1-Methylcyclopropene Improves Ethylene Tolerance of Unrooted Herbaceous Cuttings but Delays Adventitious Root Development in *Angelonia*, *Calibrachoa*, *Impatiens*, *Portulaca*, *Sutera*, and *Verbena* Cultivars

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Abstract. Knowing which herbaceous taxa are ethylene sensitive and managing exposure of unrooted terminal stem cuttings to ethylene in those taxa are critical for maintaining high-quality propagules that root readily. Of 59 taxa surveyed, freshly harvested terminal cuttings of *Begonia* hybrid ‘Snowcap’, *Lantana camara* L. ‘Patriot Sunbeam’, and *Portulaca oleracea* L. ‘Fairytale Sleeping Beauty’ were sensitive to exogenous application of 1 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene, as demonstrated by leaf abscission within 24 hours of treatment. Exposure to 1-methylcyclopropene (1-MCP) at 700 $\mu\text{L}\cdot\text{L}^{-1}$ for 4 hours before ethylene treatment prevented ethylene injury in these species/cultivars. Exposing unrooted cuttings to 700 $\mu\text{L}\cdot\text{L}^{-1}$ 1-MCP induced significant endogenous ethylene biosynthesis in terminal cuttings of the five taxa tested: *Euphorbia pulcherrima* Willd. ex Klotzsch ‘Visions of Grandeur’, *Impatiens hawkeri* W. Bull ‘Sonic Red’, *Pelargonium peltatum* (L.) L’Hérit. ‘Mandarin’, *Pelargonium ×hortorum* Bailey (pro sp.) [inquinans × zonale] ‘Rocky Mountain White’, and *Petunia ×hybrida* Vilm. ‘Suncatcher Coral Prism’. Exogenous 1 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene improved adventitious rooting in two cultivars: *Begonia* hybrid Anita Louise and *Fuchsia triphylla* L. Honeysuckle. Other trials showed that 1-MCP exposure reduced root number and length of *P. ×hortorum* ‘Kardino’ and delayed adventitious rooting in all six cultivars tested: *Angelonia angustifolia* Benth. ‘Carita Lavender’, *Calibrachoa ×hybrida* Llave & Lex. ‘Terra Cotta’, *I. hawkeri* ‘Sonic Red’, *P. oleracea* ‘Fairytale Sleeping Beauty’, *Sutera cordata* Kuntze ‘Abunda Blue Improved’, and *Verbena ×hybrida* Groenl. & Ruempl. ‘Aztec Wild Rose’. Subsequent exposure to 1 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene partially mitigated the negative effects on rooting from exposing cuttings to 1-MCP.

Ethylene promotes leaf yellowing, abscission, and general senescence in unrooted cuttings of *Codiaeum variegatum* Blume. (croton), *Pelargonium ×hortorum* Bailey (pro sp.) [inquinans × zonale] (zonal geranium), and *Lantana camara* L. (lantana) as reported by Müller et al. (1998), Kadner et al. (2000), and Rapaka et al. (2007), respectively.

Although ethylene has a negative impact on cutting quality in ethylene-sensitive species, it also plays a critical role in coordinating plant growth under water stress and aiding adventitious root formation (Clark et al., 1999; Mergemann and Sauter, 2000; Sharp and LeNoble, 2002; Stepanova and Alonso, 2005).

Research shows that ethylene injury may be prevented through chemical treatments and environmental management of ethylene-sensitive, floriculture taxa. Treating plant materials with the ethylene biosynthesis inhibitors silver thiosulfate and silver nitrate and the ethylene binding inhibitor 1-MCP have proved useful. Ethylene management has been accomplished through use of perforated packaging to allow ethylene dissipation and 1-MCP sustained release mechanisms

(Kadner and Druege, 2004; Kadner et al., 2000; Macnish et al., 2004).

1-MCP disrupts downstream ethylene-mediated developmental signaling by acting as a competitor for ethylene-binding sites (Sisler, 2006). It is widely used in the produce and cut flower industries and is increasingly used on unrooted cuttings (Blankenship and Dole, 2003). 1-MCP prevented leaf yellowing of unrooted cuttings and improved rooting frequency in terminal cuttings of zonal geraniums (Kadner and Druege, 2004; Serek et al., 1998). 1-MCP stimulated ethylene biosynthesis in unrooted geranium cuttings (Kadner and Druege, 2004; Rapaka et al., 2008), and 1-MCP-treated geranium cuttings produced fewer adventitious roots compared with untreated cuttings (Rapaka et al., 2008). Since 1-MCP is a strong competitive inhibitor of ethylene binding, these results indicate that geranium ethylene biosynthesis is regulated by an autoinhibitory feedback mechanism (Kadner and Druege, 2004).

