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Effect of Sprayable 1-MCP, AVG, and NAA on Ethylene Biosynthesis, Preharvest Fruit Drop, Fruit Maturity, and Quality of 'Delicious' Apples

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***Abstract*. Effects of naphthaleneacetic acid (NAA), aminoethoxyvinylglycine (AVG), and sprayable 1-methylcyclopropene (1-MCP) alone or in combination on fruit ethylene production, preharvest fruit drop, fruit quality, and fruit maturation were examined in 'Delicious' apples (*Malus* ×*domestica* Borkh.). 1-MCP and AVG + NAA, when applied 15 days before anticipated harvest (DBAH) for untreated control trees, more effectively delayed preharvest fruit drop than AVG or NAA used alone. However, there was no significant difference in ethylene production between fruit treated with 1-MCP or AVG + NAA and those treated by AVG. Two applications of NAA increased fruit ethylene production and fruit softening, whereas AVG inhibited NAA-enhanced fruit ethylene production and fruit softening. There was no significant difference in fruit ethylene production, fruit firmness, and fruit drop control between one and two applications of 1-MCP. The concentrations of 1-MCP did not affect the efficacy of 1-MCP when applied 15 DBAH, but high concentration of 1-MCP more effectively delayed preharvest fruit drop than low concentration of 1-MCP when applied 7 DBAH. Both AVG and 1-MCP suppressed expression of 1-aminocyclopropane-1-carboxylate (ACC) synthase gene *MdACS1*, ACC oxidase gene *MdACO1*, and polygalacturonase gene *MdPG1* in fruit. Expression of *ACS5A* and *MdACO1* but not *MdACS1* in fruit abscission zones was decreased by AVG and 1-MCP. 1-MCP more effectively suppressed expression of *MdPG2* in fruit abscission zones than AVG alone.**

'Delicious' is one of the most important apple (*Malus* ×*domestica* Borkh.) cultivars grown in the United States. Excessive preharvest apple fruit drop, which occurs before fruit develop optimum red color, maturity, or size, is one of its faults and usually causes a serious economic loss (Byers, 1997). Conversely, picking fruit before adequate maturity may lead to poor storability and poor fresh and processed fruit quality. Early harvest can also result in lower yields and prices because fruit will increase in weight 5% to 7% per week and price is based on larger fruit sizes (Byers and Eno, 2002). Ideally, plant growth regulators should hold fruit on the tree for an additional 3 weeks past optimum harvest date to improve fruit size, color, and crop value by as much as 20% while maintaining fruit quality (Byers and Eno, 2002).

Naphthaleneacetic acid (NAA), a synthetic auxin, and aminoethoxyvinylglycine (AVG), an inhibitor of ethylene biosynthesis are two compounds that commercial apple growers use to delay preharvest drop of apples since registrations of daminozide (Alar) and 2,4,5-TP were canceled in 1989 and 1986, respectively. One application of NAA may delay apple fruit drop for ≈10 to 14 d after treatment, and repeated applications of NAA delay fruit abscission more than single applications (Batjer and Moon, 1945; Marini et al., 1993). However, fruit softening is usually increased by two applications of NAA or warm weather after the first application (Smock and Gross, 1947; Yuan and Carbaugh, 2007). AVG suppresses fruit ethylene production, reduces preharvest fruit drop, and delays fruit ripening in apples (Autio and Bramlage, 1982; Bangerth, 1978; Greene, 2005; Schupp and Greene, 2004; Yuan and Carbaugh, 2007). Our preliminary results showed that the combination of NAA and AVG was more effective in delaying fruit drop than were NAA and AVG alone in 'Golden Supreme' and 'Golden Delicious' apples while maintaining fruit quality (Yuan and Carbaugh, 2007).

1-Methylcyclopropene (1-MCP), an inhibitor of ethylene action, has been used to delay postharvest ripening of climacteric fruit such as apples (Blankenship and Dole, 2003). Recently, a sprayable formulation of 1-MCP became available for use in the field. Our preliminary results showed that sprayable 1-MCP more effectively delayed fruit drop than did AVG or NAA when they were applied 1 week before commercial harvest in 'Golden Delicious' apples (Yuan and Carbaugh, 2007). Elfving et al. (2007) reported that preharvest application of sprayable 1-MCP reduced 'Delicious' apple fruit ethylene production and slowed softening during and after storage, but they did not study its effect on preharvest fruit drop in 'Delicious' apples.

Apples are typical climacteric fruit characterized by a marked increase in ethylene production and respiration at ripening (Blanpied, 1972; Yuan and Carbaugh, 2007). It has been reported that concomitant with increased fruit ethylene production is increased expression of genes and activity of enzymes associated with cell wall degradation such as polygalacturonase (PG) (Bonghi et al., 2000; Brown, 1997). As a result, the middle lamellae of cells in fruit cortex and fruit abscission zone dissolves, and ultimately, the fruit becomes soft and abscises.

