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Scientific Article

Pre-harvest and pulse treatments of spermine, γ- and β-aminobutyric acid increased antioxidant activities and extended the vase life of gerbera cut flowers 'Stanza'

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Abstract

Capitulum wilting and neck bending are the two important complications that impair the post-harvest quality and vase life of the gerbera cut flowers. The present study investigates the effects of pre- and post-harvest treatments of spermine (SPER), γ-aminobutyric acid (GABA) and β-aminobutyric acid (BABA) on the vase life, qualitative features and enzyme activity of gerbera cut flowers 'Stanza'. The pre-harvest treatments (1 mM doses) were applied by foliar spraying, and the post-harvest were by pulse treatment (5 mM doses). The flowers kept their quality longer in pre and post SPER and GABA treatments. The longest vase life was recorded in pre-SPER (14 days) and pre-GABA (13 days) compared to BABA treatments and controls (9 days). Neck bending was observed more frequently in controls whereas SPER and GABA showed a lower neck bending rate at 9 days after harvest. The highest vase solution uptake, total soluble solids, total flavonoid, total protein, the activities of catalase, peroxidase, superoxide dismutase, phenylalanine ammonia-lyase, and ascorbate peroxidase, besides the lowest neck bending, electrolyte leakage, malondialdehyde, H_2O_2 and polyphenol oxidase activity were observed in pre-SPER treatment and subsequently in pre-GABA. Pre- and post-harvest treatments with β-Aminobutyric acid (BABA) had no significant effects on cut flowers compared to SPER and GABA, although showed slightly better effects than water control. It is therefore suggested that pre-harvest treatment using SPER and GABA can improve the vase life and quality of gerbera cut flowers.

Keywords: *Gerbera jamesonii*, enzyme activity, GABA, polyamines, proline.

Resumo

Tratamentos pré-colheita e por pulso com espermina, ácido γ- e β-aminobutírico aumentam atividade antioxidante e vida de vaso de flores cortadas de gérbera 'Stanza'

O murchamento do capítulo e a flexão do pescoço são as duas complicações importantes que prejudicam a qualidade pós-colheita e a vida de vaso de flores cortadas de gérbera. O presente estudo investigou os efeitos dos tratamentos pré e pós-colheita de espermina (SPER), ácido γ-aminobutírico (GABA) e ácido β-aminobutírico (BABA) na vida de vaso, nas características qualitativas e atividade enzimática de flores de gerbera 'Estrofe'. Os tratamentos pré-colheita (doses de 1 mM) foram aplicados por pulverização foliar e os pós-colheita foram realizados por tratamento de pulso (doses de 5 mM). As flores mantiveram sua qualidade por mais tempo nos tratamentos pré e pós aplicação com SPER e GABA. A maior vida útil do vaso foi registrada no pré-SPER (14 dias) e no pré-GABA (13 dias) em comparação com os tratamentos e controles BABA (9 dias). A flexão do pescoço foi observada com mais frequência nos controles, enquanto SPER e GABA apresentaram menor taxa de flexão do pescoço aos 9 dias após a colheita. Maior absorção de solução em vaso, sólidos solúveis totais, flavonoides totais, proteína total, atividades de catalase, peroxidase, superóxido dismutase, fenilalanina amônia-liase e ascorbato peroxidase, além da menor flexão do pescoço, vazamento de eletrólitos, malondialdeído, H_2O_2 e polifenol oxidase atividade foi observada no tratamento pré-SPER e subsequentemente no pré-GABA. Os tratamentos pré e pós-colheita com ácido β-aminobutírico (BABA) não tiveram efeitos significativos nas flores cortadas em comparação ao uso de SPER e GABA, embora tenham mostrado efeitos ligeiramente melhores que o controle da água. Portanto, sugere-se o uso de tratamento pré-colheita com SPER e GABA para melhorar a vida do vaso e a qualidade das flores cortadas com gérbera.

Palavras-chave: *Gerbera jamesonii*, atividade enzimática, GABA, poliaminas, prolina.

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Introduction

Gerbera jamesonii is an important cut flower that belongs to Asteraceae family (Mehdikhah et al., 2016). Although the gerbera is very popular among consumers as a cut flower, it has a short vase life for 7-10 days depending on cultivar at 20-22 ℃ (He et al., 2006). Capitulum wilting and neck bending are the two important complications that impair the post-harvest quality and vase life of the gerbera cut flowers (Halevy and Mayak, 1981).

Polyamines such as putrescine, spermidine and spermine (SPER) are organic compounds that have two or more amino groups (Khan et al., 2008). These compounds can be bonded to biological macromolecules that take part in many biochemical and physiological processes of fruit and flowers (Ziosi et al., 2009; Simoes et al., 2018). Polyamines and ethylene have opposing effects in the process of aging and decay of cut flowers (Reid, 2004). The reduction of polyamines is associated with an increase in ethylene synthesis, implying that a balance between these regulators is effective in accelerating or delaying the aging processes of plants (Yang et al., 2000). The contradictory relationship between the synthesis of ethylene and polyamines is due to the competitive mechanism of biosynthesis of these two substances, which have a common prevalence of S-adenosine methionine (SAM) (Khan et al., 2008). In a study on red roses, polyamines (putrescine, spermidine and SPER) increased the post-harvest quality and the content of anthocyanins and therefore led to extending the vase life (Rubinowska et al., 2012). The vase life, protein content and antioxidant capacity of rose cv. 'Dolce Vita' also increased by application of SPER (Farahi et al., 2013). In a similar study, the activity of lipoxygenase enzyme was reduced and the activity of the antioxidant enzymes catalase (CAT) and ascorbate peroxidase (APX) was increased in the treated lisianthus cut flowers (Ataii et al., 2015).

