Competition for water between inflorescences and leaves in cut flowering stems of *Grevillea* 'Crimson Yul-lo'

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Running head: *Water relations in* Grevillea

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SUMMARY

Grevillea cv. 'Crimson Yul-lo' has large bright red terminal inflorescences on leafy stems and has recognised commercial potential as a cut flower crop. A major limitation is its relatively short vase-life, often terminated by early wilting of the inflorescence despite apparently turgid leaves. An investigation of the water relations of cut *Grevillea* 'Crimson Yul-lo' stems revealed that the water potential of inflorescences on intact stems in vases was significantly higher (i.e., less negative) than that of leaves from day-0 to day-3 of vase-life. Thereafter, the water potential of inflorescences declined more rapidly than that of leaves, accompanied by visible wilting of the tepals and styles of individual florets. Removal of leaves from the stems reduced both water uptake and water loss, and delayed the onset of a negative water balance in the inflorescence. Bagging of entire stems, leaves only, or inflorescences only, with micro-perforated plastic film to reduce transpiration, reducing leaf number to reduce leaf area, or supplying abscisic acid to reduce leaf stomatal aperture, all aided relative fresh weight retention by stems and extended vase-life. Four or six leaves on a stem caused greater loss in inflorescence water content than zero or two leaves. Considered collectively, these findings show competition for water between the inflorescence and the leaves in cut *Grevillea* 'Crimson Yul-lo' stems contributes to the onset of inflorescence wilting and their short vase-life.

Grevillea is a large genus within the family Proteaceae and it contains over 300 species (Joyce and Beal, 1999), many of which are grown world-wide (Costin and Costin, 1988; Joyce and Beal, 1999; Joyce, 2004). Many grevilleas, especially hybrids of sub-tropical and tropical species, are woody shrubs or small trees with attractive large, colourful inflorescences and soft, divided fern-like foliage that make them appealing as landscape plants. Their inflorescences also have commercial potential as cut flowers (Costin and Costin, 1988; Joyce, 2004), but a major limitation to their use as cut flowers is their relatively short vase-life of often less than 1 week (Faragher, 1989; Joyce *et al.*, 1996; Joyce and Beal, 1999; Joyce, 2004). Cut stems of *Grevillea* 'Crimson Yul-lo' (*Grevillea banksii* × *Grevillea* 'Misty Pink') have large bright-red terminal inflorescences consisting of 90–120 florets at various developmental stages arranged along a single floral rachis (Figure 1A, B), but the inflorescences have a vase-life of only three-four days in water.

A number of factors influencing the longevity of cut *Grevillea* flowers have been studied. The vase-life of *Grevillea* 'Majestic' inflorescences harvested in Winter was generally longer than that of Summer-harvested inflorescences (Vuthapanich *et al.,* 1993). The vase lives of *Grevillea* 'Sylvia' and *Grevillea* 'Honey Gem' were dependent upon the harvest maturity stage, with optimum maturity being characterized by opening of the lowest florets (Joyce and Beal, 1999). Addition of sucrose to vase solutions improved longevity of cut *Grevillea* 'Sylvia' inflorescences (Ligawa *et al.*, 1997). *Grevillea* flowers are classified as 'very low' to 'medium' ethylene producers with a 'non-climacteric' nature (Setyadjit *et al.*, 2004a). Nonetheless, their vase lives may be shortened by ethylene production during senescence (Joyce and Beal, 1999), but silver thiosulphate (STS) pulse treatment can extended the vase-

life of *Grevillea* 'Majestic' inflorescences because the Ag^+ ion blocks the ethylene binding sites (Vuthapanich *et al.*, 1993). Pretreatment of *Grevillea* 'Kay Williams' and 'Misty Pink' with 1-methylcyclopropene, a gaseous inhibitor of ethylene perception, protected inflorescences against subsequent exposure to ethylene (Macnish *et al.*, 2000). However, 1-methylcyclopropene had no effect in the absence of exogenous ethylene. The longevity of cut *Grevillea* 'Sylvia' inflorescences was extended by dipping them in a solution of 6-benzylaminopurine (Setyadjit *et al*., 2004b), but vase solutions containing gibberellic acid did not affect vase-life (Setyadjit *et al.*, 2006).

