

BENEFICIAL EFFECT OF CARBOHYDRATE SOLUTIONS ON POSTHARVEST CHARACTERISTICS OF CUT ALSTROEMERIA

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Abstract. *Exogenous applications of trehalose and sucrose in vase solutions increased the vase life and some physiological characteristics of cut Alstroemeria cv. Mayfair. A continuous supply of trehalose limited fresh weight loss and increased total carbohydrate content in the leaves. 60 mM trehalose did not increase the anthocyanin level in petals. Results indicate that content of carbohydrate in petals increased continuously up to day 10 and was not significantly different among all treatments. In contrast, higher concentration of sucrose (60 mM) did not improve vase life, but significantly increased pigment content in leaves. The longevity of leaves was improved by both sucrose (3.7 day) and trehalose (4.7 day). Trehalose considerably delayed leaf yellowing in cut Alstroemeria flowers during vase life, apparently due to increased carbohydrate content in the leaves. Moreover, trehalose causes the preservation of the green colour, which is considered as a good parameter to evaluate the state of the leafy flowering stem.*

Key words: *alstroemeria, carbohydrate, leaf yellowing, pigments, trehalose*

INTRODUCTION

An exogenous supply of carbohydrates is usually beneficial in maintaining quality and longevity of cut flowers. Traditionally, among the different types of sugars, sucrose has been found to be the most commonly used sugar in prolonging vase life of cut flowers. Numerous studies have noted increased vase life when sucrose was used in vase solutions for cut Rosa (Borochoy et al. 1976, Liao et al. 2000, Ichimura et al. 2003). Sucrose treatment delayed the time to visible senescence of carnation (Hoeberichts et al. 2007). Sucrose in vase solution enhanced longevity of carnations (Verlinden & Garcia 2004). Studies conducted by Shahri et al. (2010) with ornamental flowers of family Ranunculaceae in different concentrations of

sucrose reveals enhanced vase life in cut spikes of *Aquilegia vulgaris* and *Consolida ajacis*. Bayogan et al. (2008) reported that treatment with sucrose increased postharvest life of Bird-of-Paradise. Similar results were also obtained with sweet pea (Ichimura et al. 1998), *Agapanthus praecox* (Burge et al. 2010) and *Bougainvillea glabra* (Moneruzzaman et al. 2010). In contrast, sucrose in the vase solution of *Lilium* 'Stargazer' did not lead to increased vase life (Han 2003). Trehalose is a non-reducing disaccharide that occurs in a large range of organisms, such as bacteria, fungi, nematodes and crustaceans. This sugar accumulates to adapt cells against dehydration, salinity, freezing and heat stress (Wiemken 1990, Crowe et al. 1998). As a vase solution component, trehalose was more effective than sucrose in preventing senescence of cut gladiolus spikes (Otsubo & Iwaya-Inoue 2000). It has been reported that addition of trehalose to vase solution, enhanced vase life of tulip flowers (Iwaya-Inoue & Takata 2001). It was suggested that trehalose-treated petals were able to retain water for a longer time, thereby delaying wilting and abscission. Yamada et al. (2003) demonstrated that supplying exogenous trehalose in vase solution tends to increase vase life of gladiolus petals. This may be due to decreasing nuclear fragmentation in gladiolus petals, indicating that it may exert suppressive effects on apoptotic cell death. Ranwala and Miller (2009) found that trehalose increased vase life in cut *Tulipa*, although not as much as sucrose, and phytotoxicity was observed in trehalose-treated stems, where progressive blackening occurred on distal leaf regions and progressed to basal regions. *Alstroemeria* is one of the more popular cut flowers but leaf yellowing is one of the first indicators of the deterioration of flowering *Alstroemeria* stems and its leaves are yellowed before petal abscission (Mutui et al. 2006). It has been demonstrated that the onset of yellowing is associated with chlorophyll breakdown (Jordi et al. 1995). The objectives of this study were to 1) compare the dynamics of carbohydrate pools during the postharvest phase in petals and leaves of cut *Alstroemeria* stems supplied with sucrose or trehalose in the vase solution, 2) develop *Alstroemeria* flower quality (color development, longevity and delay abscission), and 3) maintain the green colour of leaves until petals abscission.