The purposes of this investigation were to: 1) study the effect of NAA and AVG alone or in combination on control of preharvest fruit drop and maintenance of on-tree fruit quality in 'Delicious' apples; 2) evaluate the effect of concentration, timing, and frequency of application of sprayable 1-MCP on preharvest fruit drop and fruit quality in 'Delicious' apples; and 3) determine the effect of AVG and sprayable 1-MCP on the expression of genes related to ethylene biosynthesis and cell wall degradation in fruit cortex and fruit abscission zones.

Materials and Methods

Expt. 1: Delicious (2006)

Plant material and treatments. To determine the effects of AVG and NAA alone or in combination, and concentration, timing, and frequency of sprayable 1-MCP on preharvest fruit drop and fruit quality, 66 10-year-old 'Bisbee Delicious'/Mark located at the Alson H. Smith, Jr. Agricultural Research and Extension Center, Winchester, VA, were selected and grouped into six blocks of 11 trees each in Sept. 2006. A randomized complete block design was used. AVG (ReTain; Valent BioSciences Corp., Libertyville, IL) at 125 $mg \cdot L^{-1}$ and NAA (Fruitone N; AMVAC Corp., Newport Beach, CA) at 20 $mg \cdot L^{-1}$ alone or in combination were applied on 6 Sept., 15 d before anticipated harvest (DBAH), or on 14 Sept., 7 DBAH. A sprayable formulation of 1-MCP (Rohm and Haas Company, Spring House, PA) at 160 or 320 $mg \cdot L^{-1}$ was applied on 6 Sept., 15 DBAH, or on 14 Sept., 7 DBAH. All spray solutions contained surfactant Silwet L-77 (Loveland Products, Greelay, CO) at 0.624 $mL \cdot L^{-1}$. Spray treatments were applied to runoff with a low-pressure hand-wand sprayer. One tree in each block was not sprayed and served as a control.

Determination of fruit abscission, fruit ethylene evolution, fruit maturity, and fruit quality. To determine fruit abscission rate, two limbs of ≈30 fruit each on each tree were tagged. Fruit on tagged limbs were counted on 6 Sept. 2006 before any fruit abscission, and then fruit remaining on tagged limbs were counted weekly thereafter until 1 Nov.

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Six fruit were collected from each tree at 1- to 4-week intervals beginning on 1 Aug. and ending on 26 Oct. 2006. Fruit were enclosed in a 3.785-L container and incubated for 3 h. One milliliter of gas sample was withdrawn from the sealed container through the rubber septum affixed to the lid, and ethylene concentration was measured with a gas chromatograph equipped with an activated alumina column and an FID detector (model 3700; Varian, Palo Alto, CA) (Yuan and Carbaugh, 2007).

To determine fruit maturity and quality, 10 fruit were sampled weekly from each tree beginning on 21 Sept. and ending on 26 Oct. 2006. Fruit red color was estimated visually on each fruit to the nearest 10%. Fruit firmness was measured on two sides of each fruit with an Effegi penetrometer (model FT 327; McCormick Fruit Tech, Yakima, WA) with an 11.1-mm tip. Soluble solids concentration (SSC) was measured with an Atago handheld refractometer (model N1; McCormick Fruit Tech) using a composite sample of juice resulting from penetrometer testing of 10 fruit from each treatment in each replicate. Each apple fruit was cut in half transversely, fruit with water core were counted, and then flesh starch was evaluated by dipping half of each apple in iodine solution for ≈15 s. The degree of staining was rated on a scale of 1 to 8, in which 1 = staining of the entire cut surface and 8 = absence of staining (Poapst et al., 1959). No phytotoxicity or other negative effects on trees were observed.

Total RNA extraction and real-time quantitative polymerase chain reaction. Forty fruit were collected from each tree, treated by sprayable 1-MCP at 0 or 160 $mg \cdot L^{-1}$ and AVG at 125 $mg \cdot L^{-1}$ on 6 Sept., 15 DBAH, of three blocks on 28 Sept. (all compounds were effectively inhibiting fruit abscission). The fruit were immediately separated into cortex and fruit abscission zone. Fruit abscission zones were collected by cutting 1 mm at each side of the abscission fracture plane. For fruit cortex, 10 fruit were randomly selected from the 40 fruit of each tree, peeled, cored, and sliced. Harvested tissues were immediately frozen in liquid nitrogen and stored at –80 °C for extraction of RNA. Total RNA was extracted from fruit abscission zones and fruit cortex as described by Wan and Wilkins (1994). DNA was removed from each RNA sample using the TURBO DNA-free™ Kit (Ambion Inc., Austin, TX). Real-time polymerase chain reaction was performed using primers that span an intron in 1-aminocyclopropane-1-carboxylate (ACC) oxidase gene *MdACO1* to confirm that each RNA sample was free of genomic DNA contamination according to Dal Cin et al. (2005).