Although the above-mentioned factors have been studied, investigation of the rapid wilting of inflorescences has not been undertaken. Inflorescence wilting is often the first symptom of senescence observed in cut *Grevillea* stems held in water. At the same time, leaves on the stems remain visually acceptable (i.e., turgid and apparently healthy). Cut flowers wilt because of an imbalance between water uptake from the vase solution via the stem, and water loss as transpiration from stomata and across cuticular surfaces (Mayak *et al.*, 1974; Halevy and Mayak, 1981; Hu *et al*., 1998; Zieslin, 1989; van Doorn, 1997). Poor water relations of cut rose flowers were attributed to abstraction of water from the petals and stems into the leaves (Hu *et al*., 1998). The proportion of cut rose flowers that developed bent neck or wilting was reduced if fewer leaves were left on the cut stems (Carpenter and Rasmussen, 1974; Zieslin *et al*., 1978). Internal competition for water may contribute to the short vase-life of *Grevillea* inflorescences versus leaves on the same stem. This study examined the water relations of cut *Grevillea* 'Crimson Yul-lo' stems. It tested the hypothesis that competition

for water in favour of the leaves leads to inflorescence wilting that characterises the short vase-life of cut *Grevillea* 'Crimson Yul-lo' stems.

MATERIALS AND METHODS

Plant materials

Grevillea 'Crimson Yul-lo' stems were harvested at the commercial maturity stage of 'mature flowers with style looped to length of perianth tube' (Figure 1 A-C, Setyadjit *et al*., 2004a). For the different experiments, they were harvested serially from August through October (Spring season) from 4-year-old plants grown at a flower farm near Gatton (152°20′E, 27°33′S), Queensland, Australia. They were harvested in the morning (*ca.* 09:00 h) and immediately placed upright in buckets with tap water to a depth of *ca.* 10 cm and held in shade until transported, within 1 h of harvest, to the post-harvest laboratory at The University of Queensland, Gatton. During transport, buckets containing stems were covered with a clear plastic film shroud to minimise moisture loss. Upon arrival at the laboratory, the lowermost leaves from all stems were trimmed off, and the stem ends were recut under deionised water to give a stem length of *ca.* 35 cm. Thereafter, all stems, each with a single terminal inflorescence, were placed upright in plastic buckets containing deionised water.

Experiment design and treatments

Four experiments were conducted in a vase-life evaluation room maintained at 20º ± 1ºC and 60 ± 10% RH under irradiation at 12 µmol m^{-2} s^{-1} (from cool-white fluorescent tubes) for a daily light period of 12 h. In each experiment, all stems were placed individually into 150

ml glass vases containing an anti-microbial solution (10 mg l^{-1} available chlorine) provided as the sodium salt of dichloroisocyanurate (DICA; Joyce *et al.*, 2000). Low-density polyethylene film was used to cover the mouth of each vase to limit solution evaporation. Vases with cut stems were arranged on benches in a randomised complete block design.

Experiment 1. Removal of leaves or inflorescences: Cut stems were subject to three treatments: intact stem; all leaves removed; or, inflorescence removed below the lowest floret. Organs were excised using a scalpel blade.

Experiment 2. Retention of different numbers of leaves: Cut stems were subject to four treatments: no leaves; two leaves; four leaves; or, six leaves retained.

Experiment 3. Bagging of leaves or inflorescences: Cut stems were subject to four treatments: whole intact stem; whole stem above the vase bagged; all individual leaves bagged; or, inflorescence bagged. Bagging was with micro-perforated polyethylene bags (with 0.5 mm diameter perforations occupying 0.8% of the total perforated area). The open end of each bag was tied off using string.

