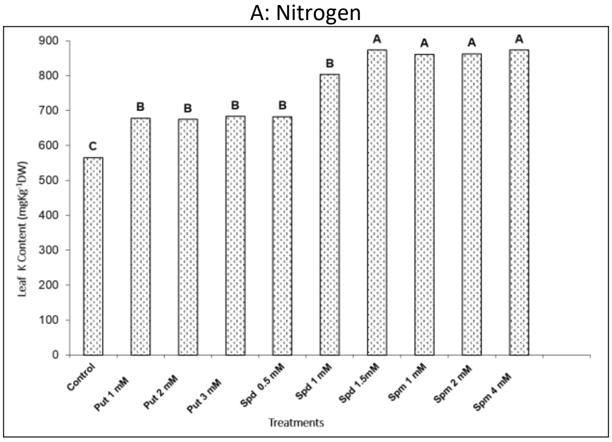
Malondialdehyde (MDA) content was measured according to the method of Mashhadi-Akbar-Boojar and Hosseini Farahi (Boojar and Farahi, 2011). The reaction mixture (4 ml) comprised 1 ml enzyme extract, 2 g trichloracetic acid (TCA), and thiobarbituric acid (TBA). The MDA content was assayed at 532 and 600 nm for control and samples, respectively.



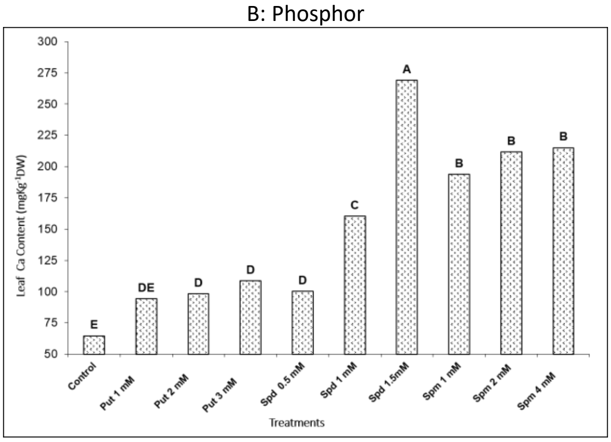
A: Nitrogen



B: Phosphor



C: Potassium



D: Calcium

Fig. I. Effect of different polyamine foliar applications on absorption and accumulation of macronutrient contents in leaves of Dulce Vita rose plants grown in hydroponic culture; A: Nitrogen, B: Phosphor, C: Potassium, and D: Calcium). Mean values with similar letters in each figure are not significantly different (P≤0.01) using Duncan's Multiple Range Test (DMRT).

Statistical Analysis

One-way ANOVA was performed and the collected data were analyzed using MSTAT-C software. Means were compared using least significant differences (LSD) test.

Results

Vase life

Compared to control, the highest level of Spm and Spd treatment significantly extended vase life of cut Dulce Vita flowers up to approximately 2 days (Table 2). Application of Put did not increase vase life. Similar response was observed in treatments with the other two polyamines at lower concentrations.

Effect of polyamines on leaf mineral nutrient contents

Leaf analysis indicated that all applied PAs significantly improved mineral absorption and accumulation (Fig. I). Among the applied PAs, Spm and Spd significantly improved mineral contents of all elements while Put induced a significant increase only in the contents of K and Ca.

Table 2
Effect of exogenous application of Put, Spd, and Spm on vase life of hydroponic grown Duce Vita rose flowers

Treatments	Vase life (Day)
Control	14.16 bd
Put 1 mM	14.16 bc
Put 2 mM	15.00ab
Put 3 mM	15.33 ab
Spd 0.5 mM	13.00 c
Spd 1 mM	15.33 ab
Spd 1.5mM	15.83 a
Spm 1 mM	14.50 abc
Spm 2 mM	15.26 ab
Spm 4 mM	16.00 a

There was a great variation in the effects of different concentrations of Spd resulting in terms of the maximum accumulation at the highest concentration (1.5 mM). Spm treatment resulted in an increasing trend with concentration increment, but there was no a significant difference among different concentrations. Put did not show much difference between its various concentrations, and did not result in a significant effect in most treatments. Amongst the treatments of the study, 1.5 mM Spd had the highest efficiency in improving mineral contents of leaves. Also, amongst the applied PAs, Spm had a high level of mineral absorption at all concentrations in the study. Moreover, Spd was mostly effective at 1.5 mM concentration, and Put did not have a significant effect on most minerals.