γ-aminobutyric acid (GABA) is a non-proteinaceous amino acid with four carbon atoms in its structure and is widely found in most prokaryotes and eukaryotes organisms. GABA has been studied in plants mainly as a proline-like metabolite (Wang et al., 2014). GABA increases as a signal in response to environmental stresses and leads to the accumulation of proline in the plant by increasing the activity of (S)-1-pyrroline-5-carboxylate and suppressing the activity of pyruvate dehydrogenase (Mashhoud et al., 2016). Proline maintains the stability of proteins and enzymes stabilizes membranes and regulates the pH of cells (Das and Roychoudhury, 2014). Aghdam et al. (2016) reported a positive effect of GABA on reducing chilling damage in *Anthurium* cut flowers and prolonging their vase life. They reported that the GABA-treated flowers had a lower EL and MDA and exhibited delayed aging by delaying the expression of genes associated with aging (Aghdam et al., 2016). GABA has been proven to be accumulated through environmental factors (such as low-temperature shock) by mediating acidity of the cytosol and increasing calcium levels inside cells (Shelp et al., 1995), playing roles on reactions involving signal transduction, cellular conduction, insect defenses, acidity regulation, energy balance, response to stress (such as decay fungi), metabolism of nitrogen and carbon.

β-aminobutyric acid (BABA) is also an isomer of the amino acid aminobutyric acid that plays a role in plants signaling (Roberts, 2007). BABA is well-known for its ability to induce plant disease resistance and to increase resistance to abiotic stresses when applied to plants (Bouche and Fromm, 2004). The application of BABA played a role in controlling a wide range of post-harvest rots (such as gray rot), which significantly delayed plant tissue firmness and prevented the increase in MDA and activity of pectin degrading enzymes such as pectin methylesterase.

Based on their functions, it seems that these compounds have a significant potential for improving the post-harvest indices of horticultural crops. Therefore, this research was conducted to study the pre- and post-harvest effects of SPER, GABA and BABA on enzyme activity and vase life of gerbera cut flowers 'Stanza'.

Materials and methods

Plant materials and chemical compounds

Gerbera flowers 'Stanza' were treated at pre-harvest by spraying 1 mM spermine (pre-SPER), γ-Aminobutyric acid (pre-GABA), β-Aminobutyric acid (pre-BABA) twice, at two and four days before commercial harvesting stage. Distilled water was used as control (pre-control). Pre-treated and water sprayed flowers were cut in the early morning and they were immediately placed upright in buckets filled with distilled water and transferred to the post-harvest laboratory. The flower stem ends were re-cut into length of 45 cm under water to remove air emboli and prevent vascular blockage. Water-sprayed cut flowers were subjected to post-harvest pulse treatment of 5 mM spermine (post-SPER), γ-Aminobutyric acid (post-GABA), β-Aminobutyric acid (post-BABA) for 1 h. Distilled water was used as control (post-control). Then, cut flowers were placed into bottles containing 300 ml of 150 ppm 8-hydroxyquinoline and 1% sucrose as a vase solution. Each replicate contained 10 cut flowers with an identical height of 45 cm. The flowers were kept at 20±1 ºC, 65±5% RH and 14 h of lightness at 20 μmol m^{-2} s^{-1}. Vase solutions were changed every three days.

Cut flower characteristics

In order to evaluate the vase life, petal wilting (>60%) and neck bending (>90°) or breaking were considered as the end point. Neck bending was measured at 9 days postharvest using a protractor (0 to 180°). Fresh weight (FW) of cut flowers was measured by a digital scale (0.01 g precision) at harvest time and during storage. Vase solution uptake (VSU) was calculated by the following equation:

$$VSU\ (ml\ kg^{-1}\ FW\ day^{-1}) = (St_{ı}\text{-}St) \qquad Eq\ (1)$$

Where St is the weight of the vase solution (in g) at day 0, 3, 6, 9, and $St_{ı}$ is the weight of the vase solution (in g) on the previous day.

Total soluble solids (TSS) was measured at room temperature by a digital refractometer. For this purpose, 5 g of stem tissue extract was prepared and the amount of TSS was immediately measured**.** To determine the electrolyte leakage (EL), pieces with the same thickness (1 g) were cut from petals by hand punching. Then, they were washed by distilled water and were placed inside tubes containing 10 ml of distilled water on a shaker (at 150×g) for 4 h. EC_1 was recorded by an EC meter (model DDS-22 C). To determine EC_2, the samples were autoclaved for 20 min at 12 °C to release all the electrolytes inside the cells. Then, they were cooled at room temperature and the final electrical conductivity (EC_2) of each sample was recorded. The EL was calculated according to equation 2.

