



Salicylic acid retards senescence and makes flowers last longer in *Nicotiana plumbaginifolia* (Viv)

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Abstract Salicylic acid (SA) is known to be a plant signalling molecule that plays an important role in growth, development and defence response in plants. During the present study the effect of exogenous application of SA on the senescence of cut *Nicotiana plumbaginifolia* flowers was investigated. The buds were subjected to different concentrations (0.05, 0.1, 0.15, 0.20 and 0.25 mM) of SA. A separate set of flowers kept in distilled water designated the control. The flowers treated with various concentrations of SA resulted in improved flower longevity besides maintaining higher membrane stability index, soluble proteins and sugar fractions. SA treatment decreased the α -amino acid, total phenol content, lipid peroxidase and lipoxygenase activity. The flowers treated with SA showed a significant increase in activity of antioxidant enzymes like superoxide dismutase, catalase and ascorbate peroxidase. Among various concentrations used, 0.05 mM SA was found to be most effective in enhancing the flower longevity. Thus, exogenous SA could maintain membrane integrity by increasing antioxidant system activity, thereby retarding the senescence of cut *N. plumbaginifolia* flowers.

Keywords Antioxidant enzymes · Lipoxygenase · Salicylic acid · Flower longevity

Introduction

Flower senescence is accompanied by many physiological and biochemical changes which include membrane leakage, degradation of macromolecules and modifications in ultra structure and oxidative stress (Rani and Singh 2014; Saeed et al. 2014, 2016). Petal senescence is commonly accompanied by morphological, biophysical and biochemical deterioration, decline in the protein content, lipid fluidity in the membranes and an increase in protease activity (Arora et al. 2007; Rani and Singh 2014; Saeed et al. 2016). During the last decade involvement of reactive oxygen species (ROS) in senescence mechanism has gained a significant importance (Gill and Tuteja 2010). The accumulation of ROS beyond physiological levels leads to oxidative stress in the cells, which in turn causes membrane disruption, lipid peroxidation, macro-molecular degradation, DNA breakage and ion leakage (Sharma et al. 2012). The membrane disruption caused by ROS due to increased oxidative stress is one of the major factors responsible for quality deterioration of cut flowers and arguably is the main challenge for the florists in the flower trade worldwide. For scavenging ROS, the antioxidant enzymes involved are peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT) (Gerailoo and Ghasemnezhad 2011; Saeed et al. 2014, 2016). The main focus of many researchers is to delay the onset of senescence in order to prolong the vase life of cut flowers in floriculture. With the improvement in scientific knowledge augmented with technology, the flower senescence has opened new vistas in plant science.

Salicylic acid (SA) has been studied extensively both as a plant growth regulator and for its potential role in the maintenance of postharvest quality of vegetables, fruits and cut flowers (Ezhilmathi et al. 2007). SA plays a vital role in

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plant growth and development processes and is widely distributed within the plants (Saeed et al. 2016). It not only influences cut flower quality and longevity but is also involved in the regulation of many physiological processes (Hassan and Ali 2014; Saeed et al. 2016; Langroudi et al. 2020). Exogenous application of SA may induce ion uptake, regulate the stomatal movement and transpiration, thereby reducing the postharvest water loss (Eraslan et al. 2007; Hassan et al. 2007). SA acts as an endogenous regulator for flower induction by stimulating flowering (Pacheco et al. 2013). It has a prominent role in reducing the oxidative stress by enhancing the activity of various antioxidant enzymes viz., CAT, SOD, POD and ascorbate peroxidase (APX), maintaining membrane integrity of cut flowers (Tareen et al. 2012). Keeping in view the considerable role of salicylic acid in orchestrating various physiological responses, the present investigation was aimed at studying the effect of exogenous application of salicylic acid for extending the decorative life and quality attributes of isolated flowers of *N. plumbaginifolia* with an aim to modulate flower senescence in this beautiful flower from Solanaceae.

Materials and methods

Isolated floral buds of *N. plumbaginifolia* were collected at 800 h when the buds were at stage III (one day before anthesis) from Kashmir University Botanic Garden (KUBG). These harvested floral buds were brought to the laboratory, cut to a uniform pedicel length of 3 cm and divided into six sets, each set comprising of 25 vials with 5 mL of respective test solutions. Each set was supplied with different concentrations of SA viz., 0.05 mM, 0.10 mM, 0.15 mM, 0.20 mM and 0.25 mM. A separate set of 25 vials containing buds held in distilled water (DW) designated the control. The experiment was conducted under laboratory conditions with relative humidity (RH) of $60 \pm 10\%$, 12 h light period a day and average temperature of $20 \pm 2^\circ\text{C}$. The day of transfer of isolated flowers to test solutions was designated as day zero.

