

GA₄₊₇ PLUS BENZYLADENINE IN COMBINATION WITH SUCROSE IMPROVES POSTHARVEST LEAF AND INFLORESCENCE QUALITY IN *Lilium* ‘Alma Ata’

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ABSTRACT

The interaction between foliar treatment with 100 mg·dm⁻³ of both gibberellic acid 4+7 (GA₄₊₇) and benzyladenine (BA) and vase solution containing 3% sucrose was analysed in cut *Lilium* ‘Alma Ata’. GA₄₊₇+BA considerably delayed leaf senescence, suppressed anthocyanin accumulation in the leaves of plants held in the sucrose solution and improved the average longevity of the flowers and the vase life of the stems. Sucrose in the vase solution strongly reduced the abscission of leaves and contributed to the enlargement of the top flower. The number of significant interactions between the treatments indicated that the investigated factors acted dependently mainly on flower quality, while their action on leaf quality was mostly independent. Results show that combined treatment with growth regulators and sucrose may considerably increase postharvest quality of cut *Lilium* ‘Alma Ata’.

Key words: *Lilium*, senescence, postharvest, gibberellic acid 4+7, benzyladenine, sucrose

INTRODUCTION

Oriental lilies are distinguished from other groups of lilies by their large flowers and leaves, but also by higher production costs and subsequently a higher final price for the customer. In commercial cultivation, Oriental lilies are predominantly grown to be sold as cut flowers. However, soon after the onset of flowering, leaves on harvested stems are subjected to

the process of senescence. In addition, further development of upper floral buds can be disrupted.

Senescence of leaves on cut lily stems develops gradually, starting from lower leaves, and results in the loss of its green colour which changes to light green, yellow and finally dark brown. This is aesthetically undesirable, therefore, if those leaves do

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not fall off, it is common practice to remove them manually. It has been shown that leaf yellowing in cut lilies can be prevented by the application of gibberellins and cytokinins. For instance, Franco and Han [1997] found that the application of gibberellic acid (GA₃) and benzyladenine (BA) delayed the onset of yellowing in excised leaves of *Lilium longiflorum* Thunb. In *Lilium* 'Stargazer', leaf senescence, induced by keeping the stems in darkness at low temperature, can be delayed by the foliar application of GA₄₊₇ [Ranwala and Miller 2000]. In *Lilium* 'Pollyanna', the application of GA₃ and combination of GA₃ and BA delayed senescence-related structural changes in the leaf mesophyll tissue [Tabuchi et al. 2005]. Rabiza-Świder et al. [2015b] found that GA₃ effectively postponed chlorophyll loss in Oriental lily 'Rialto'. Due to well-established positive effects of gibberellins and cytokinins in delaying leaf senescence in lilies, the application of Promalin® (Valent BioSciences Corporation), in which GA₄₊₇ and BA are present in equal mass concentration, is frequently recommended [Han 1996; Whitman et al. 2001; Celikel et al. 2002; van Doorn and Han 2011].

Cut lilies also often suffer from bud abortion, reduction in size of flower buds, and incomplete flowering or failure to flower. This could be caused primarily by keeping the plants in conditions in which leaves cannot produce carbohydrates needed for the completion of bud development and subsequent anthesis such as cold storage without light [van Doorn and Han 2011]. Carbohydrate shortage is more pronounced in upper flower buds which are, because of acropetal development of the inflorescence, at the moment of harvest less developed [van der Meulen-Muisers et al. 2001]. This may pose a serious problem for florists, as lily stems bearing four to seven flower buds are the most frequent on the market. Thus, it is commonly recommended to add sucrose to the holding solution. The beneficial effects of sugar on cut lilies are already well known: flowers have a longer lifespan, the size and number of successfully opened buds are increased, the number of aborted buds is lower and flowers containing anthocyanins have a more intense colour [Han 2003; Barbosa et al. 2006; Burchi et al. 2010; Arrom and Munné-Bosch 2012a; Rabiza-Świder et al. 2015a]. On the other

side, sucrose application often exhibits negative effects on leaf quality, enhancing yellowing or even causing blackening [Han 2003; Rabiza-Świder et al. 2012; Prisa et al. 2013]. For this reason, florists rarely add sucrose to holding solutions or, if they do so, they have to remove leaves which lowers the market value of the lilies.

Here we examined the effect of GA₄₊₇+BA in combination with sucrose on the postharvest quality of cut *Lilium* 'Alma Ata'. We have characterised some senescence-related changes in leaves, the blackening of leaves caused by the accumulation of anthocyanins, as well as the postharvest development and longevity of flowers. Although the effects of separate or combined application of growth regulators and sucrose are already well established [van Doorn and Han 2011 and references therein], this is, to our knowledge, the first analysis of possible interaction between the treatments.

