https://doi.org/10.1590/1678-4499.20220207

POSTHARVEST TECHNOLOGY
Article

Postharvest conservation of lisianthus inflorescences with bioregulators

Cristiane Calaboni[1,*], Ricardo Alfredo Kluge[1], Ana Paula Preczenhak[1], Claudia Fabrino Machado Mattiuz[2]

1. Universidade de São Paulo – Ciências Biológicas – Piracicaba (SP), Brazil.
2. Universidade de São Paulo – Produção Vegetal – Piracicaba (SP), Brazil.

Received: Oct. 17, 2022 | **Accepted:** Mar. 9, 2023

Section Editor: Juliana Sanches

***Corresponding author:** cristiane.calaboni@gmail.com

How to cite: Calaboni, C., Kluge, R. A., Preczenhak, A. P. and Mattiuz, F. M. (2023). Postharvest conservation of lisianthus inflorescences with bioregulators. Bragantia, 82, e20220207. https://doi.org/10.1590/1678-4499.20220207

ABSTRACT: Cut flowers are known for their beauty and variety of colors and shapes. However, they quickly lose their commercial value after harvest due to the intensity of physiological processes that result in senescence. This work aimed to evaluate the effects of bioregulators on the postharvest longevity of lisianthus flowers (Eustoma grandiflorum cv. Flare Deep Rose) by applying a pulsing solution for 24 hours. The treatments consisted of 70 µM of 6-benzylaminopurine (BAP); 5 µM of gibberellic acid (GA3); 10 µM of abscisic acid (ABA); and deionized water as control. Turgidity, floral development, total and reducing sugar contents, respiration rate, colorimetry, anthocyanin contents, phenolic compound contents, and phenylalanine ammonia-lyase (PAL) enzyme activity were evaluated. BAP resulted in higher PAL enzyme activity and greater accumulation of anthocyanins when compared to the other treatments. The treatment GA3 resulted in the highest increase in respiration rate during storage, causing a larger number of inflorescences with wilting and senescence symptoms, reducing postharvest quality. The treatment ABA resulted in greater turgidity and floral opening, delayed senescence, and maintained respiration rate due to the greater total sugar contents on the fourth and 12th days. The application of ABA contributes to the maintenance of inflorescence quality for lisianthus at postharvest, but it reduces anthocyanin contents, providing petals with lighter colors.

Key words: *Eustoma grandiflorum*, cut flower, abscisic acid, gibberellic acid, 6-benzylaminopurine.

INTRODUCTION

Lisianthus (*Eustoma grandiflorum*) is an important cut flower widely used in floral arrangements due to the beauty of its inflorescences and variety of colors (Chuang and Chang 2013). The inflorescences are large with long stems, which provides easy handling. However, flowers are highly perishability products due to the ephemeral nature of their tissues; physiological processes occur intensively and, thus, they lose their commercial value in a short period after harvest (Nowak and Rudnicki 1990).

The stem cutting triggers senescence processes that are irreversible in flowers accelerates water loss and loss of color and brightness of petals, which are the main causes of product depreciation (Dias 2016, Ma et al. 2018). Color loss is detrimental to the decorative quality of floral stems, resulting in reduced commercial value, and it is related to reductions in accumulation of pigments during senescence, such as anthocyanins and carotenoids (Mattiuz et al. 2010, Park et al. 2021).

Senescence is a process highly controlled by bioregulators, as well as the other stages of plant development; thus, these compounds can be effective when used as preservative solutions at post-harvest of flowers (Favero et al. 2020). The bioregulator 6-benzylaminopurine (BAP) can induce resistance to biotic and abiotic stress because it can reduce free radical activity in the plant (Kamran et al. 2021). Thus, good results have been obtained in pulsing treatments with BAP delaying senescence in chrysanthemum, and lisianthus (Kaur and Singh 2015, Musembi et al. 2013).

Gibberellic acid (GA3) has shown good results for postharvest maintenance of several inflorescences, such as anthurium and lisianthus. It can maintain the stability of cell membranes and, thus, reduce senescence of cut flowers (Emongor 2004, Musembi et al. 2013, Simões et al. 2018). Postharvest application of abscisic acid (ABA) can induce tolerance to water stress in petunia and pelargonium, and reduce leaf chlorosis in lily (*Lilium oriental* cv. Sorbonne), which depreciates the stems (Runkle et al. 2007, Geng et al. 2015).

Carbohydrate balance is an important factor in flower postharvest; its effects on quality maintenance and inhibition of senescence symptoms are attributed to the importance of carbohydrates as substrate for respiration, structural function, and maintenance of osmotic pressure (Halevy and Mayak 1979, Gupta and Dubey 2018). Reductions in carbohydrate levels are connected to the consumption of plant energy reserves; the application of postharvest treatments can alter these levels and assist in maintaining the quality of inflorescences after cutting (Cavasini et al. 2018).

Considering this information and the need for using technologies that reduce the impact of senescence symptoms, which depreciate inflorescences and, consequently, generate large postharvest losses and economic losses to growers, the use of preservative solutions is an effective alternative for maintaining the quality and reducing the effects of senescence (Nowak and Rudnicki 1990, Gupta and Dubey 2018).

The application of bioregulators favors anthocyanin biosynthesis and, as a result, preserves the color of petals for a longer storage period after harvest. Thus, this work aimed to evaluate changes, caused by bioregulators (BAP, GA3, and ABA), in petals of open flowers of lisianthus (*Eustoma grandiflorum* cv. Flare Deep Rose).

METHODS

Stems of lisianthus (*Eustoma grandiflorum* cv. Flare Deep Rose) were harvested in an area of the Monalisa Flores company, in Paranapanema, SP, Brazil (23º23'19"S, 48º43'22"W, and 610 m of altitude). The established harvest point was two or three open flowers per inflorescence; the flowers were harvested, packed, and transported, under refrigeration, to the Postharvest Physiology and Biochemistry Laboratory of the Universidade de São Paulo (Piracicaba, SP, Brazil). In the laboratory, the stems were standardized at 50 cm in length, and leaves were removed from the first 15 cm of the lower part of the stem. Then, they were randomized for the application of treatments.