Experiment 4. Abscisic acid (ABA) treatment: Cut stems with six leaves were subject to four treatments: no ABA in the vase; 0.04 mM ABA in the vase solution; water (solvent) sprayed onto leaves on alternate days; or, 0.04 mM ABA sprayed onto leaves on alternate days. All treatment solutions contained solution 0.1% (v/v) ethanol because ABA was initially dissolved in a small aliquot of ethanol before being diluted for use, and all vase solutions contained DICA.

Water potential

In experiment 1, water potentials of the inflorescence and of the youngest fully expanded leaf on intact cut stems were measured daily using a pressure chamber (Turner, 1988). The sampled inflorescence or leaf was enclosed in a non-perforated plastic film wrap immediately after excision, and the inflorescence rachis or leaf petiole was inserted into a rubber gland within the lid of the pressure chamber. The pressure chamber was sealed and pressurized with industrial grade N_2 at a rate of 0.03 MPa s^{-1}. Water potential was recorded from the pressure gauge at the point where xylem fluid started to exude from the cut surface.

Water uptake, water loss, and water balance

The weights of each vase, with and without cut stems, were recorded daily during the vase-life evaluation period. Average daily water uptake was calculated using the formula: water uptake (g $stem^{-1}$ d^{-1}) = (S_{t-1} - S_t); where S_t is the weight of vase solution (g) at t = day-1, -2, -3, etc., and S_{t-1} is the weight of vase solution (g) on the previous day. Average daily water loss was calculated using the formula: water loss (g $stem^{-1}$ d^{-1}) = (C_{t-1} - C_t); where C_t is the combined weights of the cut stem and vase (g) at t = day-1, -2, -3, etc., and C_{t-1} is the combined weights of the stem and vase (g) on the previous day. The water balance was calculated as water uptake minus water loss.

Relative fresh weight (RFW) and water content

The fresh weights (FW) of cut stems were measured daily during the evaluation period

using a balance. The RFW of cut stems was calculated using the formula: RFW (%) = $(FW_t/FW_{t=0}) \times 100$; where FW_t is the fresh weight of stem (g) at t = days-0, -1, -2, etc., and $FW_{t=0}$ is the fresh weight of the same stem (g) at t = day-0. Leaf and inflorescence dry weights (DW) were recorded separately after drying in an oven for at least 96 h at 62ºC. Water content was calculated as: (FW-DW)/DW (Jones *et al.*, 1993) on days-0, -4 and -8 using at least three replications.

Vase-life

Vase-life was evaluated daily, and was judged to have ended when 50% or more of florets on an inflorescence were deemed unattractive (Joyce *et al.*, 2000).

Statistical analyses

Experiments typically involved seven-to-nine replicate cut stems for each treatment (see individual Tables and Figures). Data were subjected to two-way analysis of variance (ANOVA) using the General Linear Model program of Minitab Release 14. Treatment means can be compared using the least significance difference (LSD) test at the 5% significance level. Linear regression was applied to the changes in leaf and inflorescence water potential during vase-life.

RESULTS

Inflorescence and leaf water potential

The water potential of inflorescences on cut stems fell gradually until day-3 (Figure 2),

when most of the florets had opened (i.e. styles reflexed). Thereafter, inflorescence water potential declined sharply to reach –2.69 MPa on day-7. The change in water potential was y = -0.30 - 0.32x, r^2=0.85. This rapid decline was accompanied by visible wilting of both the tepals and styles of individual florets (Figure 1E). In contrast, the change in water potential of leaves throughout the vase-life evaluation period was y = -1.40 - 0.16x, r^2=0.75). Over the first three days of vase-life evaluation, leaf water potential was significantly lower than inflorescence water potential (Figure 2).