MATERIALS AND METHODS

Plant materials

Flowers of *Alstroemeria* cv. Mayfair were obtained from a commercial grower (Ashianehsabz, Tehran, Iran) at commercial maturity (oldest buds about to open).

They were transported dry to the laboratory of Horticultural Sciences at University of Guilan; within 6 h of harvest. During transport stems were covered with a plastic film to minimize moisture loss (Chutichudet et al. 2011). Stems were cut to a length of 45 cm and put into vases containing solutions. Vases were then placed into a growth chamber under standard conditions (22 °C, 70% RH, 15 $\mu\text{mol s}^{-1}\text{m}^{-2}$ and 12 h day/night cycle) for postharvest evaluation of flowers. Petals and leaves were selected for analyses of carbohydrates and pigments content. Fresh weight was recorded, and tissues were immediately frozen in liquid nitrogen and stored at -80 °C until required.

Standard treatments

Cut flowers were placed individually in vases filled with 250 mL of deionized water (DI) or test solutions of sucrose (20, 40 and 60 mM) (Merck) and trehalose (20, 40 and 60 mM) (Merck).

Postharvest evaluation

Vase life

Cut flowers were observed each day for analysis of morphological study parameters, such as petal abscission and leaf yellowing. Vase life of *Alstroemeria* cut flowers was measured by determining the number of days from onset of the vase life tests to 50% petal fall or onset of leaf yellowing. Leaf yellowing was determined as the number of days when half of the leaves per stalk turned yellow (Mutui et al. 2006).

Water relations analyses

Weighing of vases with and without cut stems commenced on day 0 and continued daily (every 3 days) during the vase life period. Relative fresh weight (FW), Water uptake (WU), water loss (WL, transpiration) rates and water balance (WB) were calculated (He et al. 2006).

Pigments content

To determine anthocyanin content, samples were analyzed by pH-differential spectrometric method. Frozen petals were ground to a fine powder in liquid nitrogen and extracted with methanolic HCl at 4 °C for 24 h. The extracts were centrifuged at 10000 g at 4 °C for 15 min and the supernatant was used for spectrophotometric (PG Instruments Ltd-T80+UV/VIS) determination of anthocyanin content. The absorbance of the extracts were read at 520 and 700 nm (Giusti & Wrolstad 2000). For carotenoid and chlorophyll analysis, middle leaves were excised on day 3 and 10 during postharvest and used for the analysis. Frozen leaves were ground to a fine powder in liquid nitrogen and extracted with 5 ml pure methanol in the dark at room temperature for 24 h. Extracts were centrifuged at 5000 g at 20 °C for 5 min and the supernatant was used for spectrophotometric determination. The absorbance was read at 665, 652 and 470 nm. The

concentrations for chl a (c_a), chl b (c_b), and the sum of leaf carotenoids (c_{x+c}) were calculated with Lichtenthaler's formula (1987).

Total carbohydrate analysis

Soluble carbohydrates were determined by a phenol–sulfuric acid assay (Dubois et al. 1956). After freezing, the tissues were ground to a powder for carbohydrate extraction. The petals (0.1 g) were extracted with 5 ml HCL (2.5 N) and boiled at 100 °C in a water bath for 2 h. After cooling to room temperature, the extracts were centrifuged at 4500 g for 15 min at 20 °C to remove contaminants and the supernatant was removed. Briefly, 1 ml of sample was added to test tube with 500 μ L 5% phenol, then 2.5 ml concentrated sulfuric acid was added. The reaction of carbohydrate with phenol and sulfuric acid in aqueous solution gives a brown color and generates heat. The reaction mixture was allowed to cool to room temperature for 20-25 minutes, shaken, and the absorbance was measured at 490 nm (hexoses) and 480 nm (pentoses) in a spectrophotometer against a blank cell. The sugar concentration was obtained by referring to the standard graph. The assay for this standard glucose (Merck) graph was carried out by adding phenol and sulfuric acid to a standard glucose solution. Total carbohydrates were expressed in mg/0.1g leaf fresh weight.