Nitrogen

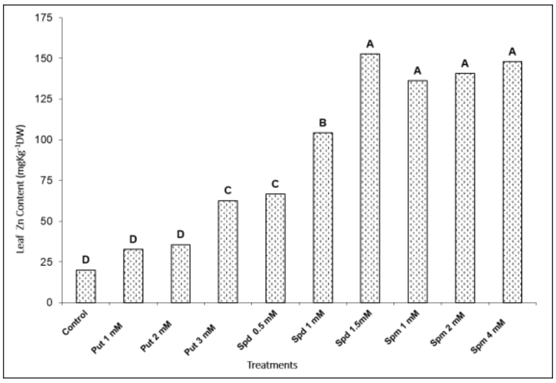
As shown in Fig. (I. a), application of PA significantly improved N contents in the leaves of the treated plants. All levels of Spm resulted in a consistent level of nitrogen while Put was only effective at 3 mM concentration, which was lower than all other treatments. The highest level of N content (2.77 % DW) was observed at 1.5 mM concentration of Spd. Absorption increment for this element was more than 2.5 folds.

Phosphorous

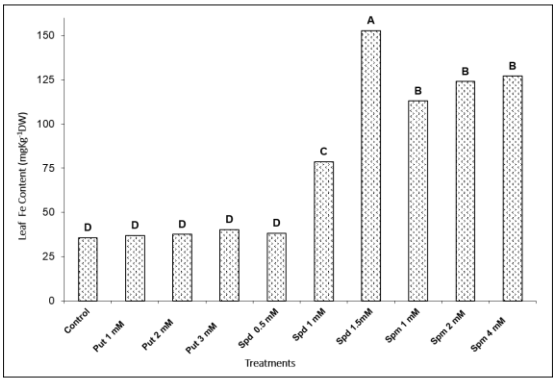
Among different treatments of the study, only Spm and high level of Spd had a significant impact on P contents of leaves in the treated plants (Fig. I. b). In fact, 1.5 mM Spd treatment resulted in the highest P content, followed by Spm. The improvement was more than 2 folds for this mineral.

Potassium

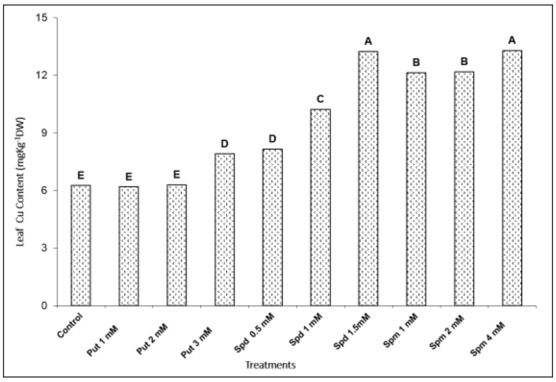
Potassium content was also enhanced by PA application and all treatments resulted in a significantly higher K content (Fig. I. c). Spm and 1.5 mM Spd treatments resulted in the maximum leaf K content while there was no significant difference amongst the treatments of the study. Although the difference between K content was significant, there was no great variation amongst the applied PAs.



A: Zinc



B: Iron



C: Copper

Fig. II. Effect of different polyamine foliar applications on absorption and accumulation of micronutrient contents in leaves of Dulce Vita rose plants grown in hydroponic culture; mean values with similar letters in each figure are not significantly different at $P \leq 0.01$ using Duncan's Multiple Range Test (DMRT).

Calcium

Leaf Ca content was similarly improved by PA application (Fig. II. d). The maximum content was observed in 1.5 mM Spd treatments (269 mg Kg^{-1} DW). This was followed by treatments with various concentrations of Spm. The improvement was more than 4 folds for calcium content in flowers treated with Spm 2 and 4 mM.

Zinc

Considering micronutrients, PA application increased Zn content in rose plants up to 7 folds (Fig. II. a). The highest concentration was observed under 1.5 mM Spd application. However, among the treatments of the study, Spm induced higher absorption in comparison to control irrespective of the concentration applied. On the other hand, the effect of Spd was significantly concentration-dependent. Finally, only the highest concentration of Put increased Zn content in comparison to control (Fig. II. a).

Iron

Fe content improved only with application of Spm and high concentrations of Spd (Fig. VI). Put was not effective in increasing Fe absorption and accumulation in leaves of Dulce Vita rose plants. Fe accumulation was 4-fold in plants treated with 1.5 mM Spd, reaching 152.7 $mgKg^{-1}DW$ while Put and low concentration of Spd were not effective in Fe absorption and accumulation.

