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Influence of type and concentration of sugars, supplemented with 8-hydroxyquinoline sulphate, on the vase life of waxflower

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ABSTRACT

A study was conducted to test the effect of 58.5 mM maltose, glucose, fructose, galactose and sucrose, and sucrose concentrations of 14.6, 29.2, 58.5 and 117.0 mM supplemented with 200 mg L⁻¹ 8-hydroxyquinoline sulphate (HQS) on the vase life and stem fresh weight changes in waxflower (Chamelaucium Desf.). The effect of the interaction between sucrose and HQS concentrations on the vase life of the cultivar 'Alba' was also investigated. All the types of exogenous sugar significantly increased the vase life of flowers, but decreased the vase life of leaves of waxflower cultivars compared with the deionized water controls, except the leaves of 'Lady Stephanie', 'Purple Pride' and 'Mullering Brook'. The flower vase life of almost all the cultivars treated with sucrose was not significantly different from the life of the cultivars kept in fructose and glucose, except 'Laura Mae Pearl', whose flower vase life in sucrose was significantly lower (9.7%) than in fructose. By contrast, the vase life of flowers of the cultivars treated with sucrose was longer than of those in maltose and galactose. At sucrose concentrations of up to 117.0 mM coupled with 200 mg L⁻¹ HQS, the flower vase life of six out of eight cultivars significantly increased, except in 'Laura Mae Pearl' and 'Mullering Brook', whose flower vase life was maximized at the concentrations of 29.2 and 58.5 mM respectively, while the vase life of their leaves decreased. Sucrose concentrations from 14.6 to 29.2 mM coupled with 50 mg L⁻¹HQS maximized vase life for both the flowers and leaves of 'Alba'. Cultivars with a longer vase life of flowers maintained stem fresh weight above the initial stem fresh weight longer.

Key words: Chamelaucium, fresh weight, HQS, sugar types, vase life

INTRODUCTION

Improvement of the vase life of cut flowers by supplying sugar in the vase solution has been widely reported (Nichols 1973, van Doorn 2001, Arrom and Munné-Bosch 2012). The demand of cut flowers for carbohydrates is mainly satisfied by the application of exogenous sugar (Stephens et al. 2011) because cut flowers have a reduced ability to conduct photosynthesis after detachment from the plant (van Staden 1995). The vase life of cut flowers has been correlated with the sugar



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content of flowers, with a higher sugar content promoting a longer vase life (Holly 1963). Adding sucrose to vase solutions or pulsing in higher sugar concentrations extended the longevity of cut Tulipa (Ranwala and Miller 2009), Rosa (Gholami et al. 2011) and Lilium flowers (van Doorn and Hanb 2011). Sugars supply materials for building structures for the plant organs and contribute to cell wall synthesis, resulting in an increased vase life of flowers (Ichimura 1998). Sugar also reduces ethylene production by the petals of cut flowers, as found in cut Dianthus, which, when treated with sucrose, significantly decreased the ethylene production of petals (Verlinden and Garcia 2004). Both mono- and disaccharides have been found in flower cells of many types of cut flowers, such as Sandersonia aurantiaca (Eason et al. 1997), Rosa (Ichimura et al. 1997), Petunia (O'Donoghue et al. 2008) and Antirrhinum majus L. (Asrar 2012) (Tab. 1). Among the different types of sugar, sucrose has been commonly used commercially to prolong the longevity of cut flowers (Pun and Ichimura 2003). Sucrose is a main component in commercial vase solutions, such as Chrysal (Chrysal, Naarden, The Netherlands), providing a carbon source for flowers and shown to have a positive effect in extending the vase life in cut Dendrobium 'Kao Sanan', 'Lovely Pink' and 'Suree Peach' (Obsuwan et al. 2013). In higher plants, the hydrolysis of sucrose provides monosaccharides of glucose and fructose, as was the case in cut Rosa (Yamada et al. 2007), which are then further metabolized by acid invertase (β -fructosidase, EC 3.2.1.26) present (in a soluble form) in the vacuoles of the petals (Ap Ree 1974, Kaltaler and Steponkus 1974, Roitsch and Gonzalez 2004).