Two micrograms of total RNA was used to synthesize cDNA in a 20-μL reaction volume using a High-Capacity cDNA Reverse Transcription Kit (Applied Biosystems, Foster City, CA). Real-time quantitative polymerase chain reaction (PCR) was performed using the Power SYBR Green PCR Master Mix Kit (Applied Biosystems) on Applied Biosystems 7500 Real-Time PCR Systems (Applied Biosystems) according to the manufacturer's instructions. Gene-specific primers were designed on nonconserved areas using Primer Expression 3.0 software (Applied Biosystems) synthesized by Integrated DNA Technologies (Coralville, IA); the primer sequences are listed in Table 1. Real-time samples were run in triplicate and the reaction volumes were 25 μL. Dissociation curves were run to determine the specificity of the amplification reactions. In addition, the amplified products by real-time quantitative PCR were sequenced as described by Dal Cin et al. (2005). After validation tests, normalization to actin was performed using the $\triangle\triangle C^T$ method described by Applied Biosystems ("Guide to Performing Relative Quantitation of Gene Expression Using Real-time Quantitative PCR"; Applied Biosystems).

Expt. 2: Delicious (2007)

Forty-eight 11-year-old 'Bisbee Delicious'/Mark located at the Alson H. Smith, Jr. Agricultural Research and Extension Center, Winchester, VA, were selected and grouped into six blocks of eight trees each in Aug. 2007. A randomized complete block design was used. AVG at 125 $mg \cdot L^{-1}$ and NAA at 10 $mg \cdot L^{-1}$ were applied on 22 Aug., 28 DBAH, and 5 Sept., 14 DBAH, respectively. The combination of AVG at 125 $mg \cdot L^{-1}$ and NAA at 10 $mg \cdot L^{-1}$ were applied on 5 Sept., 14 DBAH. Sprayable 1-MCP at 80 or 160 $mg \cdot L^{-1}$ was applied on 5 Sept., 14 DBAH, or on 12 Sept., 7 DBAH, respectively. All spray solutions contained surfactant Silwet L-77 at 0.624 $mL \cdot L^{-1}$. Spray treatments were applied to runoff with a low-pressure hand-wand sprayer. One tree in each block was not sprayed and served as a control.

Fruit on two tagged limbs of each tree were counted on 5 Sept. 2007 before any fruit abscission, and then fruit remaining on tagged limbs were counted weekly thereafter until 16 Oct. Six fruit were collected from each tree on 19 Sept. and 3 Oct. to determine fruit ethylene production. Fruit ethylene production was measured as described previously. Ten fruit were sampled from each tree on 19 Sept. and 3 Oct. for fruit quality evaluations (fruit firmness, SSC, starch staining, and fruit red color). Fruit red color, firmness,

Table 1. Gene-specific primers used for expression analysis of genes.

Gene	Accession no.	Primer left	Primer right
MdActin	CN938023	5′-TGACCGAATGAGCAAGGAAATTACT-3′	5′-TACTCAGCTTTGGCAATCCACATC-3′
MdACS1	L31347	5′-GCCTTCCGGGTTTTCGA-3′	5′-GGCGGCCACAACCATGT-3′
MdACS5A	AB034992	5′-GCAATGGTGGTCTTTTCGTATG-3′	5′-TTCGAACGTCTGCTCCTTGA-3′
MdACO1	AB030859	5′-CAGTCGGATGGGACCAGAA-3′	5′-GCTTGGAATTTCAGGCCAGA-3′
MdPG1	L27743	5′-CGCACAACAAATCCATGTCATAT-3′	5′-ACCGTGAGACAGGAAGCTTGA-3′
MdPG2	AB210897	5′-CGGTTCAGCCGACAAGTTG-3′	5′-TACGAGTGAGGAGGAGTAGATGGA-3′

Table 2. Effects of sprayable 1-MCP, AVG, and NAA on preharvest fruit drop of Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate ($mg \cdot L^{-1}$)	Cumulative fruit drop (%) 6 Sept.	14 Sept.	21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.	1 Nov.
Control	—	—	0.0 a[y]	3.8 a	19.7 a	27.8 a	43.4 a	50.7 a	63.6 a	72.9 a	91.1 a
1-MCP	15 and 7	160	0.0 a	2.7 a	5.3 c	8.6 de	8.6 e	12.1 c	14.8 d	26.9 c	64.6 b
1-MCP	15 and 7	320	0.0 a	2.8 a	5.7 c	7.7 de	11.7 de	15.2 c	21.5 cd	28.2 c	54.6 b
AVG	15 and 7	125	0.0 a	3.1 a	10.2 b	13.4 c	23.6 b	27.0 b	28.9 b	31.0 bc	31.8 c
1-MCP	15	160	0.0 a	1.9 a	3.4 c	4.7 e	8.9 e	12.1 c	20.4 cd	34.1 b	68.6 b
AVG	15	125	0.0 a	0.0 a	10.5 b	15.9 c	21.6 b	25.8 b	32.8 b	33.7 b	45.0 b
1-MCP	7	160	0.0 a	0.7 a	18.8 a	21.5 b	26.4 b	27.8 b	33.8 b	37.1 b	52.4 b
1-MCP	7	320	0.0 a	1.7 a	8.0 bc	8.9 de	12.1 d	13.2 c	22.4 c	23.7 c	51.7 b
AVG	7	125	0.0 a	0.0 a	6.4 bc	14.6 c	21.2 b	23.2 b	28.4 b	29.2 bc	33.8 c
NAA	15 and 7	20	0.0 a	2.1 a	6.5 bc	9.4 d	16.0 c	24.5 b	35.4 b	40.5 b	53.3 b
AVG +	15	125	0.0 a	1.1 a	5.7 c	6.7 de	11.0 de	13.1 c	18.4 cd	18.4 d	23.0 d
NAA	15 and 7	20									

[z]Days before anticipated harvest date, which was 21 Sept. 2006.