Copper

Applying PA improved Cu content of the plants under study (Fig. VII). The improvement was not considerable for Put while it was significantly high for Spm and high concentration of Spd. In all applied treatments, Cu leaf content increased by concentration increment. Cu absorption was also influenced by PA foliar application. Results indicated that plants treated with 1.5 mM Spm and 4 mM Spm had the highest cu content of 13.25 and 13.29 mg Kg^{-1} DW, respectively. Cu content under these treatments was 1.2-fold higher than the other treatments of the study (Fig. VII).

ACC synthase activity

Results showed that application of polyamines inhibited and reduced the activity of ACC enzyme synthase. Among the polyamines under investigation, Spm and Spd were more effective than Put in reducing the activity of ASC synthase. The lowest activity of ACC synthase was in the treatment with 4 mM Spm (9.72 nmol.h.mg $protein^{-1}$) while the highest activity of this enzyme was observed in control (29.96 nmol. h.mg $protein^{-1}$) (Fig. III. a). In other words, the activity of ASC synthase enzyme in control plants was about

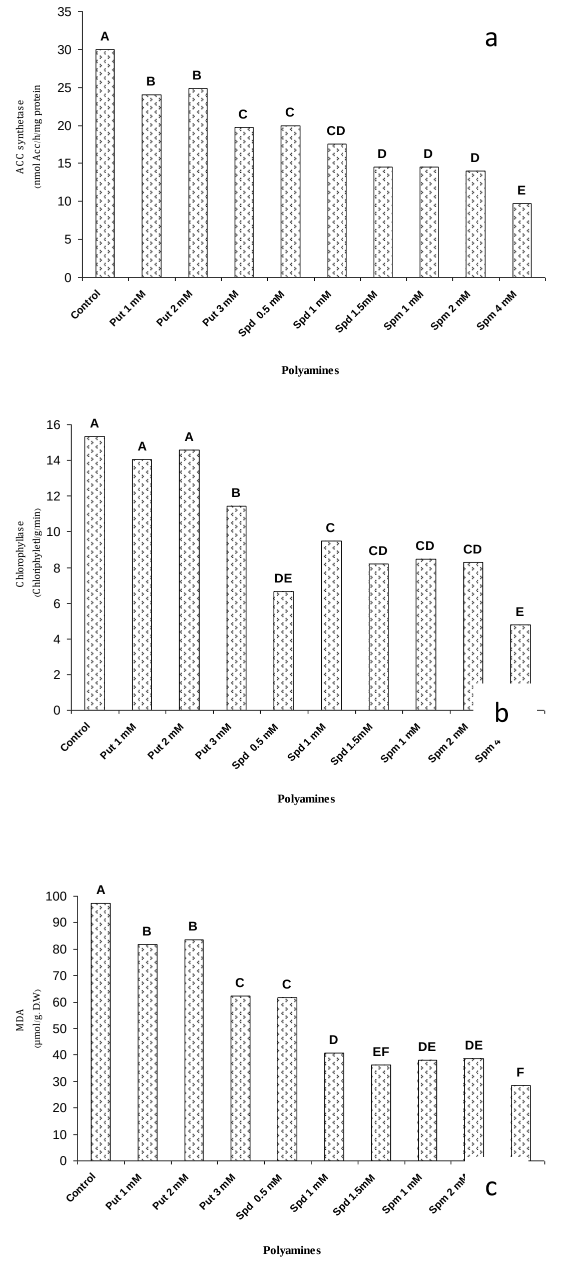


Fig. III. Effect of exogenous foliar application of Put, Spd, and Spm on ACC synthase activity (a), chlorophyllase activity (b), and malondialdehyde (MDA) production (c) in leaves of Dolce Vita rose

3 times higher than that in the plants sprayed with 4 mM Spm. Similarly, the activity of ACC synthase in treated flowers, was lower than control. In general, the activity of ACC synthase declined after day 4 of the harvest and reached its lowest level on day 12 (Fig. IV. a). The lowest level of ACC synthase activity was observed in 0.5 mM Spd.

Chlorophyllase activity

Application of polyamines decreased flower stem leaf chlorophyllase activity. Amongst treatments, 4 mM Spm decreased chlorophyllase activity by 3.2 folds compared to control plants (Fig. III. b). Changes of chlorophyllase activities after harvest showed that the activity of this enzyme increased during the first days of experiment and declined later on. The minimum activity (6.8 chlorophyllide. g. min^{-1}) was observed in 0.5 mM Spm treatment (Fig. III. b). During the experiment, the minimum chlorophyllase activity (3.92 chlorophyllide. g. min^{-1}) was observed on day 12 after harvest under 0.5 mM Spd treatment (Fig. III. b).

