Beneficial Role of 1-Methylocyclopropene for Cut Lupinus havardii Racemes Exposed to Ethephon

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Additional index words. Big Bend bluebonnet, ethylene, specialty cut flowers, senescence, desiccation, bud opening, vase life, abscission, leakage

Abstract. The raceme of Lupinus havardii Wats. (Big Bend bluebonnet) is a new greenhouse specialty cut flower, but postharvest life is limited by ethylene sensitivity. The authors studied the effects of 160 nL/L 1-Methylocyclopropene (1-MCP) with 0 to 6 days exposure to a 50-μM vase solution of ethephon [2-chloroethyl] phosphonic acid, CEPA on raceme postharvest quality indices and mature flower cell membrane permeability. With no CEPA, 1-MCP delayed postharvest losses in fresh weight and mature flower retention, and extended vase life longevity (VLL) by 1 to 4 days relative to a non-1-MCP control. With 2 days or more of CEPA, 1-MCP deferred raceme fresh weight loss and the abscission of both mature and newly opened flowers from 3 days to 5 days. There was a relatively strong protective effect of 1-MCP on raceme fresh weight, flower retention, and newly opening flowers in the presence of CEPA compared with the absence of CEPA. The greatest raceme VLL (7.2 days) was obtained for 1-MCP-treated racemes that did not receive CEPA in the vase. Although VLL was reduced by CEPA, VLL was consistently greater (by ≥2 days) after 1-MCP treatment relative to no 1-MCP treatment and irrespective of CEPA’s duration. As expected, electrolyte leakage increased with individual flower development and between 1 day and 6 days in the vase. Unexpectedly, however, the 5-day postharvest increase in leakage was intensified by 1-MCP treatment if the racemes were exposed to 1 hour of CEPA in the vase solution. Electrical conductivity measurements suggested that, in the latter treatment (+1-MCP, +CEPA), increased levels of diffusible electrolytes that had yet to be exported to the expanding apical meristem (delayed raceme development) contributed to the higher leakage. Results also demonstrate good potential for quality maintenance of L. havardii racemes by using 1-MCP, and that in addition to flower retention, raceme fresh weight and flower opening should be considered in developing VLL criteria for this new specialty crop.

Lupinus havardii (Big Bend bluebonnet) is a relatively new greenhouse-grown specialty cut flower (Davis et al., 1994; Mackay et al., 1999; Picchioni et al., 2002; Sankhla et al., 2001). The species is indigenous to the semi-arid Chihuahuan Desert of North America, and its raceme could help supply a growing demand for “spike-type” blue flowers in the U.S. cut flower industry (Young, 1997, 1999). A barrier to expanded commercialization of L. havardii is high ethylene sensitivity of its raceme.

In intact (uncut) L. havardii racemes, ethylene synthesis in a given flower begins when the flower has been open for 2 to 3 d, and subsequently proceeds acropetally along the raceme axis (Vasquez, 1998). The initiation of raceme ethylene synthesis (in the oldest, basal flowers) occurs as early as 5 to 9 d before the raceme reaches harvestable size and is brought to the postharvest environment (Mackay et al., 1999; Vasquez, 1998). After harvest and placement in a vase for 4 to 6 d at 21 °C in air and with no preconditioning treatment, desiccation and abscission of flowers at the inflorescence base are observed, by which time the functional vase life has ended (Davis et al., 1994; Mackay et al., 1999; Sankhla et al., 1999). Concurrently, expansion of the apical meristem sink results in the appearance of newly opened flowers that typically represent a 40% to 50% increase in the total number of open flowers originally present at harvest. Thus, vase life of cut L. havardii racemes is a spatially and sequentially organized process, with the most advanced developmental stage at the base, progressing to the least developmentally advanced stage at the apex. Postharvest application of the ethylene action inhibitor 1-Methylocyclopropene (1-MCP) is an environmentally safe treatment in delaying senescence of ethylene-sensitive cut flowers, such as carnation, stock, waxflower, snapdragon, and Gypsophila (Celikel and Reid, 2002; Newman et al., 1998; Serek et al., 1995a; Sierer et al., 1996). Limited data support use of 1-MCP for prolonging vase life of cut L. havardii (Picchioni et al., 2002; Sankhla et al., 2001). However, the effects of 1-MCP on delaying the expression of specific senescence-related traits along the cut axis of L. havardii are not adequately known. Therefore, the objectives of this study were to evaluate the influence of 1-MCP postharvest treatment on cut L. havardii raceme fresh weight and flower retention, apical flower opening, electrolyte leakage, and vase life longevity. We held racemes in vase solutions with or without ethephon [2-chloroethyl] phosphonic acid, or CEPA] to investigate the ability of 1-MCP to counteract the influence of an exogenous ethylene source (ethylene released from CEPA) on the aforementioned variables.

