

Polyamines and ethylene action blocker (STS) effectively augment longevity and postharvest attributes in isolated flowers of *Digitalis purpurea* L.

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Abstract

The present investigation focused on the study of the exogenous inclusion of anti-senescence biogenic polyamines (putrescine, spermidine and spermine) and ethylene antagonist silver thiosulphate on flower longevity and postharvest performance in excised flowers of *Digitalis purpurea* L. One day before the anthesis stage, *Digitalis purpurea*'s isolated buds were transported to the laboratory in distilled water. The samples were divided into five sets with one set of flower buds as control held in distilled water. The remaining four sets were respectively supplied with 0.5, 1 and 1.5 mM of putrescine (PUT), 0.1, 0.2 and 0.3 mM of spermidine (SPD), 0.2, 0.4 and 0.6 mM of spermine (SPM), 0.1, 0.2 and 0.3 mM of silver thiosulphate (STS). Including polyamines and STS in holding solutions enhanced the flower longevity of *D. purpurea* significantly compared to the control. The results indicated that the flower longevity of 14 days was recorded in 0.4 mM of spermine, followed by 13 days in 1 mM PUT, 12.5 days in 0.2 mM SPD and 12 days in 0.2 mM STS. This enhanced flower longevity corroborated with the higher values of soluble proteins, total sugars, floral diameter and membrane stability index. The improved flower longevity was also found to be positively associated with increased activities of various antioxidant enzymes viz., superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) and reduced activity of lipoxygenase (LOX). The flowers supplemented with different treatments retained a lower phenolic content compared to control. This research concluded that polyamines and STS have a profound impact on the flower longevity of *Digitalis* flowers. SPM was a more pretentious polyamine in augmenting the postharvest performance in isolated flowers of *D. purpurea*.

Key words: *Digitalis purpurea* L., antioxidant enzymes, flower longevity, senescence, silver thiosulphate, spermine

Introduction

Flower senescence is a critical challenge in the postharvest management of cut flowers. In floriculture, the main focus of researchers is to delay the onset of senescence for the extension of flower longevity. Petal death during floral senescence is accompanied by increased oxidative stress, decreased antioxidant enzyme levels, and membrane permeability loss, leading to lipid, protein, carbohydrate and nucleic acid degradation (Ahmad and Tahir, 2016). Developmental processes, including the senescence of cut flowers, are under hormonal control (Ma *et al.*, 2018). In one group of flowers, the petal senescence is highly orchestrated by ethylene (ethylene sensitive), while in another group of flowers, little or no ethylene (ethylene insensitive) is generated during the senescence (Rogers, 2012). In ethylene-sensitive flowers, it has been shown that ethylene antagonists such as silver thiosulfate (STS), amino vinyl glycine (AVG) and aminoxy acetic acid (AOA) delay the senescence of the flowers (Nisar *et al.*, 2015). STS is known to suppress autocatalytic ethylene production by inhibiting its action and providing antimicrobial activity in plant tissues (Minde *et al.*, 2019). In addition, it has also been observed that ethylene biosynthesis competitors, polyamines, exhibit anti-senescence properties in ethylene-sensitive flowers (Sobieszczuk *et al.*, 2016). Polyamines are ubiquitous nitrogen bases found in all living organisms. Evidence exists that S-adenosylmethionine

(SAM) is the precursor for both polyamines and ethylene; however, ethylene promotes senescence, whereas polyamines tend to have a delaying effect (Lokesh *et al.*, 2019).

Digitalis purpurea L., commonly called foxglove, a biennial medicinal flowering plant species, is a very popular garden material from the fifteenth century, with several available cultivars. It is the primary source of glycoside digoxin, a life-saving cardiac drug (Ravi *et al.*, 2020). *D. purpurea* also contains sugars, starch, gum, fatty matter and volatile oil, which possess antioxidant, insecticidal, antidiabetic, immunological, cytotoxic, neuro, hepatic and cardioprotective properties (Agrawal *et al.*, 2012). Besides medical uses, *D. purpurea* is cultivated in the floriculture industry as a potential cut flower (Clark *et al.*, 2010; Bergman *et al.*, 2016). The flower longevity of the foxglove is comparatively short, as ethylene accelerates the abscission of flowers. Despite being ethylene sensitive, the role of polyamines and STS in modulating flower senescence in this plant is yet to be established. Therefore, the primary aim of this study was to assess the effect of different polyamines (PUT, SPD, SPM) and STS on the postharvest performance of isolated flowers of *D. purpurea*, aiming to delay its senescence. The study could be utilized in exploring the approaches to delay the senescence in spikes of not only *D. purpurea* but also other ethylene-sensitive flowers to boost their market value in the cut flower industry.