8-hydroxyquinoline sulphate (HQS) combined with sucrose was found to be very effective in increasing the vase life and reducing respiration rate and physiological weight loss in *Dendrobium* (Dineshbabu et al. 2002) and *Gladiolus* (Beura et al. 2011). The biocide HQS is a very important germicide in the preservatives used by the floral industry (Nowak and Rudnicki 1990) to keep cut flowers fresh over extended periods. Biocides reduce the entry of bacteria and fungi, and help to prevent the blockage of xylem vessels by air and microorganisms that cause xylem occlusion (Hardenburg 1968). The use of HQS for preventing microbial growth results in an increase in water uptake by cut flowers (Reddy et al. 1996).

The effects of the types and concentrations of sugar on the vase life of cultivars have also been found to vary. While sucrose at a concentration of 146.2 mM delayed ethylene production in Dianthus caryophyllus 'White Sim', fructose, glucose and maltose used at the same concentration did not delay ethylene production (Verlinden and Garcia 2004). Similarly, combinations of glucose and aminooxyacetic acid (AOA) resulted in a longer vase life of flowers of Dendrobium compared with sucrose plus AOA used at the same rate (Rattanawisalanon et al. 2003). The response of the vase life of flowers to sucrose concentrations also varied in cut Antirrhinum, whose flower vase life increased with increasing sucrose concentration from 7.31 to 14.6 mM, reaching a maximum at the concentration of 14.6 mM, and then decreased with increasing concentrations to 29.2 mM, when used in combination with 200 mg L-1 HQS (Ichimura and Hisamatsu 1999).

The vase life of flowers of *Chamelaucium uncinatum* 'Alba' was extended with the presence of sucrose at a concertration of 58.5 mM in the vase water, but this concentration of sucrose damaged the leaves (Joyce and Jones 1992). Treatment with 58.5 mM sucrose plus 200 mg L⁻¹ HQS significantly increased the vase life of *C. uncinatum* cultivars (Joyce 1988). Increasing sucrose concentrations up to 146.2 mM, combined with 200 mg L⁻¹ HQS,

Table 1. Literature references on the presence of mono- and disaccharides in the flower cells of cut flowers

	Reference	Type of sugar				
Cultivar		Ν	Disaccharide			
		Fructose	Glucose	Galactose	Sucrose	
Rosa Carl Red	Ichimura et al. 1997	\checkmark				
Rosa Rote Rose	Ichimura et al. 1997	\checkmark	\checkmark		\checkmark	
Rosa Sonia	Ichimura et al. 1997	\checkmark	\checkmark		\checkmark	
Sandersonia tubers	Eason et al. 1997	\checkmark			\checkmark	
Petunia Mitchell	O'Donoghue et al. 2008			\checkmark		
Antirrhinum majus Yellow Butterfly	Asrar 2012	\checkmark	\checkmark			

Note: $\sqrt{\text{means similar to the previous one}}$

decreased the vase life of flowers and leaves of *C. uncinatum* 'Purple Pride' (Joyce 1988). However, there has been no extensive research on the effects of different types and concentrations of sugar, and the effects of the interaction between sucrose and HQS concentrations on the vase life of cultivars of different waxflower species. The aim of this study was to evaluate the effect of different types and concentrations of sugar on the vase life of a range of waxflower cultivars. Also, an effective vase solution with a combination of HQS and sucrose concentrations was determined.

MATERIAL AND METHODS

Plant material

Flowering stems of Chamelaucium uncinatum (Myrtaceae) 'Purple Pride', 'Alba' and 'Mullering Brook', C. megalopetalum × C. uncinatum 'Bridal Pearl', 'Denmark Pearl', 'Laura Mae Pearl' and 'Crystal Pearl', C. uncinatum × C. megalopetalum 'WX87', C. sp. Gingin \times (C. uncinatum \times C. uncinatum) 'WX97', C. floriferum × C. uncinatum 'Lady Stephanie' and (C. uncinatum × Verticordia grandis) × Verticordia grandis 'WX73' were harvested early in the morning from July to October 2012, from mature (5-year-old) bushes cultivated under irrigation and fertigation (Seaton and Poulish 2010) at Medina Research Station (32°13'18"S, 115°38'50"E) of the Department of Agriculture and Food Western Australia (DAFWA). Flowering stems of approximately 60 cm in length with 50-70% of the flowers open were cut from an average of five bushes, and the cut ends of the stems were immediately placed upright in buckets of clean water, and then transported by an air-conditioned vehicle at approximately 20°C to the postharvest laboratory of DAFWA in South Perth, the journey taking about 35 minutes (Seaton et al. 2010, Seaton and Joyce 1996). In the laboratory, cut stems were randomly chosen and cut shorter under water to a length of 30 cm (measured from the cut end to the most extreme opened-flower) for vase life assesement.