Materials and Methods

Crop cultivation, harvest, and initial handling. Culture of L. havardii ‘Texas Sapphire’ plants was carried out under greenhouse conditions described previously (Picchioni et al., 2002). Inflorescences (racemes) were harvested at 112, 130, and 138 d after transplanting and between 0700 and 0900 h. Cut racemes had yet to abscise flowers or express senescence-related desiccation or darkening of the standard petal (Dracup and Kirby, 1996), and were of the marketable size of 40 to 55 cm in length while supporting a minimum of 20 to 30 fully opened flowers (Mackay and Davis, 1998). A flower was considered fully open when the blue standard petal with yellow banner was fully reflexed and folded at its margins. Immediately after cutting, initial fresh weight and fully open flower number per raceme were recorded, and the proximal
the laboratory for CEPA treatment and 10 d after harvest (following the 12-h 1-MCP exposure, thus comprising eight total treatments). The vase solutions included a control (200 mL deionized water without CEPA) and CEPA treatments of 0, 2, or 6 d. All four CEPA treatments were established with or without previous 1-MCP treatment at 24 h after harvest (following the 12-h 1-MCP exposure). CEPA was applied for either 0 h or 1 h. There were two races per vase replication (to exclude the pedicel), and were placed in separate flasks containing 75 mL deionized water (20 total flowers per raceme position per replication). Any abscised flowers were excluded. The flowers were gently swirled and after 24 h, the electrical conductivity (EC) of the decanted waters was measured. At this time, the flowers (without solution) were frozen in liquid N₂, and the decanted solution was returned to its respective flask containing the frozen flowers. After an additional 24 h in the efflux solution, a final EC measurement was obtained, and the relative leakage ratio (RLR) was then calculated as EC before freezing divided by EC after freezing. The EC readings were first adjusted by subtracting the background EC of the deionized water (10 µS·cm⁻¹).

**Statistical analysis**

All experiments were set up with five replications per treatment combination. A replication (experimental unit) was one raceme in a vase for Expts. 1 and 2, and a pair of racemes per vase for Expt. 3. Response variables analyzed by analysis of variance (ANOVA) included VLL and the daily fresh weight, flower retention, and NNOF for Expts. 1 and 2, and RLR for Expt. 3. Experiments 1 and 2 were first analyzed separately, as a split plot with a completely randomized design on the whole plot and whole-plot treatments in a 2 (1-MCP × 4 CEPA exposure duration) factorial. Number of days in vase was the split-plot factor. ANOVA was performed for each experiment using the GLM procedure of the Statistical Analysis System (SAS Institute, 1998). Similar results were obtained for each experiment, but data were processed as a pooled mean for each experiment.
ANOVA and performed using the MIXED procedure of SAS (SAS Institute, 1990). The pooled analysis was similar to the separate analyses, except that the whole-plot treatments were in a 2 (1-MCP) × 4 (CEPA exposure duration) × 2 (experiment) factorial. Linear and quadratic polynomial contrasts were performed as posthoc tests for the CEPA main effect when it did not interact with 1-MCP. Mean and se were also calculated.