Statistical analysis

The experiment was conducted in a completely randomized design. Statistical analysis was performed by SAS software (SAS Institute Inc. 2004). The data collected was the mean of values from three replicates. Data were analyzed by GLM and means were compared by Tukey test at a significance level of 0.01.

RESULTS

Vase life

The analysis of variance of sucrose and trehalose addition to vase water on *Alstroemeria* cv. Mayfair at 22 °C has been shown in Table 1. Trehalose influenced important factors of cut stem postharvest quality, e.g.: vase life of petals and leaves. All trehalose concentrations markedly extended cut stem vase life compared to the control (Table 1). The longest vase life (14 days) was observed in the case of 60 mM trehalose solution compared to other treatments. In the sucrose treated cut flowers, 60 mM of sucrose solution had no effect on vase life, but 40 mM sucrose significantly increased the vase life for *Alstroemeria* as compared to the control. There was no significant difference in vase life between 40 mM sucrose and 60 mM trehalose. The longevity of leaves was improved by both sucrose (3.7 day) and trehalose (4.7 day). All concentrations of trehalose delayed the

onset of 50% leaf yellowing in *Alstroemeria* (Table 1). As the concentration of trehalose increased, there was a parallel increase in the number of days to 50% leaf yellowing, but holding *Alstroemeria* cut flowering stems in high concentration of sucrose (60 mM) tended to increase leaf yellowing.

Water relations

The results indicated that trehalose solution promoted fresh weight in cut *Alstroemeria*. Maximum relative fresh weight was observed for flowers kept in 60 mM trehalose solution and significantly delayed senescence in cut flowers. Different concentrations of sucrose had no significant effect on relative fresh weight during the first days of the experiment (Table 1). Decline in water uptake followed a similar pattern to that of fresh weight, although the rate of this decline did not vary between all treatments (data not shown). There were no significant differences in water loss (WL, transpiration) rates and water balance (WB) of cut stem among all treatments.

Pigment content

The analysis of chlorophyll and anthocyanin contents during postharvest conditions confirmed that trehalose maintains pigments level in petals and leaves of *Alstroemeria*. Highest anthocyanin content was observed in the 40 mM trehalose solution, but higher concentration of trehalose did not increase anthocyanin level in petals (Table 2). Also, anthocyanin level was higher in 40 mM sucrose as compared to the control and other concentrations of sucrose. In our experiments, treatment of cut stems with trehalose was more effective in delaying decrease in chlorophyll content than sucrose treatments. The total chlorophyll content measured at day 3 of postharvest was similar in all treatment (both sucrose and trehalose), but on day 10 of vase life concentrations of chlorophyll a, b and total chlorophyll in leaves of cut stems treated with trehalose were significantly higher than in those of other treatments (Table 2). There was no significant change in the carotenoid content between treatments, but the carotenoid content was reduced by time (Table 2). Chlorophyll concentration in the leaf tissue of *Alstroemeria* was much higher when compared to carotenoid concentrations.

Total carbohydrate

The results presented significant differences among the treatments and within each organ. At the beginning of the experiment, the leaves of the cut stems had sugar concentrations similar to that in petals, however total

carbohydrate content in petals continuously increased up to the end of vase life (Table 3). The results of this study show that in comparison to the untreated control, trehalose and sucrose did not affect the total carbohydrate content in petals. In contrast, exogenous trehalose resulted in a substantial increase in the total carbohydrate content in leaves. Also, trehalose affected sugar content of leaves compared to petals and increases in carbohydrate content (hexose and pentose) compared to other treatments. Interestingly, yellowing of leaves was observed in lower leaves of cut stems of *Alstroemeria* treated with trehalose (20, 40 and 60 mM), whereas upper leaves remained green. In contrast, all the leaves on cut stems treated with sucrose exhibited yellowing at end of the vase life.