MATERIAL AND METHODS

Plant material and treatments. The plants of Oriental hybrid lily 'Alma Ata' were grown from February until May in a commercial glasshouse (natural light conditions, minimum and maximum temperatures during cultivation were 12°C and 30°C, respectively). The substrate (pH 6.2) was composed of approximately equal vol/vol ratio of perlite and sphagnum peat moss. Plants were fertigated from third week after planting until three weeks before harvest, three times with 1 g·dm⁻³ of 16–8–24 (N-P₂O₅-K₂O) water-soluble fertilizer with micronutrients (Idron, Agrofyll) and two times with 0.3 g·dm⁻³ of urea (46% N).

Sixty stems, each bearing five flower buds, were harvested at a mature bud stage. Half of the randomly chosen stems were sprayed with deionized water and the other half with a solution of 100 mg·dm⁻³ of benzyladenine (BA) + 100 mg·dm⁻³ of gibberellic acid 4+7 (GA₄₊₇) in deionized water. Both sprays contained 0.07% vol/vol of a surfactant Tensiofill (Agrofyll Srl). After plant surfaces were air-dried, the plants were further divided into two additional groups: one was kept in the vases with deionized water and the other in the vases with a 3% sucrose solution (in deionized water). Both solutions contained 200 mg·dm⁻³ of 8-hydroxyquino-

line hemisulfate hemihydrate (8-HQS) as an anti-microorganism agent. The vase solution was periodically refilled and completely replaced on the 9th day (middle) of the experiment. On the same day, the stems were recut underwater. During postharvest evaluations (18 days), vases with cut lily stems were placed in a room at $21 \pm 0.5^\circ\text{C}$, 60%–70% relative air humidity, for a 12 h photoperiod. Light was provided by fluorescent lamps ($8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the top of the stems).

Leaf senescence and anthocyanin content. The leaves were analysed in the following positions: upper level – five leaves below the lowermost flower, and lower level – five leaves below the upper level leaves. If not specified, the leaf material was randomly selected from both levels.

Chlorophyll and carotenoid contents were determined spectrophotometrically (Lambda EZ 201, PerkinElmer Inc.) after being extracted from leaf discs (10 mm in diameter) in 100% methanol, according to Wellburn [1994]. Chlorophyll content was also measured in intact leaves using a chlorophyll meter (CCM-200 plus, Opti-sciences Inc.) which calculates the chlorophyll content index (CCI) based on absorbance measurements at 653 nm and 931 nm. Measurements were made separately on the upper and lower leaf level.

Leaf fresh weight (FW) was measured to the nearest milligram, immediately after its detachment from the plant. Dry weight (DW) was determined after the samples were oven-dried for 24 h at 107°C . Leaf water content was calculated as $\text{FW} - \text{DW}$. Ash content was established after combusting for 4 h at 550°C . Organic matter content was calculated as $\text{DW} - \text{ash content}$.

Ammonium nitrogen was determined using the Kjeldahl method with a copper catalyst and steam distillation into boric acid, according to Thiex et al. [2002].

Ion leakage measurements were, with slight modifications, performed according to Slavikova et al. [2008]. Briefly, six leaf discs (10 mm in diameter) were cut from the middle part of leaf blades and carefully washed with deionised water to remove surface-adhered electrolytes. Afterwards, the discs were transferred to the polypropylene tubes filled with distilled water (22°C) and periodically shaken. After 24 h, initial electrical conductivity was measured (Exstik Ec400, Extech instruments). The tubes were

then boiled for 10 min to kill the cells and final measurements were conducted after the solution had cooled down to room temperature. Ion leakage was expressed as the ratio of initial/total conductivity.

For anthocyanin quantification, leaf discs (10 mm in diameter) were chopped with a razor blade into strips and transferred into vials filled with 5 ml of cold extraction solution prepared from 3M HCl : H₂O : MeOH (1 : 3 : 16 by vol., respectively). Extraction was carried out in the dark at 4°C , with periodical shaking. After 24 h, the absorbance was measured with a UV-VIS spectrophotometer (Lambda EZ 201, PerkinElmer Inc.). The anthocyanin level was calculated as $A_{530\text{nm}} - 0.24A_{653\text{nm}}$ [Gould et al. 2000].

Longevity and postharvest development of the flowers. The flowers were visually checked every day and times of anthesis and deterioration were recorded. Flowers were classified as deteriorated when the tepals started to wilt. At that moment, the whole flower was removed. The vase life of the stem represented the period from the moment of opening of the first flower until at least two flowers remained on the stem with no signs of wilting. The rate of increase in the size of the flower bud from the beginning of the experiment until the moment of anthesis was determined by recording the length of the fourth and the fifth (the upper) flower bud daily.

Statistical analysis. The experiment was arranged as a Randomized Complete Block Design with five replicates. Each plot consisted of three vases holding one plant.

To analyse the data, a two-way ANOVA was performed using SAS 9.1.3 software (SAS Institute Inc.). The mean values were separated using Fisher's LSD test. We used alpha levels of 0.05 and 0.01 for all statistical tests.