For Expt. 3, separate ANOVAs were performed for each fully opened flower position (lower and upper). Data were analyzed as a 2 (1-MCP) × 2 (CEPA exposure duration) × 2 (days in vase) factorial in a completely randomized design using the SAS GLM procedure (SAS Institute, 1990). Mean and se were also calculated.

Results

Raceme fresh weight, mature flower retention, flower expansion (NNOF), and vase life longevity (Expts. 1 and 2). For all responses, there were some significant interactions involving the experiment factor, but the basic patterns were similar (even though statistically significant) across the two experiments. Therefore, we report only those results averaging over the two experiments. For the pooled analysis of Expts. 1 and 2, there were significant three-way 1-MCP × CEPA × days in vase interactions for fresh weight, flower retention, and NNOF (Figs. 1–3). There were also significant two-way interactions for 1-MCP × days in vase, 1-MCP × CEPA, and CEPA × days in vase, as well as significant main effects. We focus on the three-way interaction 1-MCP × CEPA × days in vase, because it provides complete information about the relationship between 1-MCP and CEPA over time. In addition, we report the 1-MCP × days in vase interaction (averaging over CEPA level) for a practical assessment of the effect of 1-MCP on vase life when ethylene exposure cannot be controlled or predicted (e.g., shipping, transporting, and storing).

The three-way 1-MCP × CEPA × days in vase interaction is apparent in Figs. 1 through 3. Without 1-MCP or CEPA treatment, a net fresh weight gain of 2% to 9% was observed during the first 4 d of vase life (Fig. 1A). Thereafter, these racemes steadily lost fresh weight so that after 10 d of vase life, they had retained an average of 69% of their original fresh weight recorded at harvest (day 0). If the non-1-MCP-treated racemes stood in the presence of CEPA, with 60% of the original flowers still attached to the rachis, 1-MCP treatment, and provided that CEPA was gradually but much less pronounced than in the presence of CEPA, with 60% of the original flowers still attached to the rachis.

By day 10, the 1-MCP-treated (non-CEPA) racemes had retained an average of 76% of their original fresh weight, or 7% more than in the non-1-MCP, non-CEPA controls.

However, there were similar rates of fresh weight decline in the latter treatments during the last half of vase life. CEPA accelerated fresh weight loss from racemes treated with 1-MCP, but did so 2 d later than without 1-MCP (day 5 vs. day 3, respectively). Also, at days 5 and 10 of vase life, fresh weight retention with 1-MCP + CEPA averaged, respectively, ≥18% and 7% higher than it did in racemes that were exposed to CEPA but not 1-MCP.

Three days after harvest, there were 80% to 95% reductions in the retention of mature (fully opened) flowers (flower retention) initially present at harvest (e.g., increases in flower abscission) for the non-1-MCP-treated racemes that were exposed to CEPA in the vase solution (Fig. 2A). By day 5, these racemes were essentially devoid of flowers. Complete (100%) abscission contributed less than 5% to fresh weight losses shown in Fig. 1. Loss in flower retention on non-1-MCP-treated racemes not held in CEPA was gradual but much less pronounced than in the presence of CEPA, with 60% of the original flowers still attached to the rachis on day 10. Increased flower retention was observed on racemes treated with 1-MCP (Fig. 2B) compared with those not treated with 1-MCP.

Unlike the 87% to 60% flower retention on days 5 and 10 respectively in the non-1-MCP, non-CEPA treatment, the racemes that received 1-MCP and lacked CEPA had retained essentially all their flowers up to day 7, 94% on day 8, and 82% on day 10. After postharvest 1-MCP treatment, CEPA accelerated abscission, particularly if applied longer than 2 d. However, 1-MCP delayed CEPA-induced abscission by 2 d beyond that observed without 1-MCP treatment. At day 5, at least 40% of flowers were still retained by the 1-MCP-treated plus CEPA-treated racemes, although flower retention approached 0% by day 10.