The bioregulators BAP (CAS 1214-39-7), GA_3 (CAS 77-06-5), and ABA (CAS 21293-29-8) were obtained from the Sigma-Aldrich® company.

The treatments consisted of bioregulators pulsing solutions for 24 hours at the rates 0 µM (deionized water; control), 70 µM BAP, 5 µM GA3, and 10 µM ABA, which were determined through preliminary tests. After applying the treatments, the stems were kept in acrylic pots containing 500 mL of a solution of deionized water and sodium dichloroisocyanurate at the concentration of 0.25%. The pots were stored under air temperature of 20°C and relative air humidity of 80 ± 2%.

A completely randomized experimental design was used, in a factorial arrangement, with four bioregulators pulsing solutions and four days of evaluation. Four replications of three stems were used, and evaluations were carried out every four days (zero, four, eight, and 12 days). Petal samples were collected, frozen in liquid nitrogen, freeze-dried, ground, and stored at -80°C for further biochemical analysis. Freeze-drying of the samples was carried out using a device operating at temperature of -55 ± 5°C and pressure of 1×10^{-2} to 3×10^{-2} mbar (0.001 to 0.003 kPa) (Liotop L108, São Paulo, Brazil), and then milled in an analytical mill (A11 Basic; IKA® Werke GmbH & Co. KG, Staufen, Germany).

According to visual analysis, buds that were at suitable developmental stage for full opening and flowers that were open at the time of harvest were quantified. Grades were assigned as follows:

- Bud;
- Early anthesis;
- Full opening;
- Senescent flowers.

Using the same structures, the following grades were assigned to determine the turgidity:

- Wilted;
- Slightly wilted;
- Turgid.

Total and reducing sugar contents–25 mg of petals, 25 mg of leaves, and 250 mg of stem–were used for sugar extraction. Each sample was immersed in 5 mL of 80% ethanol, stirred, and placed in a water bath at 60°C for 30 minutes. The samples were then centrifuged at 6,440 × g (Jouan BR4i, Paris, France) for 5 minutes; the supernatant was collected, transferred to 15-mL tubes, and then 5-mL ethanol was added, and the procedure was repeated. Then, 80% ethanol was added to complete the volume to a final extract of 10 mL.

Total sugars were quantified according to the phenol-sulfuric methodology of Dubois et al. (1956), and reducing sugars were quantified according to the Somogyi-Nelson methodology (Nelson 1944). Readings were carried out in a spectrophotometer (Biochrom Libra S22 UV-Vis, Cambrige, United Kingdom) at 490 nm for total sugars and 540 nm for reducing sugars. The results were expressed as mg glucose per g of dry matter.

Respiration rate in inflorescences was monitored by gas chromatography. The CO_2 evolution was determined by placing three stems in acrylic vases containing 500 mL of water and maintaining them in an airtight container for 1 hour. Gas samples of 0.5 mL were collected from each container and injected into a gas chromatograph device (Thermofinigan, model Trace GC Ultra) equipped with a flame ionization detector (FID) and a stainless-steel column of 1/8" and 4-m long, prepared with Porapak N 50/80. The temperatures of the column, injector, and detector were 110, 140, and 200°C, respectively; hydrogen was used as carrier gas at a flow rate of 25 mL min^{-1}. Respiration rate was expressed as mL of CO_2 per kg of fresh matter per hour (mL $CO_2 \cdot kg^{-1} \cdot h^{-1}$).

About colorimetry, readings were carried out using a Minolta CR-400 colorimeter in six flowers per replication. Five readings were carried out on the inner side of each flower. The results were calculated based on the parameters L, a*, and b* and expressed as luminosity (light-to-dark range) and chromaticity (color intensity). Chromaticity was calculated according to the Eq. 1 (Gonnet 1998):

$$C = (a^{*2} + b^{*2})^{0.5} \quad (1)$$

Regarding total anthocyanin contents, the method described by Lee and Francis (1972), with modifications, was used. Anthocyanin was extracted from a dry sample of 100 mg using 1% methanol-acidified HCl, and the extract was kept at 4°C for 12 hours. Absorbance readings were carried out at 510 nm (Biochrom Libra S22 UV-Vis, Cambrige, United Kingdom). The results were expressed in mg per g of dry matter.

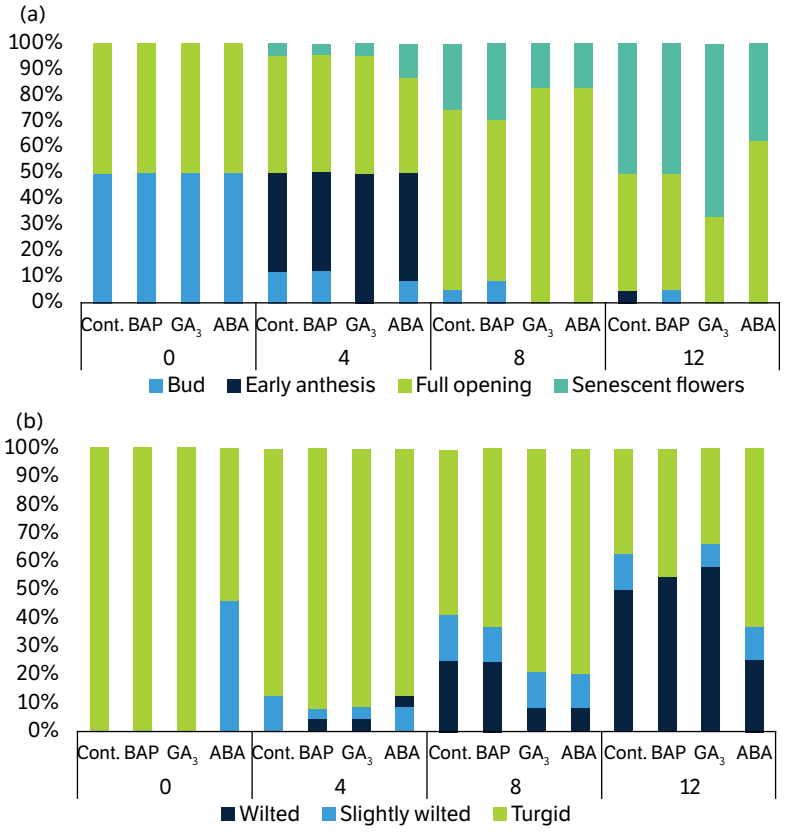
Phenylalanine ammonia-lyase (PAL) enzyme activity (EC 4.3.1.5) was evaluated using the methodology proposed by Peixoto et al. (1999), with modifications. PAL was extracted from a dry sample of 100 mg and homogenized in 10 mL of cooled sodium borate buffer (0.1 mol·L^{-1}, pH 8.8) containing polyvinylpyrrolidone 10 (50 g·L^{-1}) and β-mercaptoethanol (0.0002 mol·L^{-1}). The solution was centrifuged at 6,440 × g for 15 min at 4°C (Jouan BR4i, Paris, France), and the supernatant was collected, resulting in an enzyme extract. The whole process was conducted at 17°C. The reaction was carried out at room temperature (25 ± 1°C); 1 mL of the enzyme extract was incubated at 37°C for 1 hour in 1 mL sodium borate buffer (0.2 mol·L^{-1}, pH 8.8) and 1 mL L-phenylalanine (0.1 mol·L^{-1}). The reactions were stopped by the addition of 0.1 mL of hydrochloric acid (6 mol·L^{-1}), and the amount of t-cinnamic acid was estimated in triplicate by measuring the absorbance at 290 nm. The data were expressed as μkatals per g of dry matter.