RESULTS

Leaf quality. On day 0, when the lily stems were cut, all leaves appeared uniformly dark green. During the course of the experiment, the majority of plants foliar-treated with water, held both in water and in sucrose solution, gradually lost their dark green colour. Leaf colour started to shift to light green on day 6, then turned yellow from day 10 and became dark

brown from day 13. All changes in colour always progressed from the lowermost leaves upward. At the same time, the colour of the leaves in plants foliar-treated with growth regulators just slightly changed and this was visible only in the lowermost leaves, which acquired somewhat of a lighter green nuance.

Non-destructive measurements of chlorophyll content showed that the level of chlorophyll in lower leaves gradually diminished in all treatments. However, chlorophyll loss was considerably delayed in plants treated with growth regulators (both in those held in water and in sucrose solution). On day 9 (middle of the experiment) and day 18 (end of the experiment), relative chlorophyll content in the lower leaves of plants foliar-treated with growth regulators were about 2- and 5-fold higher, respectively, than in plants treated with water (tab. 1). In the upper leaves, relative chlorophyll content on day 9 did not differ significantly between water treated and growth regulator treated plants. However, on day 18, the upper leaves of plants treated with growth regulators contained 4.5-fold higher chlorophyll level than plants treated with water (tab. 1). Spectrophotometric analysis at the end of the experiment showed that carote-

noid content in leaves of growth-regulator treated plants was also significantly higher than in plants treated with water (tab. 1). Vase content neither influenced the level of photosynthetic pigments nor interacted with the foliar treatment.

At the end of the experiment, leaf fresh weight and water content were significantly higher in plants foliar-treated with growth regulators (about 1.4-fold) than in plants foliar-treated with water. Leaf dry weight and content of organic matter were influenced by both foliar treatment and vase content, though the latter exerted a stronger effect: leaf dry weight and organic matter content were both about 1.3-fold higher in leaves of plants kept in sucrose as compared to those kept in water (tab. 2). In addition, the Kjeldahl nitrogen content in the plants treated with growth regulators was significantly higher (about 1.6-fold) than in water-treated plants (tab. 2). Conductivity measurements showed that both factors independently influenced membrane leakage. The lowest leakage was measured in the plants treated with growth regulators and kept in sucrose and was 2.3-fold lower than in plants foliar-treated with water and kept in vases with water (tab. 2).

Table 1. The effects of foliar treatment and vase content on photosynthetic pigment content in leaves of cut *Lilium* 'Alma Ata' stems

Specification	CCI – lower leaves			CCI – upper leaves			Total Chl ($\mu\text{g}\cdot\text{cm}^{-2}$)	Total Car ($\mu\text{g}\cdot\text{cm}^{-2}$)
	day 1	day 9	day 18	day 1	day 9	day 18	day 18	day 18
Foliar treatment	NS	**	**	NS	NS	**	**	**
Vase content	NS	NS	NS	NS	NS	NS	NS	NS
Foliar treatment \times vase content	NS	NS	NS	NS	NS	NS	NS	NS
Foliar: water	55.15	23.99 b	8.50 b	72.58	58.17	14.23 b	13.98 b	3.36 b
Foliar: GA ₄₊₇ + BA	57.54	48.81 a	42.09 a	71.27	68.90	63.91 a	57.38 a	7.73 a
Vase: water	58.40	33.66	25.30	73.62	58.18	40.15	38.13	5.77
Vase: sucrose	54.29	39.15	25.29	70.23	68.88	37.98	33.23	5.32
Water \rightarrow water	57.53	22.75	10.05 b	73.23	52.73	12.85	16.52	4.03
GA ₄₊₇ + BA \rightarrow water	59.27	44.56	40.55 a	74.00	63.63	67.45	59.73	7.51
Water \rightarrow sucrose	52.77	25.23	6.95 b	71.93	63.60	15.60	11.43	2.69
GA ₄₊₇ + BA \rightarrow sucrose	55.80	53.06	43.63 a	68.53	74.16	60.37	55.02	7.94

NS – not significant, * significant at $P < 0.05$, ** significant at $P < 0.01$. CCI – chlorophyll content index, Total Chl – total chlorophyll content, Total Car – total carotenoid content. Values are means of 15 replicate stems. Means with different letters within columns are significantly different at $P < 0.05$ using LSD test

Table 2. The effects of foliar treatment and vase content on fresh weight (Fw), dry weight (Dw), contents of water, organic matter, ash and Kjeldahl nitrogen, and conductivity in leaves of cut *Lilium* 'Alma Ata' stems on day 18