Apical meristematic growth during vase life, expressed as NNOF, was similar whether or not racemes received the postharvest 1-MCP treatment, and provided that CEPA was omitted from the vase solution (Fig. 3A and B). In both non-CEPA treatments, there were ≥18 newly opened flowers at the apex by day 9, and on average, fewer than one newly opened flower had abscised between days 9 and 10. Abscission of newly opened flowers was markedly increased after 2, 4, or 6 d of CEPA vase solution treatment. The NNOF on non-1-MCP-treated plus CEPA racemes averaged ≥2.7 on day 2, which...
persisted throughout the vase life observation.

By contrast, the 1-MCP main effect on flower retention, and NNOF relevant to a postharvest environment wherein ethylene exposure can-...
of the newly introduced VLL (Ichimura et al., 2000; Serek et al., 1994). Therefore, continued efforts to extend VLL should be considered in those efforts.

The current findings support the concept of the newly introduced L. havardii could increase consumer demand and incentives for commercialization. Based on our findings, 1-MCP and CEPA treatments and 2, 4, or 6 d of CEPA exposure (50 μL·L⁻¹) together with 1-MCP treatment at 160 nL·C⁻¹·L⁻¹ still afforded a 1-d delay in fresh weight declination below the harvest average (Fig. 1), a 4-d delay in observable abscission of mature flowers (Fig. 2), and a 2-d extension of VLL (Fig. 5). The 1-MCP × days in vase interaction, graphically illustrated across CEPA exposure time (Fig. 4), shows the beneficial effects of using 1-MCP on ‘Texas Sapphire’ racemes under postharvest environments in which the presence of exogenous ethylene or concentration of ethylene sensitivity are not known. This situation may arise while storing, transporting, or retailing cut flowers. Under these ethylene-‘masked’ conditions, the protective effect of 1-MCP persisted for 3 d or longer, depending on raceme response variable.

Enhanced raceme desiccation, mature flower drop, and newly opened flower drop began at vase life day 5 in the 1-MCP + CEPA treatments (Figs. 1–5). This may indicate that 1-MCP-treated racemes regained sensitivity to ethylene, as has been proposed in other cut flower studies (Cameron and Reid, 2001; Macnish et al., 2000). The transitory influence of 1-MCP is thought to result from the synthesis of new ethylene receptor molecules not present at the time of 1-MCP treatment (Sisler and Serek, 1997; Vasquez, 1998). Thus, 1-MCP appears to be of particular value in counteracting deleterious effects of exogenous ethylene in ‘Texas Sapphire’ postharvest environments.

Although the protective effects of 1-MCP were most pronounced in the presence of CEPA, data also suggest that 1-MCP at least partially suppressed action of biosynthesized ethylene. That is, the relatively subtle effect of 1-MCP without CEPA still afforded a 1-d delay in fresh weight declination below the harvest average (Fig. 1), a 4-d delay in observable abscission of mature flowers (Fig. 2), and a 2-d extension of VLL (Fig. 5).

Postharvest 1-MCP treatment delayed the CEPA-induced raceme desiccation, mature flower drop, and newly opened flower drop by 2 d. Although 50 μL of a relatively low CEPA concentration for cut flower studies (Chanasut et al., 2003), it greatly accelerated declines in fresh weight and flower retention of ‘Texas Sapphire’, which confirms high ethylene sensitivity of this inflorescence (Sankhla et al., 1999, 2001; Vasquez, 1998). Thus, 1-MCP appears to be of particular value in counteracting deleterious effects of exogenous ethylene in ‘Texas Sapphire’ postharvest environments.

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2002; Cho et al., 2001; Han, 1998, 2003; Ichimura et al., 2000; Serek et al., 1994). Therefore, continued efforts to extend VLL of the newly introduced L. havardii could increase consumer demand and incentives for commercialization. Based on our findings, 1-MCP should be considered in those efforts.