$$EL\% = (EC_1 / EC_2) \times 100 \quad \text{Eq (2)}$$

The total phenolic compounds content of stems was measured by the method described by Tunc-Ozdemir et al. (2009). To measure total flavonoid, the aluminum calorimetry method was performed according to the method described by Zhishen et al. (1999). Malondialdehyde content (MDA) was used to determine the peroxidation of membrane lipid according to Zhishen et al. (1999). To assay free proline content of cut flower stems, 0.5 g of homogeneous samples collected from stem neck were mixed with 5 ml of aqueous 5-sulfosalicylic acid 3%. After centrifugation for 20 min at 12000×g, 1 ml of the supernatant was used to measure free proline content at 520 nm (Scinco, S-3100) as described by Bates et al. (1973). Enzyme activity was measured using the samples were stored at -80 °C. 0.5 grams of stem tissue was thoroughly homogenized in 50 ml of potassium phosphate buffer 50 mM containing polyvinylpyrrolidone (PVP) with pH 7.5. Then, the extracts were centrifuged at 10000×g at 4 °C for 15 min. The clear transparent was used to measure enzymatic activity. Content of hydrogen peroxide ($H_2O_{2)}$ was measured according to Esfahani and Mostajeran (2011). Total protein content was measured using the Bradford method (Bradford, 1976). Aliquot amounts of the supernatant sample were used directly for catalase activity (CAT) assays, and 1.0 ml of the sample was transferred to a dialysis bag and was dialyzed for 24 h at 4 ºC against 10 mM potassium phosphate buffer at pH of 7.8 to measure superoxide dismutase activity activity (SOD). CAT activity was assayed spectrophotometrically at 290 nm as described by Chandlee and Scandalios (1984). The activity was expressed as Unit kg^{-1} FW, as for all other enzymes. SOD activity was assayed by the method of Wayne et al. (1987). One unit of SOD activity was defined as the amount of enzyme required to cause 50% inhibition in the rate of nitro blue tetrazolium reduction measured at 560 nm (Scinco, S-3100). The enzyme activity was expressed as Unit kg^{-1} FW. To assess peroxidase activity (POD), 3 ml of the reaction mixture was used, which contained 2.77 ml of potassium phosphate buffer (50 mM, pH of 7.8), 100 µl of 1% H_2O_2, 100 µl of 2% guaiacol, and 30 µl of enzyme extract. POD activity was assayed using a spectrophotometer (Scinco, S-3100) at 470 nm for 3 min as described by Chance and Maehly (1955). To assess polyphenol oxidase activity (PPO), 3 ml of the reaction mixture was used, which contained 2.77 ml of potassium phosphate buffer (50 mM, pH of 7.8), 200 µl of 0.02 M pyrogallol, and 100 µl of enzyme extract. PPO activity was assayed using a spectrophotometer (Scinco, S-3100) at 420 nm (Putter, 1974). For measuring phenylalanine ammonia-lyase activity (PAL), the reaction mixture containing 200 µl of enzyme extract, 6 µM phenylalanine, and 0.5 M Tris-HCl buffer with pH of 8 was used. The reaction was terminated after 60 min at 37 °C by adding 50 µl of 5 N HCl. Ascorbate peroxidase activity (APX) was measured by at 290 nm according to the method described by Zhang et al. (2013). PAL activity was determined as the rate of conversion of L-phenylalanine to trans-cinnamic acid at 290 nm by method of Beaudoin-Egan and Thorpe (1985).

Statistical analysis

Data for each times investigation (At harvest, 3, 6 and 9 day) were individually analyzed using the general linear models procedure of SAS (SAS Institute, Inc., Cary, NC) as a completely randomized design with four replications. Means were compared by Duncan's test at P=5%.

Results

Pre- and post-harvest treatments on the vase life and flower neck bending

The longest vase life was recorded in pre-SPER (14 days) and pre-GABA (13 days) compared to the control (9 days). Neck bending was observed most frequently in control whereas all treatments showed a lower neck bending rate at 9 days. The lowest rate of neck bending was observed in pre-SPER, pre-GABA, post-SPER and post-GABA respectively. BABA pre- and post treatments showed no significant difference in the vase life, although, a lower neck bending was observed in BABA treatments than control (Figure 1 and Figure 2).

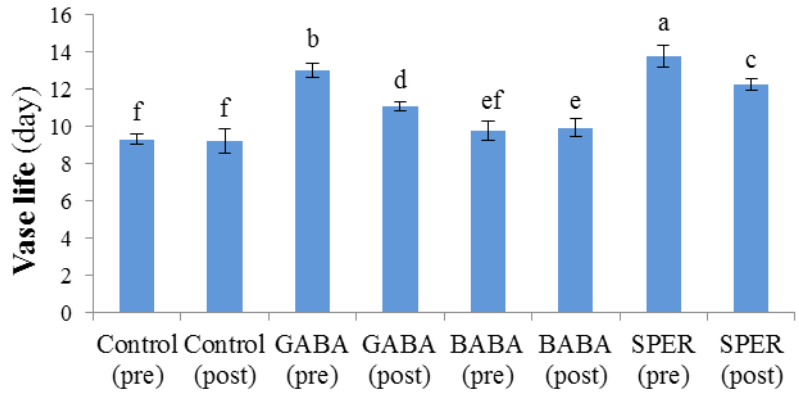

Fig. 1. The effect of treatments on the vase life (d) of gerbera cut flowers 'Stanza' (* Means with the similar letter (s) in each row are not significantly different at the P < 0.05 level of Duncan's multiple range test. Standard errors (error bars) of four independent biological replicates (n = 4) each replicate included 10 cut flowers).