Experimental design

Experiment 1: Sugar type treatments

Two disaccharides (sucrose and maltose) and three monosaccharides (glucose, fructose and galactose) were all at a concentration of 58.5 mM and supplemented with 200 mg L⁻¹ HQS. The vase life of flowers and leaves in the different sugars was compared for 'Bridal Pearl', 'Denmark Pearl', 'Laura Mae Pearl', 'Crystal Pearl', 'WX87', 'WX97', 'Lady Stephanie', 'WX73', 'Mullering Brook' and 'Purple Pride' with the vase life in deionized water (DI) used as a control. The experiment was arranged in a completely randomized design, and each treatment was repeated eight times with 1 stem per replication.

Experiment 2: Sucrose concentrations

A two-factor experiment was conducted to test the effect of different sucrose concentrations on vase life for the different cultivars. The sucrose concentration factor included 0.0, 14.6, 29.2, 58.5 and 117.0 mM sucrose prepared by dissolving 0, 5, 10, 20 and 40 g of table sugar in 1 L of deionized water. The cultivar factor included the cultivars 'Bridal Pearl', 'Denmark Pearl', 'Laura Mae Pearl', 'WX97', 'Lady Stephanie', 'WX73', 'Mullering Brook' and 'Purple Pride'. HQS at a concentration of 200 mg L⁻¹ was added to the vase water containing sucrose. This completely randomized experiment was designed with each treatment repeated eight times with 1 stem per replication.

Experiment 3: Sucrose vs. HQS

A factorial experiment was conducted to test the effect of the combination of sucrose at concentrations of 14.6, 29.2, 58.5 and 117.0 mM and HQS at concentrations of 50, 100, 200 and 400 mg L⁻¹ on the vase life of the cultivar 'Alba'. Deionized water was used as a control. The experiment was arranged in a completely randomized design with eight replications for each treatment and 1 stem per replication.

Experimental conditions

Vase life was assessed in a controlled-room at 20 \pm 2°C, 60 \pm 10% RH, with a 12 h photoperiod. The light flux densities were 8 µmol m⁻² s⁻². In each experiment, all stems were individually placed in 250 mL plastic vases, each containing one of the above vase solutions.

Measurements of the vase life of flowers and leaves

The vase life of flowers was determined when 50% of opened flowers were fully closed or showed damage to the petals. For the genotypes whose flowers had dropped before closing, the end of vase life was determined when 50% of opened flowers had dropped. The vase life of leaves was determined when 50% of the leaves were fully desiccated or yellow.

Assessment of the relationship between the vase life of flowers and the number of days when stem fresh weight was above or below the initial stem fresh weight

The number of days when stem fresh weight was above the initial stem fresh weight was recorded as a period of time from the day the stems had been placed in the vase solutions to the day when their fresh weight equalled the initial stem fresh weight. The number of days when stem fresh weight was below the initial stem fresh weight was determined as the vase life of flowers (days) minus the number of days when stem fresh weight was above the initial stem fresh weight.

Statistical analysis

The vase life of flowers and leaves resulting from treatment effects (sugar type × genotype, sucrose concentration × genotype, and the factorial treatment of sucrose concentration × HQS concentration) was analyzed with 2-way ANOVA using the statistical package Genstat XV (Lawes Agricultural Trust, Rothamsted Experimental station, UK). Treatment means were compared by LSD at p < 0.05 and the means (\pm SE) were shown as appropriate. Where possible, comparisons between the means were made using Duncan's Multiple Range Test.

