Ornamental Horticulture
ISSN 2447-536X | HTTPS://ORNAMENTALHORTICULTURE.EMNUVENS.COM.BR/RBHO
SBFPO Sociedade Brasileira de Floricultura e Plantas Ornamentais

SCIENTIFIC ARTICLE

Cerium nitrate and salicylic acid on vase life, lipid peroxidation, and antioxidant enzymes activity in cut lisianthus flowers

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Abstract

Lisianthus is a major cut flower, but it has a short vase life. To prolong postharvest longevity and improve quantitative and qualitative traits of cut lisianthus flowers, an experiment was conducted on the basis of a Completely Randomized Design with eight treatments on 120 flower sprays in three replications. The experimental treatments included salicylic acid (SA) at the rates of 50, 100 and 200 mg L^{-1}, cerium nitrate [$Ce(NO_3)_3$] at the rates of 20, 40, 80, and 200 µM, and control (distilled water). The results revealed that the flowers treated with 40 µM $Ce(NO_3)_3$ and those treated with 100 mg L^{-1} SA had the longest vase life of 15.42 and 15.20 days, respectively. Also, these treatments were most effective in improving water uptake, reducing microbial load at the stem end, and enhancing petals' protein content. The lowest malondialdehyde (18.65 nmol g^{-1} fresh weight) was related to the treatment of 40 µM $Ce(NO_3)_3$ and 100 mg L^{-1} SA. These treatments showed the lowest polyphenol oxidase (PPO) activity, too. The activity of ascorbate peroxidase (APX) and peroxidase (POD) antioxidant enzymes was significantly higher in the flowers treated with 40 µM $Ce(NO_3)_3$ and 100 mg L^{-1} SA. The treatment of 200 mg L^{-1} SA had negative effects on all the recorded traits. So, it can be concluded that the treatment of cut lisianthus flowers with 40 µM $Ce(NO_3)_3$ and 100 mg L^{-1} SA can prolong their postharvest longevity by reducing lipid peroxidation and increasing the activity of antioxidant enzymes.

Keywords: *Eustoma grandiflorum* 'Pink Picotee', ascorbate, peroxidase malondialdehyde, polyphenol oxidase, vase solution.

Resumo

Nitrato de cério e ácido salicílico na vida de vaso, peroxidação lipídica e atividade de enzimas antioxidantes em flores cortadas de lisianthus

Lisianthus é uma flor de corte importante, mas tem vida de vaso curta. Para prolongar a longevidade pós-colheita e melhorar as características quantitativas e qualitativas de flores cortadas de lisianthus, um experimento foi conduzido com base em um Projeto Completamente Randomizado com oito tratamentos em 120 pulverizações de flores em três repetições. Os tratamentos experimentais incluíram ácido salicílico (SA) nas taxas de 50, 100 e 200 mg L^{-1}, nitrato de cério [$Ce(NO_3)_3$] nas doses de 20, 40, 80 e 200 µM e controle (destilado água). Os resultados revelaram que as flores tratadas com 40 µM Ce $(NO_3)_3$ e aquelas tratadas com 100 mg L^{-1} SA tiveram a maior vida útil de vaso de 15,42 e 15,20 dias, respectivamente. Além disso, esses tratamentos foram mais eficazes em melhorar a absorção de água, reduzindo a carga microbiana na extremidade do caule e aumentando o conteúdo de proteína das pétalas. O menor malondialdeído (18,65 nmol g^{-1} de peso fresco) foi relacionado ao tratamento de 40 µM Ce $(NO_3)_3$ e 100 mg L^{-1} SA. Esses tratamentos também apresentaram a menor atividade da polifenol oxidase (PPO). A atividade das enzimas antioxidantes ascorbato peroxidase (APX) e pe-roxidase (POD) foi significativamente maior nas flores tratadas com 40 µM Ce $(NO_3)_3$ e 100 mg L^{-1} SA. O tratamento com 200 mg L^{-1} SA teve efeitos negativos em todas as características registradas. Assim, pode-se concluir que o tratamento de flores cortadas de lisianthus com 40 µM $Ce(NO_3)_3$ e 100 mg L^{-1} SA pode prolongar sua longevidade pós-colheita, reduzindo a peroxidação lipídica e aumentando a atividade de enzimas antioxidantes.

Palavras-chave: *Eustoma grandiflorum* 'Pink Picotee', ascorbato, malondialdeído peroxidase, polifenol oxidase, solução de vaso.

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https://doi.org/10.1590/2447-536X.v26i4.2227
Received July 27, 2020 | Accepted Sept 22, 2020 | Available online Oct 13, 2020

Area Editor: Bruno Trevenzoli Favero

Introduction

Lisianthus (*Eustoma grandiflorum*) is a major cut flower from the family Gentianaceae (Saeedi et al., 2015). Cut lisianthus flowers exhibit short vase life due to their susceptibility to ethylene (Ichimura et al., 1998) and xylem blockage (Sharifzadeh et al., 2014). In 2001, the production of lisianthus cut flowers in Japan, Europe and the United States was reported at 129, 122 and 14 million branches, respectively (Harbaugh, 2007). In 2016, in terms of production volume, lisiantos was ranked sixth among the ten best-selling flowers in the world with 69 million euros. The area under cultivation and the amount of lisianthus production in Iran in 1396 were 85.4 hectares and 152.6 million branches, respectively. Since postharvest longevity is a key attribute of cut flower supplies to target markets, researchers have always been looking for ways to extend postharvest longevity of these precious perishable products (Silva, 2008; Kader, 2003).