Materials and methods

For this study, isolated buds of *D. Purpurea*, one day before the anthesis stage (Fig. 1), were obtained from Kashmir University Botanic Garden (KUBG) and transported to the laboratory in distilled water. The flowers were divided into five sets designated as Control, PUT, SPD, SPM and STS. The treatment concentrations include 0.5, 1 and 1.5 mM of PUT, 0.1, 0.2 and 0.3 mM of SPD, 0.2, 0.4 and 0.6 mM of SPM, 0.1, 0.2 and 0.3 mM of STS and each concentration, including control, comprised of 15 replicates. Among these treatments, PUT, SPD and SPM were used as continuous holding solutions, while STS was applied as a pulse treatment for one hour. The day isolated buds were exposed to different treatments was designated as day zero (D0). Various physiological and biochemical parameters from the petal tissues were measured on day 2 and day 4 after being transferred to their respective test solutions. The experiment was performed under stable conditions with a relative humidity (RH) of $60 \pm 10\%$, a light duration of 12 h per day and an average temperature of 23 ± 2 °C.

Assessment of flower longevity and floral diameter: The average longevity of the flowers was counted from the day of transfer of isolated flowers to their respective testing solutions and was determined to be terminated when the last flower lost its aesthetic value. Floral diameter was recorded on day two and day 4 of the experiment as the mean of two perpendicular measurements across the flower.

Membrane stability index (MSI): The MSI evaluated in the form of solute leakage of the petal tissues was calculated by incubating 100 mg of petal tissue in 5 mL deionized water at 25 °C for 30 min and 100 °C for 15 min (Sairam, 1994). MSI was computed as under:

$$\text{MSI} = [1 - (C1/C2)] \times 100$$

C1 represents the conductivity of the samples incubated at 25 °C and C2 represents the conductivity at 100 °C, after recording the values on Elico CM180 Conductivity meter.

Protein: For the estimation of proteins, 1 g of petal tissue was macerated in 100 mM phosphate buffer of pH 7.2 containing 10 % polyvinyl pyrrolidone (PVP), 1 mM EDTA, 1 % Triton X-100, 10 % glycerol, 1 mM Dithiothreitol (DTT) and 150 mM NaCl. The mixture was centrifuged utilizing a refrigerated centrifuge at 12,000xg at 5 °C for 15 min. Proteins were calculated using an appropriate volume of aliquot obtained from the collected supernatant following Lowry *et al.* (1951).

Estimation of sugar fractions and phenols: One g of chopped petal tissue from each treatment was fixed in hot 70% ethanol,

macerated and centrifuged thrice. Total phenols, reducing, non-reducing and total sugars were measured from a suitable aliquot of supernatant. Total phenolics were determined using the Swain and Hillis technique (1959) with gallic acid as the standard. Nelson's method (1944) was used to estimate reducing sugars with glucose as the standard. Non-reducing sugars were converted to reducing sugars by invertase to estimate total sugars. The amount of non-reducing sugars was calculated from the difference between total and reducing sugars. Total phenols and sugar fractions (reducing, non-reducing and total sugars) were measured on days 2 and 4 after the flowers were transferred to the respective test solutions.

Enzyme extraction and assays

Superoxide dismutase activity (SOD): One g of petal tissue was homogenized and thoroughly mixed with 0.1 mM potassium phosphate buffer (pH = 7.8) containing 0.1 mM EDTA, 1 % PVP and 0.5 % (v/v) Triton X-100. The mixture was centrifuged at 15,000xg for 10 min. The supernatant was collected and then filtered using Mira cloth before being utilized for the enzyme assay. The activity of SOD was calculated following the method of Dhindsa *et al.* (1981) by observing the inhibition of photochemical reduction of nitroblue tetrazolium (NBT). The reaction mixture contained 0.1 mM EDTA, 50 mM sodium carbonate, 0.1 mL of the enzyme extract, 75 µM nitroblue tetrazolium (NBT) and 13 mM methionine in 50 mM phosphate buffer (pH = 7.8) in a total volume of 3 mL. To the reaction mixture, adding 2 µM riboflavin and putting the test tubes in water bath at 25°C and illuminating with a 30 W fluorescent lamp initiated the reaction. The test tubes were kept in dark after the reaction was stopped by switching off the light. Other identical, unilluminated test tubes acted as blanks. Absorbance was measured at 560 nm. The amount of enzyme that prevents photoreduction of NBT to blue formazan by 50 percent compared to the reaction mixture kept in darkness without the enzyme extract has been defined as one unit of SOD activity. The SOD activity was expressed as units $\text{min}^{-1} \text{mg}^{-1}$ protein.