Four experiments were conducted to gain a better understanding of the effect of ethylene and 1-MCP treatments on cutting establishment of several floriculture crop species as such information may be useful for developing practical methods for improving cutting survival and rooting. Expt. 1 tested the two-part hypothesis that, when floriculture crop stem cuttings from a broad range of herbaceous taxa are surveyed, a subset will be found to be ethylene sensitive, and taxa will differ in response to 1-MCP and ethylene pretreatments during vegetative propagation. Expt. 2 tested the hypothesis that exposing cuttings to 1-MCP promotes endogenous ethylene synthesis using five taxa (*Euphorbia pulcherrima* ‘Visions of Grandeur’, *Impatiens hawkeri* ‘Sonic Red’, *Pelargonium peltatum* ‘Mandarin’, *P. ×hortorum* ‘Kardino’, and *Petunia ×hybrida* ‘Suncatcher Coral Prism’). Expt. 3 tested the hypothesis that exposing cuttings to 1-MCP affects time to form adventitious roots in six taxa (*Angelonia angustifolia* ‘Carita Lavender’, *Calibrachoa ×hybrida* ‘Terra Cotta’, *I. hawkeri* ‘Sonic Red’, *Portulaca oleracea* ‘Fairytale Sleeping Beauty’, *Sutera cordata* ‘Abunda Blue Improved’, and *Verbena ×hybrida* ‘Aztec Wild Rose’). Expt. 4 tested the hypothesis that 1-MCP and ethylene influence root development in ‘Kardino’ zonal geranium cuttings.

Materials and Methods

Plant material: production and maintenance of stock plants. Terminal, three-leaf, stem cuttings of the 59 taxa in Tables 1 and 2 plus ‘Visions of Grandeur’ poinsettia (Expt. 3) and ‘Kardino’ zonal geranium (Expt. 4) were rooted in plastic pots containing soilless substrate (Fafard P3; Conrad Fafard Inc., Agawam, MA) under intermittent mist. Once rooted, these plants were maintained as stock plants and irrigated manually with unamended water, 600 mg·L⁻¹ N liquid fertilizer (20N-4.37P-16.6K; Ultrasol, SQM North America, Atlanta, GA), or flowable

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Table 1. Effect of 1-MCP and ethylene on rooting cuttings of 12 taxa. Rooting was scored after 3 weeks: 3 = more than five roots ≥ 2 cm, 2 = more than five roots but fewer than five ≥ 2 cm, 1 = callus and or roots present with all roots < 2 cm, and 0 = no callus or roots. Means are an average of 12 single cutting replications. (Y) and (N) following species/cultivar names indicate that leaves did or did not abscise, respectively, within 24 h of exposing cuttings to $1.0 \mu\text{L}\cdot\text{L}^{-1}$ ethylene.

Species/cultivar	1-MCP (0 $\text{nL}\cdot\text{L}^{-1}$) and ethylene ($\mu\text{L}\cdot\text{L}^{-1}$)			1-MCP (700 $\text{nL}\cdot\text{L}^{-1}$) and ethylene ($\mu\text{L}\cdot\text{L}^{-1}$)			Significance of main effects and interaction		
	0	0.1	1.0	0	0.1	1.0	MCP	Ethylene	Interaction
<i>Angelonia angustifolia</i> Carita Lavender (N)	1.9	1.6	1.8	1.8	1.8	1.0	NS	NS	*
<i>Begonia</i> hybrid Anita Louise (N)	2.8	3.0	3.0	2.9	3.0	3.0	NS	*	NS
<i>Begonia</i> hybrid Miss Murry (N)	2.3	2.1	2.0	2.0	1.9	2.0	*	NS	NS
<i>Begonia</i> hybrid Snowcap (Y)	3.0	3.0	2.4	2.7	2.8	2.8	NS	NS	**
<i>Begonia</i> hybrid cultivar 3 (N)	2.0	1.9	1.7	1.8	1.7	2.0	NS	NS	*
<i>Calibrachoa hybrida</i> Terra Cotta (N)	3.0	3.0	3.0	2.9	2.9	2.7	*	NS	NS
<i>Euphorbia pulcherrima</i> Christmas Star (N)	0.7	1.0	0.4	1.0	0.2	0.7	NS	NS	*
<i>Fuchsia triphylla</i> Honeysuckle (N)	1.8	2.5	2.8	2.0	2.2	2.8	NS	**	NS
<i>Lantana camara</i> Patriot Sunbeam (Y)	2.0	2.0	0.2	2.0	2.0	2.0	***	***	***
<i>Pelargonium xhortorum</i> Rocky Mountain White (N)	3.0	2.7	2.7	2.8	2.8	2.4	NS	*	NS
<i>Pelargonium peltatum</i> Amethyst (N)	2.5	3.0	2.2	3.0	2.9	2.8	*	NS	NS
<i>Portulaca oleracea</i> Fairytales Sleeping Beauty (Y)	3.0	3.0	3.0	3.0	3.0	3.0	NS	NS	NS