Flower longevity

Longevity of isolated flowers was measured as the time taken in days by an open flower to show visible signs of senescence like inrolling of petals and loss of turgidity.

Floral diameter

Diameter of 10 flowers from each treatment was recorded on day 2 and 4 of transfer to different concentrations of

salicylic acid and was taken as mean of two perpendicular measurements of the flower.

Membrane stability index (MSI)

Solute leakage of the petal tissues was calculated by incubating 250 mg of petal tissue in 5 mL of deionized water at 25°C for 30 min and 100°C for 15 min (Sairam 1994). The conductivity of the samples incubated at 25°C was designated as C1 and those incubated at 100°C was designated as C2 after recording the values on Elico CM180 conductivity meter. MSI was computed as:

$$\text{MSI} = \left[1 - \frac{C1}{C2} \right] \times 100$$

Lipid peroxidation

Lipid peroxidation, expressed as $\mu\text{mols MDA g}^{-1} \text{fw}$, was determined by the method of Heath and Packer (1968). 0.5 g of petal tissue was macerated in 15 mL of 0.1% trichloroacetic acid (TCA) and centrifuged at $15,000 \times g$ for 10 min under refrigeration. 1 mL of supernatant was taken and mixed with 4 mL of 0.5% TBA diluted in TCA (20%). The reaction was started by incubating the mixture at 95°C in water bath for 25 min and ended by placing the reaction mixture in ice. Absorbance was taken at 532 and 600 nm. Non-specific absorbance was subtracted from the value obtained at 532 nm.

Estimation of tissue constituents

Protein estimation and specific protease activity

For protein estimation, 1 g of petal tissue was macerated in 100 mM (pH 7.2) phosphate buffer. The mixture was centrifuged at $12,000 \times g$ at 4°C in a refrigerated centrifuge for 15 min. Soluble proteins were estimated from an aliquot of the supernatant by the method of Lowry et al. (1951). Specific protease activity was estimated by homogenizing 1 g petal tissue in 15 mL chilled 0.1 M phosphate buffer (pH 6.5) and centrifuged for 15 min at $500 \times g$ in a (Remi K-24) refrigerated centrifuge at -5°C . The supernatant was used for the assay of protease activity by a modification of the method as described by Tayyab and Qamar (1992).

Estimation of α -amino acids and total phenols

α -Amino acids were estimated by the method of Rosen (1957) using glycine as the standard.

Total phenols were estimated by the method of Swain and Hillis (1959) using gallic acid as standard.

Estimation of sugars

Reducing sugars were estimated by the method of Nelson (1944) using D-glucose as the standard. Total sugars were estimated after the enzymatic conversion of non-reducing sugars into reducing sugars by invertase. Non-reducing sugars were calculated as the difference between total sugars and reducing sugars.

Determination of antioxidant enzyme activity

Lipoxygenase (LOX) activity was determined by the method of Axelrod et al. (1981). 0.5 g of petal tissue was macerated in 1 mL extraction buffer containing 50 mM potassium phosphate buffer (pH 6.5), 10% polyvinyl pyrrolidone (PVP), 0.25% Triton X-100 and 1 mM phenyl methyl sulfonyl fluoride (PMSF). 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 μ L crude petal extract to the reaction mixture and absorbance was recorded at 234 nm for 5 min.