Salicylic acid (SA) is a plant growth regulator and a naturally occurring phenolic compound that is highly capable of controlling and reducing postharvest loss of different horticultural products. SA plays a significant role in the control of ethylene synthesis and activity, the reduction of respiration, and the build-up of resistance to diseases and oxidative stresses (Ding et al., 2002; Wollaston et al., 2003; Asghari and Aghdam, 2010). The positive effect of SA has been reported in prolonging postharvest longevity of gladiolus (Ezhilmathi et al., 2007), carnation (Kazemi et al., 2011) and lisianthus (Kazemi et al., 2011). Researchers argue that SA prolongs postharvest longevity of cut flowers by reducing ethylene synthesis (Bayat and Aminifard, 2017; Sirvastava and Dwivedi, 2000), inhibiting the growth and propagation of microorganisms and improving water uptake (Bayat and Aminifard, 2017; Mashhadian et al., 2012).

With the occurrence of stress in plants, the balance between the production and decomposition of oxygen active species is disturbed, under these conditions oxidative stress occurs. Increasing the production and activity of reactive oxygen species causes the destruction of macromolecules and accelerates aging in petals and other plant tissues. Plants resist the damaging effects of oxidative stress through various defense systems, including the enzymatic antioxidant defense system such as SOD, POD and CAT (Gerailoo and Ghasemnezhad, 2011; Kumar et al., 2008). SA as a compound extends the vase life of cut flowers is able to directly decompose reactive oxygen species; it also indirectly inhibits the activity of reactive oxygen species by regulating the activity of antioxidant enzymes and reduces the damaging effects of oxidative stress (Gerailoo and Ghasemnezhad, 2011). Mansouri (2012) reported that the treatment of chrysanthemums with SA contributed to maintaining membrane structure, hindering fresh weight loss, and increasing vase life. In the study of Alaey et al. (2012), the application of SA to the preservative solution of cut rose flowers resulted in the scavenging of reactive oxygen species (ROS) and the improvement of water uptake and prolonged the longevity of the cut flower versus the control. As well, SA application to the vase solution of rose 'Yellow Island' cut flowers retarded aging process by strengthening the antioxidant system and inhibiting the oxidative stress (Gerailoo and Ghasemnezhad, 2011). Kazemi et al. (2012) found that the application of 1.5 mM SA + 3% sucrose in the vase solution of cut carnation flowers reduced bacterial activity, ACC-oxidase activity, and malondialdehyde content significantly. It also preserved the cut flowers for a longer time after harvesting by enhancing membrane stability. The vase life in this treatment was 11 days and in control was 7.1 days. Therefore, this treatment increased the vase life compared to the control by 3.9 days.

Cerium (Ce) is a key trace element on the Earth that influences plant growth and development positively (Yin et al., 2009; He and Loh, 2000). This element has antibiotic (Huang, 2002) and antioxidant properties (Yin et al., 2009; He and Loh, 2000). Cerium compounds are also known in particular for their uses in topical burn treatments due to their bacteriostatic and bactericidal effects. Later, studies confirmed the antiseptic effects of cerium(III) chloride, Ce(III) nitrate, and Ce(IV) sulfate and demonstrated particular susceptibility of both gram-negative and gram-positive bacteria (which tend to coat burn wounds) to their effects. Cerium(III) nitrate in particular is a widely used treatment for burn wounds, exhibiting nearly a 50% reduction in death rate for patients with life-threatening burns when compared to patients who were administered silver nitrate treatments (Jessica and Yuji, 2015). There are reports on the role of this compound in alleviating the destructive effects of oxidative stresses (Wu et al., 2014; Liang et al., 2006) and improving the activity of ASA-GSH cycle, which is essential for reducing lipoperoxidation (Liu et al., 2016; Houa et al., 2018).

In postharvest physiology, cerium nitrate [$Ce(NO_3)_3$] is used to prolong the longevity of cut flowers. The application of $Ce(NO_3)_3$ to the vase solution of rose cut flowers (Wang et al., 2017) and *Lilium longiflorum* cut flowers (Houa et al., 2018) enhances their longevity by increasing antioxidant activity and strengthening ASA-GSH cycle. According to Zheng and Guo (2018), the treatment of carnation cut flowers with $Ce(NO_3)_3$ reduced the accumulation of MDA and strengthened the metabolism of ascorbate and glutathione in petals. It also preserved the longevity of the cut flowers for a longer time by helping to maintain membrane stability. The present study aimed to shed light on the effect of pulse treatment of salicylic acid and cerium nitrate [$Ce(NO_3)_3$] on the vase life and the related traits of cut lisianthus 'Pink Picotee' flowers.

