Stem end blockage in cut *Grevillea* 'Crimson Yul-lo' inflorescences

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Abstract

Grevillea 'Crimson Yul-lo' inflorescences have cut flower potential, but their vase life is short. End of vase life is characterised by early wilting. The possibility of physiologically mediated stem end blockage was investigated. Hydraulic conductance of 2 cm long stem end segments declined rapidly and remained lower throughout vase life than that of 2 cm long stem segments from immediately above. Re-cutting daily to remove basal 2 cm stem ends increased solution uptake, delayed declines in inflorescence water potential and water content, and improved inflorescence vase life. S-Carvone is a potential inhibitor of wound related suberin formation, via inhibition of phenylalanine ammonia-lyase, and vase solution treatments with S-carvone (0.318 and 0.636 mM) delayed the decline in hydraulic conductance of basal 2 cm long stem end segments and decreases in vase solution uptake and relative fresh weight of cut stems, and extended vase life. Treatments with the catechol oxidase inhibitor 4-hexylresorcinol (2.5-10 mM) also delayed stem end blockage. These findings suggest that stem end blockage in cut *G.* 'Crimson Yul-lo' stems is physiologically mediated.

Keywords: Cut flowers; *Grevillea*; Hydraulic conductance; Vase life; Water relations

1. Introduction

There are over 300 *Grevillea* species (Proteaceae) (Joyce and Beal, 1999). Some species and many hybrids with large colourful inflorescences have cut flower potential (Costin and Costin, 1988; Joyce and Beal, 1999; Joyce, 2004; French *et al*., 2005). However, their vase life is often

<1 week (Faragher, 1989; Joyce *et al.*, 1996; Joyce and Beal, 1999; Joyce, 2004). End of vase life is often associated with rapid wilting of the inflorescence (Joyce *et al.*, 1996; He *et al.*, 2006).

Blockage of water conducting xylem vessels contributes to the short vase life of most cut flowers (Mayak *et al.*, 1974; Halevy and Mayak, 1981; van Doorn, 1997). Stem blockage may be microbial and/or physiological. Loubaud and van Doorn (2004) reported stem blockage in *Viburnum opulus* (cv. Roseum) and rose (*Rosa x hybrida* cv. Red One) due mainly to living bacteria and their decay products. However, stem blockage in *Astilbe x arendsii* (cvs. Gult and Erica) was related mainly to wound induced physiological processes involving catechol oxidase and peroxidase. Wound related deposition of lipid-phenolic complexes (e.g. suberin) has been identified as a possible cause of stem end blockage (Williamson *et al.*, 2002).

Formation of phenolic suberin compounds begins with synthesis of trans-cinnamic acid from phenylalanine, and is catalysed by phenylalanine ammonia-lyase (PAL) (Stafford 1974). Treatment with S-carvone delayed the increase of PAL activity and suberin formation in potato tubers (Oosterhaven *et al.* 1995a). S-carvone supplied in the vase solution extended the vase life of cut *Hakea francisiana* (Proteaceae) (Williamson *et al.*, 2002). Treatment with 4-hexylresorcinol (4-HR), an inhibitor of catechol oxidase which oxidizes phenolics (Dawley and Flurkey, 1993), delayed the wilting of chrysanthemum stems (van Doorn and Vaslier, 2002). As PAL and catechol oxidase are involved in wound reactions, stem end blockage may be a response to cutting.

G. 'Crimson Yul-lo' [*G. banksii* (red form) × *G.* 'Misty Pink'] has attractive bright red terminal inflorescences. However, its vase life is short and early wilting of inflorescences may be due to

stem end blockage. The present study investigates the hypothesis that physiological stem end blockage occurs in *G.* 'Crimson Yul-lo' flower stems during vase life and results in inflorescence wilting.

2. Materials and methods

2.1. Plant material

G. 'Crimson Yul-lo' flowering stems were harvested when most florets on an inflorescence were at the commercial maturity stage of 'mature flowers with style looped to length of perianth tube' (Setyadjit *et al*., 2004). They were harvested from 4 year old in-ground plants at a flower farm near Gatton (152°20′E, 27°33′S), Queensland, Australia. Harvests were in the morning (ca. 09:00 h) from May through June in Autumn 2005. Harvested flowering stems were immediately stood upright into buckets partially filled with tap water. They were kept in shade in the field until transported within 1 h of harvest to the postharvest laboratory at The University of Queensland, Gatton. During transport, buckets containing stems were covered with a plastic film shroud to minimize moisture loss. Upon arrival at the laboratory, the lowermost leaves from all stems were trimmed off. The stem ends were re-cut under deionised water to give stem lengths of approximately 35 cm. Thereafter, all stems with their single terminal inflorescence and 4-5 leaves were stood into plastic buckets containing deionised water.