[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).

1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

Table 3. Effects of sprayable 1-MCP, AVG, and NAA on fruit ethylene production in Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate ($mg·L^{-1}$)	Fruit ethylene production ($\mu L·kg^{-1}·h^{-1}$ FW)							
			1 Aug.	6 Sept.	21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.
Control	—	—	0.001 a[y]	0.001 a	1.438 b	3.922 b	4.736 b	4.336 b	6.467 b	7.881 a
1-MCP	15 and 7	160	0.001 a	0.001 a	0.018 c	0.047 c	0.132 c	0.859 c	7.433 b	7.926 a
1-MCP	15 and 7	320	0.001 a	0.001 a	0.017 c	0.099 c	0.125 c	1.571 c	6.878 b	7.803 a
AVG	15 and 7	125	0.001 a	0.001 a	0.021 c	0.093 c	0.076 c	0.023 d	0.035 e	0.055 c
1-MCP	15	160	0.001 a	0.001 a	0.008 c	0.116 c	0.117 c	2.223 c	7.423 b	5.907 a
AVG	15	125	0.001 a	0.001 a	0.037 c	0.108 c	0.051 c	0.020 d	0.512 d	0.577 b
1-MCP	7	160	0.001 a	0.001 a	0.043 c	0.109 c	0.222 c	0.741 c	2.830 c	4.982 a
1-MCP	7	320	0.001 a	0.001 a	0.014 c	0.112 c	0.135 c	1.246 c	3.791 c	6.316 a
AVG	7	125	0.001 a	0.001 a	0.025 c	0.124 c	0.052 c	0.020 d	0.060 e	0.289 b
NAA	15 and 7	20	0.001 a	0.001 a	8.651 a	9.412 a	19.657 a	11.362 a	10.652 a	7.125 a
AVG +	15	125	0.001 a	0.001 a	0.047 c	0.096 c	0.036 c	0.054 d	0.125 de	0.203 b
NAA	15 and 7	20								

[z]Days before anticipated harvest date, which was 21 Sept. 2006.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

SSC, and flesh starch were measured as described previously.

Statistical analyses. Statistical analyses included analysis of variance, Duncan's multiple range test, and regression analysis using Statistical Analysis Systems Software for PC (SAS Inst., Cary, NC).

Results

Expt. 1

Delicious (2006). Preharvest fruit drop was reduced by 1-MCP, AVG, and NAA regardless of concentration, timing, and frequency of applications (Table 2). There was no difference in fruit drop control between NAA and AVG except on 28 Sept. and 4 Oct. when two applications of NAA more effectively reduced fruit drop than did AVG. There was no difference in fruit drop control between one and two applications of AVG either. AVG + NAA was more effective in the control of fruit drop than AVG or NAA alone. Overall, 1-MCP more effectively reduced fruit drop than did either AVG or NAA alone until 26 Oct. except for 1-MCP at 160 $mg·L^{-1}$ applied 7 DBAH, but there was no difference in fruit drop control between 1-MCP and AVG + NAA except for 1-MCP at 160 $mg·L^{-1}$ applied 7 DBAH. When 1-MCP at 160 $mg·L^{-1}$ was applied 15 DBAH and 1-MCP at 320 $mg·L^{-1}$ was applied 7 DBAH, they more effectively delayed fruit drop than did 1-MCP at 160 $mg·L^{-1}$ applied 7 DBAH, but there was no difference in fruit drop control between 1-MCP at 320 $mg·L^{-1}$ applied 7 DBAH and 1-MCP at 160 $mg·L^{-1}$ applied 15 DBAH. There was also no difference in fruit drop control between one and two applications of 1-MCP except for 1-MCP at 160 $mg·L^{-1}$ applied 7 DBAH, which had less effect in delaying fruit drop than other 1-MCP treatments.