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

1-MCP = 1-methylcyclopropene; NS = Nonsignificant.

lime (Limestone F, Cleary Chemical Inc., Dayton, NJ) as needed to maintain a target pour-through electrical conductivity of 2.0 to 3.5 $\text{dS}\cdot\text{m}^{-2}$ and pH of 5.8 to 6.2. Plants were thoroughly watered before harvesting cuttings. Greenhouse air temperatures were 24 ± 5 °C day/ 18 ± 2 night °C. Average daily light integral during the experiment was $11 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, calculated from periodic measurements of photon flux density at plant height using a quantum light sensor (Apogee Instruments, Inc., Logan, UT).

1-MCP and ethylene treatments. In all experiments, single-node stem cuttings or larger as appropriate of similar size and age were harvested. Cuttings were placed into 900-mL glass jars covered by a damp paper towel moistened with deionized water. Jars were placed into 210-L gas tight chambers and exposed to either 0 or 700 $\text{nL}\cdot\text{L}^{-1}$ 1-MCP (EthylBloc; Floralife Inc., Walterboro, SC) for 4 h, the minimum reentry time for 1-MCP. In all but Expt. 2, jars were divided randomly and equally among three ethylene treatment chambers following 1-MCP treatment. The 0 $\mu\text{L}\cdot\text{L}^{-1}$ chamber contained activated charcoal to absorb ambient ethylene. Chamber atmospheres were adjusted to 0, 0.1, or 1.0 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene, and cuttings remained in the chambers for a standard overnight treatment of 20 h.

Rooting of cuttings. In all experiments, cuttings were inserted into bedding plant flats containing soilless substrate (Fafard P3; Conrad Fafard Inc.) and placed under intermittent mist operating at 6 s every 6 min for the first 48 h then, 6 s every 10 min for 10 d from 0600 to 2000 HR. Temperature and light conditions were the same as for stock plants.

Data collection: Expt. 1. Cuttings were taken from the 59 taxa listed in Tables 1 and 2 and exposed to MPC and ethylene treatments and rooted as described above. They were observed daily for two ethylene injury symptoms: leaf yellowing and leaf abscission. Cuttings were classified as “Yes” if one or more abscised leaves were observed and “No” if no leaf abscission was observed 24 h after placement into rooting flats. Degree of rooting was recorded

Table 2. Forty-seven taxa exhibiting no effect of 1-MCP or ethylene on leaf abscission after 24 h or rooting after 21 d.

