Mycorrhiza (1999) 9:161–166

ORIGINAL PAPER

Ylva L. Besmer · Roger T. Koide

Effect of mycorrhizal colonization and phosphorus on ethylene production by snapdragon (*Antirrhinum majus* L.) flowers

Accepted: 14 June 1999

Abstract We determined the effects of phosphorus (P) concentration and mycorrhizal colonization on ethylene production by flowers of snapdragons (*Antirrhinum majus* L.). Mycorrhizal colonization in a soil-less medium did not significantly affect the total number of flowers per spike or flower P concentration, but it significantly increased flower vase-life and significantly decreased flower ethylene production. This demonstrates for the first time that mycorrhizal colonization can have a non-localized effect on host ethylene production. The reduction in ethylene production caused by mycorrhizal colonization was as large as the variation in ethylene production among snapdragon cultivars. Thus, mycorrhizal colonization may be a viable alternative to toxic ethylene inhibitors such as silver thiosulfate. Increased fertilizer P concentration (15 versus 3 μg P ml^{-1}) significantly increased plant fresh weight and the total number of flowers per spike. In contrast to mycorrhizal colonization, increased fertilizer P concentration resulted in an increase in ethylene production. There was no significant effect of fertilizer P concentration on vase-life. This suggests that factors other than ethylene have at least partial control over vase-life. Postharvest amendment of individual flowers with phosphate also significantly increased flower ethylene production. Phosphorus apparently does not mediate the mycorrhizal effect because mycorrhizal colonization decreased ethylene production without significantly influencing flower P concentration. Moreover, treatment with phosphate increased flower ethylene production. Mycorrhizal colonization did not significantly influence response to exogenous ethylene.

Key words Vase-life · Ethylene sensitivity · Postharvest quality

Y.L. Besmer · Roger T. Koide (✉)
Department of Horticulture, The Pennsylvania State University, University Park, PA 16802 USA
e-mail: rxk13@psu.edu, Fax: +1-814-863-6139

Introduction

The vase-life of cut flowers is a commercially important trait. For snapdragons (*Antirrhinum majus* L.), one of the prime causes of senescence of cut flowers is the production of ethylene (Rogers 1992). To prolong vase-life, snapdragon stems are often treated with compounds that inhibit ethylene production, such as silver thiosulphate (STS, Anderson et al. 1993). Since STS has proven to be of environmental concern, other methods to prolong vase-life are being investigated (Anderson et al. 1993; Kaur and Palta 1997).

Colonization by mycorrhizal fungi has previously been shown to increase the vase-life of cut flowers (Wen 1991; Wen and Chang 1995) but the mechanism involved is unknown. There has been some speculation that greater vase-life of mycorrhizal plants is caused by better vascular development (Wen 1991; Chang 1994). Another mechanism could involve ethylene. McArthur and Knowles (1992) showed that endogenous ethylene production was significantly reduced in potato roots when colonized by mycorrhizal fungi. The possibility exists, therefore, that the prolonged vase-life of cut flowers from mycorrhizal plants is due to decreased ethylene production. The objective of this study was to determine the effects of mycorrhizal colonization on cut flower vase-life, ethylene production and ethylene sensitivity in snapdragons. We also investigated whether P mediates the mycorrhiza effect.

Materials and methods

Three experiments were conducted. In the first, we determined the effect of mycorrhizal colonization on shoot growth, flower longevity, flower ethylene production and response to exogenous ethylene for two hybrid snapdragons differing in sensitivity to ethylene. In the second experiment, we evaluated the effect of fertilizer P concentration on growth, flower longevity and flower ethylene production for the same snapdragon hybrids. In the third experiment, we determined the effect of P on flower ethylene production by adding phosphate directly through the cut peduncle of snapdragon flowers.