Ethylene production of fruit from control trees was very low before fruit ripening and rapidly increased when fruit started to ripen (21 and 28 Sept.) (Table 3). Two applications of NAA at 20 $mg·L^{-1}$ increased fruit ethylene production, whereas AVG and 1-MCP inhibited fruit ethylene production and delayed

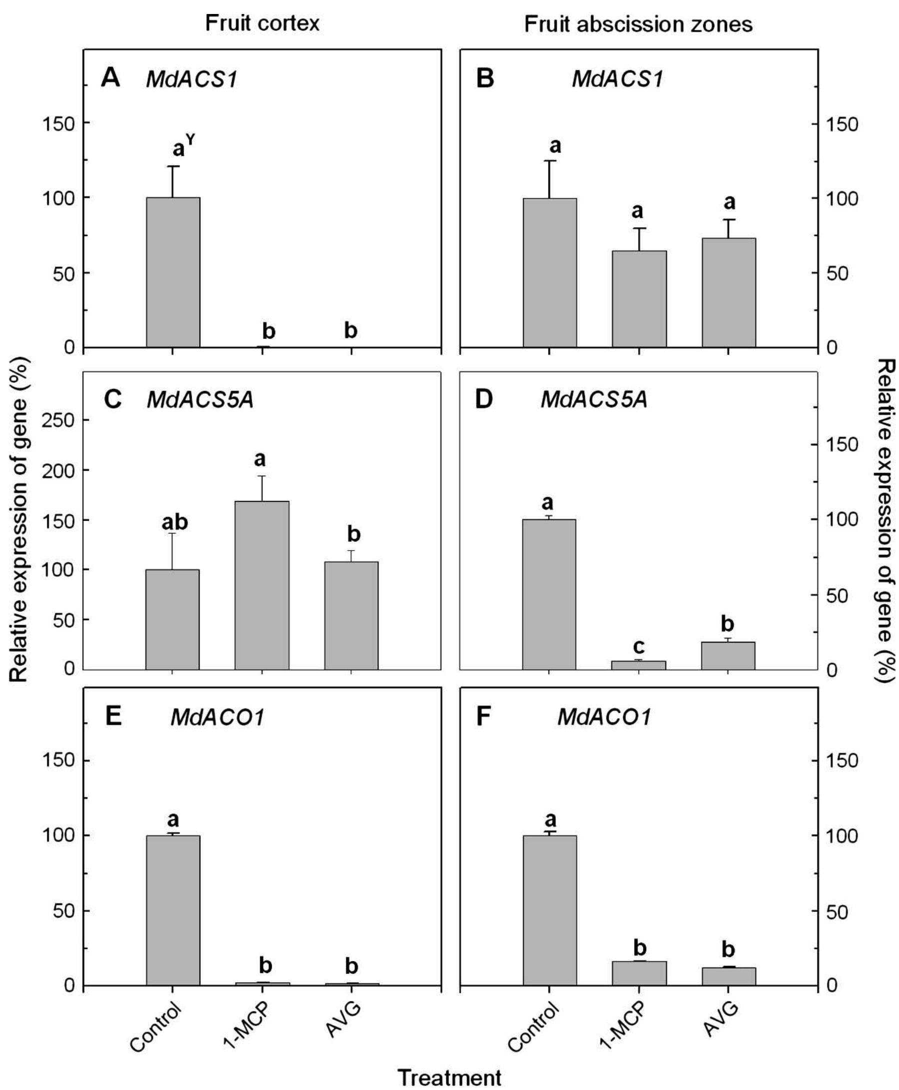

Fig. 1. Real-time quantitative polymerase chain reaction analysis of expression of *MdACS1*, *MdACS5A*, and *MdACO1* in fruit cortex (**A**, **C**, and **E**) and fruit abscission zones (**B**, **D**, and **F**) from 'Bisbee Delicious' apple trees treated with 1-methylcyclopropene (1-MCP) at 160 $mg·L^{-1}$, aminoethoxyvinylglycine (AVG) at 125 $mg·L^{-1}$, and naphthaleneacetic acid (NAA) at 20 $mg·L^{-1}$. 1-MCP and AVG were applied on 6 Sept., 15 d before anticipated harvest (DBAH), and NAA was applied on 6 Sept., 15 DBAH, and 14 Sept., 7 DBAH. The mRNA levels of *MdACS1 MdACS5A*, and *MdACO1* were normalized using actin. Data are means ± SE (n = 3). [y]Mean separation by Duncan's multiple range test ($P = 0.05$). The values of *MdACS1 MdACS5A*, and *MdACO1* in fruit cortex and fruit abscission zones of untreated control 'Delicious' apples were arbitrarily set to 100%.

the onset of fruit ethylene climacteric. Concentration, timing, and frequency of applications of 1-MCP and AVG did not affect the efficacy of 1-MCP and AVG in inhibiting fruit ethylene production. Addition of AVG reduced fruit ethylene production stimulated by NAA. However, the effect of 1-MCP on fruit ethylene production decreased by 11 Oct. and stopped by 18 Oct, whereas AVG alone or AVG + NAA inhibited fruit ethylene production through 26 Oct.