Species/cultivar
<i>Abutilon megapotamicum</i> (A. Spreng.) A. St.-Hil. & Naudin
<i>Alternanthera dentata</i> (Moench) Scheygr. New Burgundy
<i>Alternanthera dentata</i> Party Time
<i>Alternanthera dentata</i> Red
<i>Begonia</i> hybrid Frosty
<i>Begonia</i> hybrid Tom Ment
<i>Begonia</i> hybrid cultivar 3
<i>Begonia</i> hybrid cultivar 4
<i>Centradenia hybrida</i> Purple Showers
<i>Graptophyllum pictum</i> Griff.
<i>Hemigraphis alternata</i> T.Anderson
<i>Impatiens hawkeri</i> W. Bull Fanfare Orange
<i>Impatiens hawkeri</i> Sonic Red
<i>Impatiens hawkeri</i> Sonic White
<i>Impatiens hawkeri</i> Super Sonic Peach
<i>Impatiens hawkeri</i> Super Sonic Red
<i>Impatiens hawkeri</i> Super Sonic White
<i>Impatiens walleriana</i> Hook. f. Fiesta Pink Ruffle
<i>Iresine herbstii</i> Hook. Purple Lady
<i>Pelargonium xhortorum</i> Bailey (pro sp.) [inquinans $\times$ zonale] Blues
<i>Pelargonium xhortorum</i> Charleston
<i>Pelargonium xhortorum</i> Tango
<i>Pelargonium peltatum</i> (L.) L'Hérit Beach
<i>Pelargonium peltatum</i> Lambda
<i>Pelargonium peltatum</i> Mandarin
<i>Pelargonium peltatum</i> Picasso
<i>Pelargonium peltatum</i> Ragtime
<i>Pelargonium peltatum</i> White Blizzard
<i>Perilla frutescens</i> L. ex B.D.Jacks. var. <i>crispa</i> (Benth.) H.W.Li Magilla
<i>Petunia xhybrida</i> Vilm. Suncatcher Coral Prism
<i>Plectranthus ciliatus</i> E.Mey. Gold Coin
<i>Plectranthus ecklonii</i> Benth. Mona Lavender
<i>Plectranthus tomentosus</i> Benth. ex E.Mey. Nicollella
<i>Plectranthus amboinicus</i> (Lour.) Spreng.
<i>Plectranthus madagascariensis</i> Benth.
<i>Salvia officinalis</i> L. Tricolor
<i>Scaevola aemula</i> R. Br. Blue Wonder
<i>Solenostemon scutellarioides</i> (L.) Codd Aurora
<i>Solenostemon scutellarioides</i> Dark Copper
<i>Solenostemon scutellarioides</i> Rustic Orange
<i>Solenostemon scutellarioides</i> cultivar 4
<i>Streptocarpus xhybridus</i> Voss
<i>Strobilanthes dyeriana</i> Mast.
<i>Sutera cordata</i> Kuntze Abunda Blue Improved
<i>Torenia fournieri</i> Linden ex Fourn. Summer Wave Blue
<i>Tradescantia zebrina</i> G.Don Zebrina
<i>Verbena x hybrida</i> Groenl. & Ruempl. Aztec Wild Rose

1-MCP = 1-methylcyclopropene.

3 weeks after propagation as follows: 3 = ≥ 2 cm in length, 1 = callus development or more than five roots ≥ 2 cm in length, 2 = presence of one to five roots ≤ 2 cm, and 0 = more than five roots but no more than five no roots.

Data collection: Expt. 2. Cuttings were taken from ‘Sonic Red’ impatiens, ‘Mandarin’ ivy geranium, ‘Suncatcher Coral Prism’ petunia, ‘Visions of Grandeur’ poinsettia, and ‘Rocky Mountain White’ zonal geranium. Cutting weights were recorded before exposing them to 1-MCP treatment as described above and storing them in sealed 900-mL glass jars in darkness at $20 \pm 1^\circ\text{C}$ for 7 d. Ethylene concentration in jar headspace was measured and used to calculate ethylene per gram initial fresh weight generated by the cuttings on days 1, 3, 5, and 7 in storage. Ethylene concentration was measured with a gas chromatograph (Varian 3400; Varian Inc., Walnut Creek, CA) fitted with a glass column (Porapak Q, 80–100 mesh, 183 cm $\times$ 2 mm; Sigma-Aldrich, Inc., St. Louis, MO) running at 120°C injector, 120°C column, and 130°C detector (flame ionization) temperatures. Flow rates for the He carrier, H_2 , and O_2 were 30, 16, and $90\text{ mL}\cdot\text{min}^{-1}$, respectively. Injection volume was 1 mL of headspace gas drawn via a neoprene port on the jar lid.

Data collection: Expt. 3. Cuttings were taken from ‘Carita Lavender’ angelonia, ‘Terra Cotta’ calibrachoa, ‘Sonic Red’ New Guinea impatiens, ‘Fairytale Sleeping Beauty’ portulaca, ‘Abunda Blue Improved’ sutera, and ‘Aztec Wild Rose’ verbena. They were exposed to 1-MCP and ethylene treatments and rooted as described above. Observations of cutting condition and root

emergence were made daily for 10 d. Data recorded were number of abscised leaves, number of yellowing leaves at least one-third of full size, number of cuttings with emergent roots, and number of cuttings with roots $\geq 1\text{ mm}$ long.