2.2. Experiment design and treatments

Four experiments were conducted in a vase life evaluation room at 20±1°C, 60±10% relative humidity (R.H.) and 12 μmol m^{-2} s^{-1} light intensity (cool white fluorescent tubes) under a daily

light period of 12 h. In each experiment, all stems were placed individually in 150 mL capacity glass vases containing an anti-microbial vase solution of 10 $mg L^{-1}$ available chlorine provided as the sodium salt of dichloroisocyanuric acid (DICA) (Joyce *et al*., 2000; He *et al.* 2006). That is, DICA was the base constituent in all treatment solutions and was the control vase solution. DICA is a stabilized chlorine formulation that maintains free chlorine availability under chlorine demand conditions. A sheet of aluminium foil was used to cover the mouth of each vase to limit vase solution evaporation. Vases with cut flowering stems were arranged on benches in a randomized complete block (RCB) design. All solutions were freshly prepared at the beginning of the experiments and were not renewed in the course of the experiment.

Experiment 1: Hydraulic conductance. Each day during vase life evaluation, the basal 0-2 cm segment and the 2 cm segment immediately above this (denoted the 2-4 cm segment) was excised under deionised water, and hydraulic conductance was measured. **This destructive sampling was carried out on a new stem each day.**

Experiment 2: Re-cutting. Cut flowering stems were either retained intact or the basal 2 cm from the stem ends was excised daily under water. **This was carried out on the same stems each day.**

Experiment 3: S-Carvone treatments. Three concentrations of S-carvone (Sigma-Aldrich) were compared to the control vase solution; viz. 0, 0.032, 0.318 and 0.636 mM. S-carvone has reported anti-microbial activity (Stammati, et al., 1999; Iacobellis et al., 2005). However, efficacy against a range of plant pathogenic fungi and bacteria was at ≥1mM (Oosterhaven *et al.* 1995b), which is above the concentrations used in the present experiments.

Experiment 4: 4-HR treatments. Three concentrations of 4-HR (Sigma) were compared to the

104 control vase solution; viz. 0, 2.5, 5 and 10 mM.

105 The effects of S-carvone (experiment 3) and 4-HR (experiment 4), as reported in the Results
106 section, were confirmed in an experiment conducted later (July) in the 2005 flowering season.

107 *2.3. Measurements*

108 *Hydraulic conductance.* Stems were removed from their vase solution and 2 cm long segments
109 were excised under deionised water. These segments were used to measure potential hydraulic
110 conductance through the stems as described by Durkin (1979). They were maintained under a
111 pressure head of 100 cm of freshly prepared base vase (i.e. DICA) solution. The eluant was
112 collected overnight (ca.15 h).

113 *Water potential*. Water potentials of inflorescences from intact cut flowering stems were
114 measured using a Scholander pressure chamber (Turner, 1988). Individual inflorescences were
115 sampled daily. They were enclosed in a plastic bag immediately after excision. The rachis was
116 inserted into a rubber gland within the lid of the pressure chamber, and the sealed chamber was
117 pressurised with industrial grade N_2 at a rate of 0.03 MPa $.s^{-1}$. Water potential was recorded from
118 the pressure gauge at the point where xylem fluid started to exude from the surface of the cut
119 rachis.

120 *Vase solution uptake*. The weights of vases without their cut flowering stems were recorded daily
121 during the vase life evaluation period using a balance. Average daily vase solution uptake was
122 calculated by the formula: vase solution uptake rate (g $stem^{-1}$ day^{-1}) = (S_{t-1}-S_t); where, S_t is the
123 weight of vase solution (g) at t = day 1, 2, 3, etc., S_{t-1} is the weight of vase solution (g) on the
124 previous day.