Superoxide dismutase (SOD) activity was determined by macerating 0.5 g of petal tissue in pestle and mortar and homogenized 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 homogenate was centrifuged at 15,000 \times g for 10 min. The supernatant was filtered through muslin cloth and used for the enzyme assay. SOD activity was measured by the method of Dhindsa et al. (1981) by monitoring the inhibition of photochemical reduction of nitroblue tetrazolium (NBT). The reaction mixture contained 50 mM sodium carbonate, 75 μ M NBT, 0.1 mM EDTA, 13 mM methionine in 50 mM phosphate buffer (pH 7.8) and 0.1 mL of the enzyme extract in a final volume of 3 mL. The reaction was started by adding 2 μ M riboflavin and placing the test tubes in water bath at 25 °C and illuminated with a 30 W fluorescent lamp. The reaction was stopped by switching off the light and keeping the test tubes in darkness. Identical test tubes which were not illuminated served as blanks. Absorbance was measured at 560 nm and one unit of SOD activity was defined as the quantity of the enzyme which inhibits the photoreduction of NBT to blue formazan by 50% as compared to the reaction mixture kept in dark without the enzyme extract. SOD activity was expressed as units $\text{min}^{-1} \text{mg}^{-1}$ protein. Catalase (CAT) activity was estimated by the method of Aebi (1984). 0.5 g of petal tissue was macerated using pestle and mortar and homogenized in 100 mM potassium phosphate buffer (pH 7.0) containing 1 mM EDTA. The reaction mixture contained 50 mM potassium phosphate

buffer (pH 7.0), 12.5 mM H₂O₂, 50 μ L enzyme extract and distilled water to make the volume to 3 mL. Reaction was started by adding H₂O₂ and CAT activity was determined by the consumption of H₂O₂ for 3 min at 240 nm and was expressed as $\mu\text{mol H}_2\text{O}_2$ reduced $\text{min}^{-1} \text{mg}^{-1}$ protein.

For the determination of ascorbate peroxidase (APX) activity, flower petals were macerated in 100 mM sodium phosphate buffer containing 5 mM ascorbate, 10% glycerol and 1 mM EDTA. The APX activity was determined in 1 mL reaction mixture containing 50 mM potassium phosphate buffer (pH 7.0), 0.1 mM ascorbate and 0.3 mM H₂O₂. The decrease in the absorbance was recorded for 3 min at 290 nm (Chen and Asada 1989).

OD conversion into enzyme activity

$$\frac{\text{Change in Abs/MinTotal Volume (ml)}}{\text{Ext. Coefficient} \times \text{Vol. of sample take (ml)}}$$

Experimental design and data analysis

The experiments followed a completely randomized design and were performed with at least three independent biological replicates. The entire experiment was replicated three times to minimize variability between the variables. Difference between various treatments has been evaluated by simple analysis of variance and least significant difference (LSD) computed at $P_{0.05}$ using MINITAB (v15.1.2-EQUINOX_Softddl.net) software.

Results

Senescence in flowers of *N. plumbaginifolia* was characterised by the loss of petal turgidity followed by outrolling of corolla (Fig. 1). Treatment of isolated buds of *N. plumbaginifolia* with different concentrations of SA resulted in the improvement of its flower longevity and various biochemical attributes viz. soluble proteins, sugar fractions and antioxidant enzyme activities. Floral buds treated with 0.05 mM SA showed improved flower longevity (4.5 days) as compared to the other concentrations as well as control where it was 3 days (Fig. 2a). The isolated flower buds treated with different concentrations of SA showed improved flower diameter as compared to the control (Table 1). Maximum flower diameter was recorded in the floral buds on day 2 as well as on day 4 which were treated with 0.05 mM SA. Membrane stability index (MSI) which measures the membrane leakiness was found to decrease with increase in SA concentration and was recorded to be maximum in the tissue samples from floral buds held in 0.05 mM SA on day 2 (Table 1). Lipid



Fig. 1 Effect of various grades of salicylic acid (SA) on flower senescence in isolated flowers of *Nicotiana plumbaginifolia* on day 0 (Fig a), day 2 (Fig b), day 5 (Fig c) and day 7 (Fig d) of transfer to the

test solutions. Note: The clear difference in the flowers in vials containing 0.05 mM SA at day 5 and 7 as compared to control and other concentrations.

peroxidation (LPO) measured in terms of ($\mu\text{mol MDA g}^{-1} \text{FW}$) was found to increase with the increase in SA concentrations and registered an increase with the progression in time from day 2–4 (Fig. 2b). Tissue samples from floral buds treated with 0.05 mM SA showed maximum soluble protein content on day 2 as compared to the other concentrations including control. The concentration of soluble protein content was found to decrease with the progression in time from day 2–4 (Table 1). Specific protease activity measured as ($\mu\text{g tyr mg}^{-1} \text{protein min}^{-1}$) was found to show inverse relationship with the soluble protein content and minimum activity was registered in the tissue samples from floral buds which were held in 0.05 mM SA on day 2 (Table 1). α -Amino acid content was found to increase with the progression in time from day 2–4 and was also found to increase with the increase in SA concentrations. A higher content of total phenols was maintained by the tissue samples from floral buds held in control