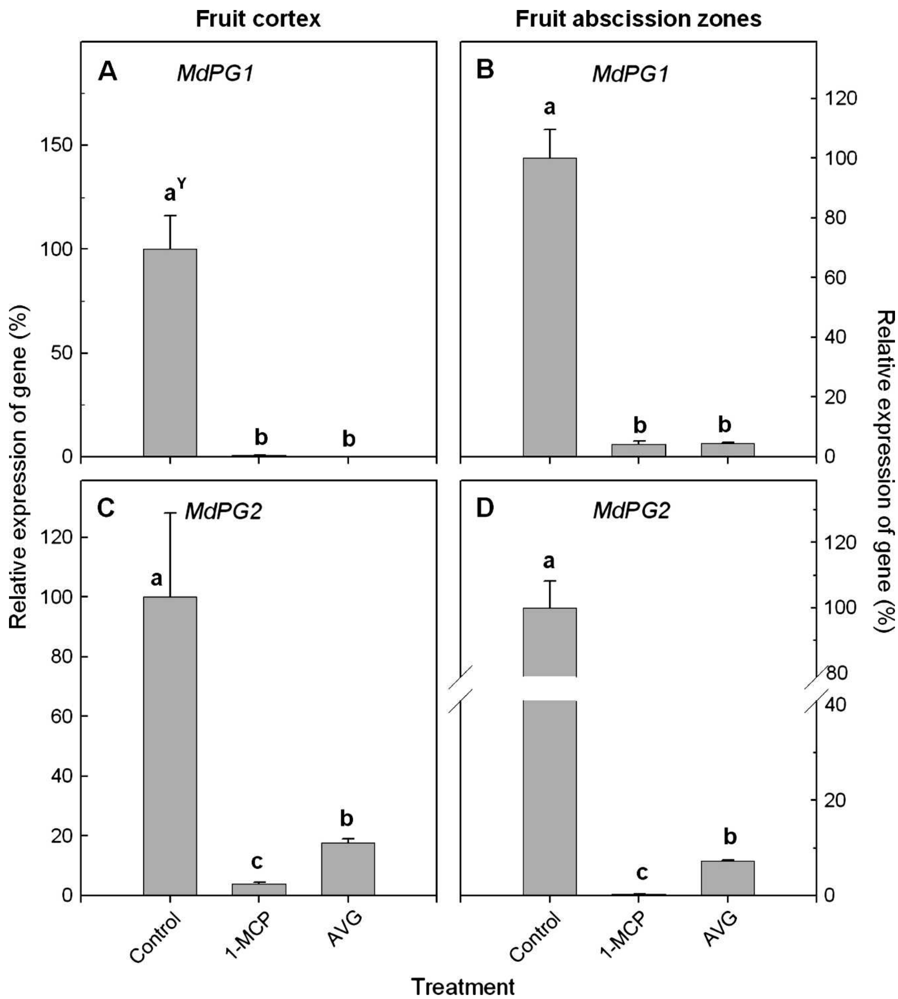

Fig. 2. Real-time quantitative polymerase chain reaction analysis of expression of *MdPG1* and *MdPG2* in fruit cortex (**A** and **C**) and fruit abscission zones (**B** and **D**) from 'Bisbee Delicious' apple trees treated with 1-methylcyclopropene (1-MCP) at 160 mg·L^{-1}, aminoethoxyvinylglycine (AVG) at 125 mg·L^{-1}, and naphthaleneacetic acid (NAA) at 20 mg·L^{-1}. 1-MCP and AVG were applied on 6 Sept., 15 d before anticipated harvest (DBAH), and NAA was applied on 6 Sept., 15 DBAH, and 14 Sept., 7 DBAH. The mRNA levels of *MdPG1* and *MdPG2* were normalized using actin. Data are means ± SE (n = 3). [Y]Mean separation by Duncan's multiple range test ($P = 0.05$). The values of *MdPG1* and *MdPG2* in fruit cortex and fruit abscission zones of untreated control 'Delicious' apples were arbitrarily set to 100%.

The expression of ACC synthase gene *MdACS1* in fruit cortex was suppressed by 1-MCP at 160 mg·L^{-1} and AVG on 28 Sept. when all compounds were effectively inhibiting fruit abscission (Fig. 1A). However, *MdACS1* expression in fruit abscission zones was unaffected by either 1-MCP at 160 mg·L^{-1} or AVG applied 15 DBAH (Fig. 1B). 1-MCP and AVG had a slight or no effect on the expression of *MdACS5A* gene in fruit cortex (Fig. 1C). On the other hand, 1-MCP and AVG inhibited the expression of *MdACS5A* in fruit abscission zones (Fig. 1D). The expression of *MdACO1* gene in both fruit cortex and fruit abscission zones was reduced by 1-MCP and AVG (Fig. 1E–F). The expression of polygalacturonase genes *MdPG1* and *MdPG2* in both fruit cortex and fruit abscission zones was reduced by 1-MCP and AVG (Fig. 2A–D).