DISCUSSION

According to the data presented here, both sucrose and trehalose increased flower longevity of *Alstroemeria* (cv. Mayfair). The optimum concentration in our experiment, 60 mM trehalose, resulted in a 3.4 days delay in senescence. Trehalose yielded the best results because exogenous trehalose may act as a continuous supply of energy retaining the turgidity of petals. Iwaya-Inoue and Takata (2001) reported that 50 mmolL⁻¹ (1.7%) was the optimum trehalose concentration in vase solution for flower longevity of tulip. Ranwala and Miller (2009) mentioned that treatment with 60 mmolL⁻¹ trehalose did not further enhance flower longevity compared to 30 mmolL⁻¹ trehalose, but further increased leaf injury. Our results were similar to those observed in gladiolus spikes by Otsubo & Iwaya-Inoue (2000). They reported that treatment with 0.1 M trehalose prolonged vase life of cut gladiolus (cv. Fujinoyuki) spikes by 2 days. Trehalose has been shown to suppress not only water loss but also cell death in the petals (Yamada et al. 2003). Trehalose also preserves cell viability and decreased nuclear fragmentation (Otsubo & Iwaya-Inoue 2000; Yamada et al. 2003). Feeding flowers with different concentrations of sucrose does not improve their vase life. Vase life registered a decrease with the increase in sucrose concentration. The lack of effect by 60 mM sucrose treatment on the vase life of *Alstroemeria* can possibly be attributed to microbial infection. He et al. (2006) mentioned that low water uptake is often due to occlusions located mainly in the basal stem end. Sugars in the vase solution accelerate bacterial growth, which may lead to stomatal closure as a result of water deficit (van Doorn 1997).

Our results are in agreement with those reported by Shahri et al. (2010), who found that sucrose at 0.05 M and 0.2 M significantly enhanced vase

Table 1. Flower longevity and fresh weight of cut *Alstroemeria* stems treated with different sugar solutions*.

Treatment	Petal longevity (day)	Leaf yellowing (day)	Fresh weight (%)		
			2 day	5 day	8 day
Control (Water)	10.6 c	8.6 c	105.3 a	96.5 a	86.9 b
Sucrose					
20 mM	10.6 c	8.9 c	108.1 a	95.5 a	84.0 b
40 mM	13.3 ab	12.3 ab	107.7 a	97.1 a	87.2 b
60 mM	11 bc	9.6 bc	106.0 a	93.8 a	83.0 b
Trehalose					
20 mM	12.3 abc	11.6 abc	107.9 a	96.6 a	87.0 b
40 mM	13.3 ab	12.6 ab	107.5 a	95.8 a	88.0 ab
60 mM	14 a	13.3 a	116.8 a	108.1 a	103.9 a
HSD	2.5	3.1	7.4	14.9	16.3

*Data are means of three replicates. Means followed by the same letter within a column are not significantly different according to the Tukey test ($p=0.01$).

Table 2. Changes in the content of pigments during the postharvest phase in petals and leaves of cut *Alstroemeria* stems treated with different sugar solutions*.

Treatment	Anthocyanin (mg. L ⁻¹)		Total chlorophyll (µg. ml ⁻¹)		Total carotenoids (µg. ml ⁻¹)	
	3 day	10 day	3 day	10 day	3 day	10 day
Control (Water)	9.3 a	6.0 b	55.2 a	30.0 d	17.1 a	15.6 a
Sucrose						
20 mM	27.4 a	7.0 b	62.2 a	49.7 c	16.8 a	14.4 a
40 mM	24.5 a	15.3 ab	62.0 a	54.1 abc	16.6 a	15.2 a
60 mM	22.3 a	11.5 b	61.6 a	51.1 bc	16.4 a	13.6 a
Trehalose						
20 mM	26.2 a	16.7 ab	62.7 a	58.1 ab	16.8 a	15.0 a
40 mM	25.2 a	24.1 a	62.5 a	61.2 a	16.9 a	15.8 a
60 mM	26.2 a	5.7 b	62.1 a	61.1 a	16.6 a	14.3 a
HSD	2.9	11.6	17.2	12.0	1.58	5.82

*Data are means of three replicates. Means followed by the same letter within a column are not significantly different according to the Tukey test (p=0.01).