125 *Relative fresh weight and water content*. The fresh weights (FW) of the cut flowering stems

were recorded daily during the vase period. Relative fresh weight (RFW) of stems was calculated by the formula: RFW (%) = $(W_t/W_{t=0}) \times 100$; where, W_t is the weight of stem (g) at t = day 0, 1, 2, etc., and $W_{t=0}$ is the weight of the same stem (g) at t = day 0.

Inflorescence dry weights (DW) were recorded after drying to constant weight in an oven for at least 96 h at 62°C. Water content was calculated as: (FW-DW)/DW (Jones *et al.*, 1993). Water content was determined on days 0, 4 and 8 for 3 replicate detached inflorescences.

Vase life. The cut flowering stems were assessed daily for visual appeal during the vase life evaluation period. Vase life was judged to have ended when 50% or more of florets on an inflorescence were deemed unattractive (Joyce *et al.*, 2000). Observations of specific visible indices of inflorescence deterioration were also recorded in experiment 4. These indices were wilting of inflorescences, floret abscission, colour change from bright red to dull red, and browning of leaves.

2.4. Statistical analyses

Experiments typically involved 5−8 replicate cut flowering stems for each treatment (see individual Tables and Figs.). Data were subjected to analysis of variance (ANOVA) using the General Linear Model program of Minitab Release 14. Means were compared by the least significance difference (LSD) test at the 0.05 probability level.

3. Results

3.1 Hydraulic conductance

Hydraulic conductance of basal 2 cm long stem end segments from cut flowering stems declined rapidly during the first 2 days of the vase period (Fig. 1). Thereafter, hydraulic

148 conductance fell more gradually until day 7. In contrast, hydraulic conductance of the segment
149 immediately above the basal segment (i.e. the 2-4 cm segment) decreased approximately
150 linearly over the first 5 days. Their hydraulic conductance was consistently higher throughout
151 the vase life evaluation period than that of the basal 2 cm stem segments.

152 *3.2. Re-cutting*

153 Re-cutting stems daily by removal of the basal 2 cm from stem ends increased the vase
154 solution uptake rate throughout the vase life evaluation period compared to not re-cutting
155 (control) (Fig. 2A). Re-cutting also maintained inflorescence water potential and water content
156 over the first 4 days of the vase life evaluation period (Fig. 2B and 2C). Thereafter, these indices
157 all fell rapidly. However, re-cutting reduced the relative degree of their decline. Vase life of the
158 flowering stems was prolonged by re-cutting (Table 1).

159 *3.3. S-Carvone*

160 Vase solution treatments with S-carvone at concentrations of 0.318 and 0.636 mM
161 significantly reduced the degree of decline in hydraulic conductance of basal 2 cm long stem end
162 segments (Fig. 3A) and delayed the fall in vase solution uptake rate compared with the control
163 treatment (0 mM S-carvone) (Fig. 3B). These higher S-carvone concentrations also maintained
164 RFW for longer (Fig. 3B) and extended vase life of the flowering stems (Table 1). There were
165 no significant differences between either the control and the 0.032 mM S-carvone treatment or
166 between the 0.318 and the 0.636 mM S-carvone treatments. The beneficial effect of 0.318 mM
167 S-carvone was confirmed in a further experiment, where vase life in S-carvone (plus DICA) was
168 significantly longer (5.4 days) than in DICA alone solution (4.0 days; $n = 8$, $P = 0.05$).

169 *3.4. 4-Hexylresorcinol*

Provision of 4-HR in the vase solution at concentrations ranging from 2.5 to 10.0 mM delayed the fall in hydraulic conductance of basal 2 cm long stem end segments compared with the control treatment (0 mM 4-HR) (Fig. 4A). 4-HR treatments increased vase solution uptake rate throughout the vase life evaluation period (Fig. 4B). There were no significant differences between the control and the 2.5 mM 4-HR treatment from day 4 onwards. Also, there were no significant differences between 5.0 and 10.0 mM 4-HR treatments during the vase period. All 4-HR treatments similarly maintained RFW for longer than the control (Fig. 4C). However, they caused leaf browning and floret abscission, with the highest concentration causing the most serious phytotoxicity (data not shown). Due to foliar and floral phytotoxicity, vase life of cut flowering stems was significantly extended only by the lowest (2.5 mM) 4-HR treatment (Table 1). The beneficial effect of this treatment was confirmed in a further experiment, where vase life in 2.5 mM HR (plus DICA) was significantly longer (5.0 days) than in DICA alone (4.0 days; $n = 8$, $P = 0.05$).