RESULTS

Sugar type treatments

The flower vase life of all the cultivars was significantly (p < 0.05) extended (1.3-fold) in the vase solutions containing 58.5 mM sugar coupled

with 200 mg L⁻¹ HQS, compared with that of the controls (Tab. 2). The flower vase life of almost all the cultivars treated with sucrose was not significantly (p < 0.05) different from those treated with fructose or glucose, except for 'Laura Mae Pearl', whose vase life in fructose was significantly (p < 0.05) greater (1.1-fold) than that in sucrose. For sucrose, fructose and glucose, flower vase life increased on average 1.4-fold, and 1.3-fold for maltose and 1.2-fold for galactose compared with the DI controls (Tab. 2). However, in terms of flower vase life the response of individual cultivars to the types of sugar varied. The flower vase life of cultivars was significantly (p < 0.05) extended (from 1.2 to 1.8-fold) by the addition of sugars, except for 'WX73' in sucrose, 'Crystal Pearl', 'WX73' and 'WX97' in maltose, 'Purple Pride' and 'WX73' in glucose, 'Lady Stephanie', 'Purple Pride', 'WX87' and 'WX73' in galactose, and 'Mullering Brook' in all types of sugar, whose flower vase life was similar to that in the control (Tab. 2).

The vase life of leaves of all the cultivars was significantly (p < 0.05) decreased (by 25.8%) by the addition of 58.5 mM sugar to the vase water containing 200 mg L⁻¹ HQS, compared with the vase life in the controls (Tab. 3). For sucrose, fructose and glucose, vase life decreased by an average of 30%, and by 50% for maltose and galactose, compared with the control (Tab. 3). In terms of the vase life of leaves the response of individual cultivars to the different types of sugar varied. The leaf vase life of 'Lady Stephanie' significantly (p < 0.05) increased (on average 1.3-fold) in all the

Table 2. Effect of different types of sugar in combination with 200 mg L⁻¹ HQS on the vase life of flowers

Cultivar	Vase life of flowers (days)					Overall	
	Control	Sucrose	Maltose	Glucose	Fructose	Galactose	mean vase life
Crystal Pearl	23.9	33.3	25.3	31.6	30.8	31.4	29.4
Laura Mae Pearl	21.5	34.9	34.1	36.3	38.3	30.9	32.7
Bridal Pearl	18.4	25.0	28.0	26.1	27.8	25.1	25.1
Denmark Pearl	15.5	28.4	25.8	27.3	27.9	22.4	24.6
Lady Stephanie	15.5	20.8	18.6	19.0	23.3	18.0	19.2
WX87	14.4	18.1	17.5	18.5	18.1	15.9	17.1
WX73	13.4	15.4	12.8	14.9	17.6	13.1	14.5
Mullering Brook	12.0	15.0	10.3	13.4	13.9	12.4	12.8
WX97	11.8	19.6	13.4	18.8	18.1	16.6	16.4
Purple Pride	9.3	13.6	14.6	12.0	15.9	10.3	12.6
Overall mean of vase life	15.6	22.4	20.0	21.8	23.2	19.6	20.4

LSD (p < 0.05) for sugar types = 0.8 day, for cultivars = 1.0 day, and for sugar types × cultivars = 2.4 days by 2-way analysis of variance

Cultivar	Vase life of leaves (days)					Overall	
	Control	Sucrose	Maltose	Glucose	Fructose	Galactose	mean vase life
Crystal Pearl	38.5	19.62	9.5	22.4	19.5	20.3	21.6
Laura Mae Pearl	34.9	21.3	8.8	26.6	25.9	19.5	22.8
Bridal Pearl	29.3	16.4	8.3	11.4	10.3	10.0	14.3
Denmark Pearl	19.5	16.5	12.4	14.9	15.8	13.4	15.4
Lady Stephanie	18.5	24.6	23.3	20.9	27.1	22.1	22.8
WX87	23.8	20.1	23.0	21.8	20.6	18.3	21.3
WX73	19.1	13.3	7.0	12.9	16.1	12.4	13.5
Mullering Brook	9.9	11.5	7.5	10.5	10.3	10.5	10.0
WX97	17.4	11.9	7.8	14.4	10.6	11.8	12.3
Purple Pride	13.8	13.4	13.5	12.9	14.1	12.3	13.3
Overall mean of vase life	22.5	16.9	12.1	16.9	16.6	15.1	16.7