Catalase activity (CAT): Aebi's approach (1984) was used to calculate the catalase activity. 1 g of petal tissue was macerated and homogenized in 100 mM potassium phosphate buffer with a pH of 7.0 and 1 mM EDTA. The reaction mixture containing 50 µL enzyme extract, 50 mM potassium phosphate buffer (pH = 7.0), 12.5 mM H_2O_2 , was added with distilled water to make the final volume 3 mL. The reaction was started by adding H_2O_2 and the catalase activity was assayed by measuring H_2O_2 consumption for 3 minutes at 240 nm and was expressed as $\mu\text{mol H}_2\text{O}_2 \text{ red. min}^{-1} \text{mg}^{-1}$ protein.

Ascorbate peroxidase activity (APX): 1 g of Petal tissue was macerated and homogenized in 100 mM sodium phosphate buffer with one mM EDTA, 5 mM ascorbate and 10 % glycerol. The



Fig. 1. One day before anthesis stage of *D. purpurea* flowers used for the present study.

APX activity was determined in 1 mL reaction mixture containing 0.1 mM ascorbate, 50 mM potassium phosphate buffer (pH = 7.0) and 0.3 mM H₂O₂. The reduction in the absorbance was noted for 3 min at 290 nm (Chen and Asada, 1989).

Lipoxygenase activity (LOX): LOX activity was determined by employing the method of Axerold *et al.* (1981). 1 g of petal tissue was thoroughly mixed in 1 mL extraction buffer containing 50 mM potassium phosphate buffer (pH = 6.5), 0.25 % Triton X-100, 10 % polyvinyl pyrrolidone (PVP) and 1 mM phenyl methyl sulfonyl fluoride (PMSF). The 1 mL reaction mixture contained 50 mM Tris-HCl buffer (pH = 6.5) and 0.4 mM linoleic acid. The reaction was started by adding 10 µL crude petal extract to the reaction mixture and absorbance was measured at 234 nm for 5 minutes. The activity was expressed as µmol min⁻¹ mg⁻¹ protein.

Statistical analysis: A completely randomized experimental design was used during the investigation. Fifteen replicates (vials) were used for each treatment, with each vial containing one flower. Each value is a mean of three replicates. Treatment means were compared via analysis of variance using SPSS (SPSS version 16; Chicago, USA). The experiment was conducted twice to reduce the variance between the variables. At the 5% probability level, the least significant difference (LSD) and Standard error between replicates was calculated.

Results

Flower longevity and floral diameter: Flower senescence was accompanied by loss of turgidity followed by wilting and in rolling of petals (Fig. 2). The application of polyamines and STS resulted in a substantial increase in the flower longevity against the control. The average lifespan of the flowers of *D. purpurea* was about 6 days when transferred to DW (control). Among the polyamines tested, 0.4 mM SPM was most efficient in accentuating the flower longevity of *D. purpurea* by eight

days, followed by seven days in 1 mM PUT, 6.5 days in 0.2 mM SPD and six days in 0.2 mM STS. Exogenous use of polyamines and STS in isolated flowers of *D. purpurea* maintained a higher flower diameter than the control with maximum value from the flowers held in SPM. Flower diameter decreased from day 2 to day 4 (Fig. 3 a-b).

Membrane stability index (MSI): The treatment of *D. purpurea* cut flowers with PUT, SPD, SPM and STS resulted in substantial improvement in MSI compared to control. MSI was found to be maximum in SPM-treated flowers, followed by PUT, SPD and STS. However, the MSI values decreased steadily from day 2 to day 4 (Fig. 4).