Materials and Methods

Plant materials and treatments

To explore the effect of salicylic acid (SA) and cerium nitrate [$Ce(NO_3)_3$] on the vase life and related traits of cut lisianthus 'Pink Picotee' flowers, an experiment was carried out based on a completely randomized design. The experimental treatments were composed of $Ce(NO_3)_3$ at four rates of 20, 40, 80, and 200 µM, SA at three rates of 50, 100 and 200 mg L^{-1}, and control (distilled water)

plus 3% sucrose. The experiment was carried out at three replicates. Intact and uniformed flowers with the same size that were harvested at their bud stage were used for the trials. After their transfer to the laboratory, the flowers were recut at a height of 45 cm under water and were treated with the solutions for 24 hours. After the pulse treatment, the flowers were placed in a vase solution containing distilled water and were kept in a room at a temperature of 20 ± 2 °C, relative humidity of 70-75%, and light period of 12 hours at an intensity of 15 µM m^{-2} s^{-1} till the end of the experiment.

Trait assessments

Vase life. It was calculated by counting the days from the treatment of cut flowers with $Ce(NO_3)_3$ and SA until 50% wilting of florets (Cho et al., 2001).

Solution uptake. It was estimated by the procedure described in Kabari and Solimandarabi (2019). Accordingly, the initial solution volume (V_{t0}), final-day solution volume (V_{t1}), cut flower weight on the first day (FW), and final surface evaporation from the solution (E_t) were calculated. It is worth noting that to calculate E_t, several vases containing 250 ml distilled water were placed in different parts of the study site on the first day. The amount of water loss on the final day showed the rate of surface evaporation. Finally, the following equation was applied to estimate the rate of solution uptake in mL g^{-1} FW:

$$\text{Solution uptake (mL/g FW)} = \frac{V_{t0} - (E_t + V_{t1})}{FW}$$

Vase solution pH. It was measured on the first and last days with a digital CG824 pH-meter.

Bacteria population of the stem. Twenty-four hours after the treatments, a 2-cm sample was taken from the end of the stem, was washed with distilled water, was crashed in a fully sterilized medium, and was diluted with 0.9% normal saline serum. Then, 0.1 mL of the solution was cultured on agar. Twenty-four hours after incubation of the samples at 37 °C, the colonies of bacteria were counted (Liu et al., 2009).

Petal anthocyanin. It was measured by the procedure described in Jadid Solimandarabi et al. (2017) for which 0.5 g of fresh petal tissue was extracted with acidic ethanol on the fifth day. After filtration, the absorption by the extract was read at 535 nm with a JASCO Model V-530 spectrophotometer. Then, anthocyanin content was calculated in mg 100 g^{-1} FW by the following equation:

$$\text{Anthocyanin (mg/100 g FW)} = \frac{e \times b \times c}{d \times a} \times 100$$

in which *e* represents the sample weight, *b* denotes the sample size, *c* is the whole solution, *d* is the volume of the taken sample, and *a* is the spectrophotometer reading.

Total protein. The petals of lisianthus were sampled on the fifth day to determine their total protein content by Kjeldahl's indirect method. So, first nitrogen percentage and then protein percentage were calculated by the following equations:

$$\text{Nitrogen (\%)} = 0.56 \times t \times (a - b) \times \frac{V}{W} \times \frac{100}{DM}$$

in which *t* is the concentration of acid used for titration in mol L^{-1}, *a* is the amount of acid used for sample in mol L^{-1}, *b* is the amount of acid used as a control in ml, *v* is the volume of extract taken from digestion in ml, *w* is the plant sample weight for digestion in g, and *DM* is the plant dry matter.

$$\text{Total protein (\%)} = nitrogen \times 6.25$$

Malondialdehyde (MDA). It was calculated by Heath and Parker's (1968) method. So, 0.5 g of petal tissue was sampled by liquefied nitrogen and potassium phosphate buffer. The extract was centrifuged at 4 °C at a speed of 14,000 and 10,500 rpm and the supernatant was separated with a sampler. Then, 200 µL of the supernatant was mixed with 1000 µl of trichloroacetic acid (TCA) and thiobarbituric acid reactive substances (TBAS) and was heated in a hot water bath for 30 minutes. Immediately after that, the samples were placed in an ice-filled container for 30 minutes. The cooled mixture was centrifuged at 4 °C at 10,500 rpm for 10 minutes. Then, it was read with a spectrophotometer at 532 and 600 nm and the readings were placed in the following equation to yield MDA content in nmol g^{-1} FW.

$$\text{MDA(nmol/g FW)} = A_{532nm} - A_{600nm}$$

Peroxidase (POD) activity. It was measured by In et al. (2007) method for which some petal samples were detached from the flower branch on the fifth day and was extracted with 50 mM of potassium phosphate buffer (pH 7.0). The extract was centrifuged at 10500 rpm at 4 °C for 20 minutes. The supernatant was used as the enzymatic extract. So, 100 µL of the extract was added with 450 µL of H_2O_2 and 450 µL of guaiacol solution. Then, it was read at 470 nm with a JASCO Model V-530 spectrophotometer and POD activity was reported in nmol g^{-1} FW.