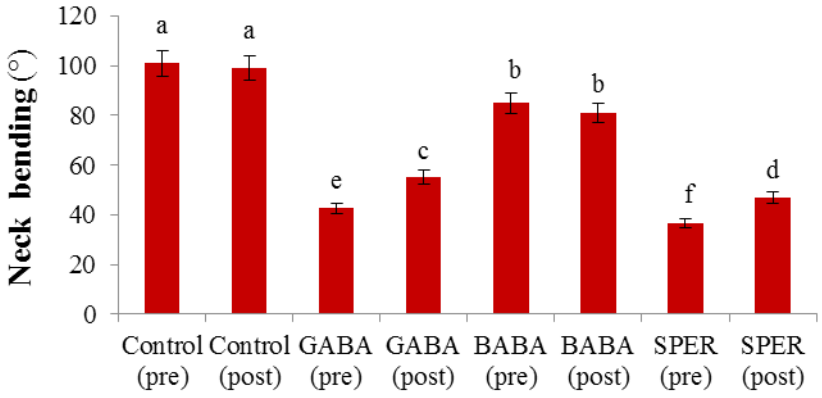

Fig. 2. The effect of treatments on neck bending (°) of gerbera cut flowers 'Stanza' (* Means with the similar letter (s) in each row are not significantly different at the P < 0.05 level of Duncan's multiple range test. Standard errors (error bars) of four independent biological replicates (n = 4) each replicate included 10 cut flowers).

FW and VSU of gerbera cut flowers

Pre-treated flowers had a higher FW than water-sprayed control samples. At post-harvest, cut flowers showed an increased in FW during three day of storage and then FW was decreased at 6 and 9 days. Following 9 days, the highest FW was observed in pre-SPER (30.70 g) then pre-GABA (30.01 g). The lowest FW during post-harvest was observed in control samples (Table 1). VSU was higher in all treatments at 9 days except in controls and pre-BABA treatment. The highest VSU was observed in pre-SPER then in pre-GABA respectively. VSU was higher in pre-SPER and pre-GABA compared to but the pre-harvest treatment of post-SPER and post-GABA was related to higher VSU than their post-harvest treatments (Table 1).

Table 1. The effect of treatments on FW, VSU, MDA, Proline, H_2O_2, TSS, EL, and Protein content of gerbera cut flowers'Stanza'.

Attributes	Time investigate	Control (pre)	Control (post)	GABA (pre)	GABA (post)	BABA (pre)	BABA (post)	SPER (pre)	SPER (post)
FW (g)	At harvest	30.36^{b}	30.30^{b}	33.08^{a}	30.30^{b}	30.76^{b}	30.30^{b}	32.90^{a}	30.30^{ij}
	3 day	30.78^{d}	30.85^{d}	36.31^{a}	33.13^{b}	31.13^{cd}	31.50^{c}	36.85^{a}	33.45^{b}
	6 day	28.26^{f}	28.32^{f}	34.82^{b}	32.06^{d}	28.95^{e}	29.23^{e}	35.28^{a}	32.51^{c}
	9 day	22.58^{ef}	22.37^{f}	30.01^{b}	27.28^{d}	22.51^{ef}	23.02^{e}	30.70^{a}	28.05^{c}
VSU (ml kg^{-1} FW day^{-1})	At harvest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	3 day	0.32^{e}	0.32^{e}	0.44^{a}	0.38^{c}	0.33^{e}	0.36^{d}	0.45^{a}	0.41^{b}
	6 day	0.23^{e}	0.23^{e}	0.35^{b}	0.30^{c}	0.23^{e}	0.26^{d}	0.37^{a}	0.31^{c}
	9 day	0.15^{f}	0.15^{f}	0.26^{b}	0.21^{d}	0.16^{f}	0.17^{e}	0.29^{a}	0.23^{c}
MDA (mmol kg^{-1})	At harvest	3.96^{a}	3.98^{a}	3.68^{c}	3.98^{a}	3.88^{b}	3.98^{a}	3.62^{d}	3.98^{a}
	3 day	4.20^{a}	4.27^{a}	3.76^{e}	4.03^{cd}	4.10^{bc}	4.16^{ab}	3.72^{ne}	3.97^{d}
	6 day	5.25^{a}	5.21^{a}	4.22^{e}	4.72^{c}	5.11^{b}	5.05^{b}	4.11^{f}	4.56^{d}
	9 day	6.80^{a}	6.75^{a}	5.22^{e}	5.92^{c}	6.67^{ab}	6.58^{b}	5.07^{f}	5.80^{d}
Proline (mmol kg^{-1})	At harvest	183.12^{a}	184.37^{a}	198.32^{c}	184.37^{a}	167.50^{b}	184.37^{a}	154.25^{d}	184.37^{a}
	3 day	189.50^{a}	189.69^{a}	197.80^{d}	185.12^{bc}	182.37^{c}	186.50^{b}	158.12^{e}	184.50^{bc}
	6 day	228.50^{a}	227.37^{a}	205.12^{c}	203.75^{c}	223.50^{b}	222.87^{b}	180.12^{e}	199.87^{d}
	9 day	261.01^{a}	262.13^{a}	216.75^{e}	231.75^{c}	253.50^{b}	251.12^{b}	205.37^{f}	225.62^{d}
H_2O_2 content (µmol g^{-1})	At harvest	1.24^{a}	1.26^{a}	1.11^{b}	1.26^{a}	1.21^{a}	1.26^{a}	1.10^{b}	1.26^{a}
	3 day	1.46^{a}	1.50^{a}	1.21^{d}	1.30^{c}	1.44^{ab}	1.40$^{\b}$	1.19^{d}	1.29^{c}
	6 day	1.98^{a}	1.95^{a}	1.41^{e}	1.61^{c}	1.89^{ab}	1.84^{b}	1.55^{cd}	1.39^{e}
	9 day	2.69^{a}	2.63^{a}	1.77^{d}	1.95^{c}	2.51^{b}	2.40^{b}	1.39^{e}	1.90^{c}
TSS (% Brix)	At harvest	5.14^{a}	5.13^{a}	5.07^{b}	5.13^{ab}	5.12^{ab}	5.13^{ab}	4.96^{c}	5.13^{ab}
	3 day	6.13^{ab}	6.20^{a}	5.56^{c}	5.70^{c}	5.93^{b}	5.96^{ab}	5.16^{d}	5.60^{c}
	6 day	4.96^{e}	4.97^{e}	5.73^{b}	6.07^{a}	5.06^{de}	5.12^{d}	5.63^{c}	6.01^{a}
	9 day	3.72^{e}	3.72^{e}	5.13^{b}	4.83^{c}	4.00^{d}	4.03^{d}	5.30^{a}	4.92^{c}
EL (%)	At harvest	19.83^{a}	19.81^{a}	18.62^{b}	19.81^{a}	19.74^{a}	19.81^{a}	18.12^{c}	19.81^{a}
	3 day	22.77^{a}	22.83^{a}	20.42^{nc}	21.97^{b}	22.81^{a}	22.47^{a}	20.17^{c}	21.60^{b}
	6 day	35.37^{a}	35.48^{a}	29.82^{d}	32.57^{c}	34.32^{b}	34.36^{b}	28.73^{e}	31.86^{c}
	9 day	67.35^{a}	67.56^{a}	55.40^{f}	61.37^{d}	66.36^{b}	65.65^{c}	53.91^{g}	59.50^{e}
Protein content (g kg^{-1})	At harvest	1.11^{d}	1.11^{d}	1.34^{b}	1.11^{d}	1.13^{c}	1.11^{d}	1.37^{a}	1.11^{d}
	3 day	1.09^{b}	1.10^{b}	1.34^{a}	1.12^{b}	1.12^{b}	1.12^{b}	1.36^{a}	1.14^{b}
	6 day	0.99^{f}	0.99^{f}	1.28^{b}	1.08^{d}	1.02^{e}	1.03^{e}	1.30^{a}	1.12^{c}
	9 day	0.87^{f}	0.86^{f}	1.16^{b}	1.01^{d}	0.89^{e}	0.90^{e}	1.21^{a}	1.07^{c}