Specification	Fw (mg·cm ⁻²)	Dw (mg·cm ⁻²)	Water (mg·cm ⁻²)	Organic matter (mg·cm ⁻²)	Ash (mg·cm ⁻²)	Kjeldahl nitrogen (mg·cm ⁻²)	Conductivity (initial/total)
Foliar treatment	**	**	**	**	*	**	**
Vase content	NS	**	NS	**	NS	NS	*
Foliar treatment × vase content	NS	NS	NS	NS	NS	NS	NS
Foliar: water	28.69 b	5.82 b	22.87 b	4.94 b	0.885 b	0.089 b	0.819 a
Foliar: GA ₄₊₇ + BA	39.52 a	6.91 a	32.60 a	5.94 a	0.975 a	0.142 a	0.513 b
Vase: water	34.00	5.64 b	28.35	4.72 b	0.927	0.114	0.756 a
Vase: sucrose	34.20	7.09 a	27.12	6.15 a	0.932	0.118	0.577 b
Water → water	27.90	5.35	22.54	4.47	0.889	0.087	0.861
GA ₄₊₇ + BA → water	40.10	5.93	34.16	4.97	0.965	0.140	0.650
Water → sucrose	29.47	6.28	23.19	5.40	0.880	0.092	0.777
GA ₄₊₇ + BA → sucrose	38.93	7.89	31.04	6.90	0.984	0.143	0.376

NS – not significant, * significant at $P < 0.05$, ** significant at $P < 0.01$. Values are means of 5 replicate stems. Means with different letters within columns are significantly different at $P < 0.05$ using LSD test

Although the main effect of the vase content on leaf photosynthetic pigments was not significant (tab. 1), plants kept in the vases with sucrose solution had significantly less abscised leaves than those in the vases with water (0.47 vs. 5.10; fig. 1A). In general, leaf abscission started from day 5, but the majority of leaves fell off within the last five days of the experiment. The process of abscission progressed from the lowermost leaves upward and was generally observed in leaves that had lost its dark green colour. The shedding of visually acceptable leaves, i.e., those that were still dark green, was also sporadically noticed in all treatments. Although both examined factors had a significant influence on the number of visually unacceptable leaves, there was also interaction between them, which resulted in a lower number of visually unacceptable leaves only in the plants foliar-treated with growth regulators and kept in the vases with sucrose solution (fig. 1B).

A significant number of leaves and stems of plants that were kept in sucrose solution and were not foliar-treated with growth regulators acquired a dark purple nuance. Spectrophotometric analysis

of the leaves of these plants indicated a considerable increase in the content of anthocyanins compared to other treatments (fig. 2). A purple nuance started to show on day 16 and only in the green areas of leaves, i.e., it did not develop in leaves or parts of leaves that had lost its green colour. Purpling was visible on both sides of the leaves but was more pronounced along the middle area of the adaxial side of the leaf. Statistical analysis detected significant interaction between the foliar treatment and the vase solution.

Inflorescence quality. In all treatments, flower buds developed without difficulty which resulted in normal anthesis of all flowers on the stems. The effect of treatments on the enlargement of flower buds was monitored only in the fourth and the fifth bud, since, at the moment of harvest, lower buds were already well developed. Neither foliar treatment nor vase solution had a significant influence on the increase in the length of the fourth flower bud. However, the increase in the length of the fifth flower bud was 42% higher in the plants kept in vases with sucrose than in the plants held in water.