Ascorbate peroxidase (APX) enzyme activity. The sampling and extracting procedure was similar to that of POD activity. APX activity was measured by the method described in Nakano and Asada (1981). So, 150 µL of the enzymatic extract was mixed with 50 mM of potassium phosphate buffer, 0.5 mM of ascorbate, and 0.1 mM hydrogen peroxide. It was read at 290 nm with a JASCO Model V-530 spectrophotometer. APX activity was measured according to Nakano and Asada (1980). The reaction mixture contained 50 mM (pH 7.0) potassium phosphate buffer (pH 7.0) 0.1 mM EDTA, 0.25 mM ascorbate, 1.0 mM H_2O_2, and 100 mL of the enzymes extract. H_2O_2-dependent oxidation of ascorbate was followed by a decrease in the absorbance at 290 nm with a JASCO Model V-530 spectrophotometer. The experiment was performed at 25 °C. The APX activity of the extract was expressed as activity U/g FW min.

Polyphenol oxidase (PPO) enzyme activity. It was measured by Nicoli et al. (1991)'s method. The enzymatic

extract was prepared same as POD enzyme. Then, a mixture was prepared of 100 µL of enzymatic extract, 2.5 mL of potassium phosphate buffer (pH 6.8), 200 µl of 0.02-M pyrogallol as the enzyme precursor (final volume reaction was 3 ml) and was read at 420 nm with a JASCO Model V-530 spectrophotometer. It was measured by Nicoli et al. (1991) method. The enzymatic extract was prepared similar to POD enzyme. Then, a mixture was prepared of 300 µL of enzymatic extract, 2.5 mL of potassium phosphate buffer (pH 6.8) 200 µl of 0.02-M Pyrogallol as the enzyme precursor and was read at 420 nm with a JASCO Model V-530 spectrophotometer. The PPO activity of the extract was expressed as activity unit/g FW min.

Data analysis

Data of the daily visits and laboratory assays were analyzed in the SPSS software package. The LSD test was applied for the comparison of data means.

Results

Vase life

The effect of the treatments was significant ($p < 0.01$) on the vase life of lisianthuses (Table 1). $Ce(NO_3)_3$ at all four levels and SA at the rates of 50 and 100 mg L^{-1} improved the vase life versus the control (11.63 days).

The most effective treatments were 40 µM $Ce(NO_3)_3$ (15.42 days) and 100 mg L^{-1} SA (15.20 days), which did not differ from 50 mg L^{-1} SA (14.78 days) significantly. The flowers treated with 200 mg L^{-1} SA exhibited the shortest vase life of 10.63 days, reflecting the negative and toxic effect of higher levels of SA on the longevity of lisianthus cut flowers. The application of $Ce(NO_3)_3$ at the rates of 80 and 200 µM resulted in the loss of the vase life as compared to its application at the rates of 20 and 40 µM; however, the former two levels improved the vase life when compared to the control (Figure 1).

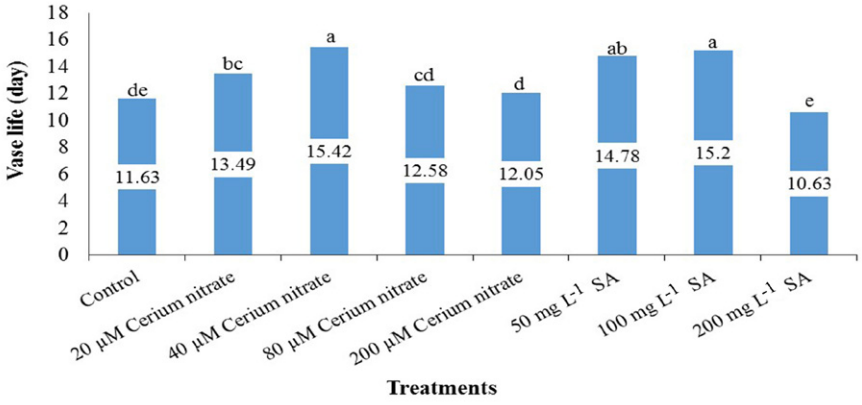

Figure 1. The effect of different rates of salicylic acid and cerium nitrate on the vase life of the cut lisianthus flowers.

Solution uptake

The solution uptake of the lisianthus cut flowers were improved by the treatments significantly ($p < 0.01$). The highest solution uptake was 1.48 mL g^{-1} FW observed in the flowers treated with 100 mg l^{-1} SA and 1.43 mL g^{-1} FW observed in the flowers treated with 40 µM $Ce(NO_3)_3$. These two treatments did not show any significant differences with one another. The treatment of 200 mg L^{-1} SA, which exhibited the shortest vase life, exhibited the lowest rate of solution uptake (1.02 mL g^{-1} FW) too (Table 2).