Total phenolic compounds were quantified using the Folin-Ciocalteu reagent, according to Randhir et al. (2002), with adaptations: 10 mL of 80% methanol was added to 0.1 g of freeze-dried lyophilized sample; the samples were stored at room temperature, protected from light, for 2 hours. The extracts were then separated, and the supernatant was collected. The reaction was carried out by adding 0.2 mL of the sample extract, 1.5 mL of distilled water, 0.1 mL of Follin-Ciocauteu reagent, and 0.2 mL of 20% calcium carbonate. It was incubated for 2 hours in the dark. Spectrophotometric readings were then carried out at 765 nm, and the results were expressed as mg of gallic acid equivalents (standard) per g of petal dry matter (EAG g·kg·L^{-1}).

Longevity was determined when the treatments presented 50% of wilted inflorescences and/or senescence symptoms such as wilting, peduncle curvature, abscission, and petal darkening. Statistical analyses were performed using the program R 3.2.5. The results were subjected to analysis of variance and expressed as mean ± standard error. The normality and homogeneity of the data were verified by the Shapiro-Wilk and Bartlett's tests, respectively. Statistical differences between means were calculated by the Tukey's test ($p \leq 0.05$).

RESULTS AND DISCUSSION

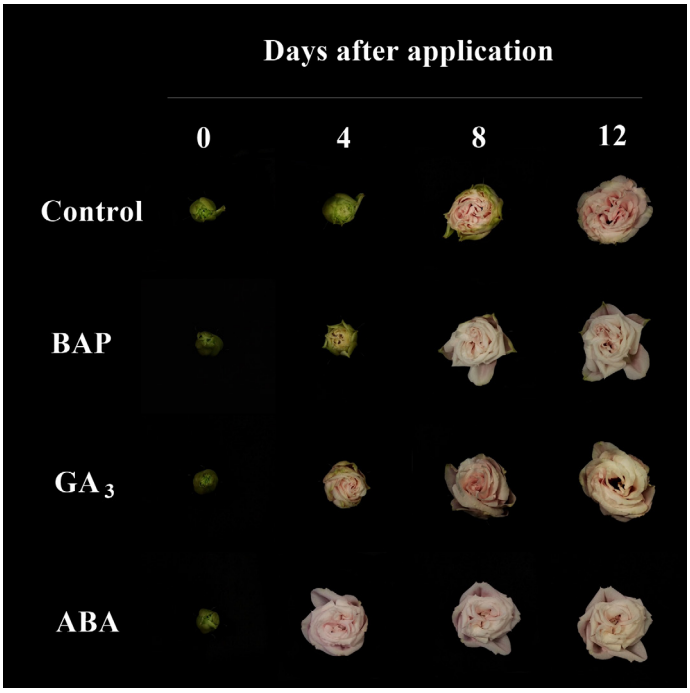
The initial floral development was advanced by the application of GA_3 and ABA bioregulators. Despite presenting the highest percentage of senescent flowers on the fourth day of storage (10%), the treatment ABA resulted in less visual quality loss after 12 days, maintaining 63% of the flowers open. Contrastingly, the application of GA_3 and BAP maintained the visual quality only during the first eight days of storage, and BAP did not differ from the control. GA_3 resulted in accelerated anthesis at four days and in a higher percentage of senescent flowers after 12 days of storage when compared to the control and the other bioregulators, resulting in discarding of stems on the 12th day (Figs. 1a, 1b, and 2).



Cont: Control; BAP: 6-benzylaminopurine; GA_3: gibberellic acid; ABA: abscisic acid.

Figure 1. (a) Development of inflorescences of lisianthus (*Eustoma grandiflorum* cv. Flare Deep Rose); (b) percentage of lisianthus inflorescences with wilting symptoms. Inflorescences treated with bioregulators and stored for 12 days at 20°C and 80% relative air humidity.

The maintenance of turgidity using ABA may be connected to its ability to regulate the water balance by controlling stomatal opening, which reduces transpiration and, consequently, the intense water loss that occurs after harvest (Halevy et al. 1974, Shimizu-Yumoto et al. 2010).



BAP: 6-benzylaminopurine; GA_3: gibberellic acid; ABA: abscisic acid.

Figure 2. Monitoring of opening of lisianthus flowers (*Eustoma grandiflorum* cv. Flare Deep Rose) treated with bioregulators and stored for 12 days at 20°C and 80% relative air humidity.