4. Discussion

Termination of vase life for many cut flowers is characterized by wilting. Wilting is generally caused by an imbalance between water uptake by the flowering stems and water loss via transpiration from their leaves and/or other organs despite their stem being held in water continuously (Halevy and Mayak, 1981; van Doorn, 1997). The relatively short vase life of *G.* 'Crimson Yul-lo' cut flowering stems is often associated with early and rapid wilting of inflorescences (He *et al.*, 2006). Data obtained in the current study on stem segment hydraulic conductance, vase solution uptake in response to re-cutting daily and provision of two different

192 inhibitors of enzymes involved in wound induced reactions collectively suggest that
193 inflorescence wilting is due to physiologically mediated stem end blockage.

194 A decline in hydraulic conductance of the basal 0-2 cm stem end segments showed that an
195 obstruction had occurred within the first 2 days of the vase life evaluation period. Hydraulic
196 conductance of the segment immediately above the basal statement was consistently higher
197 throughout vase life. Thus, blockage started at the base. Similarly, van Doorn and Vaslier (2002)
198 reported stem blockage was initially located in the basal 2 cm of cut chrysanthemum flowers
199 (*Dendranthema grandiflora* cv. Vyking). This blockage was a major factor causing severe leaf
200 wilting. Again, re-cutting daily by removal of the basal 2 cm from stem ends increased vase
201 solution uptake by the chrysanthemum stems. Similarly Williamson *et al*. (2002) found that
202 re-cutting 1 cm from the base of the stem every day increased the vase life of *Leptospermum*
203 *polygalifolium* foliage.

204 Wound induced suberization and oxidative processes are associated with stem end blockage
205 in cut flowers (Davies *et al*., 1981; Weiner and Liese, 1995; van Doorn and Cruz, 2000;
206 Williamson *et al.*, 2002; van Doorn and Vaslier, 2002; Loubaud and van Doorn, 2004). Wound
207 reactions impede the entry of micro-organisms into the open tissues of freshly cut surfaces and
208 reduce water loss (Bucciarelli *et al*., 1998). Enzymes such as PAL and catechol oxidase are
209 involved in the biosynthesis of suberin and lignin (Negrel et al., 1993; Moehs et al., 1996).
210 S-Carvone can delay the induction of PAL activity and suberin formation (Oosterhaven *et al.*
211 1995a). Provision of S-carvone in the vase solution (water) prolonged the vase life of cut *Hakea*
212 *francisiana* (Proteaceae) (Williamson *et al.*, 2002). These authors observed, by transmission
213 electron microscopy, that S-carvone treatment inhibited the early wounding response manifest

as modification to stem xylem pit membranes. Vase solution treatments for *G.* 'Crimson Yul-lo', also in the Proteaceae, with S-carvone (0.318 and 0.636 mM) delayed the fall in hydraulic conductance of basal 2 cm long stem end segments, maintained vase solution uptake rate and relative fresh weight for longer, and extended inflorescence vase life. These findings suggest that wound related formation of phenolic compounds, such as suberin, is associated with stem end blockage in cut *G.* 'Crimson Yul-lo' flowering stems. 4-HR is a specific inhibitor of catechol oxidase (Dawley and Flurkey, 1993), an enzyme that oxidizes phenolic compounds with ortho-(1,2) and vicinal (3,4,5-trihydroxy) OH-groups (Mayer, 1987). A short pulse of 4-HR (10 mM, 5 h) delayed leaf wilting of chrysanthemum and bouvardia stems (van Doorn and Vaslier, 2002; Vaslier and Doorn, 2003). The presence of 4-HR in *G.* 'Crimson Yul-lo' vase solutions delayed the decline in hydraulic conductance of basal 2 cm long stem end segments, increased vase solution uptake rate and maintained RFW for longer. Thus wound induced oxidative reactions of phenolic compounds are evidently involved in stem end blockage of cut *G.* 'Crimson Yul-lo'.