(Table 1). Total phenol content was found to increase with the progression in time from day 2–4. Treatment of isolated floral buds of *N. plumbaginifolia* with SA resulted in an increased sugar content and maximum total sugar content was registered in the tissue samples from floral buds held in 0.05 mM SA as compared to the other concentrations as well as control (Table 1). The activity of antioxidant enzymes (CAT, SOD and APX) was recorded to be maximum in the tissue samples from floral buds which were held in 0.05 mM SA and was found to decrease with the increase in SA concentrations. The activity of these antioxidant enzymes was also found to decrease with the progression in time from day 2–4 (Figs. 2b–d, 3a). Lipoxigenase activity (LOX) was recorded to increase with the increase in SA concentration and was recorded to be maximum in the tissue samples from floral buds held in 0.25 mM SA. LOX activity was also found to increase with the progression in time from day 2–4 (Fig. 3b).

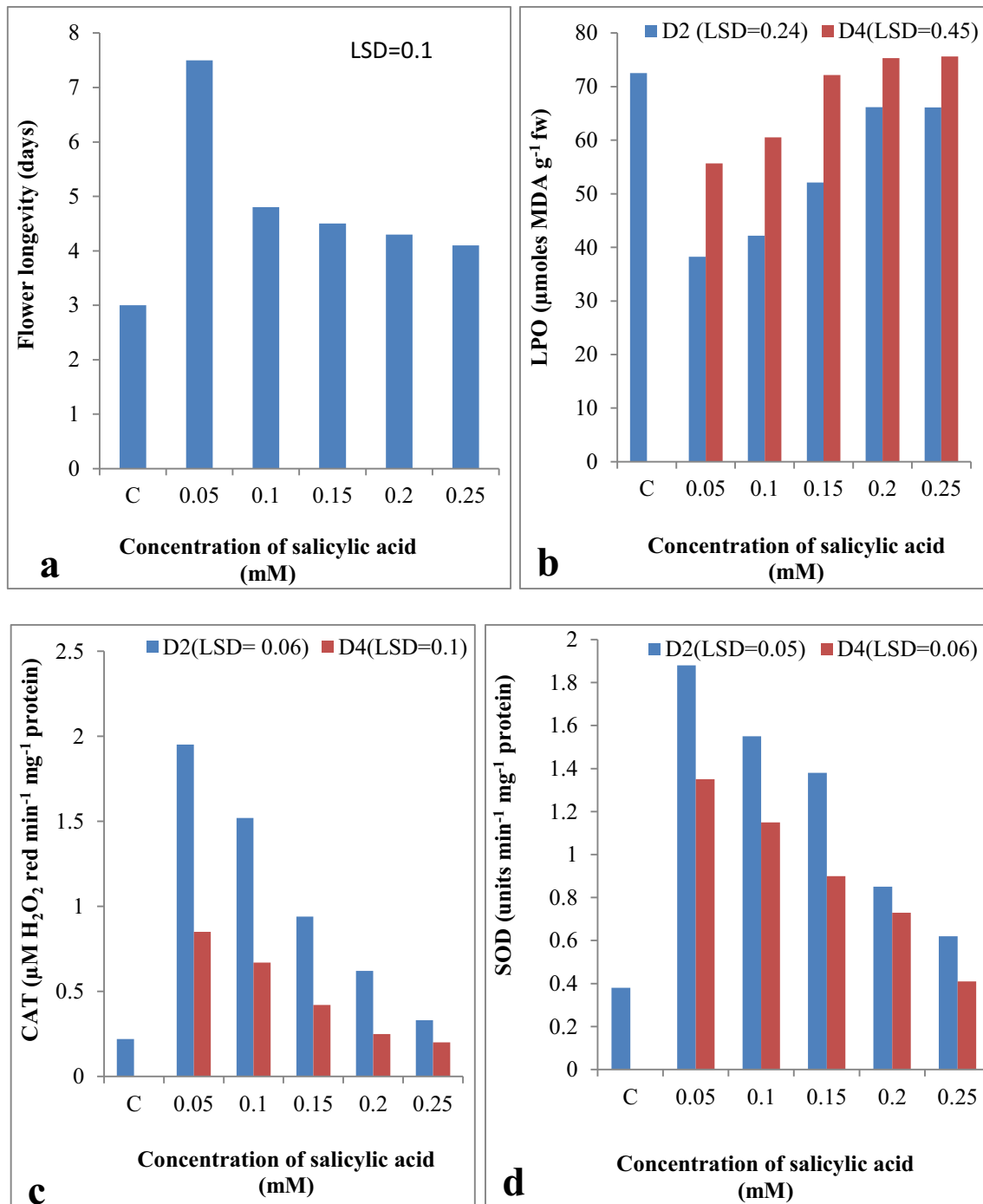


Fig. 2 Changes in flower longevity and activities of LPO, CAT and SOD in the samples from petal tissues upon treatment with different grades of salicylic acid (0.05, 0.1, 0.15, 0.20 and 0.25 mM respectively) in isolated flowers of *Nicotiana plumbaginifolia* (Viv).

Discussion

SA plays a potential role in improving the longevity of flowers, besides regulating many physiological processes. The present research was carried out to study the effect of SA on flower senescence of *N. plumbaginifolia*. SA was found to improve the flower longevity of isolated floral