Table 3. Effect of different types of sugar in combination with 200 mg L⁻¹ HQS on the vase life of leaves

LSD (p < 0.05) for sugar types = 1.3 days, for cultivars = 1.7 days, and for sugar types × cultivars = 4.1 days by 2-way analysis of variance

sugar types, and the leaf vase life of the cultivars Purple Pride, Mullering Brook and WX87 in all types of sugar, 'Denmark Pearl' in sucrose and fructose, and that of 'WX97' in glucose was similar to the vase life in the controls (Tab. 3). On the other hand, the vase life of leaves of the other cultivars significantly (p < 0.05) decreased (by half) in the vase solutions containing sugars, compared with the controls (Tab. 3). The addition of sucrose significantly (p < 0.05) extended the leaf vase life of *C. floriferum* hybrid 'Lady Stephanie' 1.3-fold, and 1.1-fold for *C. uncinatum* cultivars, but it decreased by half the leaf vase life of the cultivars with *C. megalopetalum, C.* sp. *Gingin* and *Verticordia grandis* as a parent (Tab. 3).

Sucrose concentrations

Overall, increasing sucrose concentrations increased the flower vase life of six cultivars, except that of 'Laura Mae Pearl' and 'Mullering Brook' (Fig. 1A). However, in terms of flower vase life the response to sucrose concentrations depended on the cultivar. The vase life of 'Laura Mae Pearl' was significantly (p < 0.05) extended (1.7-fold) at a sucrose concentration of 29.2 mM, compared with that in water. At a concentration of

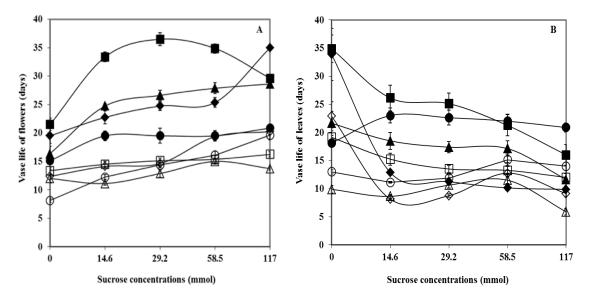


Figure 1. Vase life of flowers (Panel A) and leaves (Panel B) of 'Laura Mae Pearl' (\blacksquare), 'Bridal Pearl' (\blacklozenge), 'Denmark Pearl' (\blacktriangle), 'Lady Stephanie' (\boxdot), 'WX73' (\Box), 'WX97' (\diamondsuit), 'Mullering Brook' (Δ), and 'Purple Pride' (\circlearrowright) in different sucrose concentrations supplemented with 200 mg L⁻¹ HQS, and in deionized water. LSD (p < 0.05) for flowers = 2.2 days and for leaves = 4.0 days by 2-way analysis of variance, n = 8. Vertical bars are standard errors of means

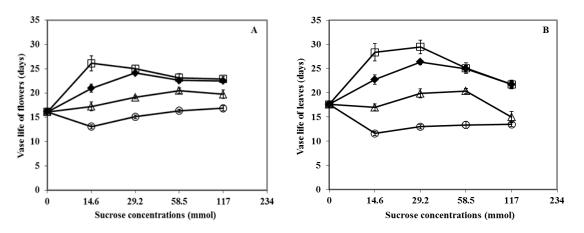


Figure 2. Effect on the vase life of flowers (Panel A) and leaves (Panel B) of *C. uncinatum* 'Alba' treated with 14.6, 29.2, 58.5 or 117.0 mmol sucrose in combination with 50 (\Box), 100 (\blacklozenge), 200 (Δ) or 400 (o) mg L⁻¹ HQS. Zero concentration of sucrose on the graphs indicates flower stems held in deionized water. Vertical bars are standard errors of means. LSD (p < 0.05) for flowers = 2.0 days and for leaves = 2.6 days, n = 8

58.5 mM, 'Mullering Brook' showed the greatest response to sucrose, where its flower vase life reached a maximum, which was a 1.3-fold increase, while the other cultivars continued to extend their lives with higher concentrations, with 'Bridal Pearl' and 'Purple Pride' increasing 1.8-fold and 1.6-fold, respectively, in 117 mM compared with the control (Fig. 1A). The cultivar WX73 did not respond to the increasing sucrose concentration compared with the control (Fig. 1A).