Experiment 1

Plant culture

Seeds of two hybrid snapdragons (*Anthirrinum majus* cv. Maryland White Improved, and experimental hybrid SN252) were kindly provided by PanAmerican Seed (Santa Paula, Calif., USA). Relative to Maryland White Improved (MWI), SN252 is significantly more sensitive to ethylene in terms of shattering of the inflorescence (Linda Laughner, PanAmerican Seed). On 22 October 1997, seeds were sown into seedling "plug" trays consisting of 200 10-ml compartments. Each cultivar was grown both with and without mycorrhizal inoculum. The medium containing mycorrhizal inoculum consisted of a 1:1 (v:v) mixture of Pro-Mix PGX and Mycorise HX (both from Premier, Riviere-du-Loup, Quebec, Canada). Mycorise HX contains approximately 2700 spores l^{-1} of *Glomus intraradices* Schenck & Smith in addition to colonized root pieces (plant species is proprietary) in a mixture of approximately 90% perlite and 10% peat moss (volume basis). Pro-Mix PGX supplies a blend of micronutrients and macronutrients sufficient for early seedling growth and consists of 60–70% peat, with the balance as vermiculite. The control medium (without inoculum) consisted of a 5:4:1 (v:v:v) mixture of Pro-Mix PGX, perlite and peat. To promote mycorrhizal fungus spore germination, a drench of 100 μg ml^{-1} Myconate (Natural Product Technologies, Inc., Okemos, Mich., USA) was applied to all trays (both inoculated and control) at the time of sowing. In our experience, this treatment substantially promotes mycorrhizal colonization. Seedlings were grown at 21 °C in a greenhouse receiving full sunlight and provided with supplementary light supplied for 14 h day^{-1} by high intensity discharge lamps. These provided an additional 150 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) at plant level. Plants were irrigated with distilled water as needed.

At 45 days, the mycorrhizal and nonmycorrhizal seedlings were transplanted into larger containers (5.5 cm deep with an opening of 6 × 5 cm) filled with approximately 150 ml of a medium consisting of PGX and perlite (1:1, v:v). The plants were placed on heating mats that maintained the soil temperature at approximately 24 °C. The ambient air temperature was maintained at 16 °C. Supplemental lighting for 14 h day^{-1} was provided by high-intensity discharge lamps yielding an additional 250 μmol m^{-2} s^{-1} PAR at plant level. All plants were fertilized with a base nutrient solution formulated with Peters Excel 15-0-15 at 100 μg N ml^{-1} N (N was 10% ammonia, 85% nitrate, 5% urea). Because the fertilizer is nutritionally complete with the exception of sulfur and phosphorus, it was supplemented with $MgSO_4 \cdot 7H_2O$ (equivalent to 39 μg S ml^{-1}) and $NaH_2PO_4 \cdot H_20$ (equivalent to 3.0 μg P ml^{-1}). At every fifth watering, plants were given tap water to flush out any accumulated salts. After 29 days in the 150-ml pots, 30 plants from each cultivar/inoculation treatment combination were transplanted into pots containing 1500 ml of the PGX:perlite (1:1) mixture and maintained under the same conditions as for the 150 ml pots in the greenhouse.

Harvest, vase-life assessment

Inflorescences (spikes) were harvested when four flowers were open, representing about 35% of the total number of flowers on each spike. Thus, spikes of each cultivar/inoculation treatment combination were harvested at the same developmental stage but not necessarily on the same day. The number of days from sowing to harvest was considered to be the vegetative period and was recorded for each spike. Measurements of shoot fresh weight and height were taken. Each spike was trimmed to a length of 50 cm measured from the top, and leaves were removed from the lower 15 cm of each spike to promote greater uniformity among spikes (Saks and Staden 1993). At the time of harvest, root samples were taken using a soil corer (diameter 2 cm), 4 cores per pot. The roots were cleared and stained, and mycorrhizal colonization was quantified by the line-intersect method (Koide and Mooney 1987).

Each spike was placed in an Erlenmeyer flask containing 200 ml distilled water, then placed in a growth chamber (25 °C, 40 μmol m^{-2} s^{-1} PAR, 10 h day^{-1}, 70% RH). Spikes were supported with a floral wire. Ten plants from each treatment combination were randomly selected and used for ethylene measurements (see below), 10 from each were treated with exogenous ethylene to measure its effects on flower abscission (see below), and the remaining 10 were used to determine vase-life. We considered the end of vase-life to be when 50% of the total number of open flowers on a spike wilted or browned.

Ethylene production by flowers

The five lower open flowers on each spike were assessed for ethylene production 11 days after harvest. The flowers were removed from the spike by cutting the peduncle with a knife. They were weighed, and the five flowers from a single spike were placed together into an unsealed 500-ml vial for 1 h to avoid the accumulation of wound ethylene. The vial contained 50 ml of distilled water to prevent wilting. After 1 h the vials were sealed. After 24 h, two 1-ml gas samples from each vial were taken through a rubber septum and injected into a gas chromatograph (Hewlett Packard 6890) with an alumina column and a flame ionization detector. An average ethylene value for each spike was calculated from the two samples. Flower P concentration was determined colorimetrically on five randomly-selected flowers per treatment (Watanabe and Olsen 1965) after digestion in a mixture of concentrated H_2SO_4 and 30% H_2O_2 at 400 °C for 1 h.