Table 1. Analysis of variance for the effect of different treatments on the measured traits

SoV	df	Vase life	Solution uptake	Bacterial population at stem end	Total anthocyanin	First day pH	Last day pH	Total protein	MDA	PPO	APX	POD
Replication	2	0.428^{ns}	0.00280^{ns}	260^{ns}	16720^{ns}	0.736^{ns}	0.488^{ns}	3.125^{ns}	6.125^{ns}	0.00000554*	12.5^{ns}	0.00000112^{ns}
Treatment	7	9.557**	0.0768**	3550*	1023584**	9.83**	6.403**	21.21*	57.7*	0.00000702**	239**	0.00016264**
Error	14	0.633	0.005109	915	19893	0.4812	0.3647	5.4107	17.55	0.00000154	12.5	0.00002112
CV (%)		6.01	5.687	23.06	15.68	14.86	11.94	21.27	17.43	10.27	21.7	19.35

*, ** and ^{ns}: Significant at $P < 0.05$, $P < 0.01$ and insignificant respectively.

Table 2. Means comparison for the effect of different treatments on the measured traits.

Treatments	Vase life (day)	Solution uptake (mL g^{-1} FW)	Bacterial population in stem end (Log_{10} CFU ml^{-1})	Total anthocyanin (mg 100 g^{-1} F.W.)	First day pH	Last day pH	Total protein (%)	MDA (nmol g^{-1} F.W.)	PPO (IU g^{-1} F.W.)	APX (IU g^{-1} F.W.)	POD| (nmol g^{-1} F.W.)
Control	11.63 de	1.11 de	161.3 ab	655 c	6.11 a	6.59 a	8.13 cd	28.30 ab	0.013 a	7.350 c	0.020 b
20 µM $Ce(NO_3)_3$	13.49 bc	1.13 de	113.6 bc	559 cd	6.15 a	6.36 ab	10.92 abc	24.44 abc	0.012 bc	11.50 bc	0.020 b
40 µM $Ce(NO_3)_3$	15.42 a	1.43 ab	81.3 c	1161 b	5.74 a	5.63 abc	13.93 a	18.65 c	0.011 bc	29.40 a	0.041 a
80 µM $Ce(NO_3)_3$	12.58 cd	1.31 bc	128.3 bc	1635 a	6.05 a	5.49 bc	12.80 ab	21.86 bc	0.012 bc	17.05 b	0.021 b
200 µM $Ce(NO_3)_3$	12.05 d	1.23 cd	156.3 ab	588 c	5.80 a	5.82 ab	9.52 bcd	27.65 ab	0.012 bc	11.85 bc	0.023 b
50 mg L^{-1} SA	14.78 ab	1.32 bc	110.0 bc	423 cd	2.75 b	4.70 c	12.06 abc	22.51 bc	0.011 bc	15.30 b	0.021 b
100 mg L^{-1} SA	15.20 a	1.48 a	110.6 bc	1872 a	2.41 b	3.44 d	13.54 ab	18.65 c	0.010 c	30.00 a	0.026 b
200 mg L^{-1} SA	10.63 e	1.02 e	187.0 a	322 d	2.30 b	2.40 d	6.56 d	30.23 a	0.015 a	7.70 c	0.018 b

*In each column, means with the similar letters are not significantly different ($p < 0.05$) using the LSD test.

The bacterial population at the stem end

The effect of different treatments was found to be significant ($p < 0.05$) on the bacterial population at the stem end (Table 1). The most population bacterial colony (187 Log_{10} CFU mL^{-1}) was related to the flowers treated with 200 mg L^{-1} SA, insignificantly differing from that of the plants treated with 200 µM $Ce(NO_3)_3$ and the control. The most successful treatments in reducing the microbial load at the stem end were 40 µM $Ce(NO_3)_3$ (81.3 Log_{10} CFU mL^{-1}), 50 mg L^{-1} SA, and 100 mg L^{-1} SA, respectively (Table 2).

Vase solution pH

According to the results of variance analysis, the effect of the treatments was significant ($p < 0.01$) on the first-day and last-day vase solution pH (Table 1). The pH of the SA-containing vase solution on both the first and last days was lower than that of the control and the solutions containing different levels of $Ce(NO_3)_3$. Overall, the vase solution pH was lower than 7, which is the appropriate pH for vase solutions, in all treatments (Table 2).

Petal protein

The results revealed that the total protein content in the petals of the lisianthuses was significantly ($p < 0.05$) decreased when they were subjected to 200 mg L^{-1} SA (6.56%). As is evident in Table 2, 20 µM $Ce(NO_3)_3$ was related to the highest petal content of 13.93%, but it did not differ from that of 50 and 100 mg L^{-1} SA and 20 and 80 µM $Ce(NO_3)_3$ significantly (Table 2).