The current findings support the concept that inflorescence fresh weight change is an important process during initiation of cut flower senescence (Brochov and Woodson, 1989; Van Doorn, 1997), and as such, is an important determinant of VLL. Waithaka et al. (2001) and Celikel and Reid (2002) reported a close temporal relationship between termination of tuberose and stock vase life, and time needed for inflorescence鲜 weight to drop below the initial value. We found a similar relationship when comparing data on fresh weight declination (Fig. 1) with VLL (Fig. 5) for ‘Texas Sapphire’ receiving any CEPA × 1-MCP combination.

Destillation during vase life of cut ‘Texas Sapphire’ racemes is confined to mature flowers originally present at time of harvest, which experience up to an =70% loss in fresh weight and express withering by 6 d of vase life (Picchioni et al., 2002). Growth of the newly opening flowers partially counteracts total raceme fresh weight declines (Fig. 1). However, there is an overriding influence of net water loss from mature flowers on total raceme fresh weight in that the loss exceeds net apical water gain by a factor of approximately three (Picchioni et al., 2007). In cut carnations, only a 25% reduction in stem fresh weight corresponded to a turgor pressure of 0 mPa and a visual expression of petal wilting (Mayak, 1987). These findings suggest that water deficits in the mature flowers of cut ‘Texas Sapphire’ are a critical factor in VLL.

For a given combination of the two 1-MCP treatments and 2, 4, or 6 d of CEPA treatment, the major losses in raceme fresh weight, flower retention, and NNOF occurred on the same day of vase life (Figs. 1–3). Postharvest 1-MCP treatment delayed the CEPA-induced raceme desiccation, mature flower drop, and newly opened flower drop by 2 d. Although 50 μL is a relatively low CEPA concentration for cut flower studies (Chanasut et al., 2003), it greatly accelerated declines in fresh weight and flower retention of ‘Texas Sapphire’, which confirms high ethylene sensitivity of this inflorescence (Sankhla et al., 1999, 2001; Vasquez, 1998). Thus, 1-MCP appears to be of particular value in counteracting deleterious effects of exogenous ethylene in ‘Texas Sapphire’ postharvest environments.

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once 1-MCP bound to ethylene receptors, its inhibition of ethylene action on raceme water balance and flower retention persisted for \( \approx 2 \) d. This hypothesis is supported by a CEPA duration-dependent effect at day 5 (Figs. 1B, 2B, and 3B), and by preliminary results we have obtained with multiple 1-MCP applications to cut ‘Texas Sapphire’ made every 2 d between 0 d and 6 d of total vase life (unpublished data).

The marginally smaller 5-d increase in RLR of upper mature flowers from racemes receiving postharvest 1-MCP but no CEPA treatment compared with flowers from racemes receiving neither 1-MCP nor CEPA (day 6 in Fig. 6A) is consistent with senescence-delaying effects of 1-MCP. Consequently, the enhanced 5-d RLR increase in both upper and lower mature flowers from 1-MCP and CEPA-treated racemes compared with racemes receiving CEPA but no 1-MCP was somewhat unexpected (day 6 in Figs. 6B and D). The EC after freezing in liquid \( N_2 \) averaged 20% higher in the +1-MCP/+CEPA treatment than in the CEPA-only treatment (EC at 6 d vase life, normalized to a per-flower basis to account for \( \approx 20\% \) abscission of mature flowers; data not shown). In similar experimental conditions using silver thiosulfate in place of 1-MCP and followed by continuous 50 \( \mu M \) CEPA in the vase solution, we observed that total export of N, P, and K from senescing, mature ‘Texas Sapphire’ flowers was 33% to 90% less than total N, P, and K export from mature flowers on racemes receiving only CEPA (unpublished data). Thus, higher electrolyte leakage in flowers from the +1-MCP/+CEPA treatment may be attributable to a greater amount of diffusible electrolytes present in the tissue. The greater amount of diffusible electrolytes may, in turn, be associated with delayed development (delayed electrolyte export) from mature flowers by 1-MCP. More research is needed to elucidate the physiological basis of interaction between ethylene action inhibitors, exogenous ethylene, cell membranes, and phloem export from mature flowers to apical tissues of the cut \( L. \) havardii inflorescence.