buds which were held in 0.05 mM SA as compared to the other concentrations as well as control, where it was only 3 days. SA has also been found to induce flowering in *Lemna gibba*, *Spirodela polyrrhiza* and *Wolffia microscopia* (Khurana and Maheshwari 1980, 1983; Huang et al. 2015). The role of SA in improving flower longevity is possibly due to the reduced rates of ethylene biosynthesis

Table 1 Effect of different concentrations of salicylic acid (SA) on the floral diameter, membrane stability index, soluble proteins, specific protease activity, α -amino acids, total phenols and sugar fractions (total, reducing and non-reducing) in isolated flowers/petal tissues of *Nicotiana plumbaginifolia*

Daysafter transfer	Control (DW)	0.05 mM SA	0.1 mM SA	0.15 mM SA	0.20 mM SA	0.25 mM SA	LSD P = 0.05
<i>Floral diameter (cm)</i>							
2	3.4	3.9	3.5	3.1	2.5	3.0	0.06
4	–	3.3	3.1	2.9	2.2	2.5	0.08
<i>Membrane stability index (%)</i>							
2	30.0	81.0	74.0	60.0	55.5	40.1	0.56
4	0	65.13	43.2	37.8	25.4	19.1	919.4
<i>Solubleproteins (mg g⁻¹ fw)</i>							
2	2.21	7.84	5.13	4.33	3.89	3.90	0.05
4	0	4.32	3.76	3.24	2.89	1.76	0.07
<i>Specific protease activity ($\mu\text{g tyr mg}^{-1}$ protein min^{-1})</i>							
2	2.15	1.45	1.88	2.40	2.64	2.88	0.11
4	0	1.60	2.31	2.87	3.22	3.50	0.09
<i>α-amino acids (mg g⁻¹ fw)</i>							
2	16.32	7.52	9.04	9.86	10.15	10.66	0.09
4	0	9.32	11.04	11.56	13.21	15.32	0.06
<i>Total phenols (mg g⁻¹ fw)</i>							
2	2.58	2.16	3.33	4.07	4.65	5.21	0.08
4	0	3.25	3.50	4.86	5.06	6.42	0.07
<i>Total sugars (mg g⁻¹ fw)</i>							
2	10.10	17.56	14.22	12.18	12.04	11.42	0.09
4	0	8.25	8.20	7.87	6.92	6.60	0.11
<i>Reducing sugars (mg g⁻¹ fw)</i>							
2	6.50	9.14	7.25	6.22	5.25	4.22	0.13
4	0	4.20	4.15	4.66	3.41	4.15	0.19
<i>Non-reducing sugars (mg g⁻¹ fw)</i>							
2	3.60	8.42	6.97	5.96	6.79	7.20	0.08
4	0	4.05	4.05	3.21	3.51	2.45	0.09