Leaf or inflorescence removal

Water uptake and water loss by intact cut stems were higher over days-2 and -3 of vase-life than at day-0 (Figure 3A,B). Thereafter, both water uptake and loss declined sharply. These changes led rapidly to a negative water balance (Figure 3C). Removal of leaves markedly lowered water uptake and water loss (Figure 3A,B). Consequently, there was only a small initial increase in water uptake and water loss. After day-3, there was a rapid but non-parallel drop in both water uptake and water loss that led to a negative water balance (Figure 3C). Compared with the rapid decline in water balance of intact cut stems, the onset of negative water balance for stems with leaves removed was more gradual. Removal of inflorescences reduced initial water uptake and water loss compared with intact stems (Figure 3A,B). After day-4, there were parallel and rapid falls in water uptake and water loss (Figure 3A,B). The net effect of these parallel responses was a zero water balance that persisted throughout the vase-life evaluation period (Figure 3C).

RFW of intact cut stems peaked on day-1 of vase-life (Figure 4A). However, if leaves had

been removed, the RFW peak was delayed a further day. Stems with inflorescences removed, maintained approximately constant RFW during the vase-life evaluation period (Figure 4A).

Retention of different leaf numbers

Reducing the number of leaves on stems prolonged the vase-life of cut stems (Table I, experiment 2). The fewer the leaves on stems, the longer was the vase-life.

No differences in RFW were observed between cut stems with zero or two leaves or between stems with four or six leaves throughout vase-life evaluation (Figure 4B). During the evaluation period, RFW peaked on day-2 for all leaf number manipulation treatments. Thereafter, the RFW of stems with zero or two leaves tended to fall more slowly than that of stems with four or six leaves. Differences were significant between RFW of four- and six-leaf treatments compared with the 0-leaf treatment on days-4 and -5 (Figure 4B).

Bagging leaves or inflorescences

All bagging treatments extended the vase-life of cut stems, more so when whole stems or inflorescences were bagged (Table I).

Bagging of whole stems or inflorescences increased the RFW on day-3 of vase-life of cut stems compared with intact unbagged stems (Figure 4C). Bagging the leaves only also increased stem RFW, but the effect was not as pronounced.

ABA treatments

Vase-life was extended by the vase solution containing ABA (Table I), but not by spraying

leaves with ABA solution.

Provision of ABA (0.04 mM) in the vase solution enabled RFW of stems to remain significantly higher from day-3 until day-7 of the vase-life evaluation period (Figure 4D). Spray application of ABA did not, however, significantly increase the RFW of cut stems over the control-sprayed stems (Figure 4D).

Water content of inflorescences and leaves

Water content of inflorescences declined more rapidly than in leaves throughout the vase-life evaluation period (Figure 5A,B). Removing progressively more leaves slowed the loss of inflorescence water content, particularly over the first 4 d of vase-life evaluation (Figure 5A). In contrast, reducing the number of leaves on stems had only a small effect on the water content of the remaining leaves (Figure 5B).

DISCUSSION

Termination of vase-life in cut stems of *Grevillea* 'Crimson Yul-lo' is typically characterised by early and rapid wilting of inflorescences (Figure 1E). This characteristic is generally similar to that of flowering stems cut from other woody shrubs, such as *Thryptomene calycina* (Lindl.) Stapf. (Jones *et al.*, 1993) and *Camellia japonica* L. (Doi and Reid, 1996). Water status measurements for *Grevillea* 'Crimson Yul-lo' supported the initial hypothesis that rapid wilting of inflorescences and associated short longevity of stems is due to competition for water between inflorescences (with higher water potential) and leaves (with lower water potential), in favour of the latter.

Water potential is a direct measure of the water status of cut flowers and is thus related to wilting (Halevy and Mayak, 1981; van Doorn, 1997). Cut Geraldton waxflower (*Chamelaucium uncinatum* Shauer) foliage and flowers had similar water potentials initially (Joyce and Jones, 1992), but water potentials later decreased more in foliage than flowers. The water potential of inflorescences on cut *Grevillea* 'Crimson Yul-lo' stems in vases was significantly higher than that of leaves from day-0 to day-3 of the vase-life evaluation period (Figure 2). Thereafter, the water potential of inflorescences declined more rapidly than that of leaves and was accompanied by visible wilting of the tepals and styles of individual florets. Such a water potential gradient between flowers (petals) and leaves has also been reported for cut rose stems (Hu *et al.*, 1998). Similar water potential gradients have been reported between fruits and leaves of pear trees (Yamamoto, 1983; Behboudian *et al.*, 1994). Such internal water potential gradients can drive water redistribution from organs at higher water potential to organs at lower water potential and result in wilting of the source tissue.