Soluble proteins: Polyamines and STS maintained an elevated amount of soluble protein content, with the maximum in SPM-treated petal tissues, which gradually declined as time progressed from D2 to D4 (Fig. 5).

Phenols and sugar fractions: On day 2, the flowers held in STS showed lower phenolic content than the control, followed by SPD, PUT and SPM, but on day 4, there was a considerable increase, with the highest value in the flowers from the control (Fig. 6a).

The polyamine and STS-treated flowers had considerably increased sugar content (total, reducing and non-reducing) than the control, with the highest in the SPM samples. Sugar fractions were shown to drop dramatically from day two onwards, with the floral samples in SPM experiencing the least loss (Fig. 6b-d).

Activities of antioxidant and lipoxygenase enzyme: The activities of the antioxidant enzymes SOD, CAT and APX were increased in the petal tissues through PUT, SPD, SPM and STS (Fig. 7a-c). The expression of these enzymes was found to be considerably higher in the SPM treated floral buds compared to other examined solutions but decreased dramatically from day 2 to day 4. Treatment with polyamines and STS reduced LOX

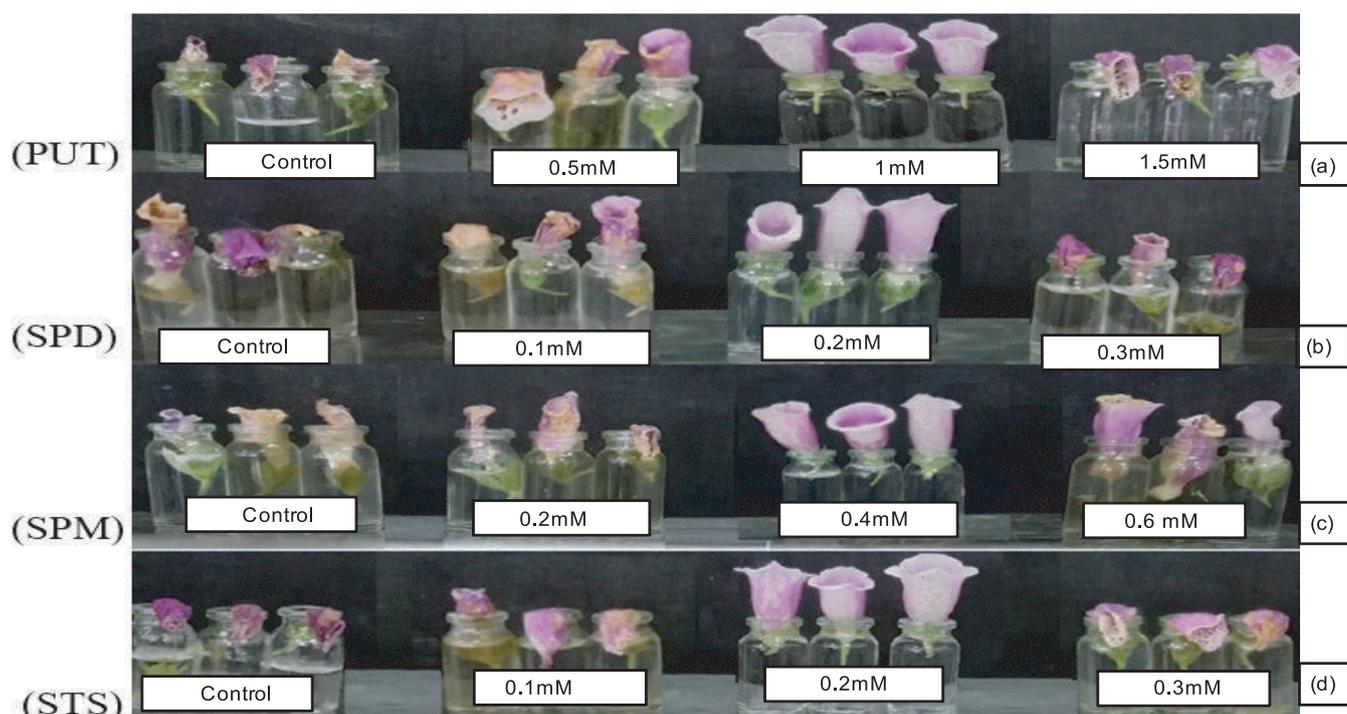


Fig. 2. Effect of different concentrations of (a) PUT, (b) SPD, (c) SPM and (d) STS on flower senescence in isolated flowers of *D. purpurea* on day 11 after transfer to their respective holding solutions.