The vase life of leaves of all the cultivars tested, except for 'Lady Stephanie', 'Purple Pride' and 'WX97', decreased with increasing sucrose concentrations. The leaf vase life of 'Lady Stephanie' was significantly (p < 0.05) increased (1.3-fold) to a maximum at the concentration of 14.6 mM, compared with that in the control. The leaf vase life of 'Mullering Brook' in sucrose concentrations from 14.6 to 58.5 mM was similar to that in the DI controls and lower in 117 mM sucrose, compared with that in the DI control. The leaf vase life of C. uncinatum cultivars was significantly (p < 0.05) increased (1.2-fold) at the concentration of 58.5 mM, and was similar to that in the control when being treated with 29.2 mM sucrose. The lower concentration of 14.6 mM and the higher concentration of 117 mM significantly (p < 0.05) decreased leaf vase life by 13.5% and 16.4% respectively. By comparison, the vase life of leaves of the remaining cultivars was decreased by 37% to 54% in the vase solutions containing sucrose, compared with the control (Fig. 1B).

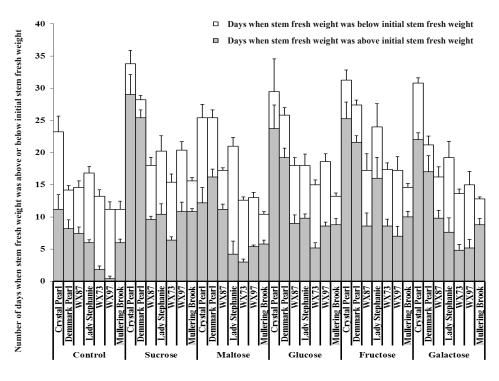
Sucrose vs. HQS concentrations

The maximum vase life of the cultivar Alba was obtained with a low concentration of sucrose in combination with a low concentration of HQS (Figs 2A and 2B). The vase life of the flowers of 'Alba' was significantly (p < 0.05) extended (1.6-fold) to a maximum in the vase solution of 14.6 mM sucrose plus 50 mg L⁻¹ HQS. As HQS concentrations increased, the maximum vase life of 'Alba' flowers decreased and occurred at high sucrose concentrations, with the maximum vase life decreasing by 35% in 117 mM sucrose plus 400 mg L⁻¹ HQS compared with the vase solution of 14.6 mM sucrose plus 50 mg L⁻¹ HQS (Fig. 2A). The vase life of flowers in increasing sucrose concentrations could not be improved by increasing HQS concentrations, with a 26% decrease in vase life occurring in 117 mM sucrose in 400 mg L⁻¹ HQS compared with 50 mg L^{-1} HQS (Fig. 2A).

The vase life of leaves was significantly (p < 0.05) extended (1.7-fold) to a maximum in the vase solution of 29.2 mM sucrose plus 50 mg L⁻¹ HQS (Fig. 2B). The maximum vase life at 29.2 mM sucrose plus 50 mg L⁻¹ HQS was significantly (p < 0.05) higher (1.5-fold) compared with the vase life in 58.5 mM sucrose plus 200 mg L⁻¹ HQS (Fig. 2B). The vase life of leaves in increasing sucrose concentrations could not be improved by increasing HQS concentrations, with a 40% decrease in vase life occurring in 117 mM sucrose in 400 mg L⁻¹ HQS compared with 50 mg L⁻¹ HQS (Fig. 2B).

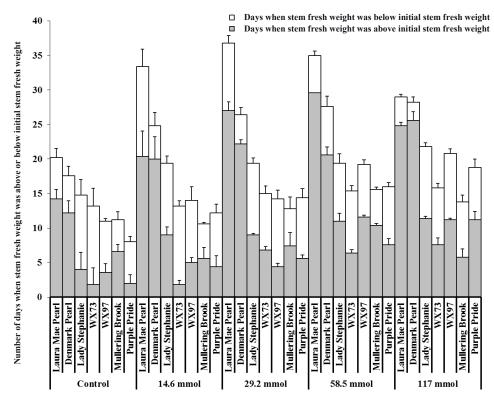
Relationship between the vase life of flowers and the number of days when stem fresh weight was above or below the initial stem weight of cultivars in different types of sugar