Removal of either leaves or inflorescences from *Grevillea* 'Crimson Yul-lo' stems reduced both water uptake and water loss (Figure 3A,B) has been reported in cut roses and carnations (Carpenter and Rasmussen, 1974; Hu *et al.*, 1998). Removal of leaves from cut *Grevillea* 'Crimson Yul-lo' stems delayed the onset of negative water balance (Figure 3C) and the delayed decrease in stem RFW (Figure 4A). In addition, reducing leaf numbers maintained RFW retention by stems (Figure 4A) and delayed the decline in water content of inflorescences (Figure 5A), thereby extending vase-life (Table I). Similarly, wilting of flowers was delayed if fewer leaves were left on cut rose stems (Carpenter and Rasmussen, 1974; Zieslin *et al*., 1978). Removal of inflorescences significantly reduced water uptake on

days-1 and -2 and reduced water loss on days-2 and -3 compared with the intact *Grevillea* 'Crimson Yul-lo' stems (Figure 3A,B).

Inflorescence removal led to maintenance of a zero water balance (Figure 3C) and maintenance of constant RFW (Figure 4A) throughout the 8 d vase-life evaluation period. The zero water balance resulted from generally parallel changes in water uptake and water loss (Figure 3A,B). Leaves evidently have greater ability to retain water than inflorescences (Figure 5A,B). Bagging of entire stems, inflorescences, or leaves with micro-perforated plastic film also helped stems maintain RFW for longer (Figure 4C) and extended the vase-life of inflorescences (Table I). Bagging can improve the water status of cut *Grevillea* 'Crimson Yul-lo' stems by reducing water loss from inflorescence evapotranspiration and leaf transpiration, as found following the bagging of broccoli inflorescences (*Brassica oleracea* L., Toivonen, 1997), and apple (Watkins and Thompson, 1992) and citrus (Porat *et al.*, 2004) fruit.

Provision of 0.04 mM ABA either in the vase solution or as a leaf spray applied on alternate days also delayed the decline in stem RFW (Figure 4D). Moreover, the ABA vase treatment prolonged inflorescence vase-life (Table I). ABA treatment can induce stomatal closure and reduce water loss in cut roses (Pompodakis and Joyce, 2003) and in Geraldton waxflower foliage (Joyce and Jones, 1992), thereby extending vase-life. Also, ABA sprays to the leaves of 'Royalty' roses on day-1 and day-3 of vase-life reduced water use and delayed senescence (Barthe *et al.*, 1991). These results suggest that reducing leaf stomatal aperture reduces leaf competition for water and improves the water status of cut *Grevillea* 'Crimson Yul-lo' stems, delays inflorescence wilting and thereby extends inflorescence vase-life.

Inflorescences of *Grevillea* ‘Crimson Yul-lo’ are covered with interlocking trichomes. Light microscope examination of hand sections and of lacquer casts of tepal surfaces revealed no evidence of stomata being present. These observations support the proposition that the leaves are stronger or more competitive sinks for water supply than the inflorescences.

In conclusion, inflorescence wilting and short vase-life of *Grevillea* ‘Crimson Yul-lo’ stems is associated with more rapid development of a negative water balance in the inflorescence than in the leaves. In the event of restricted water supply from the vase due to microbial and/or physiological stem blockage (van Doorn, 1997), the internal water potential gradient between the inflorescence (higher water potential) and the leaves (lower water potential) could drive water flow away from the inflorescence, thereby predisposing it to wilting.