DICA (10 mg L^{-1} available chlorine) was used as the base solution constituent to inhibit microbial growth in these experiments, but stabilized chorine formulations lose efficacy over time (Halevy and Mayak, 1981). Nonetheless, the early decrease in stem section hydraulic conductivity during vase life in the presence of chlorine (Fig. 1), consistently positive effects of stem end cutting on vase solution uptake by flowering stems (Fig. 2) and the early positive effects of S-carvone and of 4-HR treatments on vase solution uptake and relative fresh weight in the presence of chlorine suggest that physiological blockage and not microbial blockage was the key limiting factor. Although not reported in the literature, S-carvone could conceivably have

anti-microbial activity at the low concentrations used in the present study (see Materials and Methods). However, the beneficial effects of 4-HR in addition to those of S-carvone in the presence of DICA in increasing hydraulic conductance, improving vase solution uptake and maintaining relative fresh weight for *G.* 'Crimson Yul-lo' cut flowering stems (Figs. 3 and 4) support a physiological inhibitor of wound response role for S-carvone.

In summary, stem end blockage in cut 'Crimson Yul-lo' stems limits their vase life and is manifest as inflorescence wilting. Stem end blockage is apparently due to physiological processes that involve phenolic synthesis and oxidation and possibly suberin formation to repair the wound sustained during cutting.

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Table 1

Vase lives of cut *G.* 'Crimson Yul-lo' flowering stems with stems intact or re-cut daily by removing the basal 2 cm from stem ends (Experiment 2), with several different concentrations of S-carvone in the vase solution (Experiment 3), and with several different concentrations of 4-hexylresorcinol (4-HR) in the vase solution (Experiment 4). DICA (10 mg L^{-1} available chlorine) was included as a base constituent in the vase solutions.

Experiments	Treatments	Vase life (days)
Experiment 2	No re-cutting	4.3
	Re-cutting daily	6.3
	$LSD_{0.05}$ (n = 7)	0.7
Experiment 3	0 mM S-carvone	4.1
	0.032 mM S-carvone	4.5
	0.318 mM S-carvone	5.6
	0.636 mM S-carvone	5.8
	$LSD_{0.05}$ (n = 8)	0.8
Experiment 4	0 mM 4-HR	4.1
	2.5 mM 4-HR	4.8
	5.0 mM 4-HR	4.3
	10.0 mM 4-HR	3.8
	$LSD_{0.05}$ (n = 8)	0.6

List of Figure captions

Fig. 1. Change in hydraulic conductance of the basal 0-2 cm stem segment and segment immediately above that (the 2-4 cm segment) from cut *G.* 'Crimson Yul-lo' flowering stems during the vase life evaluation period. Vertical bar indicates $LSD_{0.05}$ for the treatment by time interaction. DICA (10 mg L^{-1} available chlorine) was included as a base constituent in the solution.

Fig. 2. Change in vase solution uptake rate (**A**), inflorescence water potential (**B**) and inflorescence water content (**C**) for intact cut *G.* 'Crimson Yul-lo' flowering stems versus those re-cut daily under solution by removal of the basal 2 cm. Vertical bars indicate $LSD_{0.05}$ for the treatment by time interaction. DICA (10 mg L^{-1} available chlorine) was included as a base constituent in the vase solutions.

Fig. 3. Change in hydraulic conductance of basal 0-2 cm stem segments (**A**), vase solution uptake rate (**B**), and relative fresh weight (**C**) for cut *G.* 'Crimson Yul-lo' flowering stems with several different concentrations of S-carvone in the vase solution. Vertical bars indicate $LSD_{0.05}$ for the treatment by time interaction. DICA (10 mg L^{-1} available chlorine) was included as a base constituent in the vase solutions.

Fig.4. Change in hydraulic conductance of basal 0-2 cm stem segments (**A**), vase solution uptake rate (**B**), and relative fresh weight (**C**) for cut *G.* 'Crimson Yul-lo' flowering stems with

several different concentrations of 4-hexylresorcinol in the vase solution. Vertical bars indicate $LSD_{0.05}$ for the treatment by time interaction. DICA (10 mg L^{-1} available chlorine) was included as a base constituent in the solution.

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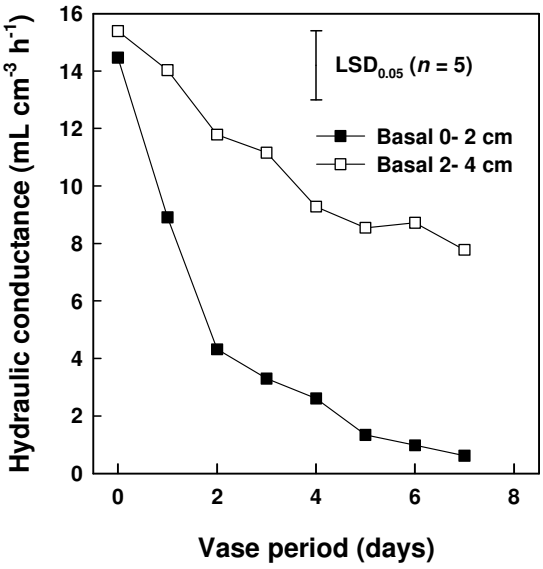

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355 Fig. 1.