In addition to present a larger number of senescent flowers, the treatment ABA resulted in a greater percentage of flowers with pronounced wilting symptoms, more than the control on the fourth day of storage. However, this trend did not continue; at the end of 12 days of storage, ABA resulted in the lowest wilting percentages. The application of GA3 markedly accelerated the loss of visual quality of flowers in the last four days of storage; in this period, there was a 45% increase in wilted flowers when compared to day 8, which is equivalent to that one found for the control. BAP presented no efficacy in controlling the flower wilting, showing no differences from the control (Figs. 1a and 1b).

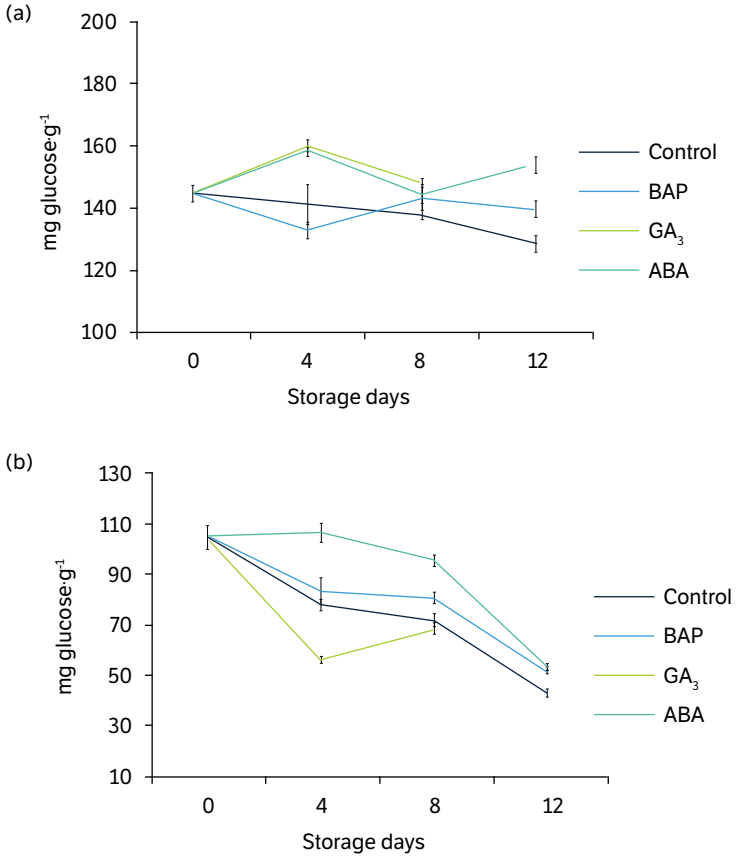
Sugar contents are involved with flower turgescence. Reducing osmotic potential through carbohydrate accumulation can increase the influx of water into flowers, maintaining the pressure potential, which is connected to cell expansion and floral opening. Moreover, flowers are the main carbohydrate drain during the inflorescence development (Waithaka et al. 2001). The inflorescences treated with ABA (310.2 $mg \cdot g^{-1}$) and GA3 (322.2 mg.g-1) showed the highest contents of total sugars at four days of storage. The treatment ABA showed higher total sugar contents (305.9 $mg \cdot g^{-1}$) than the other treatments at 12 days of storage. The treatment BAP did not show significant difference from the control (Fig. 3).

Unlike the control, which showed a constant reduction in total sugar contents, the application of ABA and GA_3 resulted in the highest contents in petals throughout the storage period. However, the visual quality result was different between these two treatments. The stems with GA_3 did not maintain the commercial quality by the 12th day of storage. In contrast to other bioregulators, the application of BAP resulted in reductions in total sugars over the first four days of storage and did not differ from the control on any day of analysis (Fig. 3a).

The metabolism of sugars was affected by the application of bioregulators, with decreases in reducing sugar contents in all treatments during storage. However, the treatment ABA had the highest contents in the first eight days of evaluation. GA_3 showed the highest decrease in reducing sugar contents on the fourth day, but, on the eighth day of evaluation, it was the only treatment that showed increases in these contents throughout the storage period. BAP had the same result as the control, with less effect on reducing sugars when compared to the other bioregulators (Fig. 3b).

ABA is a bioregulator connected to the plant physiological response to stress, conferring adaptation to the environment. It induces the formation of reactive oxygen species that act as abiotic stress signaling molecules, which is important for the adjustment of metabolism, causing stomatal closure. Reactive oxygen species cause cell damages. However, these damages are reduced when cells have high energy reserves (Mittler and Blumwald 2015, Choudhury et al. 2017).

The total and reducing sugars in stems treated with ABA in the first days of storage (Fig. 3) may have reduced damages caused by senescence. Soluble sugars can have antioxidant action, protecting the cell against oxidative stress (Keunen et al. 2013, Peshev et al. 2013). In addition, ABA can increase translocation of endogenous carbohydrates to flowers and buds, making the osmotic potential more negative and intensifying water uptake, which aids in maintaining turgidity and opening of buds (Emongor 2004, Shimizu-Yumoto et al. 2010).



BAP: 6-benzylaminopurine; GA_3: gibberellic acid; ABA: abscisic acid; *vertical bars represent the standard error of the mean (n = 4).

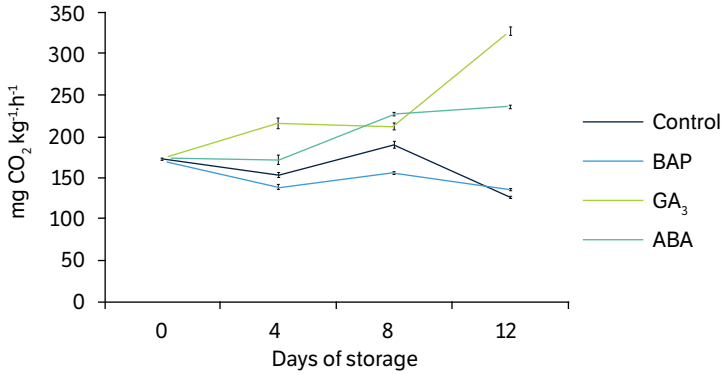
Figure 3. (a) Total sugars and (b) reducing sugars in petals of lisianthus flowers (*Eustoma grandiflorum* cv. Flare Deep Rose) treated with bioregulators and stored for 12 days at 20°C and 80% relative air humidity.