Data collection: Expt. 4. Cuttings were taken from ‘Kardino’ zonal geranium stock plants and exposed to 1-MCP and ethylene treatments and rooted as described above. Data recorded after 21 d included number of abscised leaves, number of yellowing leaves at least one-third of full size, number of roots $\geq 1\text{ mm}$ long, length of the five longest roots, and root area. Root area was determined using a digital area meter (Model 3100; LICOR, Lincoln, NE). Rooted cuttings were dried at 70°C for 72 h and root and shoot dry weights were recorded.

Statistical analysis. Statistical procedures were performed using SAS software version 9.2 (SAS Institute, Cary, NC). Expt. 1 was conducted as a completely randomized design (CRD) with 12 cuttings as replicates in a factorial design of the 2 1-MCP treatments by the 3 ethylene treatments. Statistical analysis was conducted using PROC GLM.

Expt. 2 was conducted as a CRD with three jars (each containing six cuttings) as replicates within each of two 1-MCP treatments. Statistical analysis was conducted using PROC GLM.

Expt. 3 and 4 were conducted as randomized complete block designs. There were six individual cuttings per cultivar within each of six treatments, created by the factorial design of two 1-MCP treatments by three ethylene treatments, within each of three blocks.

Statistical analysis of Expt. 3 data were conducted using analysis of variance (ANOVA) in combination with several methods of means testing and regression. Time to root emergence main effects were analyzed using PROC MIXED at $P \leq 0.05$. The Weibull function $Y = a(1 - \exp\{-[(X-l)/k]^c\})$ was used to analyze adventitious rooting response (Dias, 2001) with model terms as follows: Y is the percentage of cuttings with roots on day X , a the total percent of rooted cuttings on a given day, l the number of days to the onset of rooting, and k the number of days from onset to maximal rooting. The dimensionless parameter c estimates the symmetry of the germination distribution around the normal curve ($c > 3.60$ = negative asymmetry, $c < 3.26$ = positive asymmetry, and $3.26 \leq c \leq 3.60$ = symmetry). Nonlinear regression, PROC NLIN, was used at $P \leq 0.05$. Model terms were evaluated for significance by comparison of F values at $\alpha = 0.05$.

Root development data in Expt. 4 were tested for main effects with ANOVA using a general linear model. Subsequent comparisons between treatments or means of

Fig. 1. Cumulative concentration of ethylene in dark-stored, 900 mL, sealed jars containing ‘Sonic Red’ impatiens, ‘Mandarin’ ivy geranium, ‘Suncatcher Coral Prism’ petunia, ‘Visions of Grandeur’ poinsettia, and ‘Rocky Mountain White’ zonal geranium cuttings. Points represent mean ($n = 3$) $\pm$ 1 SE ethylene concentration quantified 1, 3, 5, and 7 d after exposure to $700\text{ nL}\cdot\text{L}^{-1}$ 1-MCP ($\blacklozenge$) or left untreated ($\square$). Linear equations were generated on the entire dataset and superimposed on the means. Equations and fit are given within each graph.

combined treatments were made using orthogonal contrasts at the $P \leq 0.05$ level.

Results

Expt. 1. Ethylene-induced leaf abscission occurred in cuttings of 3 of the 59 taxa surveyed: *Begonia* hybrid ‘Snowcap’, *Lantana camara* ‘Patriot Sunbeam’, and ‘Fairytale Sleeping Beauty’ portulaca (Table 1).

Leaves abscised within 24 h and only when treated with $1.0 \mu\text{L}\cdot\text{L}^{-1}$ in all three of the ethylene-sensitive cultivars. However, begonia and portulaca cuttings defoliated by ethylene were rooted rapidly while ethylene-defoliated lantana cuttings rooted slowly (personal observation). Prior exposure to 1-MCP prevented ethylene-induced leaf abscission in the three cultivars exhibiting ethylene sensitivity, reducing the number of

abscised leaves per cutting from close to 1.0 to 0 in all three cultivars. Significant leaf yellowing was not observed in any treatment for any of the 59 taxa.