Overall, fruit weight increased linearly with time regardless of treatment (Table 4). Fruit weight increased ≈14.5% from 21 Sept. to 11 Oct. Fruit red color quadratically increased with time but was unaffected by 1-MCP, AVG, or NAA (Table 5). Fruit from trees treated with NAA were softer compared with fruit from control trees, whereas 1-MCP, AVG, or AVG + NAA slowed softening (Table 6). The efficacy of AVG and 1-MCP in slowing softening was not influenced by concentration, timing, and number of 1-MCP and AVG applications until 11 Oct. NAA alone significantly increased SSC except on 21 Sept. and 11 Oct., whereas only two applications of 1-MCP at 160 mg·L^{-1} reduced SSC on 21 Sept. (Table 7). Starch degradation as indicated by starch rating was increased by NAA but decreased by 1-MCP and AVG (Table 8). AVG reduced NAA-caused starch degradation. Water core was reduced by AVG and 1-MCP but increased by NAA on 4 Oct. (Table 9).

Expt. 2

Delicious (2007). NAA, 1-MCP, AVG, and AVG + NAA delayed preharvest fruit

Table 4. Effects of sprayable 1-MCP, AVG, and NAA on fruit weight of Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate (mg·L^{-1})	Fruit wt (g) 21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.	Significance
Control	—	—	199.7 a[y]	204.7 a	209.7 a	217.6 a	229.1 ab	228.9 ab	
1-MCP	15 and 7	160	194.3 a	205.2 a	206.5 a	228.2 a	238.9 ab	246.1 ab	
1-MCP	15 and 7	320	206.0 a	215.3 a	225.2 a	242.2 a	243.1 ab	257.5 a	
AVG	15 and 7	125	199.0 a	204.1 a	213.9 a	233.5 a	242.5 ab	228.4 ab	
1-MCP	15	160	193.9 a	207.3 a	208.6 a	217.8 a	226.7 b	232.1 ab	
AVG	15	125	202.1 a	205.8 a	216.4 a	231.6 a	242.5 ab	241.1 ab	
1-MCP	7	160	198.1 a	203.6 a	204.5 a	227.8 a	243.8 ab	236.9 ab	
1-MCP	7	320	201.6 a	215.7 a	208.7 a	229.4 a	241.6 ab	239.8 ab	
AVG	7	125	208.6 a	206.9 a	213.9 a	228.0 a	257.0 ab	259.6 a	
NAA	15 and 7	20	201.9 a	209.0 a	220.5 a	243.3 a	262.4 a	244.7 ab	
AVG +	15	125	192.5 a	196.8 a	202.8 a	217.4 a	225.0 b	216.2 b	
NAA	15 and 7	20							
Mean			199.8	206.8	211.9	228.8	241.2	239.2	L**Q[NS]

[z]Days before anticipated harvest date, which was 21 Sept. 2006.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).
[NS], [**]Nonsignificant or significant at $P = 0.01$, respectively.
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

Table 5. Effects of sprayable 1-MCP, AVG, and NAA on fruit red color of Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate (mg·L^{-1})	Fruit red color (%) 21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.	Significance
Control	—	—	91.1 a[y]	94.4 a	96.9 a	97.3 a	97.9 a	97.8 a	
1-MCP	15 and 7	160	87.6 a	95.3 a	95.8 a	97.4 a	98.3 a	97.4 a	
1-MCP	15 and 7	320	88.5 a	94.9 a	96.5 a	96.5 a	98.1 a	97.7 a	
AVG	15 and 7	125	90.3 a	94.9 a	95.2 a	98.0 a	97.7 a	97.8 a	
1-MCP	15	160	90.1 a	94.0 a	96.2 a	97.7 a	98.3 a	97.5 a	
AVG	15	125	91.7 a	95.7 a	96.0 a	96.9 a	97.5 a	98.1 a	
1-MCP	7	160	88.5 a	94.0 a	96.8 a	96.6 a	97.9 a	98.1 a	
1-MCP	7	320	89.0 a	90.8 a	95.9 a	96.0 a	97.0 a	96.6 a	
AVG	7	125	89.5 a	94.3 a	95.5 a	97.6 a	97.3 a	97.7 a	
NAA	15 and 7	20	91.2 a	95.3 a	96.2 a	97.0 a	97.3 a	97.0 a	
AVG +	15	125	93.1 a	95.7 a	96.2 a	96.5 a	97.9 a	97.3 a	
NAA	15 and 7	20							
Mean			90.1	94.5	96.1	97.1	97.8	97.6	L*Q*

[z]Days before anticipated harvest date, which was 21 Sept. 2006.
[y]Mean separation within columns by Duncan's multiple range test (P = 0.05).
*Significant at P = 0.05.
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

Table 6. Effects of sprayable 1-MCP, AVG, and NAA on fruit firmness of Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate (mg·L^{-1})	Fruit firmness (N) 21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.
Control	—	—	71.2 bc[y]	69.4 b	67.6 b	63.6 d	61.0 a	54.3 d
1-MCP	15 and 7	160	75.6 a	73.0 a	69.9 a	69.0 ab	64.1 a	55.2 cd
1-MCP	15 and 7	320	73.9 ab	74.3 a	70.3 a	66.3 abcd	64.5 a	56.9 bcd
AVG	15 and 7	125	74.8 a	73.0 a	70.3 a	69.4 a	65.4 a	62.3 a
1-MCP	15	160	75.6 a	72.5 ab	70.3 a	67.6 abc	64.5 a	56.9 bcd
AVG	15	125	73.4 ab	73.4 a	69.4 a	67.2 abc	65.0 a	60.5 ab
1-MCP	7	160	73.9 ab	72.1 ab	69.4 a	68.1 abc	64.1 a	57.8 abcd
1-MCP	7	320	73.4 ab	73.4 a	69.4 a	65.8 bcd	64.1 a	59.2 abc
AVG	7	125	72.5 ab	72.1 ab	69.0 a	65.4 cd	64.1 a	58.7 abcd
NAA	15 and 7	20	68.1 c	65.8 c	52.1 c	44.0 f	37.8 b	33.8 e
AVG +	15	125	73.0 ab	73.0 a	69.4 a	68.1 abc	63.2 a	62.3 a
NAA	15 and 7	20						