Table 3. Effects of exogenous trehalose and sucrose treatment on content of carbohydrates during the postharvest phase in petals and leaves of cut *Alstroemeria* stems*.

Treatment	Total carbohydrate petal (mg.g ⁻¹ FW)						Total carbohydrate leaf (mg.g ⁻¹ FW)					
	Hexose (490 nm)		Pentose (480 nm)		Hexose (490 nm)		Pentose (480 nm)		Hexose (490 nm)		Pentose (480 nm)	
	5 day	10 day	5 day	10 day	5 day	10 day	5 day	10 day	5 day	10 day	5 day	10 day
Control (Water)	0.6 a	0.48 a	0.61a	0.49 a	0.6 a	0.42 c	0.62 a	0.43 c	0.6 a	0.42 c	0.62 a	0.43 c
Sucrose												
20 mM	0.57 a	0.48 a	0.58 a	0.47 a	0.62 a	0.46 b	0.64 a	0.48 b	0.62 a	0.46 b	0.64 a	0.48 b
40 mM	0.64 a	0.44 a	0.65 a	0.45 a	0.56 a	0.47 b	0.59 a	0.43 bc	0.56 a	0.47 b	0.59 a	0.43 bc
60 mM	0.63 a	0.47 a	0.64 a	0.49 a	0.61 a	0.46 b	0.63 a	0.47 b	0.61 a	0.46 b	0.63 a	0.47 b
Trehalose												
20 mM	0.64 a	0.5 a	0.65 a	0.51 a	0.58 a	0.51 a	0.6 a	0.52 a	0.58 a	0.51 a	0.6 a	0.52 a
40 mM	0.64 a	0.49 a	0.65 a	0.5 a	0.59 a	0.51 a	0.6 a	0.52 a	0.59 a	0.51 a	0.6 a	0.52 a
60 mM	0.61 a	0.5 a	0.63 a	0.5 a	0.6 a	0.53 a	0.62 a	0.54 a	0.6 a	0.53 a	0.62 a	0.54 a
HSD	0.11	0.14	0.1	0.14	0.13	0.03	0.11	0.04	0.13	0.03	0.11	0.04

*Data are means of three replicates. Means followed by the same letter within a column are not significantly different according to the Tukey test ($p=0.01$).

life of cut spikes of *Aquilegia vulgaris* and *Consolida ajacis*, respectively, but a drastic reduction in vase life was recorded in flowers supplied with higher concentrations of sucrose. It is suggested that sucrose induces the closure of stomata, eventually reducing the loss of water, thereby reducing transpiration and maintaining fresh mass (Marousky 1969, Chen et al. 2001). Verlinden and Garcia (2004) demonstrated that accumulation of the mRNA of ethylene biosynthetic pathway genes decreased in carnation petals. Water uptake for all the treatments increased up to day 2 and decreased thereafter. The present study also demonstrated that exogenous trehalose (60 mM) increased fresh weight of cut stems. This effect is probably due to the presence of trehalose and its osmoprotectant roles. This experiment suggests that cut stem water relation was not the main factor influencing vase life. The postharvest life of leaves was good, averaging 13.3, 12.6 and 12.3 days for the 60 and 40 mM trehalose and 40 mM sucrose solutions, respectively. Indeed, there was a coincidence of petal abscission time and leaf yellowing. Trehalose is not easily broken into its two glucose molecule components, except in the presence of trehalase that can be found in cellular cytoplasm with a neutral pH or within vacuoles with a pH of 4.5 (Crowe et al. 1984). This property of trehalose caused stability in leaves and has moved slowly from the tissue. In contrast, the toxic effects of exogenous trehalose on shoot tip of *Cuscuta reflexa* (Veluthambi et al. 1981), bracts in gladiolus florets (Otsubo & Iwaya-Inoue 2000), and tulip leaves (Iwaya-Inoue & Takata 2001, Ranwala and Miller 2009), have been reported. This suggests that leaves have only a limited capacity to metabolize exogenous trehalose and utilize it (Ranwala & Miller 2009). In our results we found that trehalose was more effective in maintaining pigments of petal and leaf compared to the sucrose and control treatment. Trehalose maximizes chlorophyll content and vase life of leaves greater than sucrose due to the supply of carbohydrate and carbon availability. It is proposed that this sugar is involved in osmoregulation, removal of free radicals and stabilization of the hydrated structure of proteins to maintain membrane integrity and protein stability under various stress conditions (Crowe et al. 1992). Carotenoids are synthesized in chloroplasts and are essential for protecting tissues against photo-oxidative damage in the green tissues of higher plants (Britton 1998).