* The effects of experimental treatments are individually comparing horizontally at each time investigation (at harvest, 3, 6 and 9 days) in each attributes. Results are means of four replications (n = 4) each replicate included 10 cut flower samples. At each time of postharvest keeping, data per attributes with the same letters within rows and columns are not significantly different at the $P < 0.05$ level of Duncan's multiple range test. (pre and post show application of treatments at pre- and post-harvest).

MDA, proline, and H_2O_2 content of gerbera cut flowers

The lowest MDA and H_2O_2 contents were observed at harvest, increasing during the vase life up to 9 days. At 9 days the lowest MDA and H_2O_2 content were recorded in pre-SPER then in pre-GABA treatments, and subsequently in post-SPER and post-GABA treatments (Table 1). A lesser amount of proline was produced in flowers sprayed with spermine at pre-harvest (pre-SPER). The same, the lowest proline content was observed in pre-SPER (205.37 mmol kg^{-1}) at 9 days. Whereas, proline content reached the highest amount in controls and BABA treatments at 9 days (Table 1).

TSS, EL, and protein content

TSS of flower neck was increased in all treatments from harvest up to 3 days. After that, TSS showed a significant decrease from day 3 to day 9 post-harvest in BABA and control treatments as opposed to SPER and GABA treatments. According to the results, the highest (5.30 % Brix) and the lowest (3.72% Brix) of TSS content were observed in pre-SPER treatment and control samples respectively at 9 days (Table 1). The EL increased over the vase life time. The lowest EL at 9 days was recorded in flowers sprayed by SPER then GABA (pre-SPER and pre-GABA) (Table 1). In the same way, the protein content of cut flowers decreased by increasing the storage time in vase solution. The highest amount of proteins belonged to cut flowers sprayed with SPER and GABA at pre-harvest, whereas the lowest protein content was recorded in control samples (Table 1).

CAT, POD, SOD, APX, and PAL activity of gerbera cut flowers

The highest CAT activity was observed in pre-SPER (182.37×10^3 U kg^{-1}) and pre-GABA (172.36×10^3 U kg^{-1}) respectively, at 9 days (Table 2). CAT activity decreased during post-harvest storage from day 0 to 9 days, but all treatments caused a higher CAT activity compared to control at 9 days (Table 2). POD activity also showed a decreasing pattern during the vase life from harvest to 9 days. The highest POD activity was recorded in pre-SPER (0.337×10^3 U kg^{-1}) and pre-GABA (0.296×10^3 U kg^{-1}) respectively on day 9 (Table 2). BABA treatments had no significant effects on POD activity compared to controls (Table 2).

SOD activity increased drastically during 3 days, and then decreased into the background level in BABA treatments and controls at 9 days. The highest SOD activity was related to pre-SPER (43.75×10^3 U kg^{-1}), pre-GABA (37.12×10^3 U kg^{-1}), post-SPER (31.50×10^3 U kg^{-1}) and post-GABA (26.50×10^3 U kg^{-1}) treatments, respectively. Although the SOD activity decreased in SPER and GABA pre-harvest and post-harvest treatments, it was still about two-fold higher than controls (Table 2).