MDA production

Polyamine treatment decreased the production of MDA as a destructive biomarker in leaves of rose flower. Application of 4 mM Spm reduced MDA production more than 3 folds and consequently, the least MDA level (28.4 μmol. g. D.W^{-1}) was observed in rose flowers treated with 4 mM Spm (Fig. II. c). During vase life of flowers, MAD content increased in all the treatments (Fig. III. c). By applications of 0.5 mM Spd, MAD content increased up to 141 μmol. g. D.W^{-1} while c) content in control flowers was 195 μmol. g. D.W^{-1} on day 12 after harvest (Fig. III. c).

Discussion

Previous reports on cut flowers have suggested that senescence delay is the reason for vase life increase when PA is applied. In their study, (Sivaprakasam et al., 2009)reported three days delay in deterioration of cut gladiolus flowers under 5 mM Spm treatment. Similarly, senescence delay in gladiolus flowers by application of polyamine was reported (Raju Dantuluri et al., 2008). They considered cell membrane permeability improvement as the reason behind vase life increase. Scientists argued that the production of ethylene inhibitors by PA-treated flowers is involved in increased vase life of cut flowers(Desmedt et al., 2021). Likewise, some researchers reported that vase life improvement in cut rose flowers by 0.1 mM Spm application through reduced ethylene production(Farooq et al., 2021). Similarly, Dastyaran and Hosseini Farahi (2015) found foliar application of 2 or 4 mM Put

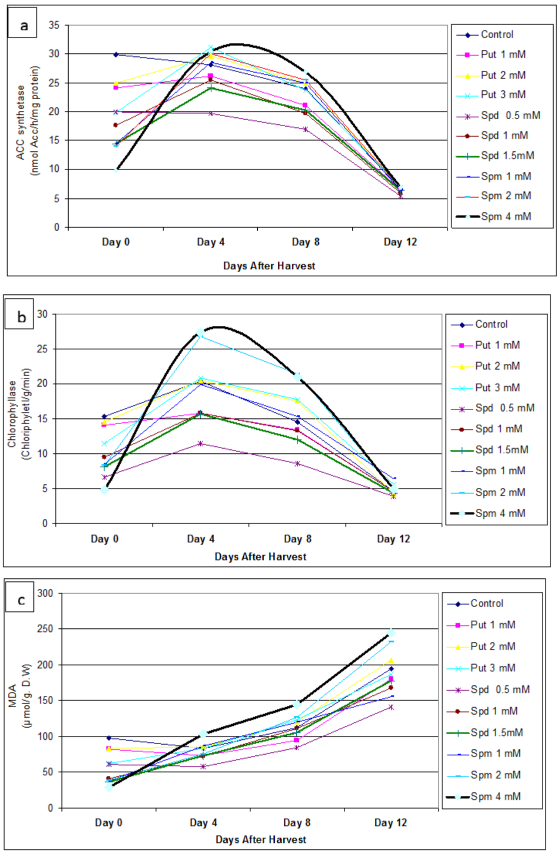


Fig. IV. Changes in ACC synthase activity (a), chlorophyllase activity (b), and malondialdehyde (MDA) content (c) of Dolce Vita rose flower leaves after polyamine foliar application during 12 days.

with humic acid during plant growth as an effective treatment to improve reproductive characteristics of Dulce Vita roses(Dastyaran and Hosseini Farahi, 2015). The same researchers observed that vase life of Dulce Vita rose flowers significantly increased under Put treatment, and flowers of the treated plants lasted 4 more days compared to control. The best treatment for vase life extension was 4 mM Put + 400 mgl^{-1} HA (Dastyaran and Hosseini Farahi, 2015). Similar finding has been reported by Farjadi Shakib and coworkers (Farjadi Shakib et al., 2013)for vegetative characteristics of Persian cyclamen. They reported that application of Spd increased number of flowers and vase life of the native flower. PA application has also been reported to increase number of florets in *Freesia hybrida* cut flowers (Adil et al., 2021).