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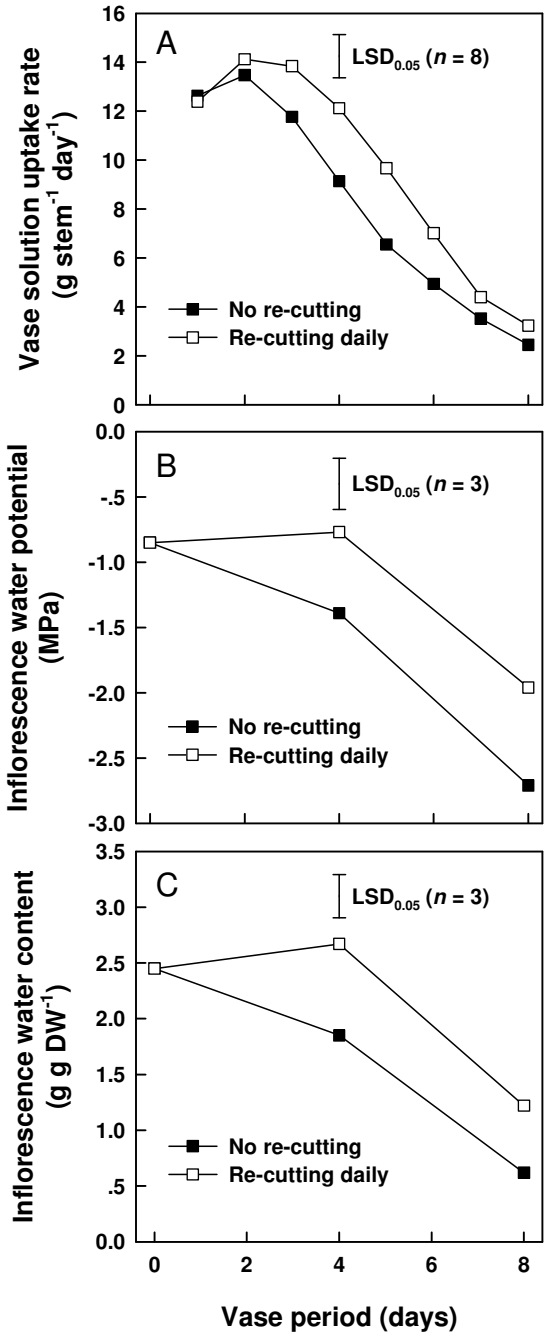

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359 Fig. 2.

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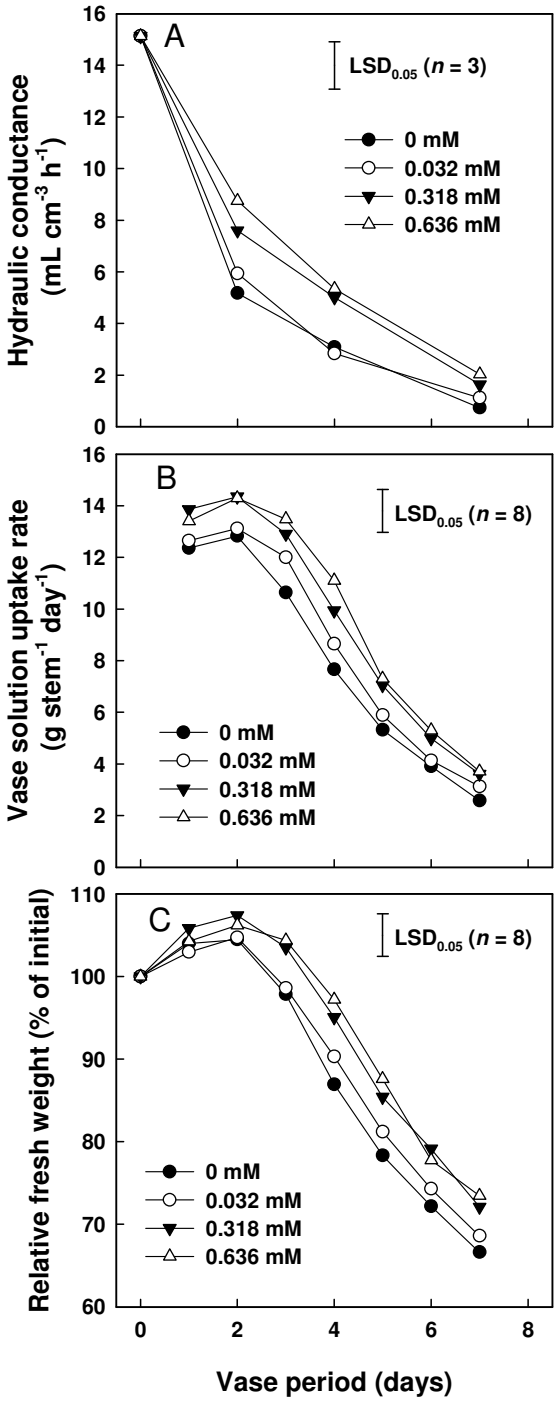