The long vase life of cultivars in sugars had a higher number of days when stem fresh weight was above



Different genotypes in different types of sugar

Figure 3. Relationship between the vase life of flowers and the number of days when stem fresh weight was above or below the initial stem fresh weight for different cultivars in 58.5 mmol of sucrose, maltose, glucose, fructose and galactose supplemented with 200 mg L⁻¹ HQS. DI water was used as a control. Vertical bars are standard errors of means, n = 5



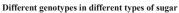


Figure 4. Relationship between the vase life of flowers and the number of days when stem fresh weight was above or below the initial stem fresh weight for different cultivars in different sucrose concentrations supplemented with 200 mg L^{-1} HQS. DI water was used as a control. Vertical bars are standard errors of means, n = 5

the initial stem fresh weight (DFWA) compared with the number of days when stem fresh weight was below the initial stem fresh weight (DFWB) (Fig. 3). DFWA of cultivars in all the types of sugar was higher (2.0-fold) than that in the controls. Overall for the cultivars, DFWA for sucrose, fructose or glucose was 108%, 85.2% or 51.3% higher than DFWB, respectively, while DFWA for galactose was 40.3% higher than DFWB. By contrast, DFWA for maltose and the control was 13.4% and 35.3% lower than DFWB, respectively. DFWA of the cultivars with C. megalopetalum as a parent and C. uncinatum 'Mullering Brook' in the vase solutions was 116.3% and 81.9% greater than DFWB, while DFWA of the C. floriferum hybrid 'Lady Stephanie', the C. sp. Gingin hybrid 'WX97' and the Verticordia grandis hybrid 'WX73' was 17.2%, 48.1% and 35.6% lower than DFWB, respectively (Fig. 3).

Relationship between the vase life of flowers and the number of days when stem fresh weight was above or below the initial stem weight of cultivars in different concentrations of sucrose

The vase life of flowers of cultivars in different concentrations of sucrose increased with increasing DFWA over DFWB (Fig. 4). DFWA of cultivars in all the sucrose concentrations was higher (with a 2.0-fold increase) than that in the control. DFWA of cultivars in 58.5 and 117 m mol L⁻¹ was 90.6% and 92.9% greater than DFWB, respectively, while DFWA of cultivars in 29.2 and 14.6 mM was 60.9% and 18.7% higher than DFWB, respectively. By contrast, DFWA of cultivars in the control was 14.0% lower than DFWB (Fig. 4).

DISCUSSION

The increase in the vase life of flowers achieved by supplying sucrose and HQS was consistent with the results obtained for *C. uncinatum* 'Purple Pride' (Joyce 1988). It was also consistent with sugar providing a carbohydrate source for the flower (Ichimura and Suto 1999). Increased vase life of cut flowers by sugar application has been attributed to the increased water uptake by the flowers through increasing the osmotic concentration of the florets and leaves (Pun and Ichimura 2003). In waxflower, sugar was most effective when applied to vase solutions in combination with a biocide, such as HQS, to prevent the growth of microorganisms in xylem vessels and maintain water uptake, thus prolonging the longevity of cut flowers (Asrar 2012), although HQS can become toxic.

The greater response of waxflower to sucrose, glucose and fructose is consistent with the findings in cut Rosa, where fructose, glucose and sucrose were the main soluble carbohydrates decreasing slowly during the vase life (Ichimura et al. 1999). Decreased sucrose conversion to a respirable carbohydrate occurs when there is loss of sucrose synthase and invertase activities (Yamada et al. 2007, Kumar et al. 2008). The lower vase life response to maltose and galactose is associated with the fact that they are rare types of sugar in flowers (Tab. 1) and may not be as readily respired as sucrose, and therefore are less effective in increasing the vase life of waxflower. The increase in vase life in vase solutions containing fructose or glucose may be due to the flower cells being supplied with an increased respiratory substrate to maintain stem water balance and stem fresh weight above the initial stem fresh weight for a longer time when compared with maltose or galactose. The way in which different sugar types affect the vase life of flowers is unclear. However, a study on Petunia 'Mitchell' by O'Donoghue et al. (2008) showed that the galactose content in petals decreased sharply over 2.0 days after flower opening, whereas the amounts of other sugars showed little change over that time. This suggested that the loss of galactose might also affect the vase life of flowers. Variation in genotype postharvest response to sucrose was reported in Protea 'Sylvia', whose vase life did not improve with a sucrose pulse at 584.8 mM (Stephens et al. 2011), while a 584.8 mM sucrose pulse (24 h, 25°C) reduced leaf blackening in Protea neriifolia R. Br. and increased the vase life of flowers (McConchie and Lang 1993).