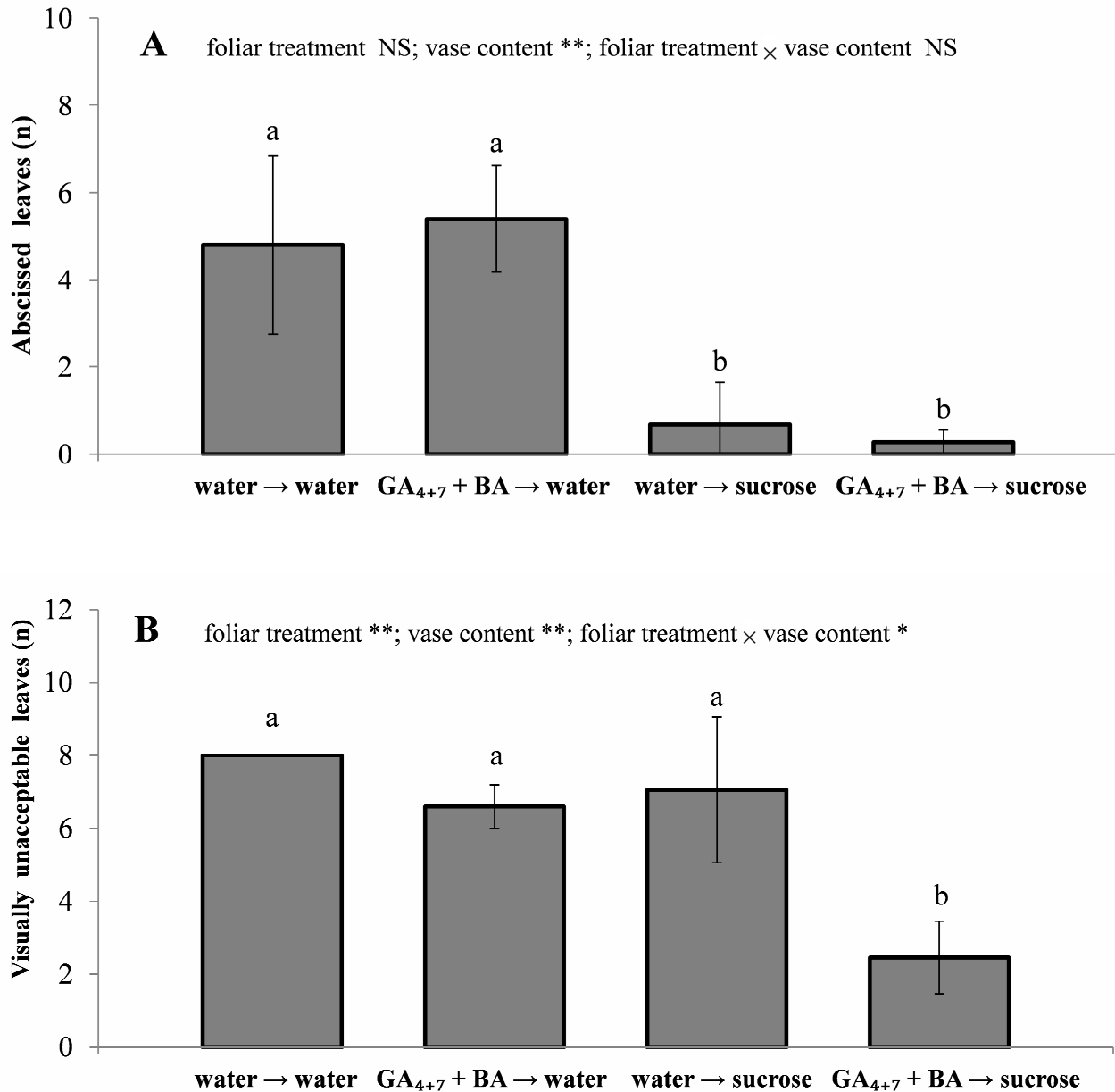


Fig. 1. Effects of foliar treatment and vase content on leaves of cut *Lilium* 'Alma Ata' stems. Harvested plants were sprayed with water or 100 mg·dm⁻³ each of GA₄₊₇ and BA. The plants were then held either in the vases with water or in the vases with 3% sucrose solution. A. The number of abscised leaves. B. The number of visually unacceptable leaves. Values are means of 15 replicate stems. Vertical bars denote standard deviation. Columns with different letters are significantly different at $P < 0.05$ using LSD test. NS – not significant, * significant at $P < 0.05$, ** significant at $P < 0.01$

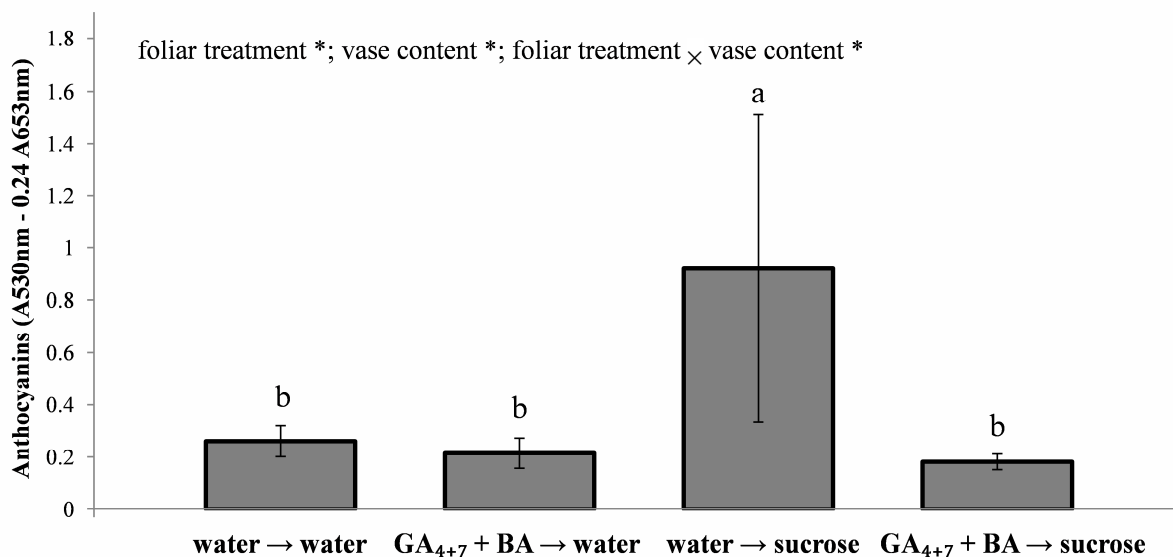


Fig. 2. Effects of foliar treatment and vase content on the anthocyanin level in leaves of cut *Lilium* 'Alma Ata' stems. Harvested plants were sprayed with water or 100 mg·dm⁻³ each of GA₄₊₇ and BA. The plants were then held either in the vases with water or in the vases with 3% sucrose solution. Values are means of 15 replicate stems. Vertical bars denote standard deviation. Columns with different letters are significantly different at $P < 0.05$ using LSD test. NS – not significant, * significant at $P < 0.05$, ** significant at $P < 0.01$