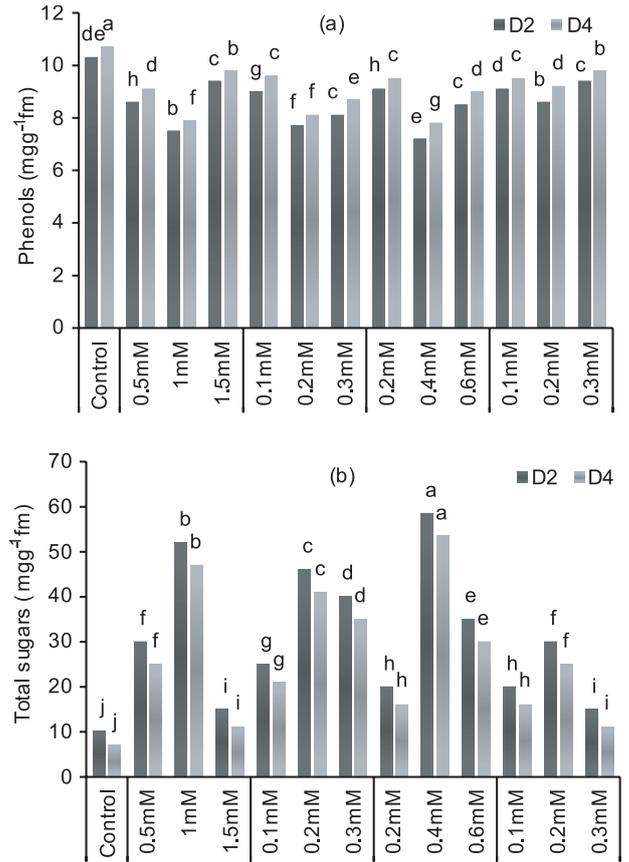
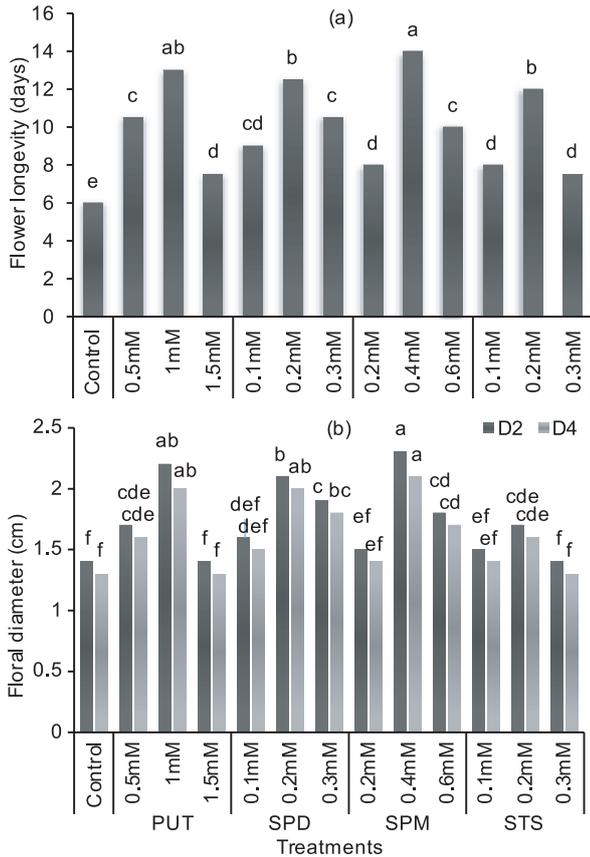


Fig. 3. Effect of different concentrations of PUT, SPD, SPM and STS on (a) Flower longevity and (b) Floral diameter in isolated flowers of *D. purpurea*.