On the fourth day of storage, the treatment ABA showed an advance in the opening of the floral buds, with an increase in total sugar contents (Fig. 3a). Floral opening is a result of the development and expansion of petal cells, which are processes regulated by the presence of soluble carbohydrates in the tissues (Pun and Ichimura 2003, In et al. 2006).

The increase in sugars caused by application of ABA in cut flowers may reflect the ability of the bioregulator to interfere with the metabolism of these compounds present in petals and leaves (Geng et al. 2015). Studies have reported the ability of bioregulators to affect the activity of the enzyme invertase, which is responsible for the hydrolysis of sucrose into hexoses (Trouverie et al. 2004, Pan et al. 2006). Sucrose is translocated from leaves through the phloem to other tissues, in which it is hydrolyzed by the invertase, and ABA can increase the activity of this enzyme (Tauzin and Giardina 2014).

The application of GA3 also affected sugar contents in lisianthus petals. There were an increase in total soluble sugar contents and a decrease in reducing sugars on the fourth day of storage (Fig. 3). These results may be connected to the increase in respiration of plants in this treatment throughout the 12 days of storage (Fig. 3). Thus, unlike ABA, GA3 probably did not accumulate enough sugars to supply the respiration rate, consuming sugar reserves of petals and inducing senescence.

Accelerated metabolism may be involved in the anticipation of floral bud opening in the treatment GA_3, as the transport of soluble sugars from leaves to petals was probably promoted by exogenous GA_3, inducing carbohydrate loading in the flowers (Aloni et al. 1986, Murcia et al. 2018). Gibberellins can increase hydrolysis of starch, fructans, and sucrose into glucose and fructose, reducing the osmotic potential of tissues, facilitating the influx of water to upper parts of the stem (Emongor 2004). Thus, floral opening occurred as a response to the maintenance of turgidity caused by GA_3 until the eighth day of storage (Figs. 1b, 2, and 4).



BAP: 6-benzylaminopurine; GA_3: gibberellic acid; ABA: abscisic acid; *vertical bars represent the standard error of the mean (n = 4).

Figure 4. Respiration rate of inflorescences of lisianthus (*Eustoma grandiflorum* cv. Flare Deep Rose) treated with bioregulators and stored for 12 days at 20°C and 80% relative air humidity*.

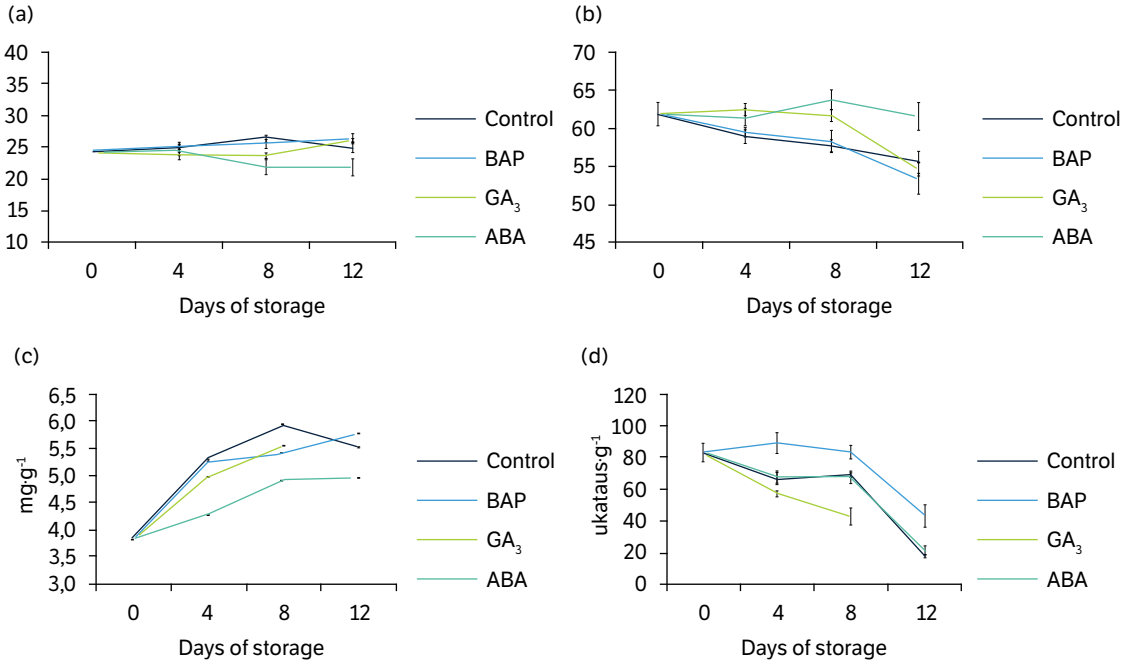
The effect of sugars on the senescence of different plant organs has not yet been fully elucidated, but it is known that carbohydrates can delay senescence when they are present at high levels in inflorescences, and that low levels of these sugars in petals and leaves can induce senescence (Wojciechowska et al. 2018).

The application of bioregulators showed different effects on the color chromaticity and luminosity of lisianthus petals (Figs. 5a and 5b). The treatment BAP showed a significant difference in anthocyanin contents only on the 12th day of storage (Fig. 5c).

The BAP treatment showed higher PAL activity, although the activity of this enzyme decreased over time in all treatments (Fig. 5d). Exogenous BAP can induce the expression of genes linked to the anthocyanin biosynthesis pathway, causing accumulation of this pigment (Das et al. 2012). However, there was no significant difference in luminosity and chromaticity between BAP and the control (Figs. 5a and 5b).