Petal anthocyanin content

The effect of the treatments was significant ($p < 0.01$) on the petal anthocyanin content (Table 1). Table 2 displays that the highest petal anthocyanin content was observed in the plants treated with 100 mg L^{-1} SA (1,872 mg 100 g^{-1} FW) and those treated with 80 µM $Ce(NO_3)_3$ (1,635 mg 100 g^{-1} FW). The application of 200 mg L^{-1} SA resulted in the lowest petal anthocyanin among all the treatments (Table 2).

MDA content

The effect of the treatments was significant ($p < 0.05$) on the peroxidation of lipids or MDA (Table 1). The highest rate of MDA accumulation was related to the flowers treated with 200 mg L^{-1} SA (30.23 nmol g^{-1} FW), but it did not show significant differences from that of the control and the flowers treated with 20 and 200 µM $Ce(NO_3)_3$. The treatments of 40 µM $Ce(NO_3)_3$ and 100 mg L^{-1} SA (18.65 nmol g^{-1} FW) both performed the best in controlling lipid peroxidation and reducing MDA accumulation (Table 2).

Enzyme peroxidase (POD)

Based on the results, the application of 40 µM $Ce(NO_3)_3$ increased peroxidase activity significantly ($p < 0.01$) as compared to the control. The lowest activity of this enzyme (0.018 nmol g^{-1} FW) was obtained from the application of 200 mg L^{-1} SA, which was not significantly different from that of the control and the treatments of 20, 80, 200 µM $Ce(NO_3)_3$ and 50 and 100 mg L^{-1} SA (Table 2).

Enzyme ascorbate peroxidase (APX)

APX activity was significantly ($p < 0.01$) increased when the flowers were treated with 100 mg L^{-1} SA (30 IU g^{-1} FW) and 40 µM $Ce(NO_3)_3$ (29.40 IU g^{-1} FW). The lowest APX activity (7.35 IU g^{-1} FW) was related to the control, but not differing from that of 200 mg L^{-1} SA significantly (Table 2).

Enzyme polyphenol oxidase (PPO)

The effect of the treatments was found to be significant ($p < 0.01$) on PPO activity (Table 2). The highest activity was observed in the plants treated with 200 mg L^{-1} SA (0.015 IU g^{-1} FW) and the control (0.013 IU g^{-1} FW) and the lowest was 0.010 IU g^{-1} FW observed in those treated with 200 mg L^{-1} SA (Table 2).

Discussion

Salicylic acid (SA) and cerium nitrate [$Ce(NO_3)_3$] were recognized as compounds that prolong vase life and escalate the relevant traits in cut lisianthus flowers. As was already mentioned within the results, higher rates of the applied compounds, especially SA at the rate of 200 mg L^{-1}, had a negative and toxic effect on the vase life and related traits. SA increases hydrogen peroxide and oxygen free radicals to induce resistance in plants in the early stages of stress. These compounds are gradually eliminated by the enzymatic and non-enzymatic defense systems of the plant (Rohi et al., 2010). Due to the increased peroxidation of lipids with the use of 200 mg L^{-1} SA, it seems that the application of high concentrations of SA has caused the overproduction of oxygen radicals and oxidative stress that the plant's antioxidant system is able to control of these factors is not destructive and ultimately causes tissue damage and reduced vase life. The toxic effect is to increase lipid peroxidation (MDA) and reduce vase life. This is probably due to the increase in H_2O_2 and free radicals. Asghari and Aghdam (2010) argue that the appropriate and non-toxic concentration of SA should be specified for each crop through frequent experiments and trials. In the study of Geriloo and Ghasemnezhad (2011), the application of 150 mg L^{-1} SA increased the vase life of cut rose 'Yellow Island', but its increase to 200 mg L^{-1} had negative impacts on the measured traits. Negative effects of reduced vase life include premature wilting of petals and increased lipid peroxidation. Also, Kazemi et al. (2011) showed that the vase life of lisianthuses was significantly extended with the application of 2 mM SA, but when SA was applied at the rate of 4 mM, the vase life was shortened. Moreover, Cavasini et al. (2015) found that a dose of 1000 mg L^{-1} of SA was detrimental to the vase life of cut lisianthus. The negative effect of high levels of SA on the vase life and related traits has also reported for cut carnation (Kazemi et al., 2011) and chrysanthemum (Mansouri, 2012), which is consistent with our findings.

In addition to high rates of SA, $Ce(NO_3)_3$ at the rates of 80 and 100 µM performed poorly in improving the quantitative and qualitative traits of the cut lisianthus flowers as compared to 20 and 40 µM. Although these treatments

outperformed the control in most cases, the findings may show the negative impact of higher concentrations of $Ce(NO_3)_3$ on the longevity of cut lisianthus flowers. The negative effect of high $Ce(NO_3)_3$ rates have also been reported on the longevity of cut Lilium (Houa et al., 2018) and rose flowers (Wang et al., 2017), which is in agreement with our findings.

It has been shown that the vase solution pH is a determinant factor dictating solution uptake by cut flowers. The best pH for vase solutions has been found to be <7 (Nell, 2002; Edrisi, 2009). In our study, all the treatments had pH < 7, and the lowest was for SA treatments.