The flowers kept as control did not last up to day 4 hence indicated as 0

because SA has been found to block the conversion of ACC to ethylene (Bueno and Del Rio 1992; Gerailoo and Ghasemnezhad 2011; Hassan and Ali 2014). It has also been reported that SA improves translocation of sugars in plants which could build up more resources accumulation in turn improves the longevity of flowers (Ezhilmathi et al. 2007; Saeed et al. 2016). Application of SA in *Gladiolus* has been shown to increase the vase life of the flower by taking part in cell multiplication and elongation and in turn improves its flower longevity (Anjum et al. 2001; Saeed et al. 2016). One more reason for increased flower longevity due to application of SA could be manifested because salicylic acid considerably extends the flower longevity with increase in the activity of antioxidant enzymes and decreased ROS production. Treatment of cut *Gerbera* flowers with SA was found to increase its vase life due to

increased antioxidant enzyme activity and decrease ROS production (Yuping 2009; Heidarneshadian et al. 2017). Studies have also shown that SA could improve flower longevity by lowering the respiration rate and copying with the biotic stress (Eraslan et al. 2007; Kazemi and Shokri 2011; Saeed et al. 2016). In addition to this, it has also been revealed that SA extends vase life in association with inhibition of ethylene production in *Alstroemeria peruviana*, *Gerbera jamesonii*, *Lilium asiaticum*, *Polianthes tuberosa* and *Rosa hybrida* (Bayat and Aminifard 2017; Kazemi et al. 2018).

The reason for increase in floral diameter could be due to the fact that SA might delay dehydration either due to increase in solution uptake or lowering the water loss. Treatment of *Gladiolus* flowers with SA showed delayed dehydration of flowers and enhanced the fresh weight and

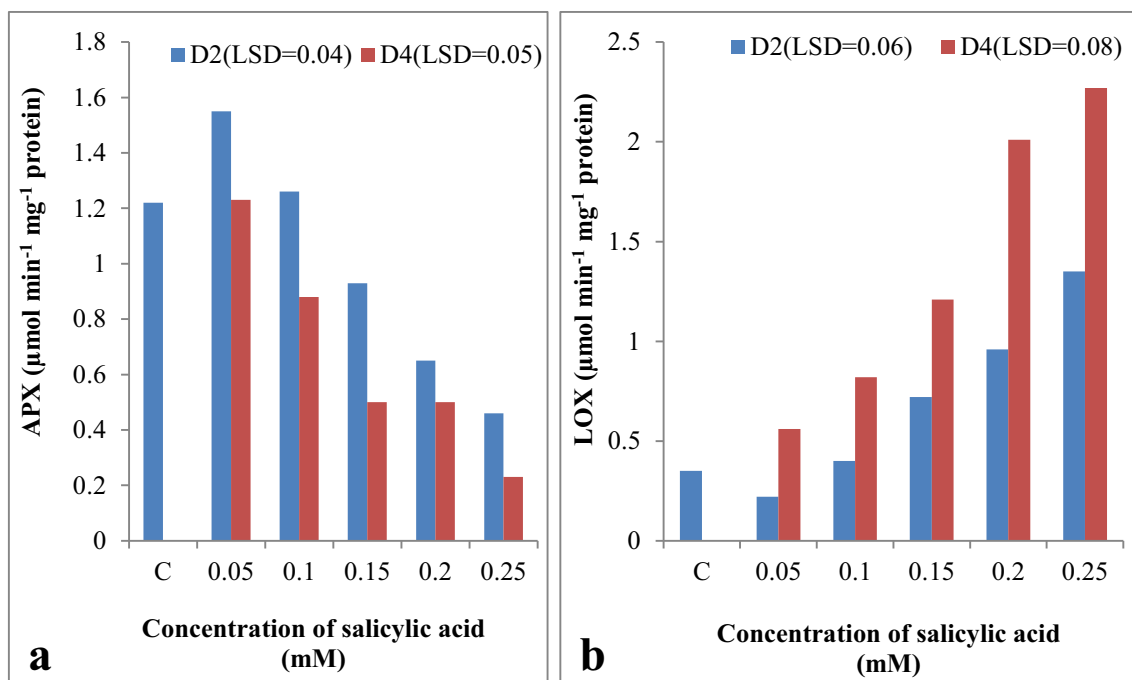


Fig. 3 Changes in activities of APX and LOX in the samples from petal tissues upon treatment with different grades of salicylic acid (0.05, 0.1, 0.15, 0.20 and 0.25 mM respectively) in isolated flowers of *Nicotiana plumbaginifolia* (Viv).