Leaf yellowing, the visible sign of senescence, is due to preferential degradation of chlorophyll over carotenoids (Matile 1992). The present study indicates that carotenoids content in leaves was lower than concentrations of chlorophyll a, b and total chlorophyll. Similar results were found by Oliveira Neto et al. (2009) working with *Sorghum bicolor*. Moreover water deficit promoted strong fall in the levels of carotenoids and

chlorophylls. The degradation of the pigments is linked with the decrease of the synthesis and/or degradation of carotenoids, because carotenoids are accessory pigments in the absorption and transference of light, and are used as chlorophyll protectors during the photo oxidation process (Sharma & Hall 1991). In anthocyanin biosynthesis, sugars could act as precursors of metabolic processes and as a signaling molecule in promoting gene expression (Weiss 2000).

In the present study, anthocyanins increased with trehalose treatment, but higher concentration of trehalose (60 mM) lead to decline in anthocyanin content. The reason for reduced anthocyanin may be inadequate separation of organelles in one type of cell. The onset of senescence may relate to low carbohydrate levels in one cellular compartment, such as cytosol, while there is no such low level in other compartments, for example the vacuole (van Doorn & Woltering 2008). These results are similar to those reported by Han (2003), who demonstrated that sucrose in the vase solution of 'Stargazer' Lilium did not increase vase life, but did increase opening of secondary buds and anthocyanin content. Research on the uptake of exogenous sugars in cut flower stems has revealed the presence of sucrose and trehalose in vase solution increased carbohydrate content in cut stem. Comparison of sugar profiles in leaves and petals in the experiment indicates that concentration of carbohydrate in the leaf of the stems treated with trehalose was maintained continuously up to day 10, but in cut stem treated with sucrose carbohydrate decreased by day 10, while the concentration of carbohydrate in petals increased continuously up to day 10 and was not significantly different between all treatments. These findings suggesting the start of yellowing that may be associated with the decrease in carbohydrate levels in leaves and competition between leaves and petals for carbohydrate may contribute to the short vase life of cut flowers.

CONCLUSION

The results obtained from the present study provided novel insights into improving cut flower longevity and delaying yellowing processes in Alstroemeria cut stems. 40 mM sucrose solution as well as 40 and 60 mM trehalose extended the time to 50% petal fall and 50% leaf yellowing. The best postharvest treatment for Alstroemeria was a 60 mM solution of trehalose. It can thus be concluded that trehalose has a potential for improving cut flower longevity. Trehalose causes the preservation of green colour, which is considered a good parameter to evaluate the state of the

leafy flowering stem. Therefore, carbohydrate supply may determine the length of vase life of cut flowers. These results also suggest that more elaborate studies are needed to be conducted on flowers to make a generalized argument on the relationship between trehalose and petal abscission.