1-MCP treatment affected adventitious rooting on cuttings from 4 of the 59 taxa (Table 1). In two cases rooting was enhanced (‘Patriot Sunbeam’ lantana and *Pelargonium peltatum* ‘Amethyst’) and in two cases rooting was reduced (*Begonia*

Fig. 2. Adventitious root development of 1-MCP treated (■) and untreated (▲) cuttings of ‘Carita Lavender’ angelonia, ‘Terra Cotta’ calibrachoa, ‘Sonic Red’ impatiens, ‘Fairytale Sleeping Beauty’ portulaca, ‘Abunda Blue Improved’ sutera and ‘Aztec Wild Rose’ verbena. Points represent mean (n = 3) percentage of cuttings with at least one root ≥ 10 mm each day for 10 d after 1-MCP treatment. Solid lines are fitted Weibull curves. Shaded areas are the 95% confidence interval for each line. Parameter estimates l , k and c are followed by the respective standard error in parentheses. The parameter a (the total percentage rooted) is not included as it was universally estimated as 1 with no SE.

hybrid 'Miss Murry' and 'Terra Cotta' calibrachoa).

Ethylene treatment significantly affected adventitious rooting of cuttings from four taxa (Table 1). In two cases more and longer roots (*Begonia* hybrid 'Anita Louise' and *Fuchsia triphylla* L. 'Honeysuckle') and in two cases fewer and shorter roots ('Patriot Sunbeam' lantana and 'Rocky Mountain White' zonal geranium) were observed in cuttings exposed to ethylene (Table 1).

Leaf abscission and adventitious rooting were unaffected by ethylene and 1-MCP exposure for the majority of taxa tested (Table 2).

Expt. 2. Cuttings from all five taxa tested produced significantly more ethylene when stored after exposure to 1-MCP compared with untreated cuttings of the same cultivar and the degree of response differed greatly among taxa (Fig. 1). 'Suncatcher Coral Prism' petunia cuttings generated $1.05 \mu\text{L}\cdot\text{L}^{-1}\cdot\text{g}^{-1}$ fresh weight ethylene, while 'Sonic Red' New Guinea impatiens cuttings produced $0.13 \mu\text{L}\cdot\text{L}^{-1}\cdot\text{g}^{-1}$ fresh weight ethylene by day seven (Fig. 1). Untreated cuttings for these two taxa produced 0.08 and $0.04 \mu\text{L}\cdot\text{L}^{-1}\cdot\text{g}^{-1}$ fresh weight ethylene over the same period, respectively. The other three taxa fell between these two extremes in ethylene synthesis following 1-MCP exposure but had similarly low ethylene production when untreated (Fig. 1).

Expt. 3. All cuttings from all six cultivars produced adventitious roots by 10 d, but time to 100% root emergence was significantly longer when cuttings were treated with 1-MCP in all taxa tested (Fig. 2). The delay in days was 0.39, 0.73, 1.00, 0.59, 0.31, and 0.60 for angelonia, calibrachoa, impatiens, portulaca, sutera, and verbenia, respectively.

1-MCP delayed first root emergence. For example, first root emergence of 1-MCP-treated impatiens cuttings was 1.70 d later than for cuttings without 1-MCP exposure. Rooting of the two varieties that took the longest time to root without 1-MCP, 'Sonic Red' New Guinea impatiens and 'Carita Lavender' angelonia, was further delayed by 1-MCP treatment to a greater degree than varieties that took less time to root without 1-MCP. For example, 1-MCP treatment delayed initial root emergence 0.36 d on portulaca cuttings, a rapidly rooting species, whereas 1-MCP delayed initial root emergence 1.70 d on impatiens cuttings, a more slowly rooting species.

Expt. 4. Leaf abscission was greater for cuttings treated with 1-MCP and $0.1 \mu\text{L}\cdot\text{L}^{-1}$ ethylene than for cuttings treated with $0.1 \mu\text{L}\cdot\text{L}^{-1}$ ethylene only (Fig. 3). Leaf yellowing was negligible, and no significant differences among treatments in leaf yellowing were noted (data not shown).