Increasing the concentration of sucrose resulted in an increase in the supplied carbohydrate source (Nichols 1973) and osmosis concentration (Pun and Ichimura 2003), and in increased flower vase life of waxflower, confirming the result obtained for C. uncinatum cultivars (Joyce 1988). Competition for sugar between flower-buds, opening-flowers and older flowers shortened the vase life of flowers of Lilium (van der Meulen-Muisers et al. 1995). The flowers of 'Purple Pride' and the cultivars with C. megalopetalum as a parent are larger than the flowers of the remaining cultivars (Macnish et al. 2004), which may have resulted in a higher demand for carbohydrates as indicated by the shorter vase lives in our study. Increasing sucrose concentrations may have satisfied the requirement of these cultivars

for carbohydrates and consequently increased the vase life of flowers. The decrease in the vase life of leaves in increasing sucrose concentrations could have been caused by osmotic stress in the leaves due to the use of high sugar concentrations. Joyce (1988) reported that sucrose at a concentration of 146.2 mM in combination with 200 mg L⁻¹ HQS desiccated the leaves of C. uncinatum cultivars through osmotic stress. However, in this study a 40% lower sucrose concentration of 58.5 mmol damaged the leaves of almost all the cultivars, except for 'Lady Stephanie' and the cultivars of C. uncinatum (Fig. 1B). The leaves of these cultivars may not have been damaged by sugar, indicating that those leaves did not take up as much sugar as the leaves of stressed cultivars. The vase life response of cultivars to glucose or fructose concentrations was also similar to the vase life response of cultivars to sucrose concentrations (data not shown).

Increasing the concentration of sucrose in combination with higher concentrations of HQS increased the vase life of 'Alba' (Fig. 2A). The response of the cultivar Alba to sucrose may indicate a different response to that found in Gladiolus, where lower concentrations prolonged the vase life of florets by increasing water uptake, whereas higher concentrations seemed to impede water uptake (Bravdo et al. 1974). Sucrose in combination with biocides has become an important preservative for several floral cut flowers (Pun and Ichimura 2003). Application of HQS, an antimicrobial agent (Ketsa et al. 1995), increased water uptake and fresh weight, and consequently the vase life of cut Rosa (Ichimura et al. 1999). HQS coupled with sucrose increased flower quality, water uptake, fresh weight, flower freshness and reduced respiration rate and physiological weight loss in Dendrobium (Dineshbabu et al. 2002) and Gladiolus (Beura et al. 2011). However, HQS at high concentrations can become toxic and decreases the vase life of 'Alba'. The optimal concentrations of sucrose and HQS for increasing the vase life of 'Alba' were far below those reported for 'Purple Pride' (Joyce 1988).

CONCLUSIONS

- Critical levels of sugars were found for a range of cultivars to be from 14.6 to 29.2 mM in combination with low HQS levels at 50 to 100 mg L⁻¹, and this depended on the type of sugar.
- 2. Fructose, glucose and sucrose were the most effective sugars in increasing the vase life of waxflower as compared to galactose.

- 3. The sugar concentration that improved the vase life of both flowers and leaves was from 14.6 to 29.2 mM.
- 4. HQS at 200 mg L⁻¹ can become toxic, but a quarter of this amount extended vase life. The vase life of flowers of cultivars increased with increasing number of days when stem fresh weight was above the initial stem fresh weight.

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AUTHOR CONTRIBUTIONS

All of the authors contributed extensively to the work presented in this paper. C.D.D. – conducted the research work, collected and analyzed data, and wrote the research paper; K.S. – designed the experiments, provided the samples, offered suggestions and corrected the manuscript; Z.S. – offered suggestions and corrected the manuscript.

CONFLICT OF INTEREST

Authors declare no conflict of interest.

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