Table 3. The effects of foliar treatment and vase content on flower longevity (in days) of cut *Lilium* 'Alma Ata'

Specification	1st flower	2nd flower	3rd flower	4th flower	5th flower	Average: 1st – 5th
Foliar treatment	**	**	**	**	**	**
Vase content	NS	NS	NS	**	NS	NS
Foliar treatment × vase content	**	*	**	*	NS	**
Foliar: water	8.37 b	8.53 b	8.33 b	7.70 b	6.37 b	7.86 b
Foliar: GA ₄₊₇ + BA	10.13 a	10.20 a	9.90 a	9.36 a	7.61 a	9.45 a
Vase: water	9.27	9.59	8.86	7.99 b	6.62	8.49
Vase: sucrose	9.23	9.13	9.37	9.06 a	7.33	8.83
Water → water	7.80 c	8.46 c	7.66 c	6.73 b	5.73	7.28 c
GA ₄₊₇ + BA → water	10.73 a	10.73 a	10.06 a	9.26 a	7.57	9.69 a
Water → sucrose	8.93 b	8.60 c	9.00 b	8.66 a	7.00	8.44 b
GA ₄₊₇ + BA → sucrose	9.53 b	9.66 b	9.73 ab	9.46 a	7.66	9.21 a

NS – not significant, * significant at $P < 0.05$, ** significant at $P < 0.01$. Values are means of 15 replicate stems. Means with different letters within columns are significantly different at $P < 0.05$ using LSD test

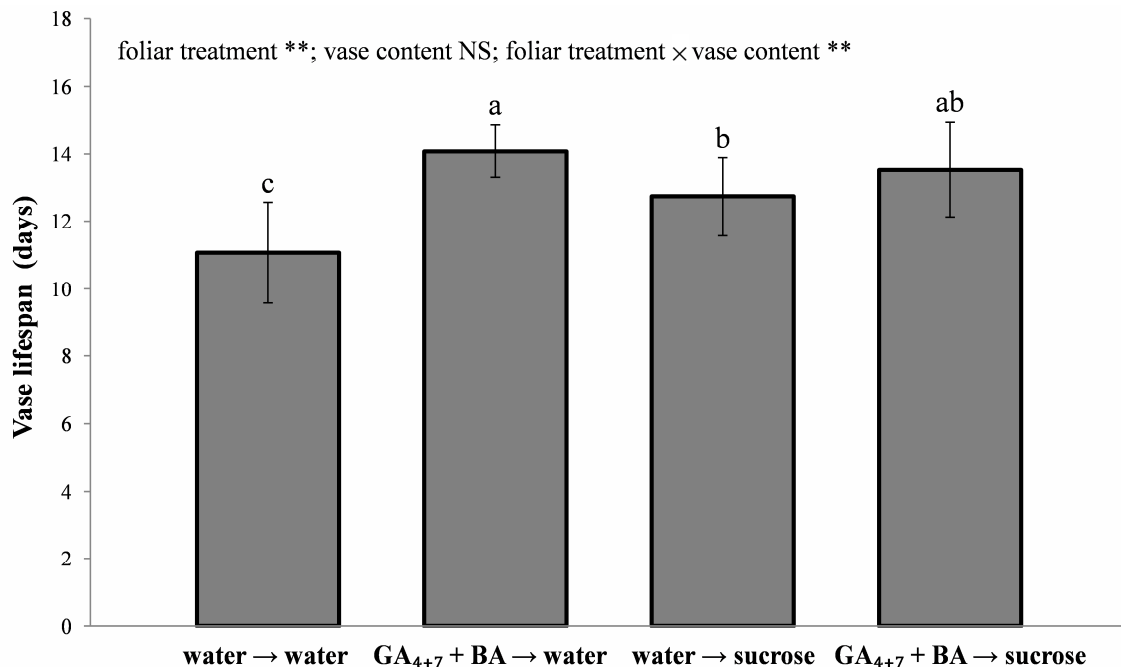


Fig. 3. Effects of foliar treatment and vase content on the vase life of cut *Lilium* 'Alma Ata' stems. Harvested plants were sprayed with water or 100 mg·dm⁻³ each of GA₄₊₇ and BA. The plants were then held either in the vases with water or in the vases with 3% sucrose solution. Values are means of 15 replicate stems. Vertical bars denote standard deviation. Columns with different letters are significantly different at $P < 0.05$ using LSD test. NS – not significant, * significant at $P < 0.05$, ** significant at $P < 0.01$

The period from the anthesis of the first to the fifth flower bud on the stem did not show statistically significant differences between treatments, taking on average 7.04 days. The fourth flower had a significantly lower longevity than any of the lowest three, while the fifth (i.e., top) flower had the shortest lifespan (tab. 3).