Previous findings on cut flowers have shown that application of PAs influenced mineral contents of the treated plants. Polyamines can act as an additional source of nitrogen; moreover, they can increase nitrogen uptake and storage in nitrogen-containing compounds such as amino acids. On the other hand, they protect the plant from stress by forming amino acids. Phosphorus plays an important role in reproductive and growth of plants, since it is present in important compounds such as ATP, NADP, NAD, ans nucleic acid and coenzymes (Xiao et al., 2018; Yousefi et al., 2019). Studies indicated the vital role of potassium in photosynthesis and its direct effect on photosynthetic pigments and carbon dioxide uptake (Tränkner et al., 2018). In their study, Abdel Aziz Nahed et al. (Abdel Aziz et al., 2009) found that foliar application of Put (50-200 mgl^{-1}) increased absorption of N, P, and K and their contents in leaves of gladiolus. Researches have also reported increased N content in leaves of salt-stressed *Myrtus communis* treated with Put(Yao et al., 2023). Dastyaran and Hosseini Farahi (2015) observed that application of Put in combination with humic acid increased uptake and concentration of microelements such as N, P, K, Ca, and Mg in leaves of Dulce Vita roses. Similar finding was observed by Abd El-Dayem (2015) for N, P, and K minerals in snap bean cv. Bronco by application of 20 mgl^{-1} Put. El Habba et al. (2016) observed that application of Put at the concentration of 50 ppm resulted in the highest content of N, P, and K in leaves and stems of *Populus euramericana* trees. Besides, P and K contents in roots of the trees were significantly affected and increased. Yousefi et al. (2019) recorded the highest nitrogen, phosphorous, and potassium concentrations in exogenous application of 1 mM Spm on *Rosa hybrida* cv. Herbert Stevens.

In a similar study on *Nymphoides peltatum*, Xue (2008) observed that exogenous application of Spm and Smd increased Zn content and could overcome Zn deficiency and improve mineral balance under mineral deficiency condition. One researcher observed that pre-treatment of salinity-stressed rice plants with 1 mM Spd improved grain yield and K content of leaves while it did not have a significant impact on the composition of the other micronutrients under study(Nounjan and Theerakulpisut, 2023). Rezvanpour et al. (2015) observed that by application of PAs (Put, Spm, and Spd) both as soil drench and foliar application improved growth and development of the plant as well as the content of various minerals such as N, P, K, Mg, Fe, and Zn of *Freesia hybrida* leaves.

Various mechanisms have been suggested for mineral absorption improvement by PA application. PAs increase photosynthesis and consequently lead to a better mineral absorption(Borromeo et al., 2023). Some other researchers have recommended better mycorrhizal development as the reason for improved mineral absorption. Dunn and Becerra-Rivera, reported that PAs regulate root development and its interaction with microbes(Dunn and Becerra-Rivera, 2023). Liang et al. (Liang et al., 2022)reported that application of Put along with Arbuscular mycorrhizal fungi and Put synthesis inhibitor (Difluoromethylornithine) increased P content in root and leaf of *Citrus tangerine*. In another study, Zhang and coworkers (Zhang et al., 2022)observed that exogenous application of Put and Spd significantly increased root dry weight in citrus trees. Our findings indicated that in Dulce Vita rose leaves, foliar application of Spd increased Fe uptake at 1.5 mM concentration and Cu uptake at 1.5 and 4 mM concentrations. Moreover, Spd (1.5 mM) and Spm (1.2 and 4 mM) enhanced zinc uptake. Zinc interacts with plant hormones, stimulates antioxidant enzymes, and increases cell membrane stability (Sharma et al., 2022). Therefore, application of polyamines in flowers can increase cell membrane stability and reduce MAD content, improve zinc uptake, and finally enhance vase life, as our findings showed.

Polyamines are involved in some physiological processes such as senescence as a competitive demand for SAM (S-Adenosyl-L-methionine); they are also considered inhibitors of ethylene production (Stolarska et al., 2023). Interaction of ethylene and polyamines in the conversion of SAM to ACC pathway has been proposed. The exogenously supplied Put and Spd suppressed ACC transcripts in aged orange discs (Harpaz-Saad et al., 2018) On the other hand, Spm and Spd are synthetized by the aminopropyl moieties, which is derived from SAM. As SAM is a precursor of ethylene, the production of ethylene is prevented (Zhang et al., 2019). Previous research indicated that application of Put on *Bougainvillea buttiana* (Lin et al., 2021), *Gladiolus* (Abdel Aziz Nahed et al., 2009), and *Rosa hybrida* (Yousefi et al., 2019) delayed senescence. In this study, the use of Spm and Spd caused a significant reduction in chlorophyllase activity and MAD content. Zhang et al. (2019) stated that Put reduced chlorophyllase activity by inhibiting chlorophyllase gene expression in broccoli, especially BoCLH2 and maintaining membrane stability beside chlorophyll degradation delay.