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REFERENCES

- Bayogan, E.R.V., Jaroenkit, T., Paull, R.E. (2008): Postharvest life of Bird-of-Paradise inflorescences. *Postharvest Biology and Technology* 48: 259-263.
- Borochoy, A., Mayak, S., Halevy, A.H. (1976): Combined effects of abscisic acid and sucrose on growth and senescence of rose flowers. *Physiologia Plantarum* 36: 221-224.
- Britton, G. (1998): Overview of carotenoid biosynthesis. In: Britton, G, Liaaen-Jensen S, Pfander H, eds. *Carotenoids*, Basel: Birkha user, 3: 13-147.
- Burge, G.K., Morgan, E.R., Seelye, J.F., Clark, G.E., McLachlan, A., Eason, J.R. (2010): Prevention of floret abscission for *Agapanthus praecox* requires an adequate supply of carbohydrate to the developing florets. *South African Journal of Botany* 76: 30-36.
- Chen, W.S., Liao, L.J., Chen, C.Y., Huang, K.U. (2001): Kinetin, Gibberellic acid and sucrose affect vase life in *Oncidium* spp. *Acta Botanica Gallica* 148: 177-181.
- Chutichudet, P., Chutichudet, B., Boontiang, K. (2011): Influence of 1-MCP fumigation on flowering weight loss, water uptake, longevity, anthocyanin content and colour of Patumma (*Curcuma alismatifolia*) cv. Chiand Mai Pink. *International Journal of Agricultural Research* 6: 29-39.
- Crowe, J.H., Carpenter, J.F., Crowe, L.M. (1998): The role of vitrification in anhydrobiosis. *Annual Reviews* 60: 73-103.
- Crowe, J.H., Crowe, L.M., Chapman, D. (1984): Preservation of membranes in anhydrobiotic organism: The role of trehalose. *Science* 223: 209-217.
- Crowe, J.H., Hoekstra, F.A., Crowe, L.M. (1992): Anhydrobiosis. *Annual Reviews* 54: 579-599.
- Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A., Smith, F. (1956): Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28: 350-356.
- Giusti, M.M., Wrolstad, R.E. (2000): *Characterization and Measurement of Antocyanins by UV-Visible Spectroscopy*, John Wiley&Sons, Inc.
- Halevy, A.H., Mayak, S. (1979): Senescence and postharvest physiology of cut flowers, Part 1. *Horticultural Reviews* 1: 204-236.
- Han, S.S. (2003): Role of sugar in the vase solution on postharvest flower and leaf quality of oriental lily 'Stargazer'. *Hort Science* 38: 412-416.
- He, S., Joyce, D.C., Irving, D.E. (2006): Competition for water between inflorescences and leaves in cut flowering stems of *Grevillea* 'Crimson Yul-lo'. *Journal of horticultural science & biotechnology* 81: 891-897.
- Hoeberichts, F.A., van Doorn, W.G., Vorst, O., Hall, R.D., van Wordragen, M.F. (2007):