floral diameter (Saeed et al. 2016). For the survival of living organisms structure and functionality of cell membranes are important (Rubinstein 2000). Unsaturated bond in phospholipid bilayers in cell membranes are degraded by ROS which lead to the lipid peroxidation. Treatment with salicylic acid induces antioxidative defence system thereby activating the antioxidant enzymes (Sen et al. 2010; Saeed et al. 2016), whereas, in absence of salicylic acid, decline in membrane stability was observed which indicates the direct relationship between the free radical biosynthesis and membrane damage as suggested by Droillard et al. (1987). Isolated floral buds of *N. plumbaginifolia* when treated with SA showed reduced MSI and therefore increased lipid peroxidation (LPO). Such effects of SA as MSI reduction and increased LPO activity has been previously reported in *Gladiolus* by Ezhilmathi et al. (2007) and Hatamzadeh et al. (2012) MSI and LPO have been found to show inverse relationship with flower senescence as in case of *Gladiolus* flowers (Singh et al. 2008; Hatamzadeh et al. 2012; Hassan and Ali 2014). The soluble proteins play important role till final stages of vase life. As a result, high protein content of SA treated flowers may help them improve their postharvest longevity. Petal senescence has been found to be associated with the loss of proteins (Kenis et al. 1985; van Doorn and Stead 1994). The protein concentration in petals of cut daylily flowers rapidly decreased due to the significant protein degradation (Lay-Yee et al. 1992). As a result of this protein degradation there occurs dismantling of membranes

(Woolhouse 1984). This progressive deterioration of membrane bilayer accompanied by senescence may be due to the loss of membrane protein function (Thompson 1974). Sugars plays an important role in suppressing the occurrence of programmed cell death (PCD) and senescence is a form of developmental PCD (van Doorn and Woltering 2008). They have been found to limit the occurrence of PCD and in turn delay the senescence of flowers in *Gladiolus* (van Doorn and Woltering 2008; Hassan and Ali 2014). Salicylic acid also improves the water uptake and sugar translocation in plants which could accumulate more resources and exert turgor pressure and in turn delay flower senescence as seen in case of *Gladiolus* flowers (Ezhilmathi et al. 2007; Saeed et al. 2016).

SA treated flowers showed significantly higher SOD activity compared to the control. Several studies have confirmed that vase life of flowers is modulated by antioxidants, suggesting the involvement of ROS in senescence (Gerailoo and Ghasemnezhad 2011; Hassan and Ali 2014). In the present study SOD activity declined during the vase life of the flowers. These results are in accordance with the pattern of SOD activity during senescence in carnation and daylily (Panavas and Rubinstein 1998; Ezhilmathi et al. 2007; Gerailoo and Ghasemnezhad 2011; Langroudi et al. 2020). Floral buds of *N. plumbaginifolia* treated with SA showed increased CAT and APX activities. *Lisianthus* cut flowers treated with SA also showed higher activities of CAT and APX associated with lower H₂O₂ accumulation during vase life (Ataï et al.

2015). Hassan and Ali (2014) have reported that SA treatment considerably prolonged the vase life and minimized the weight loss of *Gladiolus* spikes and alleviated the oxidative stress in cut flowers during postharvest senescence. An increase in floret antioxidant enzyme activities (CAT and APX) was observed in SA treated spikes compared to the control. The activities of antioxidant enzymes are measured as a response against oxidative stress (Zhou et al. 2014; Ataï et al. 2015). SA treatment enhanced the production of antioxidant enzymes which scavenge the ROS. The decline in membrane integrity of *Lisianthus* cut flowers was alleviated by treatment with SA, which was associated with an increase in CAT and APX activity in treated flowers. It can be argued that SA has a role in the induction of antioxidant enzymes and/or might also act as a scavenger of ROS, thus maintaining membrane integrity for extended period (Ataï et al. 2015). LOX activity was also found to increase gradually after harvest in case of Rose cut flowers. Similar results were observed in tulips and *Gladiolus* (Jones and McConchie 1995; Ezhilmathi et al. 2007). An increase in LOX activity has been correlated with an increase in cell membrane permeability and senescence in daylily (Panavas and Rubinstein 1998) and rose (Fukuchi-Mizutani et al. 2000).

Conclusion

The study was an attempt to investigate the role of SA in delaying the senescence of *N. plumbaginifolia* flowers. SA improved floral longevity/delayed flower senescence by maintaining membrane integrity and increasing the antioxidant enzymes CAT, SOD and APX activities, which led to diminishing H₂O₂ accumulation. The effects of SA treatment on retarding flower senescence was due to increased antioxidant enzyme activities and thus reduced lipid peroxidation and maintained membrane stability. The present study shows that there is a lot of potential for studying the role of salicylic acid signalling in orchestrating flower senescence at molecular level with great future implications.

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