Results of our study showed that polyamines increased vase life through their possible effect on ethylene biosynthesis pathway, their impact on increasing the uptake of mineral elements, and ultimately their effect on enzymes and biochemical pathways.

Conclusion

Constructive effect of PAs on various vegetative and nutritional aspects of hydroponic Dulce Vita cut rose flowers was observed in the present study. Generally, amongst the Pas investigated in this study, Spm had the most beneficial effect on the studied features while Put did not have a significant impact on most of the studied parameters compared to control, or its impact was very little. On the other hand, Spd demonstrated a favorable effect applied at the highest concentration. Improved vegetative characteristics under PAs application can be explained by their influence on cell elongation, division, and development of tissues and organs, as various features of plant growth and development are associated with biochemical and enzymatic changes implemented by exogenous PA application.

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References

Abd El-Dayem, H.M.M., M.A.M. Mady, M.M.M. Abd El-All and R.S.M. Eid. 2015. Effect of Some Antioxidants, Potassium and Arbuscular Mycorrhiza on Growth, Yield and Quality of Snap Bean Plants Grown Under Water Stress Levels. *Annals of Agricultural Sciences Moshtohor*. 53(1): 15–30.

Abdel Aziz, N. G., L. S. Taha and S. M. Ibrahim. 2009. Some studies on the effect of putrescine, ascorbic acid and thiamine on growth, flowering and some chemical constituents of gladiolus plants at Nubaria. *Ozean J Appl Sci,* 2, (2) 169-179.

Adil, A. M., E. E. Ahmed, A. T. Al-Chalabi and A. F. Al-Ma'athedi. 2021. Effect of planting time and corms treatment with gibberellic acid on growth, flowering, and vase life of 'Corona'. *Journal of Horticultural Research,* 29, (2) 23-30.

Alhaithloul, H. A., M. H. Soliman, K. L. Ameta, M. A. El-Esawi and A. Elkelish. 2019. Changes in ecophysiology, osmolytes, and secondary metabolites of the medicinal plants of Mentha piperita and Catharanthus roseus subjected to drought and heat stress. *Biomolecules,* 10, (1) 43.

Boojar, M. M. A. and M. H. Farahi. 2011. The role of antioxidative enzymes in copper tolerance strategy of Mimosaceace prosopis farcta growing in a copper mine. *International Journal of Plant Biology,* 2, (1) e1.

Borromeo, I., F. Domenici, M. Del Gallo and C. Forni. 2023. Role of Polyamines in the Response to Salt Stress of Tomato. *Plants,* 12, (9) 1855.

Dastyaran, M. and M. Hosseini Farahi. 2015. Effects of humic acid and puterscine on vegetative properties and vase life of rose in soilless culture system. *Journal of Soil and Plant Interactions-Isfahan University of Technology,* 5, (4) 241-250.

Desmedt, W., W. Jonckheere, V. H. Nguyen, M. Ameye, N. De Zutter, K. De Kock, J. Debode, T. Van Leeuwen, K. Audenaert and B. Vanholme. 2021. The phenylpropanoid pathway inhibitor piperonylic acid induces broad-spectrum pest and disease resistance in plants. *Plant, Cell & Environment,* 44, (9) 3122-3139.

Dunn, M. F. and V. A. Becerra-Rivera. 2023. The Biosynthesis and functions of polyamines in the interaction of plant growth-promoting rhizobacteria with plants. *Plants,* 12, (14) 2671.

El-Ghait, A., A. Gomaa, A. Youssef and A. El-Nemr. 2022. EFFECT OF SOME GROWTH SUBSTANCES AND CHEMICAL FERTILIZATION ON VEGETATIVE GROWTH AND CHEMICAL COMPOSITION OF MATTHIOLA INCANA L. PLANT. *Scientific Journal of Flowers and Ornamental Plants,* 9, (3) 167-182.

El Habba, E., N.G. Abdel Aziz, A.M.Z. Sarhan, A. M. S. Arafa, N. M. Youssef. 2016. Effect of Putrescine and Growing Media on Vegetative Growth and Chemical Constituents of *Populus euramericana* Plants. *Journal of Innovations in Pharmaceuticals and Biological Sciences*, 3 (1): 61-73.

Emami, A. 1996. Plant analysis methods. Technical Bulletin No. 982. Plant, Soil and Water Research Institute. Tehran, Iran.