Vascular blockage by microorganisms is a major factor implicated for short postharvest longevity of cut flowers. In the present study, the microbial load at the stem end was decreased with the application of $Ce(NO_3)_3$ and SA at lower rates, which was followed by the increased uptake of water. Since the vividness of cut flowers is directly related to water uptake, the positive effect of SA and $Ce(NO_3)_3$ on improving the vase life of cut lisianthus flowers can be attributed to their capability in suppressing microbial load at stem ends and establishing balance in water uptake.

Researchers argue that SA is an antibacterial compounds that prolongs the vase life of cut flowers by reducing the growth and propagation of microorganisms and inhibiting vascular blockage (Mori et al., 2001; Alaey et al., 2011). In addition to the antibacterial activity of SA, its association has been reported in controlling stomatal movements, regulating evapotranspiration, adjusting aging-related genes, controlling oxidative stresses, and finally, improving the longevity of horticultural products (Mori et al., 2001; Asghari and Aghdam, 2010; Alaey et al., 2011).

In the study of Alaey et al. (2011), it was found that the application of SA to the vase solution of rose 'Black Magic' cut flowers improved postharvest longevity through increasing water uptake. Bayat and Aminifard (2017) obtained the longest vase life of the cut flowers of alstroemeria, gerbera, Lilium, rose, and tuberose by applying 300 mg L^{-1} SA. They attributed the positive effect of SA on the vase life of cut flowers to its impact on preserving water uptake and its antioxidative property. There are reports on the improvement of vase life and the related traits in the cut flowers of lisianthuses and carnations (Kazemi et al., 2011) and chrysanthemums (Mansouri, 2012; Mashhadian et al., 2012) when SA is applied at lower rates, which is consistent with our findings.

Cerium is an antibiotic (Huang, 2002) and antioxidant (He and Loh, 2000; Yin et al., 2009) whose positive effect in the form of $Ce(NO_3)_3$ has been reported on the postharvest longevity of cut carnations (Zheng and Guo, 2018) and roses (Wang et al., 2017). Houa et al. (2018) reported that the application of $Ce(NO_3)_3$ in the vase solution of Lilium cut flowers prolonged their postharvest longevity by enhancing water uptake and influencing the ASA-GSH cycle. The glutathione ascorbate cycle is one of the enzymatic defense systems of plants in purifying reactive oxygen species and maintaining membrane stability under stress. Ascorbate peroxidase, 1,2-hydroascorbate reductase and glutathione reductase are some of the enzymes in this cycle that play an important role in the clearance of hydrogen peroxide and reactive oxygen species (Zheng and Guo, 2018; Mittler and Zilinskas, 1994). Cerium is effective in increasing the activity of enzymes in this cycle (Zheng and Guo, 2018; Wang et al., 2017).

The senescence of cut flowers is associated with MDA content and the extent of lipid peroxidation so that MDA content increases as a cut flower approaches the end of its vase life (Shan and Zhao, 2015; Song et al., 2014). In our experiment, the treatments that exhibited longer vase life had lower MDA content. It has been documented that SA reduces lipid peroxidation by scavenging ROS and adjusting the activity of antioxidant enzymes (Ezhilmathi et al., 2007). Kazemi et al. (2011) reported that when SA was applied, MDA accumulation was decreased in cut lisianthus flowers, which is similar to our finding. In the study of Mansouri (2012), the treatment of cut chrysanthemum flowers with 0.1 and 1 μM SA reduced MDA accumulation, but the application of 10 and 100 μM SA increased it and influenced the postharvest longevity of the cut flowers adversely. In the present study, SA reduced MDA at the rates of 50 and 100 mg L^{-1}, but when it was increased to 200 mg L^{-1}, MDA accumulation was increased in the petals. Therefore, it can be concluded that the application of SA at high rates had a toxic impact on the lipids of the membrane and reduced the vase life of cut lisianthus flowers by increasing MDA accumulation.

$Ce(NO_3)_3$ inhibited lipid peroxidation or MDA accumulation in the petals of lisianthus and preserved the cut flowers for a longer time. The positive effect of $Ce(NO_3)_3$ on reducing MDA accumulation has been reported for the cut flowers of Liliums (Houa et al., 2018) and carnations (Zheng and Guo, 2018) too, which is similar to our findings. Wang et al. (2017) attributed the effect of $Ce(NO_3)_3$ on prolonging the vase life of cut rose flowers to the preservation of membrane structure through reducing lipid peroxidation and MDA accumulation.

The antioxidant enzymes were more active in the cut lisianthus flowers that had longer vase life. Antioxidant systems play a remarkable role in hindering the destructive effects of stresses and ROS in plants. POD and APX are antioxidant systems whose increased activity retards senescence (Shan and Zhao, 2015, Ataii et al., 2017). During petal aging and stress occurrence, the production of reactive oxygen species such as hydroxide radicals, hydrogen peroxide and superoxide anions increases in the plant. Accumulation of these molecules in the cell causes oxidative stress and damage to membranes and other macromolecules, leading to plant death. Plants use a variety of defense systems, including an antioxidant defense system against oxygen free radicals. Therefore, under stress conditions, the antioxidant defense capacity increases. SOD, CAT, PO, APX, etc. are among the antioxidant enzymes that protect the plant against damage caused by oxidative stress. These enzymes purify and remove reactive oxygen species. In fact, antioxidant enzymes oxidize by giving electrons to their oxygen free radicals and neutralize the oxidizing power of active oxygen species, thus preventing oxidative damage and the natural process of plant growth. They maintain the natural process of plant growth (Rohi et al., 2010; Carlos et al., 1996; Mittler, 2002).