Response to exogenous ethylene application

After having been in the growth chamber (see above) for 3 days, spikes were transferred to a water-jacketed incubation chamber (approximately 0.34 m^3) held at 20 °C. Because different plants matured at slightly different rates, there were variable numbers of spikes in the incubation chamber during the course of this part of the study. Irrespective of the number of spikes, the ethylene concentration within the incubation chamber was maintained at 1 μg ml^{-1} by the tri-gas control sensor of the chamber. Ethylene concentration was carefully checked by independent gas chromatographic analysis. After 48 h, each flower was pulled gently to determine whether an abscission zone had formed in the peduncle and the percentage of abscised flowers was recorded.

Statistical analysis

Measured traits were analyzed using the multifactor analysis of variance procedure of the Statgraphics programs (STSC 1991) following log transformation of data when necessary. Main effects and interactions were considered significant when $P \leq 0.05$. For single-factor analyses, means were separated using the Least Significant Difference Method and differences were considered significant when $P \leq 0.05$.

Experiment 2

Plant culture

On 12 September 1997, seeds of the MWI and SN252 hybrid snapdragons (see above) were sown into seedling "plug" trays as in experiment 1 containing a mixture of Pro-Mix PGX, perlite and Canadian peat (5:4:1, v:v:v). All seedlings were nonmycorrhizal. The trays were placed on capillary mats in a greenhouse and maintained as in experiment 1. After 34 days, when the second true leaf had expanded, the seedlings were transplanted into 150-ml containers filled with PGX:perlite (1:1) as in experiment 1 and moved to a greenhouse section maintained at 16 °C (air temperature) with 100 μmol m^{-2} s^{-1} PAR supplemental light supplied by incandescent lamps 14 h day^{-1}. All plants were fertilized with

the base nutrient solution amended with $MgSO_4 \cdot 7H_2O$ as in experiment 1. Half the plants were randomly designated low P (solution P concentration was 3.0 μg P ml^{-1} in the form of $NaH_2PO_4 \cdot H_2O$) and the other plants were designated high P (solution P concentration was 15.0 μg P ml^{-1}). At every fifth watering, plants were given tap water to flush out excessive nutrients. After 27 days in the 150-ml containers, 20 plants from each cultivar/P treatment combination were transplanted into 1500-ml pots as in experiment 1 and maintained at the P concentrations previously established.

Harvest, vase-life assessment

Harvesting and postharvest handling of plant material was as in experiment 1, but because P concentration affected the number of flowers developed on each spike, spikes from the high P plants were harvested when 6–8 flowers had opened compared to 4 flowers for low P plants. Ten plants from each treatment were randomly selected and observed for vase-life (as in experiment 1) and the other 10 were used for ethylene measurements.

Ethylene production by flowers

Ethylene measurements were made with the gas chromatagraph as in experiment 1, except that two flowers on each spike were assessed 9 days after opening. Individual flowers were weighed and placed in 150-ml clear glass vials containing 20 ml distilled water to prevent wilting. To avoid measuring wound ethylene, the vials were left unsealed for 30 min. Following that, flowers were enclosed for 3 h in the laboratory at approximately 21 °C. Two 1-ml gas samples from each vial were injected into the gas chromatograph and the average value calculated. The mean of the values for the two flowers from a single spike was taken to represent that spike.