There was less synthesis of anthocyanins in the treatment ABA (Fig. 5c), which affected color parameters, causing an increase in luminosity and reduction in chromaticity (Figs. 5a and 5b). The higher the luminosity, the lighter the analyzed surface. Chromaticity is a parameter related to color purity. Thus, the higher the chromaticity, the more intense the color of petals, which can be connected to anthocyanin contents present in the lisianthus petals (Uddin et al. 2001).

In this context, the reduction in anthocyanin contents resulted in a lighter hue in petals in inflorescences treated with ABA. This result was probably due to the deviation of the biosynthesis route, with formation of other types of flavonoids instead of anthocyanins. Flavonoids are among the main non-enzymatic antioxidants produced during oxidative stress (Baskar et al. 2018), whereas ABA induces formation of reactive species for signaling and plant adaptation to this stress (Choudhury et al. 2017).



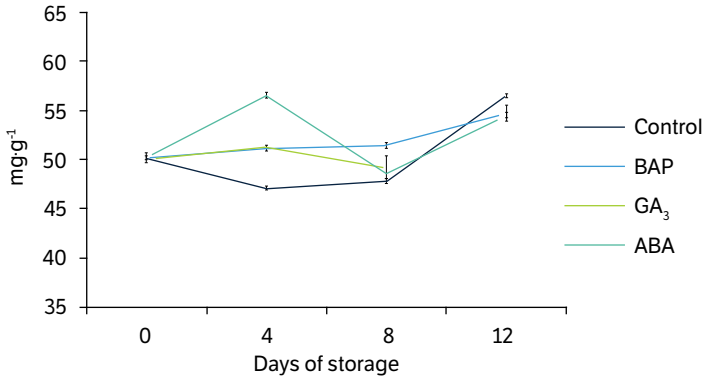
BAP: 6-benzylaminopurine; GA_3: gibberellic acid; ABA: abscisic acid; *vertical bars represent the standard error of the mean (n = 4).

Figure 5. (a) Chromaticity; (b) luminosity; (c) anthocyanin contents; and (d) phenylalanine ammonia-lyase activity in petals of lisianthus (*Eustoma grandiflorum* cv. Flare Deep Rose) treated with bioregulators and stored for 12 days at 20°C and 80% relative air humidity*.

These results explain the reduction in anthocyanin accumulation and the greater formation of total phenolics in the first days of storage in the treatment ABA (Fig. 6), with no effect on PAL enzyme activity (Fig. 5d). In addition, plants exposed to oxidative stress increase endogenous ABA and may form proanthocyanidins at the expense of anthocyanins, resulting in flowers with lighter petals. Proanthocyanidins are involved in induction of tolerance and expression of stress response genes (Luo et al. 2016, Li et al. 2019).

The postharvest application of GA_3 in lisianthus increased anthocyanin contents until the fourth day and probably accelerated the development of inflorescences, leading to senescence (Figs. 1 and 5c). The same result was found for chrysanthemums cultivars (Flippo, Recital, and Bronze Repim); the application of increasing rates of GA_3 in a preservative solution accelerated the senescence of leaves and flowers, reducing the vase life of inflorescences (Brackmann et al. 2005).

Although PAL showed the lowest activity in the treatment GA_3, there was an increase in anthocyanin contents in the first days of storage (Fig. 5c and 5d). However, total phenolic compounds did not change (Fig. 6), indicating that the treatment induced formation of anthocyanins to the detriment of other phenolics in the first days of storage. Gibberellins act indirectly in the expression of genes linked to the anthocyanin biosynthesis pathway; however, the expression of these genes begins to decrease after anthesis (Weiss et al. 1995).



BAP: 6-benzylaminopurine; GA_3: gibberellic acid; ABA: abscisic acid; *vertical bars represent the standard error of the mean (n = 4).

Figure 6. Total phenolic contents of lisianthus (*Eustoma grandiflorum* cv. Flare Deep Rose) treated with bioregulators and stored for 12 days at 20°C and 80% relative air humidity*.

CONCLUSION

The application of ABA during postharvest of lisianthus contributes to maintenance of inflorescence quality. However, it reduces anthocyanin contents, resulting in petals with lighter colors. The application of GA_3 accelerates the senescence, reducing postharvest quality of inflorescences.

AUTHORS' CONTRIBUTION

Conceptualization: Calaboni, C., Mattiuz, C. M. F. and Kluge, R. A.; **Methodology:** Calaboni, C., Mattiuz, C. M. F. and Preczenhac, A. P.; **Writing – Original Draft:** Calaboni, C.; **Writing – Review and Editing:** Mattiuz, C. M. F., Kluge, R. A. and Preczenhac, A. P.; **Supervision:** Mattiuz, C. M. F. and Kluge, R. A.

DATA AVAILABILITY STATEMENT

All dataset were generated and analyzed in the current study.

FUNDING

Fundação de Amparo à Pesquisa do Estado de São Paulo
https://doi.org/10.13039/501100001807
Grant no. 2019/01156-0

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
https://doi.org/10.13039/501100002322
Finance Code 001.

ACKNOWLEDGMENTS

We acknowledge Cooperflora cooperative members for providing the plant material for this work.

REFERENCES

Aloni, B., Pashkar, T. and Libel, R. (1986). The possible involvement of gibberellins and calcium in tipburn of Chinese cabbage: study of intact plants and detached leaves. Plant Growth Regulation, 4, 3-11. https://doi.org/10.1007/BF00025344

Baskar, V., Venkatesh, R. and Ramalingam, S. (2018). Flavonoids (antioxidants systems) in higher plants and their response to stresses. In D. K. Gupta, J. M. Palma and F. J. Corpas (Eds.). Antioxidants and antioxidant enzymes in higher plants (p. 253-268). Cham: Springer.