APX activity also showed a decreasing pattern during post-harvest storage from harvest to 9 days. However, the results showed that pre-treatments of SPER and GABA caused higher APX activity compared to the controls and other treatments at harvest time. Again pre-SPER (0.417×10^3 U kg^{-1}) and pre-GABA (0.376×10^3 U kg^{-1}) were the best treatments that kept the enzyme activity at a higher level at 9 days (Table 2). Same to APX, PAL activity showed a decreasing pattern in all treatments during post-harvest storage. PAL activity was the highest in pre-GABA treatment at harvest time. All treatments showed a higher PAL activity than control samples at 9 days and the highest amount was belong to pre-SPER (0.197×10^3 U kg^{-1}) and pre-GABA (0.181×10^3 U kg^{-1}) respectively (Table 2).

Table 2. The effect of treatments on CAT, POD, SOD, PAL, Total phenol, Flavonoid and PPO activity of gerbera cut flowers 'Stanza'.

Attributes	Time investigate	Control (pre)	Control (post)	GABA (pre)	GABA (post)	BABA (pre)	BABA (post)	SPER (pre)	SPER (post)
CAT activity ($U\ kg^{-1}$)×10^3	At harvest	181.87^{d}	181.87^{d}	218.75^{b}	181.87^{d}	190.87^{c}	181.87^{d}	229.91^{a}	181.87^{d}
	3 day	183.87^{d}	184.12^{d}	221.25^{b}	186.12^{d}	192.75^{c}	185.12^{d}	229.75^{a}	187.51^{d}
	6 day	134.86^{f}	135.50^{f}	209.74^{b}	169.37^{d}	139.00^{e}	140.62^{e}	218.49^{a}	177.87^{c}
	9 day	102.51^{f}	103.12^{f}	172.36^{b}	143.00^{d}	109.87^{e}	110.37^{e}	182.37^{a}	150.40^{c}
POD activity ($U\ kg^{-1}$)×10^3	At harvest	0.395^{c}	0.398^{c}	0.467^{b}	0.398^{c}	0.415^{c}	0.398^{c}	0.510^{a}	0.398^{c}
	3 day	0.356^{d}	0.354^{d}	0.441^{b}	0.381^{c}	0.371^{cd}	0.373^{cd}	0.486^{a}	0.383^{c}
	6 day	0.228^{e}	0.231^{e}	0.385^{b}	0.279^{d}	0.242^{e}	0.249^{e}	0.422^{a}	0.318^{c}
	9 day	0.124^{e}	0.126^{e}	0.296^{b}	0.193^{d}	0.127^{e}	0.136^{e}	0.337^{a}	0.237^{c}
SOD activity ($U\ kg^{-1}$)×10^3	At harvest	16.62^{b}	16.87^{b}	24.01^{jab}	16.87^{b}	18.25^{b}	16.87^{b}	27.49^{a}	16.87^{b}
	3 day	46.62^{g}	47.50^{fg}	64.13^{b}	52.03^{d}	48.37^{ef}	49.04^{e}	69.25^{a}	58.02^{c}
	6 day	35.37^{f}	35.25^{f}	58.62^{b}	46.90^{d}	37.11^{e}	37.76^{e}	63.13^{a}	50.37^{c}
	9 day	15.50^{ef}	14.87^{f}	37.12^{b}	26.50^{d}	15.79^{ef}	16.53^{e}	43.73^{a}	31.51^{c}
APX activity ($U\ kg^{-1}$)×10^3	At harvest	0.475^{d}	0.480^{d}	0.542^{b}	0.480^{d}	0.492^{c}	0.480^{d}	0.581^{a}	0.480^{d}
	3 day	0.436^{d}	0.430^{d}	0.521^{b}	0.461^{c}	0.451^{cd}	0.451^{cd}	0.566^{a}	0.463^{c}
	6 day	0.308^{e}	0.310^{e}	0.465^{b}	0.361^{d}	0.322^{e}	0.327^{e}	0.502^{a}	0.39^{c}
	9 day	0.206^{e}	0.206^{e}	0.376^{b}	0.273^{d}	0.205^{e}	0.216^{e}	0.417^{a}	0.316^{c}
PAL activity ($U\ kg^{-1}$)×10^3	At harvest	0.276^{b}	0.278^{b}	0.302^{a}	0.278^{b}	0.275^{b}	0.278^{b}	0.282^{b}	0.278^{b}
	3 day	0.258^{bc}	0.262^{bc}	0.283^{a}	0.255^{c}	0.258^{bc}	0.260^{bc}	0.270^{ab}	0.257^{c}
	6 day	0.186^{d}	0.183^{d}	0.237^{b}	0.210^{c}	0.186^{d}	0.190^{d}	0.246^{a}	0.216^{c}
	9 day	0.101^{g}	0.106^{fg}	0.181^{b}	0.125^{d}	0.111^{ef}	0.115^{e}	0.197^{a}	0.140^{c}
Total phenol ($g\ kg^{-1}$)	At harvest	0.465^{d}	0.459^{d}	0.615^{b}	0.459^{d}	0.500^{c}	0.459^{d}	0.631^{a}	0.459^{d}
	3 day	0.422^{e}	0.428^{e}	0.631^{a}	0.531^{c}	0.473^{d}	0.462^{d}	0.650^{a}	0.562^{b}
	6 day	0.323^{f}	0.320^{f}	0.567^{b}	0.512^{c}	0.351^{e}	0.363^{d}	0.577^{a}	0.513^{c}
	9 day	0.213^{e}	0.207^{e}	0.487^{a}	0.397^{c}	0.256^{d}	0.261^{d}	0.500^{a}	0.436^{b}
Flavonoid ($g\ kg^{-1}$)	At harvest	$0.196j^{d}$	0.197^{d}	0.242^{b}	0.197^{d}	0.213^{c}	0.197^{d}	0.254^{a}	0.197^{d}
	3 day	0.193^{e}	0.190^{e}	0.253^{a}	0.216^{c}	0.207^{d}	0.203^{d}	0.259^{a}	0.228^{b}
	6 day	0.152^{d}	0.150^{d}	0.241^{a}	0.218^{b}	0.162^{c}	0.166^{c}	0.248^{a}	0.225^{b}
	9 day	0.103^{e}	0.096^{e}	0.196^{b}	0.167^{c}	0.113^{d}	0.120^{d}	0.206^{a}	0.176^{c}
PPO activity ($U\ kg^{-1}$)×10^3	At harvest	2.83^{a}	2.84^{a}	2.53^{c}	2.84^{a}	2.71^{b}	2.84^{a}	2.32^{d}	2.84^{a}
	3 day	3.27^{ab}	3.30^{a}	2.67^{e}	3.02^{d}	3.21^{bc}	3.14^{c}	2.52^{f}	3.01^{d}
	6 day	2.88^{a}	2.91^{a}	2.49^{e}	2.74^{c}	2.81^{b}	2.78^{b}	2.42^{f}	2.67^{d}
	9 day	2.73^{a}	2.77^{a}	2.35^{e}	2.59^{c}	2.72^{ab}	2.70^{b}	2.30^{f}	2.56^{d}