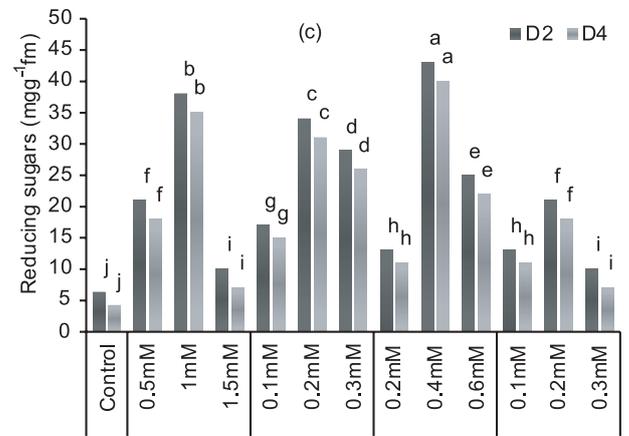
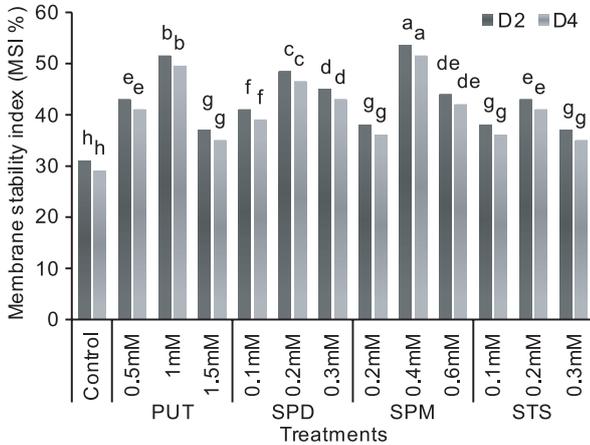


Fig. 4. Effect of different concentrations of PUT, SPD, SPM and STS on Membrane Stability Index in isolated flowers of *D. purpurea*.

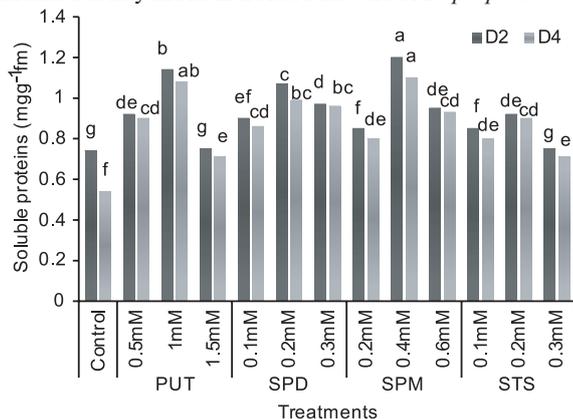


Fig. 5. Effect of different concentrations of PUT, SPD, SPM and STS on Protein content in isolated flowers of *D. purpurea*.

Fig. 6. Effect of different concentrations of PUT, SPD, SPM and STS on (a) Phenolic and (b-d) Sugar content in isolated flowers of *D. purpurea*.