Farjadi Shakib, M., R. Naderi and M. Mashhadi Akbar Boujar. 2013. Effects of spermidine spray on morphological, physiological and biochemical characteristics of Cyclamen persicum Miller. *Journal of Plant Ecophysiology,* 5, (13) 96-113.

Farooq, S., M. L. Lone, S. Parveen, F. Altaf and I. Tahir. 2021. Polyamines accentuate vase life by augmenting antioxidant system in cut spikes of Consolida ajacis (L.) Schur. *Ornamental Horticulture,* 27, 495-504.

Gaurav, A. K., Namita, D. Raju, M. Ramkumar, M. Singh, B. Singh, S. G. Krishnan, S. Panwar and A. M. Sevanthi. 2021. Genetic diversity analysis of wild and cultivated Rosa species of India using microsatellite markers and their comparison with morphology based diversity. *Journal of Plant Biochemistry and Biotechnology,* 1-10.

Ghorbani, H., A. Ebrahimzadeh, B. Eftekhari Sis and M. B. Hasanpouraghadm. 2018. Impact of exogenous spermine application on the vase life of cut rose flowers 'Dolce Vita'. *Journal of Ornamental Plants,* 8, (1) 57-66.

Harpaz-Saad, S., T. Azoulay, T. Arazi, E. Ben-Yaakov, A. Mett, Y. M. Shiboleth, S. Hortensteiner, D. Gidoni, A. Gal-On and E. E. Goldschmidt. 2007. Chlorophyllase is a rate-limiting enzyme in chlorophyll catabolism and is posttranslationally regulated. *The Plant Cell,* 19, (3) 1007-1022.

Harpaz-Saad, S., G.M. Yoon, A.K. Mattoo and J.J. Kieber. 2018. The Formation of ACC and Competition between Polyamines and Ethylene for SAM. The Plant Hormone Ethylene. Vol. 44. Jhon Wily and Son. https://doi.org/10.1002/9781119312994.apr0475

Hosseini Farahi, M. and A. Aboutalebi Jahromi. 2018. Effect of pre-harvest foliar application of polyamines and calcium sulfate on vegetative characteristics and mineral nutrient uptake in Rosa hybrida. *Journal of Ornamental Plants,* 8, (4) 241-253.

Hosseini Farahi, M., B. Kholdebarin, S. Eshghi, B. Jamali and H. Reza Roosta. 2019. Changes in plant growth substances, contents and flower quality of rose cv.'Dolce Vita'in response to nitrogen sources under soilless culture conditions. *Journal of Plant Nutrition,* 42, (9) 1047-1060.

Karimi, M., F. Akbari and A. Heidarzade. 2017. Protective effects of polyamines on regulation of senescence in spray carnation cut flowers (Dianthus caryophyllus' Spotlight'). *Acta Agriculturae Slovenica,* 109, (3) 509–515-509–515.

Kasem, M. M., M. M. Abd El-Baset, A. A. Helaly, E.-S. A. El-Boraie, M. D. Alqahtani, A. Alhashimi, A. M. Abu-Elsaoud, A. Elkelish, A. G. Mancy and A. Alhumaid. 2023. Pre and postharvest characteristics of Dahlia pinnata var. pinnata, cav. As affected by SiO2 and CaCO3 nanoparticles under two different planting dates. *Heliyon,* 9, (6)

Killiny, N. and Y. Nehela. 2020. Citrus polyamines: structure, biosynthesis, and physiological functions. *Plants,* 9, (4) 426.

Liang, S.-M., F.-L. Zheng and Q.-S. Wu. 2022. Elucidating the dialogue between arbuscular mycorrhizal fungi and polyamines in plants. *World Journal of Microbiology and Biotechnology,* 38, (9) 159.

Lin, K.-H., J.-M. Li, C.-W. Wu and Y.-S. Chang. 2021. Effects of plant growth regulators and polyamines on bract longevity in Bougainvillea buttiana. *Horticulture, Environment, and Biotechnology,* 62, 149-157.

Mustafavi, S. H., H. Naghdi Badi, A. Sękara, A. Mehrafarin, T. Janda, M. Ghorbanpour and H. Rafiee. 2018. Polyamines and their possible mechanisms involved in plant physiological processes and elicitation of secondary metabolites. *Acta Physiologiae Plantarum,* 40, 1-19.