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363 Fig. 3.

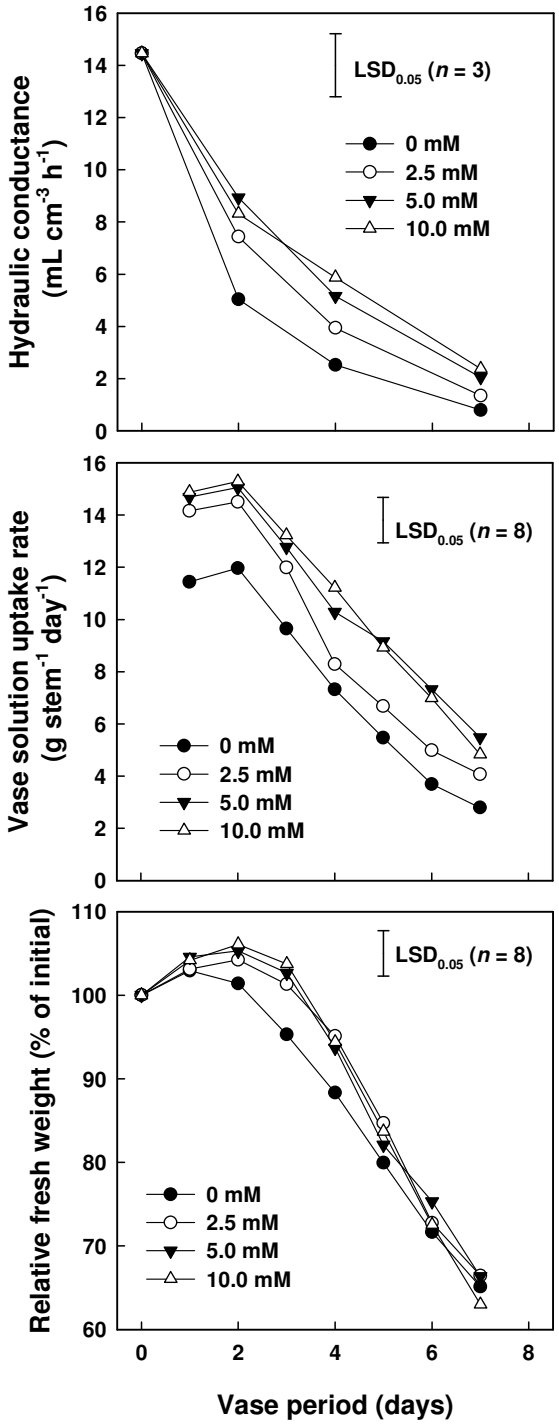
Hydraulic conductance (mL cm-3 h-1)
LSD0.05 (n = 3)
0 mM
2.5 mM
5.0 mM
10.0 mM
Vase solution uptake rate (g stem-1 day-1)
LSD0.05 (n = 8)
0 mM
2.5 mM
5.0 mM
10.0 mM
Relative fresh weight (% of initial)
LSD0.05 (n = 8)
0 mM
2.5 mM
5.0 mM
10.0 mM
Vase period (days)

Fig. 4.