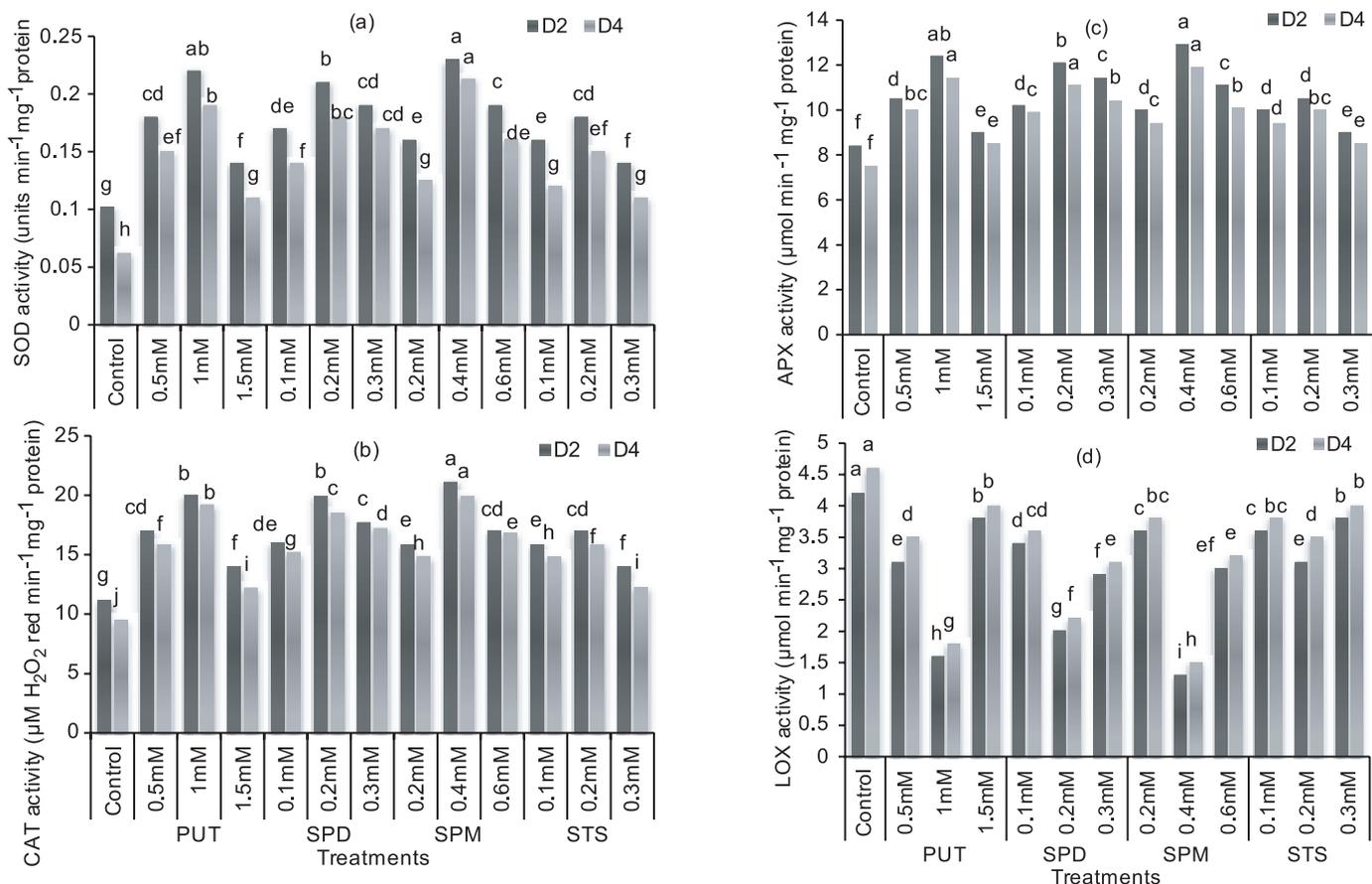


Fig. 7. Effect of different concentrations of PUT, SPD, SPM and STS on activities of antioxidant enzymes in isolated flowers of *D. purpurea*.

activity, with the least in SPM-treated floral buds. The activity of LOX increased significantly from D2 to D4 (Fig. 7d).

Discussion

During this study, SPM was found to be most efficient in improving the quality and flower longevity of the *D. purpurea* flowers by 8 days compared to other tested growth regulators. These findings are as per the earlier studies which showed that exogenous SPM increased the polyamine content of *Anthurium* flowers, delayed senescence and improved their quality (Simoes *et al.*, 2018). It has also been reported that SPM inhibited the senescence of *carnation* petals, possibly due to the corresponding inhibition of ethylene synthesis (Anwar *et al.*, 2015). Moreover, it was found that adding PUT, SPD and STS to the vase solution of the *Antirrhinum*, *Clarkia* delayed senescence and increased their longevity (Asrar *et al.*, 2012; Dar *et al.*, 2020). In addition, isolated flowers held in different polyamine and STS test solutions retained a larger floral diameter than the control. This increased floral diameter may be ascribed to greater water influx in the petal tissues due to the enrichment of carbohydrates, which increases flower turgidity (Lone *et al.*, 2021; Farooq *et al.*, 2021).

Reduced LOX activity may be attributed to improved membrane stability index in polyamine and STS treated tissue samples. This decline in LOX activity may be due to preserving sufficient proteins, phospholipids and thiols by inhibiting protease leakage into the cytoplasm from vacuoles (Dek *et al.*, 2017). Decreased LOX activity by polyamines and STS pulse may be justified by the fact that polyamines and silver prevent the production of free radicals, including O_2 and H_2O_2 , thereby improving the membrane

stability index (Dar *et al.*, 2020). Reportedly, polyamines interact with ethylene precursors and inhibit lipid peroxidation, thereby reducing cell wall damage (Palagani and Singh, 2017). Our results are also in harmony with earlier studies which revealed that ion leakage in petal tissues was reduced in the STS-treated flowers (Khella *et al.*, 2018).