The main effect of the foliar treatment was significant for two important indicators of inflorescence quality (tab. 3 and fig. 3): in the stems foliar-treated with growth regulators, the average longevity of the flowers and the vase life of the stems were 1.6 and 1.9 days longer, respectively, than in the stems treated with water. However, there was a significant interaction between the foliar treatment and the vase content indicating that sucrose solution also had a positive effect on the longevity of flowers and

stems, but only in the plants that were not foliar-treated with growth regulators (tab. 3). The average longevity of the flowers and vase life of the stems were the highest in plants treated with growth regulators and kept in the vases with water, being 2.4 and 3 days longer, respectively, than in the plants treated with water and kept in the vases with water (tab. 3 and fig. 3).

DISCUSSION

A major postproduction problem in cut Oriental lily 'Alma Ata' is leaf senescence, which starts on lower leaves and progresses upwards. Leaf senescence is generally characterized by diverse metabolic and structural changes, such as the degradation of thylakoid membranes, destruction of chlorophylls

and proteins, withdrawal of nitrogen, phosphorus and other nutrients from leaves toward other plant parts, and disintegration of cell membranes [Srivastava 2002; Lim et al. 2007]. In our study, the treatment of leaves on cut lily stems with the combination of GA₄₊₇ and BA considerably delayed the senescence of leaves, as indicated by, among others, significantly higher contents of photosynthetic pigments, organic matter, nitrogen and ash, and also by lowered ion leakage as compared to the leaves treated with water. Foliar application of growth regulators thus significantly improved postharvest leaf quality in the tested cultivar. The application of formulations containing gibberellins and cytokinins has been shown to alleviate postproduction leaf yellowing in a number of hybrid lily varieties [van Doorn and Han 2011 and references therein]. Studies performed on Oriental and Easter lilies showed that products containing only GA₄₊₇ (e.g., ProVide, Abbott Laboratories) are as effective as those containing both GA₄₊₇ and BA (such as Promalin®), indicating that GA₄₊₇ has a more important role than BA in preventing leaf chlorosis [Han 1997; Ranwala and Miller 1998]. The growth regulators effectively prevented leaf yellowing when applied through vase solution [Leonard and Nell 2004; Rabiza-Świder et al. 2015b] as well as by spraying the leaves [Han 1997]. Han [1997] found that application of GA₄₊₇ and BA prevented foliar chlorosis only in the treated leaves, indicating that the growth regulators were not mobilized in the plants.

In contrary to the strong effect of growth regulators on delaying leaf senescence, sucrose in the vase solution led only to a higher content of organic and dry matter in leaves, which could mostly be due to the uptake of sucrose from the vase solution. The vase solution did not influence chlorophyll content. In potted lily 'Stargazer', light during cold storage delayed leaf chlorosis [Ranwala and Miller 1998, 2000], while in cut 'Stargazer' the addition of sugar in vase solution led to the earlier yellowing of leaves compared to the solution without sugar [Han 2003]. Although sucrose had apparently no effect on leaf senescence in lily 'Alma Ata', it strongly reduced leaf abscission. This indicates that postproduction abscission of leaves in cut lily 'Alma Ata' could be related to the depletion of carbohydrates. Ranwala

and Miller [1998] found that providing light during the cold storage period significantly suppressed the abscission of leaves in Oriental lily 'Stargazer'.

Considering leaf senescence, the only significant interaction between the vase solution and the foliar treatment was evident with respect to the number of visually unacceptable leaves which was the lowest in the growth regulator treated plants kept in the vases with sucrose. This was apparently due to the fact that the treatment with growth regulators significantly improved leaf colour, while the sucrose supply postponed the abscission of leaves.

The darkening of leaves in cut Oriental lilies, referred to as blackening, so far has been briefly reported in two studies in which this phenomenon was linked with sucrose application. We have also observed the darkening of leaves in cut lily 'Alma Ata' as well as in some other Oriental and LA-hybrid lily varieties (data not published) when they were held in a solution containing sugars and were not previously foliar-treated with the growth regulators. In Oriental lily 'Stargazer' this process started out as the blackening of a partial area of the leaf and eventually led to the blackening of the entire leaf, indicating a phytotoxic reaction to excess levels of sugars [Han 2003]. Similarly, Rabiza-Świder et al. [2012] proposed that leaf blackening in Oriental lily 'Helvetia', caused by the presence of sucrose in holding solution, was probably due to an excessive sugar accumulation in leaves and their desiccation. The spectrophotometric analyses that we performed in lily 'Alma Ata' indicated that leaf colour change was the result of anthocyanin accumulation, which gave the leaves a dark purple coloration. The stimulating effect of sugars on anthocyanin biosynthesis has already been reported in different plant species [Teng et al. 2005; Loreti et al. 2008; Murakami et al. 2008]. Teng et al. [2005] found sucrose to be the most effective sugar in stimulating anthocyanin accumulation in *Arabidopsis* seedlings. According to Zhang et al. [2013], carbohydrate accumulation, caused by callose-blocked translocation of photosynthates from source to sink tissues, may be the proximate trigger of anthocyanin biosynthesis in leaves of *Begonia cucullata* var. *hookeri* in the autumn. In addition, results of the study conducted by Murakami et al. [2008] indicated