The findings from the current study counter prevailing concepts of postharvest biology of cut flowers in general and of \( L. \) havardii in particular. First, solute leakage determined at a given stage of vase life may be of questionable value in assessing senescence-related cell permeability change, as has been typically inferred in the floriculture senescence literature (Borochov and Woodson, 1989; Halevy and Mayak, 1979). Senescing petals of cut ‘Texas Sapphire’ racemes take on a capacity to export low-molecular weight solutes and electrolytes in response to increasing metabolic demands of the floral apical meristem (Picchioni et al., 2007). The increase in RLR appears to reflect this developmentally regulated function as a source organ rather than only an increase in permeability per se. Only recently have mineral-exporting traits of senescing petals received quantitative study (Bieleski, 2000; Verlinden, 2004).
Mature flower abscission is regarded as the major ethylene-regulated process determining the end of vase life for cut *L. havardii* racemes (Sankhla et al., 2001). However, total inflorescence fresh weight and the opening and retention of flowers are considered to be important postharvest quality attributes of other indeterminate inflorescences (Chanasut et al., 2003; Han, 1998; Ichimura and Hisamatsu, 1999). In ‘Texas Sapphire’, the latter characteristics responded in markedly similar fashion, as did mature flower retention. Fresh weight and flower opening should therefore be considered in developing commercially applicable longevity criteria for this new specialty cut flower.

_Literature Cited_

Bieleski, R.L. 2000. The bigger picture: Phloem transport through horticultural eyes. Aust. J. Plant Physiol. 27:615–624.

Borochov, A. and W.R. Woodson. 1989. Physiology and biochemistry of flower petal senescence. Hort. Rev. (Amer. Soc. Hort. Sci.) 11:15–43.

Cameron, A.C. and M.S. Reid. 2001. 1-MCP blocks ethylene-induced petal abscission of *Pelargonium peltatum* but the effect is transient. Postharvest Biol. Technol. 22:169–177.

Celikel, F.G. and M.S. Reid. 2002. Postharvest handling of stock (Matthiola incana). HortScience 37:144–147.

Chanasut, U., H.J. Rogers, M.K. Leverenz, G. Grif-fiths, B. Thomas, C. Wagstaff, and A.D. Stead. 2003. Increasing flower longevity in *Eustoma grandiflorum*. Postharvest Biol. Technol. 29:325–333.

Cho, M., F. Celikel, L. Dodge, and M.S. Reid. 2001. Sucrose enhances the postharvest quality of cut flowers of *Eustoma grandiflorum* (Raf.) Shinn. Acta Hort. 543:305–310.

Davis, T.D., S.W. George, W.A. Mackay, and J.M. Parsons. 1994. Development of Texas bluebonnets into floricultural crops. HortScience 29:1110, 1121.

Drucup, M. and E.J.M. Kirby. 1996. Lupin development guide. University of Western Australia Press, Netherlands.

Halevy, A.H. and S. Mayak. 1979. Senescence and postharvest physiology of cut flowers. Hort. Rev. (Amer. Soc. Hort. Sci.) 1:204–236.

Han, S.S. 1998. Postharvest handling of cut *Hesperantha sanguinea* Engelm. flowers: Effects of sucrose and silver thiosulfate. HortScience 33:731–733.

Han, S.S. 2003. Role of sugar in the vase solution on postharvest flower and leaf quality of Oriental lily ‘Stargazer’. HortScience 38:412–416.

Ichimura, K. and T. Hisamatsu. 1999. Effects of continuous treatment with sucrose on the vase life, soluble carbohydrate concentrations, and ethylene production of cut snapdragon flowers. J. Jpn. Soc. Hort. Sci. 68:61–66.

Ichimura, K., K. Kohata, and R. Goto. 2000. Soluble carbohydrates in *Delphinium* and their influence on sepal abscission in cut flowers. Physiol. Plant. 108:307–313.

Mackay, W.A. and T.D. Davis. 1998. ‘Texas Sapphire’ and ‘Texas Ice’ long-stem bluebonnets (*Lupinus havardii*). HortScience 33:348–349.