Exposure to $700 \text{ nL}\cdot\text{L}^{-1}$ 1-MCP before rooting influenced all rooting parameters in 'Kardino' zonal geranium cuttings (Table 3). Compared with untreated cuttings, those treated with 1-MCP had fewer (18.1 vs. 27.5) and shorter roots (22.1 mm vs. 29.8 mm) (Fig. 3). Root surface area followed the

same trend as did root number (data not shown). Root dry weight was less when 1-MCP was used, but shoot dry weight was the same with or without 1-MCP treatment (Fig. 3).

Ethylene exposure after 1-MCP exposure partially reversed inhibition of adventitious rooting. For example, root number and length of 1-MCP-treated cuttings exposed to $1 \mu\text{L}\cdot\text{L}^{-1}$ ethylene were not significantly ($P > 0.05$) different to cuttings treated with $1 \mu\text{L}\cdot\text{L}^{-1}$ ethylene only (Table 3). Considering only cuttings with no 1-MCP exposure, no significant ($P > 0.05$) difference was observed in root number or length among ethylene treatments (Fig. 3).

Discussion

This work supports previous research (Serek et al., 1998) in demonstrating that

treatment with 1-MCP decreased leaf abscission in ethylene-sensitive taxa and reduced leaf yellowing in ethylene-sensitive and insensitive species. That no significant difference was observed in leaf yellowing of zonal geranium cuttings after any 1-MCP and ethylene treatment combination may be because the cuttings used in Expt. 4 were not stored the $\approx 72 \text{ h}$ that depletes carbohydrate reserves to the point at which senescence is triggered due to the combined effect of low carbohydrate content and ethylene exposure (Rapaka et al., 2008). However, there was a significant increase in leaf abscission of zonal geranium cuttings treated with 1-MCP and subsequently exposed to $0.1 \mu\text{L}\cdot\text{L}^{-1}$ ethylene, and an observed but nonsignificant increase in leaf yellowing for this treatment. The cause may be a dosage-dependent biphasic response to ethylene as described by Pierik et al. (2006) for *Arabidopsis*

Fig. 3. Effect of 1-MCP and ethylene on leaf abscission, root length and number, and root and shoot dry weight of 'Kardino' zonal geranium cuttings after 21 d under intermittent mist. Error bars represent $\pm 1 \text{ SE}$. Statistical differences analyzed by one df contrasts are summarized in Table 3.

Table 3. Effect of 1-MCP and ethylene on leaf abscission, root length and number, and root and shoot dry weight of 'Kardino' zonal geranium cuttings after 21 d under intermittent mist. Differences between means (n = 5) were analyzed using orthogonal contrasts. Data are shown in Fig. 3.

Single degree of freedom contrast ^a	Leaf abscission	Root length	Root number	Root area	Root dry wt	Shoot dry wt
0 1-MCP vs. 700 1-MCP	*	*	*	*	*	NS
0 1-MCP vs. 700 1-MCP and 1.0 ethylene	NS	*	*	*	*	NS
0 1-MCP and 0 ethylene vs. 1.0 ethylene		NS	NS	NS	NS	NS
0 1-MCP and 0.1 ethylene vs. 1.0 ethylene	NS	NS	NS	NS	NS	NS
0 1-MCP and 0 ethylene vs. 700 1-MCP and 1.0 ethylene	NS	*	*	*	*	NS
0 1-MCP and 0.1 ethylene vs. 700 1-MCP and 0.1 ethylene	*	NS	*	NS	NS	*
0 1-MCP and 1.0 ethylene vs. 700 1-MCP and 1.0 ethylene	NS	NS	NS	NS	NS	NS
700 1-MCP and 0 ethylene vs. 700 1-MCP and 0.1 ethylene	NS	NS	NS	NS	NS	*
700 1-MCP and 0 ethylene vs. 700 1-MCP and 1.0 ethylene	NS	NS	NS	NS	NS	NS
700 1-MCP and 0.1 ethylene vs. 700 1-MCP and 1.0 ethylene	NS	NS	NS	NS	NS	NS

^aTreatments: 0 and 700 1-MCP indicate 0 and 700 nL·L⁻¹ 1-MCP; 0, 0.1, and 1.0 ethylene indicate 0, 0.1, and 1.0 µL·L⁻¹ ethylene.

NS, *Nonsignificant or significant at $P \leq 0.05$.

1-MCP = 1-methylcyclopropene.

[*Arabidopsis thaliana* (L.) Heynh.], in which a lower ethylene concentration (0.1 µL·L⁻¹) induces a specific set of physiological responses, e.g., petiole elongation, while a higher dose (1.0 µL·L⁻¹) activates senescence responses.