Experiment 3

Plant culture

On 14 May 1998, seeds of hybrid snapdragon *Anthirrinum majus* cv. Bismarck (PanAmerican Seed) were sown into seedling "plug" trays (see above) containing a mixture of equal volumes of an autoclaved sandy loam soil and medium sand (pH 5.8, 2.5 μg P ml^{-1} Olsen). This hybrid has an ethylene sensitivity intermediate between SN252 and MWI. Half the tray was inoculated with mycorrhizal inoculum (30% of total medium volume) consisting of *G. intraradices* (Schenck and Smith) grown on the roots of *Sorghum bicolor* (L.) Moench. for approximately 6 months in the mixture of soil and sand described above. The fungus was originally obtained from Native Plants Inc. (Salt Lake City, Utah, USA). The control (nonmycorrhizal) soil/sand medium received water washings of *G. intraradices* spores passed through a 37-μm sieve (Koide and Li 1989). As in experiment 1, all trays were given a drench of 100 μg ml^{-1} Myconate at sowing to promote mycorrhizal colonization of the inoculated seedlings. The seedlings were fertilized every other day with the 3 μg P ml^{-1} complete fertilizer solution described in experiment 1 and given distilled water between fertilizations as needed. The seedlings were grown without supplementary lighting and the air temperature was maintained at 21–25 °C. After 33 days, the seedlings were transplanted into 150-ml pots as described previously, containing a PGX:perlite (1:1, v:v) mixture. The seedlings were fertilized weekly with the complete nutrient solution containing 3 μg P ml^{-1} described previously.

Ethylene production by flowers

On 13 August 1998, seven flowers each from different mycorrhizal plants and five flowers each from different nonmycorrhizal plants were placed separately into 50-ml clear glass vials containing 2 ml of 15 mM $NaH_2PO_4 \cdot H_2O$. Another seven flowers from mycorrhizal plants and five flowers from nonmycorrhizal plants were placed in vials containing 2 ml of 15 mM NaCl. Because the flowers developed more rapidly on the mycorrhizal plants, the average age of mycorrhizal flowers was greater than the average age of nonmycorrhizal flowers at the time of sampling. Phosphate-treated and control flowers for a given mycorrhizal treatment, however, did not differ in age. The vials were kept in the laboratory at approximately 21 °C. After 18 h (to allow uptake of the solution in the vial), the vials were sealed and ethylene production was assessed after 3 h as in experiment 2. Flowers were then rinsed with distilled water and their P concentrations determined as in experiment 1. Roots samples were cleared and stained, and mycorrhizal colonization was quantified as in experiment 1.

Results

Experiment 1

Mycorrhizal colonization was high in both varieties when inoculated, and control plants were nonmycorrhizal (Table 1). Mycorrhizal colonization significantly increased the vegetative period for both varieties, and SN252 had a significantly longer vegetative period than MWI. There was a positive effect of colonization on shoot fresh weight and shoot height for MWI but no significant effect of colonization on SN252. Mycorrhizal colonization significantly increased vase-life, and MWI had a significantly shorter vase-life than SN252. Neither mycorrhizal colonization nor cultivar significantly influenced the number of flowers per spike. Mycorrhizal colonization significantly decreased flower ethylene production in both cultivars, and SN252 (the cultivar with the greater sensitivity to ethylene) had significantly lower rates of ethylene production by flowers than MWI. Mycorrhizal colonization did not significantly influence flower abscission following exogenous ethylene treatment, but SN252 abscised a significantly higher proportion of flowers than did MWI. Mycorrhizal colonization did not significantly increase the flower P concentration in SN252. Unfortunately the flowers for MWI nonmycorrhizal plants were inadvertently thrown out so a comparison with MWI mycorrhizal plants was not possible.

Experiment 2

The high P concentration (15 μg P ml^{-1}) significantly decreased the vegetative period and significantly increased the number of flowers per spike (Table 2). Cultivar did not significantly influence either of these traits. The positive effect of high P concentration on shoot fresh weight and shoot height was slightly greater for SN252 than for MWI, resulting in a significant interaction between cultivar and P concentration. SN252 had a significantly greater vase-life than MWI while P concentration had no significant effect on vase-life. Flower ethylene production was significantly increased

Table 1 Effect of mycorrhizal colonization and cultivar on various traits of snapdragon plants in experiment 1. Values shown are means ±se. Flower ethylene production was measured 11 days after anthesis, and flower abscission was measured 48 h after a 1 μg ml^{-1} C_2H_4 treatment. A two-factor analysis of variance was performed on all variables except root colonization and flower P concentration for which the least significant difference method was used to separate means. The same letter indicates there was no significant difference between means. Vegetative period was the period from sowing to harvest (when approximately 35% of flowers on a spike were open (*M* mycorrhizal, *NM* Nonmycorrhizal, *MWI* Maryland White Improved (PanAmerican Seed), *SN252* experimental hybrid SN252 (PanAmerican Seed)