Mackay, W.A., T.D. Davis, and D. Sankhla. 1995. Influence of scarification and temperature treatments on seed germination of *Lupinus havardii*. Seed Sci. Technol. 23:815–821.

Mackay, W.A., D. Sankhla, T.D. Davis, and N. Sankhla. 1999. Studies on postharvest performance of cut racemes of Big Bend bluebonnet. HortScience 34:503 (abstr.).

Macnish, A.J., D.H. Simons, D.C. Joyce, J.D. Faragher, and P.J. Hofman. 2000. Responses of native Australian cut flowers to treatment with 1-methylcyclopene and ethylene. HortScience 35:254–255.

Mayak, S. 1987. Senescence of cut flowers. HortScience 22:863–865.

Newman, J.P., L.L. Dodge, and M.S. Reid. 1998. Evaluation of ethylene inhibitors for postharvest treatment of *Gypsophila paniculata* L. Hortotechnology 8:58–63.

Piccioni, G.A., M. Valenzuela–Vázquez, and L.W. Murray. 2002. Calcium and 1-methylcyclopene delay desiccation of *Lupinus havardii* cut racemes. HortScience 37:122–125.

Piccioni, G.A., W.A. Mackay, and M. Valenzuela–Vázquez. 2007. Correlative supply and demand functions in *Lupinus havardii*: A forgotten side of cut flower physiology? J. Amer. Soc. Hort. Sci (In Press).

Sankhla, N., W.A. Mackay, and T.D. Davis. 1999. Effect of EthylBloc on postharvest performance and ethylene production of cut racemes of Big Bend bluebonnet. Ppce. Plant Growth Regulat. Soc. Amer. 26:190–192.

Sankhla, N., W.A. Mackay, and T.D. Davis. 2001. Extension of vase life and prevention of ethylene-induced flower shattering in *Lupinus havardii* by 1-methylcyclopene. Acta Hort. 543:75–78.

SAS Institute. 1990. SAS user’s guide: Statistics, version 6. 4th ed. SAS Institute, Cary, N.C.

Sisler, M., E.C. Sisler, and M.S. Reid. 1994. Role of ethylene in opening and senescence of *Gladiolus* flowers. J. Amer. Soc. Hort. Sci. 119:1014–1019.

Sisler, M., E.C. Sisler, T. Tirosh, and S. Mayak. 1999b. 1-Methylcyclopene prevents bud, flower, and leaf abscission of Geraldton wax-flower. HortScience 30:1310.

Sisler, E.C., E. Dupille, and M. Serek. 1996. Effect of 1-methylcyclopene and methylenecyclopropane on ethylene binding and ethylene action on cut carnations. Plant Growth Regul. 18:79–86.

Sisler, E.C. and M. Serek. 1997. Inhibitors of ethylene responses in plants at the receptor level: Recent developments. Physiol. Plant. 100:577–582.

Sisler, E.C. and M. Serek. 2003. Compounds interacting with the ethylene receptor in plants. Plant Biol. 5:473–480.

Van Doorn, W.G. 1997. Water relations of cut flowers. Hort. Rev. (Amer. Soc. Hort. Sci.) 18:1–85.

Vasquez, K.L. 1998. Ethylene production and sensitivity in *Lupinus havardii*, Big Bend bluebonnet. N.M. State Univ., Las Cruces, master’s thesis.

Verlinden, S. 2004. Changes in mineral nutrient concentrations in petunia corollas during development and senescence. HortScience 39:71–74.

Wathaka, K., M.S. Reid and L.L. Dodge. 2001. Cold storage and flower keeping quality of cut tuberoses (*Polianthes tuberosa* L.). J. Hort. Sci. Biotecnol. 76:271–275.

Young, K. 1997. Hot hues. Floral Mgt. 14:41–45.

Young, K. 1999. Hands on: Ready-to-use ideas for better business. Floral Mgt. 15:11–13.