* The effects of experimental treatments are individually comparing horizontally at each time investigation (at harvest, 3, 6 and 9 days) in each attributes. Results are means of four replications (n = 4) each replicate included 10 cut flower samples. At each time of postharvest keeping, data per attributes with the same letters within rows and columns are not significantly different at the $P < 0.05$ level of Duncan's multiple range test. (pre and post show application of treatments at pre- and post-harvest).

Phenol, flavonoid and PPO activity of gerbera cut flowers

At 9 days postharvest keeping, the highest amount of total phenol was observed in treatments of pre-SPER (0.500 g kg^{-1}) and pre-GABA (0.487 g kg^{-1}) treatments. Subsequently, treatments of post-SPER (0.436 g kg^{-1}) then post-GABA (0.397 g kg^{-1}) contained more total phenols (Table 2). The flowers were sprayed with SPER (0.206 g kg^{-1}), and GABA (0.196 g kg^{-1}) showed the highest amount of flavonoid content at harvest time and at 9 days. Also there was no significant difference between pre and post-BABA treatments, but they had higher flavonoid content than control samples (Table 2). PPO activity was reduced in flowers were sprayed with SPER and GABA at harvest time. The same, a lower PPO activity was recorded in pre-SPER and pre-GABA at 9 days, respectively (Table 2).

Discussion

Polyamines reduce ROS by increasing the antioxidant capacity of flowers. In addition, they can alleviate the destruction of membrane lipids and post-harvest loss of cut flowers by reducing lipoxygenase activity (Lee et al., 1997). All of these factors help to maintain the post-harvest quality of cut flowers . However, at pre-harvest since flowers are still attached to the mother plants, the use of pre-treatments that induces the plant's antioxidant system can outperform post-treatment because they strengthen the antioxidant system of the flowers by the uptake and synthesis of necessary supplies from the mother plant. The observation of antioxidant material in cut flowers at the harvesting stage, including phenol, flavonoids and antioxidant enzymes, confirms this claim in our study.

The prevention of peroxidation of membrane lipids is the anti-aging mechanisms of SPER (Yang et al., 2000). Similar to our results, Palagani and Singh (2017) reported that the increase in antioxidant capacity and the decrease in damages to cell walls were effective SPER in decrease of neck bending and prolonging the vase life of gerbera cut flowers. GABA is known as a stress-tolerant osmolyte that is suggested to accumulate in cells due to its osmolality and leads to the accumulation of proline in the plant. Proline accumulation maintains cellular turgor, protects cell membrane and protein structure, and metabolizes the plant by inhibiting cell water loss (Krishnan et al., 2013), these are the likely causes for higher freshness, quality and vase life of the cut flowers in our research. BABA is a compound that induces resistance to pathogens (Bouche and Fromm, 2004). In the present study, pre- and post-harvest treatments by BABA had no significant effect on the vase life of the cut flowers compared to controls, maybe due to a low concentration was used or a narrower range of activities compared to SPER and GABA.

The results showed that treatments with higher VSU had higher FW too. The increase in FW of alstroemeria cut flowers treated with SPER and putrescine (Alborz et al., 2015) and anthurium cut flowers treated with GABA under cold storage conditions reported (Soleimani-Aghdam et al., 2016). Lee et al. (1997) found that the application of polyamines improved water absorption by carnation cut flowers as compared to the control and attributed it to the preservation of stem turgor in polyamine-exposed flowers.

In our study, TSS of flower neck was increased in all treatments from harvest time up to 3 days and then it started to decrease from day 3 to day 9 post-harvest in BABA and control treatments despite of SPER and GABA treatments. This could be due to the increased respiration and post-harvest deterioration of flowers and consumption of sugars by the process of cell respiration (Danaee et al., 2013). It can reduce the TSS during the post-harvest storage of cut flowers. Dantuluri et al. (2008) reported the reduced activity of hydrolytic enzymes in gladiolus plants treated with polyamines.