	Root colonization (%, $n=10$)	Vegetative period (days, $n=30$)	Shoot fresh weight (g, $n=30$)	Shoot height (cm, $n=30$)	Vase-life (days, $n=10$)	Flowers $spike^{-1}$ ($n=10$)	C_2H_4 (nl g^{-1} h^{-1}, $n=10$)	C_2H_4 treatment Abscised flowers (%, $n=10$)	Flower P concentration (%, $n=5$)
MWI M	71.2 (4.6) a	118.3 (0.5)	27.2 (0.9)	82.3 (1.5)	13.2 (0.4)	14.6 (0.5)	0.98 (0.09)	43.8 (5.1)	0.28 (0.01) a
MWI NM	0.0	114.1 (0.4)	24.2 (0.6)	77.6 (1.1)	12.3 (0.3)	14.5 (0.4)	2.47 (0.42)	47.9 (4.6)	Lost
SN252 M	72.0 (3.1) a	120.3 (0.6)	29.3 (0.9)	92.7 (1.3)	16.8 (0.5)	14.2 (0.6)	0.60 (0.12)	72.6 (3.8)	0.26 (0.01) a
SN252 NM	0.0	116.0 (0.4)	29.5 (0.7)	92.6 (1.3)	15.5 (0.7)	14.3 (0.5)	0.99 (0.11)	69.8 (3.9)	0.28 (0.01) a
Analysis of variance									
Cultivar		0.0001	0.0840	0.0628	0.0001	0.5641	0.0001	0.0000	
M treatment		0.0001	0.0001	0.0001	0.0360	1.0000	0.0001	0.8856	
Interaction		0.9428	0.0379	0.0744	0.6986	0.8469	0.4380	0.4422	

Table 2 Effect of P treatment and cultivar on various traits of snapdragon plants in experiment 2. Values shown are means ±se. Flower ethylene production was measured 9 days after anthesis. Vegetative period was the period from sowing to harvest (when approximately 35% of flowers on a spike were open. $n=30$ except where noted. A two-factor analysis of variance was performed on all variables. Abbreviations as in Table 1

	Vegetative period (days)	Shoot fresh weight (g)	Shoot height (cm)	Vase-life (days, $n=10$)	Flowers $spike^{-1}$ ($n=10$)	C_2H_4 (nl g^{-1} h^{-1}, $n=10$)
MWI High P	115.0 (1.0)	45.7 (1.2)	90.9 (0.9)	11.3 (0.2)	20.1 (0.8)	9.24 (2.77)
MWI Low P	127.6 (1.3)	23.9 (0.4)	77.1 (0.8)	11.4 (0.3)	11.5 (0.6)	3.07 (0.50)
SN252 High P	114.7 (0.6)	47.9 (1.3)	106.5 (0.9)	14.5 (0.4)	20.6 (0.5)	2.47 (0.33)
SN252 Low P	128.9 (1.1)	23.0 (0.5)	83.7 (0.8)	14.8 (0.7)	10.4 (0.6)	1.79 (0.36)
Analysis of variance						
Cultivar	0.6477	0.8026	0.0001	0.0001	0.6411	0.0003
P treatment	0.0001	0.0001	0.0001	0.7497	0.0001	0.0039
Interaction	0.4544	0.0290	0.0001	0.8978	0.2112	0.1629

at the high P concentration, and MWI flowers had a significantly higher ethylene production than those of SN252.

Experiment 3

Mycorrhizal colonization of inoculated plants at harvest was moderate (mean 26.5%, se 2.8, $n=7$). Nonmycorrhizal plants were not colonized. The postharvest addition of P to flowers significantly increased flower ethylene production and P concentration for flowers of both mycorrhizal and nonmycorrhizal plants (Table 3).

Table 3 Effect of P treatment and mycorrhizal status on individual flower ethylene production and P concentration after 18 h P treatment for plants grown in experiment 3. Values shown are means ±se. n (M) = 7, n (NM) = 5. M and NM treatments are not comparable because M flowers were older than NM flowers at the time of measurement. Comparisons between P levels within each mycorrhiza treatment were thus made using Fisher's protected least significant difference method. Different letters indicate a significant difference between means

	C_2H_4 (nl g^{-1} h^{-1})	P concentration (%)
NM − P	0.56 (0.09) b	0.17 (0.01) b
NM + P	3.49 (0.93) a	0.24 (0.02) a
M − P	2.64 (0.90) y	0.17 (0.01) y
M + P	5.10 (0.95) x	0.25 (0.01) x

Discussion

One of our major results is the significant reduction in flower ethylene production caused by mycorrhizal colonization. This occurred for both MWI and SN252 hybrids, which differed in inherent sensitivity to exogenous ethylene. The mechanism for this effect of mycorrhizal colonization is not clear, but it does not appear to be related to flower P concentration; flowers produced by mycorrhizal and nonmycorrhizal SN252 plants did not differ significantly in P concentration.