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TABLE I

Vase-life of cut Grevillea *'Crimson Yul-lo' stems with different numbers of leaves retained (Experiment 2), with bagged leaves and/or inflorescences (Experiment 3), or with various ABA treatments (Experiment 4)*

Experiment	Treatment	Mean vase-life (d)
Experiment 2	0 leaves retained	5.9
	2 leaves retained	5.6
	4 leaves retained	4.8
	6 leaves retained	4.1
	$LSD_{0.05}$ (n = 8)	0.8
Experiment 3	Stems intact	4.1
	Stems bagged	6.4
	Leaves bagged	5.4
	Inflorescence bagged	6.0
	$LSD_{0.05}$ (n = 7)	1.0
Experiment 4	No ABA in vase-solution	4.3
	0.04 mM ABA in vase-solution	6.1
	0.1% ethanol spray	4.6
	0.04 mM ABA spray	5.3
	$LSD_{0.05}$ (n = 7)	1.2

$LSD_{0.05}$ values allow comparison of treatment means within an experiment.

List of Figure captions

FIG. 1

Grevillea ‘Crimson Yul-lo’. Panel A, a freshly-cut stem. Panel B, a fresh inflorescence. Panel C, an individual floret. Panel D, a wilted inflorescence. Panel E, a senescent cut stem 8 d after harvest. The cut stems in panels A and E are 35 cm in length.

FIG. 2

Change in water potential of inflorescences and leaves on cut *Grevillea* ‘Crimson Yul-lo’ stems during the vase-life evaluation period. Vertical bar indicates $LSD_{0.05}$ values. (n = 5).

FIG. 3

Change in water uptake (Panel A), water loss (Panel B), and water balance (Panel C) of cut *Grevillea* ‘Crimson Yul-lo’ stems with leaves or inflorescences removed. Vertical bars indicate $LSD_{0.05}$ values. (n = 9).

FIG. 4

Change in relative fresh weight (RFW) of cut *Grevillea* 'Crimson Yul-lo' stems. Panel A, with leaves or inflorescences removed (Experiment 1; $n = 9$). Panel B, with different numbers of leaves retained (Experiment 2; $n = 8$). Panel C, with leaves or inflorescences bagged with micro-perforated film (Experiment 3; $n = 7$). Panel D, with abscisic acid (ABA) in the vase solution or sprayed onto the leaves (Experiment 4; $n = 7$). Vertical bars indicate $LSD_{0.05}$ values.

FIG. 5

Changes in water content in inflorescences (Panel A) and in leaves (Panel B) on cut *Grevillea* 'Crimson Yul-lo' stems with different numbers of leaves ($n = 8$). Vertical bars indicate $LSD_{0.05}$ values.