In this experiment, polyamine and STS-treated flowers maintained higher values of soluble proteins. The degradation of proteins with increased protease activity is the first stage in the senescence of flowers (Tripathi *et al.*, 2009). Polyamines are considered to delay this senescence by either reducing ethylene production or stabilizing proteins via decreasing protease activity (Nisar *et al.*, 2015). In *Gladiolus* and *Iris*, similar results of increased protein content by using polyamines and STS have been observed (Nahed *et al.*, 2009; Ahmad and Tahir, 2018). Maintaining protein content in STS pulsed flowers indicates that protein status is essential in controlling ethylene production and improving flower longevity.

Applying polyamines and STS to the isolated flowers of *D. purpurea* resulted in an overall decrease in the phenolic content with maximum value in the flowers from control. Phenols were shown to rise rapidly toward senescence, which can be attributed to increased membrane leakiness (Shahri *et al.*, 2011). The higher phenolic content in the senescent flowers of *Dianthus* confirms our findings (Dar *et al.*, 2014). Reduced phenolic level in the STS-treated flowers of *Ranunculus* and *Dianthus* was associated with enhanced flower longevity (Shahri and Tahir, 2010; Dar *et al.*, 2014).

In addition, polyamines and STS maintained a higher sugar level in the flowers. Compared to other holding solutions, flowers held

in SPM had the highest values for sugar content. Our results augment the earlier results with *Gladiolus*, *Nicotiana*, *Consolida* (Nahed *et al.*, 2009; Nisar *et al.*, 2015; Ul Haq *et al.*, 2021). This increase in carbohydrate content can be ascribed to the ability of polyamines to slow down cellular respiration, thus retaining higher levels of internal sugars for longer duration (Ahmad and Tahir, 2016). Polyamines are thought to be closely associated with the modulation of sugar and carbohydrate biosynthesis (Mahgoub *et al.*, 2011). Increased sugar content in STS treated flowers has also been reported in various flowers such as *Limonium*, *Gladiolus*, *Lathyrus* (Khalid, 2012; Hassan *et al.*, 2014; Khella *et al.*, 2018).

Isolated flowers of *D. purpurea* held in different solutions of polyamines and STS showed increased SOD, CAT and APX activities with SPM being the most effective. Similar to our findings, increased antioxidant enzymes have been documented in *Alstroemeria* and *Anthurium* flowers treated with PUT and SPM (Alborz *et al.*, 2015; Simoes *et al.*, 2018). Plant cells are generally protected against reactive oxygen species (ROS) produced during oxidative stress by an antioxidant enzyme system such as SOD, CAT and APX activity (Zhou *et al.*, 2014). The increase in the amounts of different endogenous or exogenous polyamines results in increased elimination of ROS, which helps cells retain higher concentrations of proteins and sugars to combat senescence (Cakmak *et al.*, 2009; Hussain *et al.*, 2011). As a result, the elevated SOD, APX and CAT activities in polyamine and STS-treated samples relative to controls could explain the delayed floral senescence in *D. purpurea*.

Moreover, STS, an ethylene action inhibitor, is known to have a role in ROS scavenging and delaying the senescence of flowers (Hassan *et al.*, 2014). SOD, APX and CAT activities were also reported to decrease during the floral senescence of *Gladiolus*, *Daylily*, *Dendrobium* and *Rose* (Chakrabarty *et al.*, 2009; Rogers, 2012). Thus, it can be presumed that the elevated SOD, APX and CAT activities in polyamine and STS-treated samples relative to control could explain the delayed floral senescence in *D. purpurea*.

Our experiment attempted to evaluate the putative effect of polyamines and STS in delaying the senescence of the isolated flowers of *D. purpurea*. The study revealed that the postharvest performance of *D. purpurea* flowers was significantly improved by applying these growth regulators, preferably spermine. Despite reduced LOX activity, higher values of soluble proteins, total sugars, and SOD, CAT, and APX activity were maintained in petal tissues. This reduction in LOX activity prevented lipid peroxidation, thus preserving membrane integrity. The study showed that a preservative solution containing SPM at an appropriate concentration can augment flower longevity. The study could provide insights into the strategies to improve the postharvest performance of spikes for efficient marketing in the floriculture industry.

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