Moreover, flowers of both cultivars produced more ethylene when higher concentrations of P were applied to the soil (experiment 2), and when detached flowers of both mycorrhizal and nonmycorrhizal plants were allowed to take up phosphate (experiment 3). This latter effect was shown to be unrelated to a salt-induced decrease in osmotic potential. The mycorrhiza effect thus appears to be opposite to the phosphate effect.

McArthur and Knowles (1992) also showed a negative effect of mycorrhizal colonization and a positive effect of added phosphate on ethylene production in potato roots. They further demonstrated that water-soluble substances leached from mycorrhizal roots inhibited 1-amino cyclopropane-1-carboxylic acid (ACC) oxidase activity. However, they found that reduced ethylene production in mycorrhizal plants was confined to colonized roots. In split-root studies, the nonmycorrhizal portion of an otherwise mycorrhizal root system did not have reduced ACC oxidase activity. Our results demonstrate for the first time that mycorrhizal colonization can have a non-localized effect on ethylene production by flowers. Because flower age alone may influence ethylene production, we were careful to compare mycorrhizal and nonmycorrhizal or high P and low P flowers when they were at the same developmental stage. Our results, therefore, are not artifacts caused by different developmental rates in plants of contrasting treatments, but suggest a possible mechanism that may help explain the increase in vase-life caused by mycorrhizal colonization reported by Wen and Chang (1995).

In both experiments 1 and 2, SN252 had longer vase-life than MWI despite being more sensitive to ethylene. Perhaps this was because SN252 produced less ethylene. However, ethylene production can not be the only factor determining vase-life. In experiment 1, while there was a negative relationship between ethylene production and vase-life for each of the cultivars considered alone, the relationship was not apparent when considering both cultivars together. Moreover, in experiment 2, ethylene production was significantly affected by phosphate fertilization, but vase-life was not. Therefore, it seems clear that if reduced ethylene production is involved in the increased vase-life of flowers of mycorrhizal plants, it is not be the only factor. For example, better vascular development in mycorrhizal plants as suggested by Wen (1991) and Chang (1994) may also be involved. Indeed, Daft and Okusanya (1973) have shown that mycorrhizal maize plants possess more vascular bundles than nonmycorrhizal plants. A positive effect of mycorrhizal colonization on flower vase-life may also be due to a reduction in sensitivity to ethylene. In experiment 1, however, mycorrhizal colonization did not significantly affect floral response to exogenous ethylene. Thus it appears that the mycorrhizal effect on ethylene physiology is primarily an effect on production and not on sensitivity.

Our results and those of McArthur and Knowles (1992) are different from those obtained by Chalutz et al. (1980). Those researchers demonstrated that higher intercellular phosphate levels inhibited ethylene production in fruits, roots, shoots, fungi and bacteria. We did not measure intercellular phosphate, but we assume that it was increased as a consequence of added phosphate. The reasons for this inconsistency are not clear at this time.

In most other studies, the effects of mycorrhizal colonization on plant performance were related to increased P uptake (Smith 1980; Hayman 1983; Abbott and Robson 1984; Koide 1991). There are, however, other documented effects of mycorrhizal colonization on plant performance that are apparently unrelated to host P status, including enhanced resistance to disease (Dehne 1982; Newsham et al. 1995). Further research on the effects of mycorrhizal fungi unrelated to nutrient uptake would, therefore, appear to be warranted. Responses not mediated by increased host P status may be of particular interest when plants are grown in soil-less media. Because in soil-less media, P concentrations are not usually buffered as in soil, the enhancement of P uptake or growth by mycorrhizal fungi may be less common than in soil (Graham and Timmer 1984; Powell et al. 1985).

While the experimental hybrid SN252 demonstrated a greater sensitivity to exogenous ethylene than MWI, its flowers inherently produced less ethylene than did those of MWI. In experiment 1, the vase-life of SN252 was also approximately 3 days longer than that of MWI averaged across both treatments. Mycorrhizal colonization increased vase-life by just over 1 day, averaged across both cultivars. Thus variation in vase-life among host genotypes was significantly greater than variation caused by mycorrhizal colonization. Nevertheless, mycorrhizal colonization may be a useful non-toxic strategy for increased vase-life in plants such as snapdragon.