Nandy, S., T. Das, C. K. Tudu, T. Mishra, M. Ghorai, V. S. Gadekar, U. Anand, M. Kumar, T. Behl and N. K. Shaikh. 2022. Unravelling the multi-faceted regulatory role of polyamines in plant biotechnology, transgenics and secondary metabolomics. *Applied Microbiology and Biotechnology,* 106, (3) 905-929.

Nounjan, N. and P. Theerakulpisut. 2023. Transgenerational stress memory and transgenerational effects caused by wood vinegar and spermidine are associated with early germination of rice seeds under salt stress. *Plant Growth Regulation,* 1-14.

Raju Dantuluri, V., R. Misra and V. Singh. 2008. Effect of polyamines on post harvest life of gladiolus spikes. *Journal of Ornamental Horticulture,* 11, (1) 66-68.

Rezvanypour, S., A. Hatamzadeh, S. A. Elahinia and H. R. Asghari. 2015. Exogenous polyamines improve mycorrhizal development and growth and flowering of Freesia hybrida. *Journal of Horticultural Research,* 23, (2)

Roosta, H. R. and I. Rezaei. 2014. Effect of nutrient solution pH on the vegetative and reproductive growth and physiological characteristics of rose cv.'Grand Gala'in hydroponic system. *Journal of Plant Nutrition,* 37, (13) 2179-2194.

Sankaran, M., D. Kalaivanan, S. Mishra, P. Singh, M. S. Prasad and M. T. R. Kannan. 2022. Abstracts of ICAR-IIHR PhD thesis. ICAR-IIHR.

Yao, X.-C., L.-F. Meng, W.-L. Zhao and G.-L. Mao. 2023. Changes in the morphology traits, anatomical structure of the leaves and transcriptome in Lycium barbarum L. under salt stress. *Frontiers in Plant Science,* 14, 1090366.

Sedaghathoor, S., Z. Narouei, S. A. Sajjadi and S. Piri. 2020. The effect of chemical treatments (silver thiosulfate and putrescine) on vase life and quality of cut Chrysanthemum morifolium (Ram.) flowers. *Cogent Biology,* 6, (1) 1754320.

Sharma, A., D. Kapoor, S. Gautam, M. Landi, N. Kandhol, F. Araniti, M. Ramakrishnan, L. Satish, V. P. Singh and P. Sharma. 2022. Heavy metal induced regulation of plant biology: Recent insights. *Physiologia Plantarum,* 174, (3) e13688.

Sivaprakasam, G., V. Singh and A. Ajay. 2009. Physiological and molecular analysis of effect of spermine on senescing petals of gladiolus. *Indian Journal of Plant Physiology,* 14, (4) 384-391.

Stolarska, E., E. Paluch-Lubawa, M. Grabsztunowicz, U. Kumar Tanwar, M. Arasimowicz-Jelonek, O. Phanstiel, A. K. Mattoo and E. Sobieszczuk-Nowicka. 2023. Polyamines as Universal Bioregulators across Kingdoms and Their role in Cellular Longevity and Death. *Critical Reviews in Plant Sciences,* 1-21.

Tränkner, M., E. Tavakol and B. Jákli. 2018. Functioning of potassium and magnesium in photosynthesis, photosynthate translocation and photoprotection. *Physiologia plantarum,* 163, (3) 414-431.

Xiao, W., R.-S. Wang, D. E. Handy and J. Loscalzo. 2018. NAD (H) and NADP (H) redox couples and cellular energy metabolism. *Antioxidants & redox signaling,* 28, (3) 251-272.

Xue, W. 2008. Effects of Polyamines on Nutrient Element Absorption in the Leaves of *Nymphoides peltatum* under Zn Stress· Journal of Anhui Agricultural Sciences, (http://en.cnki.com.cn/Article_en/CJFDTotal-AHNY200830016.

Yousefi, F., Z. Jabbarzadeh, J. Amiri and M. H. Rasouli-Sadaghiani. 2019. Response of roses (Rosa hybrida L.'Herbert Stevens') to foliar application of polyamines on root development, flowering, photosynthetic pigments, antioxidant enzymes activity and NPK. *Scientific Reports,* 9, (1) 16025.

Zhang, Q., M. Liang, R. Song, Z. Song, H. Song and X. Qiao. 2022. Brassinosteroids enhance resistance to manganese toxicity in Malus robusta Rehd. via modulating polyamines profile. *Journal of Plant Physiology,* 277, 153808.

Zlesak, D. C. 2007. Rose: Rosa x hybrida. In *Flower breeding and genetics: issues, challenges and opportunities for the 21st century*:695-740: Springer. Number of 695-740 pp.