Researchers argue that SA is directly or indirectly involved in activating antioxidant enzymes (Tian et al., 2007). In indirect method, SA stimulates the antioxidant defense system in plants by producing hydrogen peroxide and oxygen free radicals. These destructive species are easily removed by the antioxidant system. In direct method, SA is able to decompose oxygen free radicals. Hassan and Ali (2014) reported that the treatment of cut gladiolus flowers with SA enhanced the activity of antioxidant enzymes and reduced the rate of aging. The increased activity of antioxidant enzymes and the lower rate of ROS synthesis have been reported in cut rose flowers treated with SA (Capdeville et al., 2003). Consistent with our findings, there are also reports on the favorable effect of $Ce(NO_3)_3$ on increasing the activity of antioxidant enzymes in cut flowers of roses (Wang et al., 2017), carnations (Wu et al., 2014), and Liliums (Houa et al., 2018).

By accelerating the oxidation of phenols, PPO increases rotting and browning of tissues during storage. If the activity of this enzyme can be reduced in some way, postharvest longevity and quality can be improved (Ali Pour et al., 2015). PPO is a strong oxidizer of phenols and its activity in plants increases with the occurrence of biotic and abiotic stresses (Mayer and Harel, 1979). Reducing the activity of this enzyme with postharvest life-prolonging compounds such as nitric oxide (Ali Pour et al., 2015), heat treatment (Dogan and Dogan, 2004), pH-reducing agents (Kang and Yu, 2005), etc. can reduce tissue browning and reduce vase life. As already mentioned in the Results section, the PPO activity was lower in the flowers that had longer vase life. In fact, the application of SA and $Ce(NO_3)_3$ inhibited the destructive activity of PPO during storage. The application of cerium alleviated the activity of PPO in the study of Shyam and Aery (2012). Sadeghi et al. (2017) reported that the application of longevity-promoting compounds to cut Alstroemeria flowers reduced PPO activity, which agrees with our findings. As the petals age, the production of proteins that are responsible for the breakdown of macromolecules increases. On the other hand, the production and activity of ROSs cause the breakdown of proteins and lipids (Eason and Webster, 1995; Lay Yee et al., 1992; Sood et al., 2006). In general, due to the imbalance between the production and degradation of proteins during stress and aging, the amount of protein in tissues generally decreases. In the present study, the amount of protein was lower in the treatments that had a shorter vase life. Due to the effect of cerium nitrate and SA in maintaining the vase life, it seems that these compounds delay the aging process and preserve the proteins in this cut flower. Delay in aging and preservation of proteins with the use of SA in this study has been reported (Bahrami et al., 2013), which is consistent with the results of the present study. Anthocyanins are antioxidant compounds belonging to the group of flavonoids that are directly involved in the breakdown of reactive oxygen species and reduce the damaging effects of stress. In the present study, the highest amount of petal anthocyanin belonged to the treatment of 100 mg L^{-1} SA and 80 mM cerium nitrate, which can indicate the positive effect of these compounds in maintaining the activity of antioxidants and delaying aging. SA has been shown to increase the production of the enzyme phenylalanine ammonialyase, which is responsible for the biosynthesis of flavonoids (Chen et al., 2006; Lu et al., 2011). Increasing the amount of anthocyanins with the use of SA in gladiolus (Rahmani et al., 2015) and increasing the accumulation of anthocyanins in potato seedlings by affecting the expression of genes involved in the synthesis of anthocyanins has been reported with the use of cerium (Qineng et al., 2006), which agrees with the results of the present study.

Conclusions

In conclusion, we found that the application of SA and $Ce(NO_3)_3$ at lower rates improved the quantitative and qualitative traits of the cut lisianthus flowers. But, their higher concentrations, especially SA at the rate of 200 mg L^{-1}, were detrimental to the postharvest traits of the cut flowers. Thus, it is recommended to use appropriate concentrations of SA (50 and 100 mg L^{-1}) and $Ce(NO_3)_3$ (40 μM) to preserve the quantitative and qualitative traits of cut flowers of lisianthus 'Pink Picotee'. Aging in cut flowers is associated with the continuous production of high levels of oxygen free radicals. Antioxidant enzymes prevent oxidative stress and damage to membranes by inhibiting reactive oxygen species, thereby preventing premature aging of flowers.

Authors contributions

DH: conceived the study, planned the experiments and analysed the data. **FP:** performed the experiments. **BK:** conceived the study, planned the experiments and analysed the data, manuscript write and review.

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