Acknowledgements We thank the American Floral Endowment for providing funding, Dr. Christopher Walsh at University of Maryland for providing valuable advice, laboratory space and equipment for the ethylene work in experiments 1 and 2, and Linda Laughner (PanAmerican Seed) for providing the seed.

References

Abbott LK, Robson AD (1984) The effect of VA mycorrhizae on plant growth. In: Powell CL, Bagyaraj DJ (eds) VA mycorrhiza. CRC, Boca Raton, Fla, pp 113–130

Anderson RD, Sanderson KC, Smith D, Williams JC (1993) Reduction of induced abscission of geranium (*Pelargonium hortorum*) petals and snapdragon (*Anthirrinum majus*) florets using three anti-ethylene compounds. Plant Growth Reg Soc Am Quart 21:144–150

Chalutz E, Mattoo AK, Fuchs Y (1980) Biosynthesis of ethylene: the effect of phosphate. Plant Cell Environ 3:349–356

Chang DCN (1994) What is the potential for management of vesicular-arbuscular mycorrhizae in horticulture? In: Robson AD, Abbott LK, Malajczuk N (eds) Management of mycorrhizas in agriculture, horticulture and forestry. Kluwer, Dordrecht, pp 187–190

Daft MJ, Okusanya BO (1973) Effect of *Endogone* mycorrhiza on plant growth. VI. Influence of infection on the anatomy and reproductive development in four hosts. New Phytol 72:1333–1339

Dehne HW (1982) Interaction between vesicular-arbuscular mycorrhizal fungi and plant pathogens. Phytopathology 72:1115–1119

Graham JH, Timmer LW (1984) Vesicular-arbuscular mycorrhizal development and growth response of rough lemon in soil and soilless media: effect of phosphorus source. J Am Soc Hortic Sci 109:118–121

Hayman DS (1983) The physiology of vesicular-arbuscular endomycorrhizal symbiosis. Can J Bot 61:944–963

Kaur N, Palta JP (1997) Postharvest dip in a natural lipid, lysophosphatidylethanolamine, may prolong vase life of snapdragon flowers. Hortscience 32:888–890

Koide RT (1991) Nutrient supply, nutrient demand and plant response to mycorrhizal infection. New Phytol 117:365–386

Koide RT, Li M (1989) Appropriate controls for vesicular-arbuscular mycorrhiza research. New Phytol 111:35–44

Koide RT, Mooney HA (1987) Spatial variation in inoculum potential of vesicular-arbuscular mycorrhizal fungi caused by formation of gopher mounds. New Phytol 107:173–182

McArthur DAJ, Knowles NR (1992) Resistance responses of potato to vesicular-arbuscular mycorrhizal fungi under varying abiotic phosphorus levels. Plant Physiol 100:341–351

Newsham KK, Fitter AH, Watkinson AR (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. Tree 10:407–411

Powell CL, Bagyaraj DJ, Clark GE, Caldwell KI (1985) Inoculation with vesicular-arbuscular mycorrhizal fungi in the greenhouse production of asparagus seedlings. N Z J Agric Res 28:293–297

Rogers MN (1992) Snapdragons. In: Larson RA (ed) Introduction to floriculture. Academic, San Diego, pp 93–112

Saks Y, Staden JV (1993) Evidence for the involvement of gibberellins in developmental phenomena associated with carnation flower senescence. Plant Growth Reg 12:105–110

Smith SE (1980) Mycorrhizas of autotrophic higher plants. Biol Rev 55:475–510

STSC (1991) Statgraphics statistical graphics system, version 5.1, STSC, Rockville

Watanabe FS, Olsen SR (1965) Test of an ascorbic acid method for determining phosphorus in water and $NaHCO_3$ extracts from soil. Soil Sci Soc Proc 29:677–678

Wen CL (1991) Effect of temperature and *Glomus* sp. on the growth and cut flower quality of micropropagated *Gerbera jamesonii*. MS thesis, National Taiwan University

Wen CL, Chang DCN (1995) Effects of temperature and *Glomus* sp. on the cut flower quality of micropropagated *Gerbera jamsoni.* Memoirs of the College of Agriculture, National Taiwan University 35:75–91