- Sucrose prevents up-regulation of senescence-associated genes in carnation petals. *Journal of Experimental Botany* 58: 2873-2885.
- Ichimura, K., Kawabata, Y., Kishimoto, M., Goto, R., Yamada, K. (2003): Shortage of soluble carbohydrates is largely responsible for short vase life of cut 'Sonia' rose flowers. *Journal of the Japanese Society for Horticultural Science* 72: 292-298.
- Ichimura, K., Mukasa, Y., Fujiwara, T., Kohata, K. (1998): Improvement of postharvest life and changes in sugar concentrations by sucrose treatment in bud-cut sweet pea. *National Research Institute of Vegetables, Ornamental Plants and Tea, Japan* 13: 41-49.
- Iwaya-Inoue, M., Takata, M. (2001): Trehalose plus chloramphenicol prolong the vase life of tulip flowers. *Hort Science* 36: 946-950.
- Jordi, W., Stoop, G.M., Kelepouris, K., van-der-Krieken, W.M. (1995): Gibberellin-induced delay of leaf senescence of *Alstroemeria* cut flowering stems is not caused by an increase in the endogenous cytokinin content. *Journal of Plant Growth Regulation* 14: 121-127.
- Liao, L.J., Lin, Y.H., Huang, K.L., Chen, W.S., Cheng, Y.M. (2000): Postharvest life of cut rose flowers as affected by silver thiosulfate and sucrose. *Botanical Bulletin of Academia Sinica* 41: 299-303.
- Lichtenthaler, H.K. (1987): Chlorophylls and carotenoids: pigments of photosynthetic membranes. *Methods in Enzymology* 148: 350-382.
- Marouskuy, F.J. (1969): Vascular blockage, water absorption, stomatal opening and respiration of cut 'Better Times' roses treated with 8-hydroxyquinoline citrate and sucrose. *Journal of the American Society for Horticultural Science* 94: 223-226.
- Matile, P., (1992): Chloroplast senescence. pp.413-40. In: Baker, NR, Thomas, H, (eds), *Crop photosynthesis: spatial and temporal determinants*. Elsevier, Amsterdam.
- Moneruzzaman, K.M., Hossain, A.B.M.S., Amru, N.B., Saifudin, M., Imdadul, H., Wirakarnai, S. (2010): Effect of sucrose and kinetin on the quality and vase life of *Bougainvillea glabra* var. Elizabeth Angus bracts at different temperatures. *Australian Journal of Crop Science* 4: 474-479.
- Mutui, T.M., Emongor, V.E., Hutchinson, M.J. (2006): The effects of gibberellin₄₊₇ on the vase life and flower quality of *Alstroemeria* cut flowers. *Plant Growth Regulation* 48: 207-214.
- Oliveira Neto, C.F., Lobato, A.K.S., Gonçalves-Vidigal, M.C., Costa, R.C.L., Santos Filho, B.G., Alves, G.A.R., Maia, W.J.M.S., Cruz, F.R., Neves, H.K.B., Lopes, M.J.S. (2009): Carbon compounds and chlorophyll contents in sorghum submitted to water deficit during three growth stages. *Journal of Food Agriculture & Environment* 7: 588-593.
- Otsubo, M., Iwaya-Inoue, M. (2000): Trehalose delays senescence in cut gladiolus spikes. *Hort Science* 35: 1107-1110.
- Ranwala, A.P., Miller, W.B. (2009): Comparison of the dynamics of non-structural carbohydrate pools in cut tulip stems supplied with sucrose or trehalose. *Postharvest Biology and Technology* 52: 91-96.
- SAS Institute Inc. (2004): SAS/STAT, Statistical Software. Version 9, SAS Institute Inc., Cary, NC.
- Shahri, W., Tahir, I., Tajamul, S.I., Ahmad, M., (2010): Response of some ornamental flowers of family Ranunculaceae to sucrose feeding. *African Journal of Plant Science* 4: 346-352.
- Sharma, P.K., Hall, D.O. (1991): Interaction of salt stress and photoinhibition on photosynthesis in barley and sorghum. *Journal of Plant Physiology* 138: 614-619.
- van Doorn, W.G. (1997): Water relations of cut flowers. *Horticultural Reviews* 18: 1-85.
- van Doorn, W.G., Woltering, E.J. (2008): Physiology and molecular biology of petal senescence. *Journal of Experimental Botany* 59: 453-480.

- Veluthambi, K., Mahadevan, S., Mehashwari, R. (1981): Trehalose toxicity in *Cuscuta reflexa*. Correlation with low trehalase activity. *Journal of Plant Physiology* 68: 1369-1374.
- Verlinden, S., Garcia, J.J.V. (2004): Sucrose loading decreases ethylene responsiveness in carnation (*Dianthus caryophyllus* cv. White Sim) petals. *Postharvest Biology and Technology* 31: 305-312.
- Weiss, D. (2000): Regulation of flower pigmentation and growth: multiple signalling pathways control anthocyanin synthesis in expanding petals. *Physiologia Plantarum* 110: 152-157.
- Wiemken, A. (1990): Trehalose in yeast, stress protectant rather than reserve carbohydrate. *Antonie van Leeuwenhoek*, 58: 209-217.
- Wingler, A. (2002): Molecules of Interest: The function of trehalose biosynthesis in plants. *Phytochemistry* 60: 437-440.
- Yamada, T., Takatsu, Y., Manabe, T., Kasumi, M., Marubashi, W. (2003): Suppressive effect of trehalose on apoptotic cell death leading to petal senescence in ethylene-insensitive flowers of *gladiolus*. *Plant Science* 164: 213-221.