Figure1

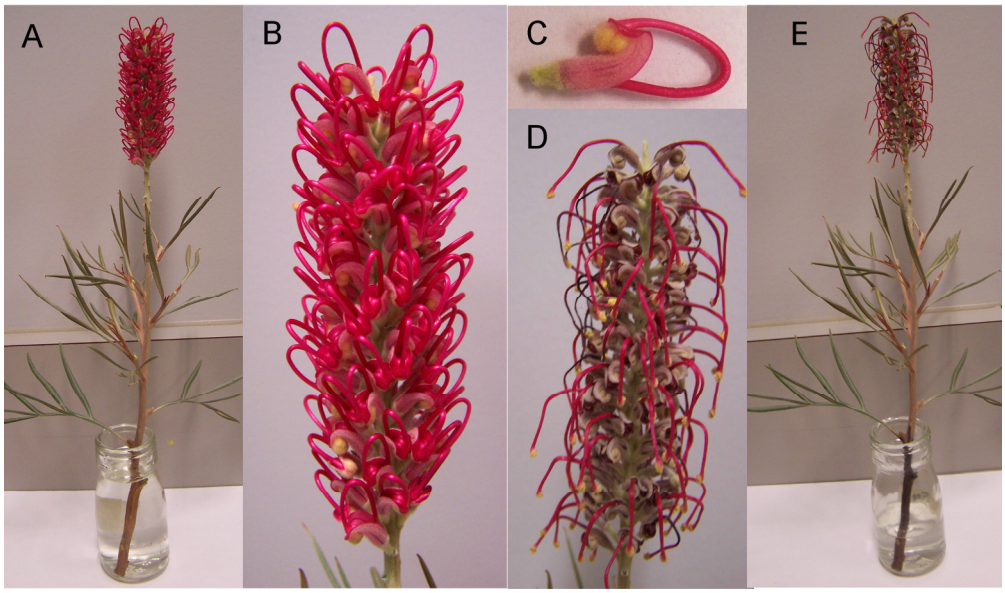


Figure 2

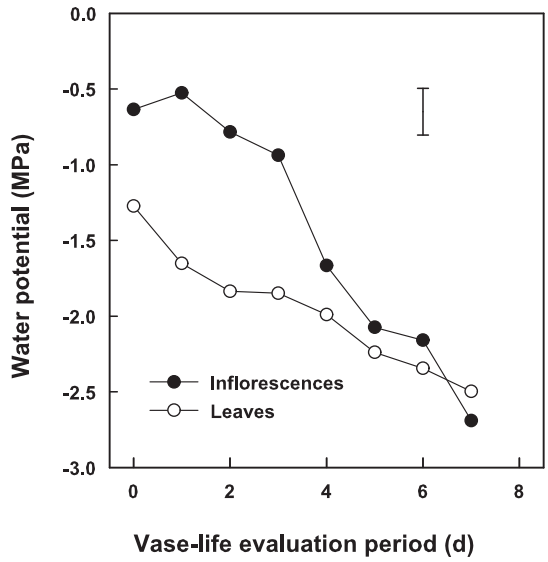


Figure 3

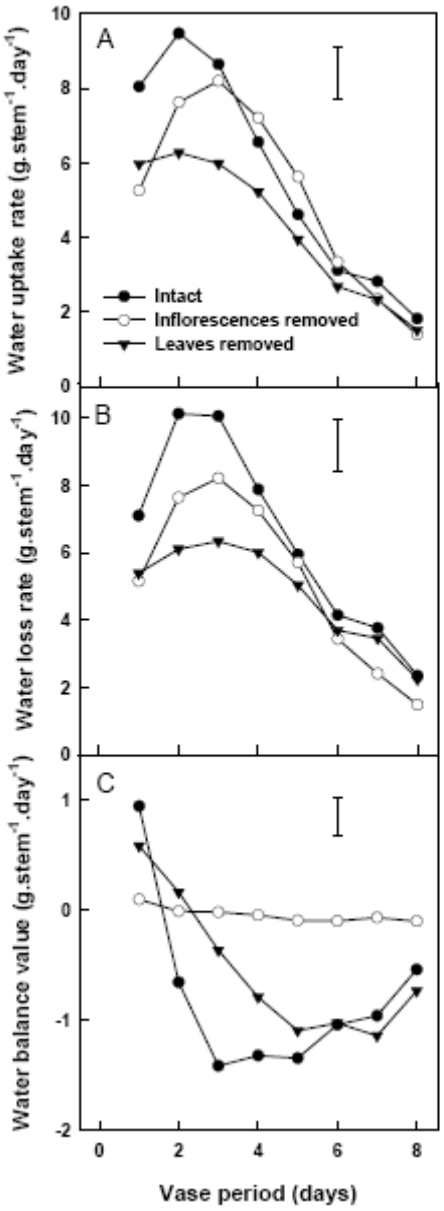

A
B
C
Intact
Inflorescences removed
Leaves removed
Water uptake rate (g.stem-1.day-1)
Water loss rate (g.stem-1.day-1)
Water balance value (g.stem-1.day-1)
Vase period (days)