that stem girdling increased foliar sugar concentrations and enhanced anthocyanin production during autumn in the leaves of *Acer saccharum*. A shift in leaf colour from green to dark purple in Oriental lilies could therefore be the sign of inadequate strength or even nonexistence of the sink that could draw out a surplus of sugar from the leaves. In our experiment, a purple hue started to show near the end of the experiment when the flowers had started to wilt, so sink strength was reduced while sucrose from the vase solution was constantly imported into the leaves. Our results indicate that foliar application of GA₄₊₇+BA suppressed anthocyanin accumulation in leaves of plants held in the sucrose solution. This is in accordance with Loreti et al. [2008], who found that gibberellins counteracted the sucrose induction of anthocyanin biosynthesis in Arabidopsis leaves.

In *Lilium* 'Alma Ata', foliar treatment with GA₄₊₇+BA extended the average lifespan of the flowers by 1.6 days. This is in accordance with previous studies which showed that flower senescence in *Lilium* could be delayed by the commercial formulation of GA₄₊₇+BA (Promalin[®]) [Ranwala and Miller 1998; Celikel et al. 2002] or by gibberellins alone [Ranwala and Miller 2002]. Exogenous gibberellic acid (GA₃) has been shown to delay petal senescence by acting antagonistically to ABA and ethylene [Saks and van Staden 1993; Hunter et al. 2004a, 2004b; Lü et al. 2014]. Cytokinins have been found to delay flower senescence in a number of ornamental species [Reid and Chen 2007]. Analysis of endogenous hormone contents in different floral tissues of *Lilium* 'Courier' revealed that cytokinin levels mostly increased in tepals before anthesis and decreased later during senescence [Arrom and Munné-Bosch 2012b].

It is well established that the addition of sucrose to vase solution may prolong the lifespan of lily flowers [Nowak and Mynett 1985; Lee and Suh 1996; Barbosa et al. 2006; Asil 2008; Rabiza-Świder et al. 2015a]. The positive effect of sucrose on flower longevity has usually been attributed to an increase in available energy for respiration and improvement in water relations. Besides, sugars may also have other effects, such as reduction of ethylene sensitivity in ethylene-sensitive flowers [van Doorn and Woltering 2008]. Arrom and Munné-Bosch [2012a] found that,

in cut lily flowers, the addition of sucrose to vase solution did not alter water content in floral organs, but delayed senescence by altering the hormonal balance in various floral tissues, among other factors. In outer tepals of the lily, sucrose treatment resulted in a considerable decrease in ABA content. It is thought that in ethylene-insensitive flowers, such as lilies, ABA has an important role in hormonal regulation of flower senescence, promoting the process [Tripathi and Tuteja 2007; Kumar et al. 2014; Cubría-Radio et al. 2017]. Thus, the positive effect of sucrose on the longevity of lily flowers could be, at least partially, the result of a decrease in ABA content in tepals. In our study, sucrose also improved the longevity of the flowers, but only in plants that were not foliar-treated with growth regulators. This suggests that sucrose did not have an additional effect on the lifespan of flowers in the presence of sufficient levels of senescence-delaying growth regulators.

Treatments did not significantly affect the increase of the fourth flower bud in *Lilium* 'Alma Ata'; however, exogenous sucrose led to an increase in the length of the fifth flower bud. These results indicate that, at the moment of harvest, the fourth flower bud was already well developed and possessed enough carbohydrates for the completion of its development. However, the fifth (i.e., the upper) flower bud was, at the moment of harvest, apparently undersized and thus benefited from sucrose uptake.

CONCLUSIONS

The number of significant interactions between the foliar treatment and the vase solution indicated that the investigated factors acted dependently mainly on flower quality, while their action on leaf quality was mostly independent. Foliar application of combination of GA₄₊₇+BA improved flower longevity and leaf colour, while sucrose in the vase solution contributed to the enlargement of the top flower and also suppressed leaf abscission. Our study also indicated that foliar application of GA₄₊₇+BA suppressed the accumulation of anthocyanins in plants held in sucrose solution. The combined treatment with growth regulators and sucrose may therefore considerably increase postharvest quality of cut *Lilium* 'Alma Ata'.

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