Brackmann, A., Bellé, R. A., Freitas, S. T. and Mello, A. M. (2005). Qualidade pós-colheita de crisântemos (*Dedrantema grandiflora*) mantidos em soluções de ácido giberélico. Ciência Rural, 35, 1451-1455. https://doi.org/10.1590/S0103-84782005000600037

Cavasini, R., Laschi, D., Tavares, A. R. and Lima, G. P. P. (2018). Carbohydrate reserves on postharvest of lisianthus cut Flowers. Ornamental Horticulture, 24, 12-18. https://doi.org/10.14295/oh.v24i1.1108

Choudhury, F. K., Rivero, R. M., Blumwald, E. and Mittler, R. (2017). Reactive oxygen species, abiotic stress and stress combination. The Plant Journal, 90, 856-867. https://doi.org/10.1111/tpj.13299

Chuang, Y. C. and Chang, Y. C. A. (2013). The role of soluble sugars in vase life of *Eustoma grandiflorum*. HortScience, 48, 222-226. http://doi.org/10.21273/HORTSCI.48.2.222

Das, P. K., Shin, D. H., Choi, S. B., Yoo, S. D., Choi, G. and Park, Y. I. (2012). Cytokinins enhance sugar-induced anthocyanin biosynthesis in *Arabdopsis*. Molecules and Cell, 34, 93-101. https://doi.org/10.1007/s10059-012-0114-2

Dias, M. D. (2016). Quality maintenance Tropical Plants. Ornamental Horticulture, 22, 256-258. https://doi.org/10.14295/oh.v22i3.961

Dubois, M., Gilles, K. A., Hamilton, J. K., Bebers, P. A. and Smith, F. (1956). Colorimetric methods for determination of sugars and related substances. Analytical Chemistry, 28, 350-356. https://doi.org/10.1021/ac60111a017

Emongor, V. E. (2004). Effects of gibberelic acid on postharvest quality and vaselife life of gerbera cut flower (*Gerbera jamesonii*). Journal of Agronomy, 3, 191-195. https://doi.org/10.3923/ja.2004.191.195

Favero, B. T., Lütken, H., Dole, J. M. and Lima, G. P. P. (2020). *Anthurium andraeanum* senescence in response to 6-benzyllaminopurine: vase life and biochemical aspects. Postharvest Biology and Technology, 161, 111084. https://doi.org/10.1016/j.postharvbio.2019.111084

Geng, X. M., Li, M., Lu, L., Okubo, H. and Ozaki, Y. (2015). ABA improved postharvest quality of cut Lilium 'Sorbonne' harvested in late period. Journal of the Faculty of Agriculture, 60, 81-86. https://doi.org/10.5109/1526317

Gonnet, J. F. (1998). Color effects of co-pigmentation of anthocyanins revisited. A colorimetric definition using CIELAB scale. Food Chemistry, 63, 409-415. https://doi.org/10.1016/S0308-8146(98)00053-3

Gupta, J. and Dubey, R. K. (2018). Factors affecting post-harvest life of flowers crop. International Journal of Current Microbiology and Applied Sciences, 7, 548-557. https://doi.org/10.20546/ijcmas.2018.701.065

Halevy, A. H. and Mayak, S. (1979). Senescence and postharvest physiology of cut Flowers - part 1. Horticultural Reviews, 1, 204-236. https://doi.org/10.1002/9781118060742.ch5

Halevy, A. H., Mayak, S., Tirosh, T., Spiegelstein, H. and Kofranek, A. M. (1974). Opposing effects of abscisic acid on senescence of rose flowers. Plant and Cell Physiology, 15, 813-821. https://doi.org/10.1093/oxfordjournals.pcp.a075070

In, B.-C., Sato, K., Ito, K., Inamoto, K., Doi, M. and Mori, G. (2006). Influences of preharvest relative humidity on yield, vase life and transpiration of cut roses. Environmental Control in Biology, 44, 257-263. https://doi.org/10.2525/ecb.44.257

Kamran, M., Danish, M., Saleen, M. H., Malik, Z., Parveen, A., Abbasi, G. H., Jamil, M., Ali, S., Afzal, S., Riaz, M., Riazwan, M., Ali, M. and Zhou, Y. (2021). Application of abscisic acid and 6-benzylaminopurine modulated morphophysiological and antioxidative defense responses of tomato (*Solanum lycopersicum* L.) by minimizing cobalt uptake. Chemosphere, 263, 128169. https://doi.org/10.1016/j.chemosphere.2020.128169

Kaur, P. and Singh, K. (2015). Influence of growth regulators on physiology and senescence of cut stems of chrysanthemum (*Chrysantemum morifolium* Ramat.) var. Thai Ching Queen. International Journal of Allied Practice, Research and Review, 2, 31-41.

Keunen, E., Peshev, D., Vangronsveld, J., Van der End, W. and Aiypers, A. (2013). Plant sugars are crucial players in the oxidative challenge during abiotic stress; extending the traditional concept. Plant, Cell & Environment, 36, 1242-1255. https://doi.org/10.1111/pce.12061

Lee, D. H. and Francis, F. J. (1972). Standardization of pigment analyses in cranberries. HortiScience, 83-84. https://doi.org/10.21273/HORTSCI.7.1.83

Li, Z., Chen, W., Zhang, C., Du, C., Shao, G., Cui, Y. and Luo, P. (2019). RcMYBPA2 of *Rosa chinensis* functions in proanthocyanidin biosynthesis and enhances abiotic stress tolerance in transgenic tobacco. Plant Cell, Tissue and Organ Culture, 441-454. https://doi.org/10.1007/s11240-019-01580-z

Luo, P., Shen, Y., Jen, S., Huang, S., Cheng, X., Xang, Z., Li, P., Zhao, J., Bao, M. and Ning, G. (2016). Overexpression of Rosa rugosa anthocyanidin redutase enhances tobacco tolerance to abiotic stress through increased ROS scavenging and modulation of ABA signaling. Plant Science, 245, 35-49. https://doi.org/10.1016/j.plantsci.2016.01.007

Ma, N., Ma, C., Liu, Y., Sharid, M. O., Wang, C. and Gao, J. (2018). Petal senescence: a hormone view. Journal of Experimental Botany, 69, 719-732. https://doi.org/10.1093/jxb/ery009

Mattiuz, C. F. M., Rodrigues, T. J. D., Mattiuz, B. H., Pietro, J. D. and Martins, R. N. (2010). Armazenamento refrigerado de inflorescências cortadas de *Oncidium varicosum* 'Samurai'. Ciência Rural, 40, 2288-2293. https://doi.org/10.1590/S0103-84782010001100007