Figure 4

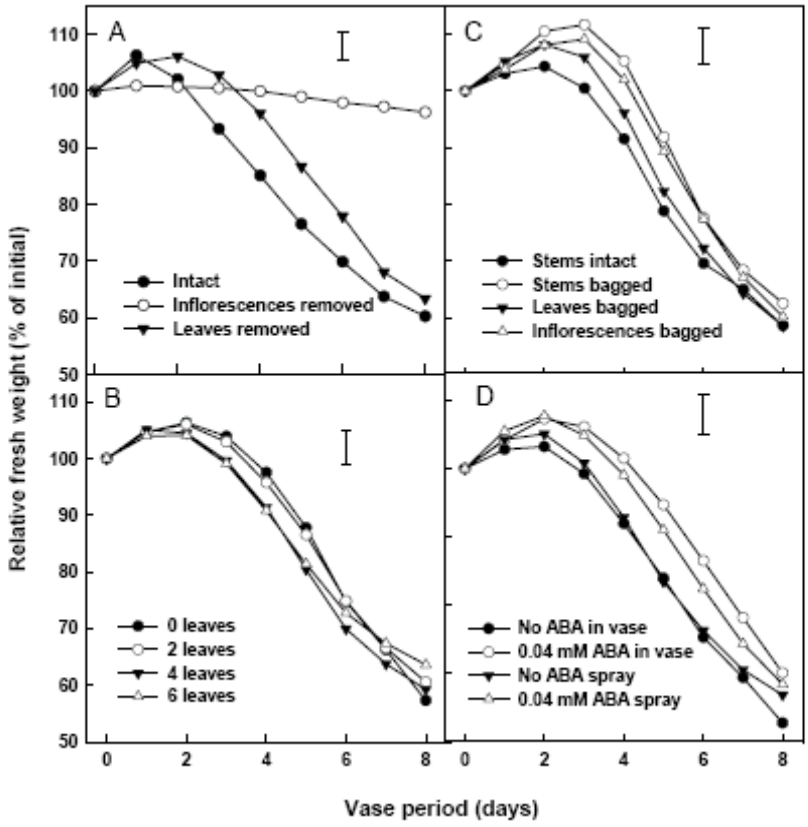
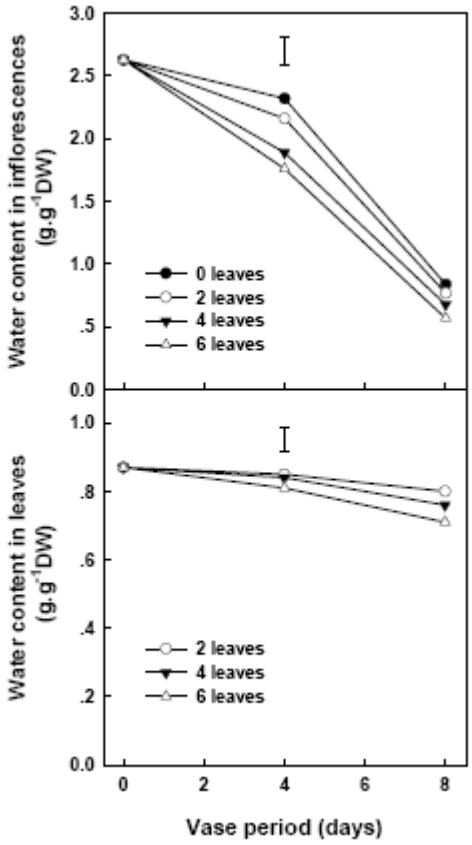

A
B
C
D
Relative fresh weight (% of initial)
Vase period (days)
Intact
Inflorescences removed
Leaves removed
0 leaves
2 leaves
4 leaves
6 leaves
Stems intact
Stems bagged
Leaves bagged
Inflorescences bagged
No ABA in vase
0.04 mM ABA in vase
No ABA spray
0.04 mM ABA spray

Figure 5


Water content in inflorescences (g.g-1DW)
3.0
2.5
2.0
1.5
1.0
.5
0.0
0 leaves
2 leaves
4 leaves
6 leaves
Water content in leaves (g.g-1DW)
1.0
.8
.6
.4
.2
0.0
2 leaves
4 leaves
6 leaves
0
2
4
6
8
Vase period (days)