By increasing the storage time, water absorption was decreased and respiration and post-harvest stress were increased. In this situation, the stress of the cell increased and reactive oxygen species (ROS) such as H_2O_2 showed a high tendency to damage cell membranes. It is reasonable to conclude that the decrease in membrane stability is most likely due to the increase in the activity of ROS and the decrease in antioxidant capacity during the vase life. Polyamines compete with ethylene precursors and increase antioxidant capacity, thereby reducing damages to cell membranes and lipid peroxidation (Kaur-Sawhney et al., 2003). Polyamines bond to anionic molecules such as proteins, phospholipids, and pectinates, which may be a reason for the decreased activity of the enzyme pectinase and MDA content in cells (Apel and Hirt, 2004). Also, the increase in antioxidant enzymes helps to maintain cellular structure against oxidative damage of ROS (Jayaprakasha et al., 2007; Bregoli et al., 2002) that these are reasons for lower EL, MDA and H_2O_2 in treatments of flowers than control samples at harvest and their post-harvest by GABA and SPER treatments.

In oxidative stresses, phenolic compounds, especially flavonoids, can bond with phospholipids by a hydrogen bond from polar heads of phospholipids, resulting in these compounds being accumulated inside and outside the membrane and preventing the damage of ROS (Michalak, 2006). Our results showed that cut flowers with higher total phenol and flavonoid content had less H_2O_2, EL and MDA content and prolonged vase life. The preservation of phenolic compounds of gerbera cut flowers treated with sodium nitroprusside has been attributed to the increase in antioxidant capacity and the decrease in PPO activity (Shabanian et al., 2018), which is consistent with our results. Also, the increase in total phenol and flavonoids content of anthurium cut flowers treated with gibberellic acid and SPER has been attributed to the increase in internal polyamines and the reduction of respiration in cut flowers (Simoes et al., 2018).

Proline is not only an indicator of stress intensity, but it can also maintain the structure of cell membranes and proteins (Das and Roychoudhury, 2014). In our study, SPER and GABA treatments reduced damages to cellular compositions of cut flowers by mitigating stress during post-harvest kept, so they reduced the amount of proline accumulation in cut flowers. Metabolites like GABA,

alcoholic sugars, and amino acids accumulate as osmolyte or antioxidants in different plant species exposed to stressful conditions and can reduce stress damage (Krishnan et al., 2013). Aghdam et al. (2016) showed that pre and post treatment of GABA increased the accumulation of proline in anthurium cut flowers during cold storage. The comparison of protein results with proline content of cut flowers showed that treatments with lower protein content had higher proline content because proline is one of the products of proteins destruction. The reduction of protein content can be a result of protein destruction under stressful conditions.

Plant cells are equipped with antioxidant enzymes to combat with ROS. These enzymes prevent damages to plant cells (Kopyra and Gwozdz, 2003). Horticultural crops lose their quality (due to the initiation of the aging process) and suffer from an increasing rate of ROS during post-harvest period partially because of their detachment from their mother plants, so the amount of feedstock and pre-antioxidant compounds decline during their kept after harvesting (Chanjirakul et al., 2008). At the post-harvest period, the content of antioxidant enzymes including CAT, SOD, APX, and POD decreases, while ROS is removed and the stress damage is alleviated, so their content decreases during the vase life of the cut flowers. Polyamines, directly or through the reduction of ROS and maintain antioxidant enzymes in plant tissues (Kakkar and Sawhney, 2003). Therefore, one of the reasons for the higher activity of antioxidant enzymes (CAT, SOD, APX, and POD) in these treatments may be less stress and respiration in these treatments. An increase in antioxidant enzymes in alstroemeria cut flowers treated with Putrescin and SPER (Alborz et al., 2015), anthurium cut flowers treated with GABA and salicylic acid (Aghdam et al., 2016) and anthurium cut flowers treated with GA_3 and SPER (Simoes et al., 2018) has been reported during their vase life, which are consistent with our results.

PAL is one of the important enzymes in plants that has a positive correlation with resistance to oxidative stress. Also, this enzyme is one of the most important enzymes in the production of phenolic compounds such as lignin (Bharti and Khurana, 1997). Lignin has been introduced as one of the most important compounds in the development of cellular strength and reduction of neck bending of gerbera cut flowers (Nazari deljou et al. 2015). Therefore, the results of the present study clearly show that treatments with longer vase life had more PAL activity and showed less neck bending and less wilting. Similar to our results, Danaee et al. (2013) observed in gerbera cut flowers that longer vase life of cut flower was due to higher PAL content and antioxidant enzymes than control.

The internal and external browning of tissues is caused by the oxidation of phenolic compounds by PPO enzyme (Crisosto et al., 2007). Polyamine treatments increase the internal polyamines of cells and can inactivate ROS and maintain cell membranes against oxidation stress, so they maintain the fluidity of the membrane, decrease H_2O_2, EL and induce browning skin of petals of cut flowers (Tassoni, 1998). Our results showed that treatments with higher quality and longer vase life had lower PPO activity. The reduction of PPO enzyme in alstroemeria cut flowers treated by SPER and putrescin has been reported by Alborz et al. (2015), which is consistent with our results for gerbera cut flowers 'Stanza'.

Conclusions

Pre-harvest treatments of SPER and GABA outperform their post-harvest treatments in maintaining the quality and vase life of gerbera cut flowers, but pre- and post-harvest treatments with BABA have no significant effects on cut flowers compared to SPER and GABA, although it shows fewer slightly better effects than water control.

Author Contributions

M.A.[0000-0001-6631-6874]: conceived the ideas and designed the study. M.A and M.M.[0000-0003-1519-7750]: analyzed the data and developed the experiments. M.A., M.M and M.S.[0000-0001-9462-7127]: participated in the interpretation the data and discussion of the results and writing of the article. All authors read and approved the final manuscript.

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