Mittler, R. and Blumwald, E. (2015). The roles of ROS and ABA in systemic acquired acclimation. The Plant Cell, 27, 64-70. https://doi.org/10.1105/tpc.114.133090

Murcia, G., Pontin, M., and Piccoli, P. (2018). Role of ABA and Gibberellin A3 on gene expression. Pattern of sugar transports and invertases in *Vitis vinífera* cv. Malbec during berry ripening. Plant Growth Regulation, 84, 275-283. https://doi.org/10.1007/s10725-017-0338-4

Musembi, N. N., Hutchinson, M. J. and Waitaka, K. (2013). The effects of 6-benzylaminopurine and gibberellic acid on postharvest physiology of lisianthus (*Eustoma grandiflorum*) flowers: I. Novel synergism improves water balance and vase life. Acta Horticulturae, 1077, 47-56. https://doi.org/10.17660/ActaHortic.2015.1077.4

Nelson, N. (1944). A photometric adaptation of Somogyi method for determination of glucose. Journal of Biologic Chemistry, 153, 375-380. https://doi.org/10.1016/S0021-9258(18)71980-7

Nowak, J. and Rudnicki, R. M. (1990). Postharvest handling and storage of cut flowers, florest greens and potted plants. Portland: Timber Press.

Pan, Q. H., Yu, X. C., Zhang, N., Zou, X., Peng, C. C., Wang, X. L., Zou, K. Q. and Zhang, D. P. (2006). Activity, but not expression, of soluble and cell wall-bound acid invertase is induced by abscisic acid in developing apple fruit. Journal of Integrative Plant Biology, 48, 536-549. https://doi.org/10.1111/j.1744-7909.2006.00251.x

Park, C. H., Yeo, H. J., Kim, Y. J., Nguyen, B. V., Park, Y. E., Sathasivam, R., Kim, J. K. and Park, S. V. (2021). Profiles of secondary metabolites (phenolic acids, carotenoids, anthocyanins, and galantamine) and primary metabolites (carbohydrates, amino acids, and organic acids) during flower development in *Lycoris radiata*. Biomolecules, 11, 248. https://doi.org/10.3390/biom11020248

Peixoto, P. H. P., Cambraia, J., Sant'Anna, R., Mosquim, P. R., Moreira, M. A. (1999). Aluminum effects on lipid peroxidation and on the activities of enzymes of oxidative metabolism in sorghum. Revista Brasileira de Fisiologia Vegetal, 11, 137-143.

Peshev, D., Vergawen, R., Moglia, A., Hideg, E., Van der Ende, W. (2023). Towards understanding vacuolar antioxidant mechanism: a role of fructans? Journal of Experimental Botany, 64, 1025-1038. https://doi.org/10.1093/jxb/ers377

Pun, U. K. and Ichimura, K. (2003). Role of sugars in senescence and biosynthesis of ethylene in cut flowers. Japan Agricultural Research Quaterly, 37, 219-224. https://doi.org/10.6090/jarq.37.219

Randhir, R., Shetty, P., Shetty, K. (2002). l-DOPA and total phenolic stimulation in dark germinated fava bean in response to peptide and phytochemical elicitors. Process Biochemistry, 37, 1247-1256. https://doi.org/10.1016/S0032-9592(02)00006-7

Runkle, E. S., Woolard, D., Campbell, C. A., Blanchard, M. G., Newton, L. A. (2007). Exogenous applications of abscisic acid improved the postharvest drought tolerance of several annual bedding plants. Acta Horticulturae, 755, 127-133.

Shimizu-Yumoto, H., Kondo, M., Sanoh, Y., Ohsumi, A. and Ichimura, K. (2010). Effect of abscisic acid on the distribution of exogenous carbon derived from sucrose applied to cut *Eustoma* flower. Journal of Horticultural Science & Biotechnology, 85, 83-87. https://doi.org/10.1080/14620316.2010.11512635

Simões, A. N., Diniz, N. D., Vieira, M. R. S., Ferreira-Lima, S. L., Silva, M. B., Minatel, I. O. and Lima, G. P. P. (2018). Impact of GA3 and spermine on postharvest quality of anthurium cut flowers (*Anthurium andaeanum*) cv. Arizona. Scientia Horticulturae, 241, 178-186. https://doi.org/10.1016/j.scienta.2018.06.095

Tauzin, A. S. and Giardina, T. (2014). Sucrose and invertases, a part of plant defense response to the biotic stresses. Frontiers in Plant Science, 5, 1-5. https://doi.org/10.3389/fpls.2014.00293

Trouverie, J., Chateau-Joubert, S., Thévenot, C., Jacquemot, M. P. and Prioul, J. L. (2004). Regulation of vacuolar invertase by abscisic acid or glucose in leaves and roots from maize plantlets. Planta, 219, 894-905. https://doi.org/10.1007/s00425-004-1289-3

Uddin, A. F. M. J., Hashimoto, F., Kaetani, M., Shimizu, K. and Sakata, Y. (2001). Analysis of light and sucrose potencies on petal coloration and pigmentation of lisianthus cultivars (in vitro). Scientia Horticulturae, v. 89, p. 75-84. https://doi.org/10.1016/S0304-4238(01)00224-2

Waithaka, K., Dodge, L. and Reid, M. (2001). Carbohydrate traffic during opening of gladiolus florets. Journal of Horticultural Science & Biotechnology, 76, 120-124. https://doi.org/10.1080/14620316.2001.11511337

Weiss, D., Van Der Luit, A., Knergt, E., Vermeer, E., Mol, J. N. M. and Kooter, J. M. (1995). Identification of endogenous gibberellins in petunias flowers. Plant Physiology, 107, 695-702. https://doi.org/10.1104/pp.107.3.695

Wojciechowska, N., Sobieszczuk-Nowicha, E. and Bagniewska-Zadworna, A. (2018). Plant organ senescence – regulation by manifold pathways. Plant Biology, 20, 167-181. https://doi.org/10.1111/plb.12672