1-MCP delayed the onset of rooting in several taxa and decreased root number and length in zonal geranium as occurred with *Hibiscus rosa-sinensis* L. and *Dendranthema grandiflorum* (Ramat.) Kitamura (Serek et al., 1998). 1-MCP reduced root number and length of 'Miss Murry' begonia and 'Terra Cotta' calibrachoa cuttings in the taxa survey. In Expt. 3, rooting delay was hardly perceptible for rapidly rooting taxa, such as 'Fairytale Sleeping Beauty' portulaca, and is likely not commercially important. With more slowly rooting taxa, such as 'Sonic Red' New Guinea impatiens and 'Kardino' zonal geranium, the delay was greater and could be a significant delay to production cycles if cuttings with fewer and shorter roots due to 1-MCP exposure result in weaker, slower growing plants. The decrease in root number caused by exposure to 1-MCP may also be a problem for rapidly rooting species and further research is warranted.

Rather than having a consistently negative effect, 1-MCP exposure had no influence on adventitious rooting of most taxa in the survey and increased root number and length of 'Amethyst' ivy geranium and 'Patriot Sunbeam' lantana cuttings. Since the taxa survey rooting evaluations were made 3 weeks after propagation it is possible that initial differences in rooting response were overcome by subsequent root development, especially in rapidly rooting taxa.

Ethylene exposure after 1-MCP treatment could completely or partially mitigate the negative impact of 1-MCP on adventitious rooting. For example, zonal geranium cuttings treated with 1-MCP and subsequently exposed to ethylene had significantly greater root numbers and lengths compared with 1-MCP-treated cuttings that were not exposed to ethylene. These observations support the results of Serek et al. (1998) and Kadner and Druege (2004). In addition, our Expt. 2 and other research (Kadner and Druege, 2004; Rapaka et al., 2008) has established that 1-MCP treatment can cause significantly increased ethylene biosynthesis in some

taxa. Because endogenous ethylene synthesis is regulated by feedback inhibition triggered by ethylene binding (Alonso and Stepanova, 2004; Wang et al., 2004), 1-MCP appears to act as an antagonist of ethylene binding thereby disrupting the feedback inhibition mechanism resulting in increased ethylene biosynthesis.

The responses to 1-MCP we observed help explain the inconsistent results reported in the literature regarding 1-MCP effects on adventitious rooting. Serek et al. (1998) treated zonal geranium cuttings with 1-MCP and rooted one group immediately and stored another group in perforated polyethylene bags for 3 d in darkness at 20 °C, and the stored cuttings had a significantly higher rooting percentage compared with 1-MCP-treated cuttings set to root immediately. Kadner and Druege (2004) treated zonal geranium cuttings with 1-MCP and placed them into polypropylene boxes with 1 L volume per 10 cuttings for 48 h in darkness at 5 or 20 °C, and the cuttings had similar numbers of roots compared with untreated stored cuttings. Cuttings in our study were placed into 210-L steel drums with plexiglass tops after 1-MCP treatment and then exposed to exogenous ethylene. Differences among studies in storage headspace mean the cuttings received varying concentrations of ethylene during storage after 1-MCP exposure. Because our results establish that subsequent ethylene exposure partially reversed 1-MCP's inhibition of adventitious rooting, it is not surprising that cuttings stored with little headspace after 1-MCP treatment, such as in Kadner and Druege (2004), exhibited no inhibition of adventitious root formation as they would have been exposed to higher doses of ethylene than those stored in containers with a larger headspace.

Taken together, this research reinforces the need to address several considerations in the rooting of herbaceous stem cuttings of any given cultivar with regard to ethylene. First is the need for a determination of ethylene sensitivity. For ethylene-sensitive cultivars, it is important to know that if the use of 1-MCP or other compounds or management methods can mitigate the negative impact of ethylene exposure on cutting quality or rooting. It is equally important to know if the methods that attenuate the negative

ethylene exposure effects themselves have a detrimental effect on adventitious rooting. Finally, it is important to ascertain whether statistically significant negative impacts on rooting are of such magnitude as to have commercial importance. For them to be useful in developing practical propagation protocols, answers to all these questions must be obtained under conditions that closely simulate real-life propagation at each step.

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