[z]Days before anticipated harvest date, which was 21 Sept. 2006.
[y]Mean separation within columns by Duncan's multiple range test (P = 0.05).
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

Table 7. Effects of sprayable 1-MCP, AVG, and NAA on soluble solids of Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate (mg·L^{-1})	Soluble solids (%) 21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.
Control	—	—	12.7 abc[y]	12.6 bcde	13.4 bc	13.8 ab	13.9 b	14.4 bc
1-MCP	15 and 7	160	12.0 d	12.3 e	12.6 c	13.6 b	13.7 b	14.2 bc
1-MCP	15 and 7	320	12.2 cd	12.8 bcde	13.3 bc	13.5 b	13.9 b	14.5 bc
AVG	15 and 7	125	12.9 abc	13.0 bcde	13.3 bc	13.9 ab	13.9 b	14.4 bc
1-MCP	15	160	12.3 bcd	12.3 de	13.0 bc	13.1 b	14.0 ab	14.0 bc
AVG	15	125	12.8 abc	13.0 bcd	13.2 bc	13.7 ab	14.3 ab	14.7 b
1-MCP	7	160	12.7 abc	12.7 bcde	13.4 bc	13.8 ab	14.0 ab	14.4 bc
1-MCP	7	320	12.4 bcd	12.4 cde	13.0 bc	13.5 b	13.7 b	14.4 bc
AVG	7	125	13.0 ab	13.1 ab	13.4 bc	13.4 b	13.8 b	14.3 bc
NAA	15 and 7	20	13.2 a	13.8 a	14.6 a	14.4 a	14.8 a	15.6 a
AVG +	15	125	12.8 abc	13.0 bcde	12.6 c	13.4 b	13.6 b	13.8 c
NAA	15 and 7	20						

[z]Days before anticipated harvest date, which was 21 Sept. 2006.
[y]Mean separation within columns by Duncan's multiple range test (P = 0.05).
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

drop (Table 10). 1-MCP and NAA was more effective in delaying preharvest fruit drop than was AVG except 1-MCP at 80 mg·L^{-1} applied 7 DBAH. NAA + AVG was more effective in the control of preharvest fruit drop than NAA, AVG, or 1-MCP alone. The concentration of 1-MCP, when applied 14 DBAH, did not affect the efficacy of 1-MCP in reducing preharvest fruit drop, but 1-MCP at 160 mg·L^{-1} more effectively reduced preharvest fruit drop than at 80 mg·L^{-1} when applied 7 DBAH. Fruit ethylene production was inhibited by AVG or 1-MCP, but one application of NAA at 10 mg·L^{-1} had no significant effect on fruit ethylene production (Table 11). 1-MCP, AVG, or AVG + NAA slowed softening, whereas NAA increased it. Starch degradation was delayed by AVG or 1-MCP. Only 1-MCP at 160 mg·L^{-1} applied 7 DBAH slightly reduced fruit red color on 3 Oct. AVG + NAA and 1-MCP, except 1-MCP at 80 mg·L^{-1} applied 14 DBAH, reduced fruit SSC.

Discussion

Our results showed that AVG + NAA more effectively delayed preharvest fruit drop than AVG or NAA alone in 'Bisbee Delicious' apples although there was no difference in fruit ethylene production between AVG and AVG + NAA, suggesting that there is an additive effect between NAA and AVG in controlling fruit abscission. These results are in agreement with our previous reports in 'Golden Supreme' and 'Golden Delicious' apples (Yuan and Carbaugh, 2007). Fruit ethylene production and fruit drop were unaffected by one and two applications of AVG, which is consistent with previous report in 'Golden Supreme' apples (Yuan and Carbaugh, 2007). Two applications of NAA reduced fruit abscission although it enhanced fruit ethylene production and fruit softening. This indicates that NAA reduces preharvest fruit drop not through reducing ethylene production and plays a different role in fruit abscission and fruit softening. Similarly, NAA, but not AVG, reduced preharvest fruit drop caused by ethephon (Byers, 1997). Addition of AVG delayed NAA-enhanced fruit softening and starch degradation but did not affect fruit red color. This has been attributed to the action of AVG in inhibiting NAA-stimulated ethylene production (Yuan and Carbaugh, 2007). Therefore, the use of AVG + NAA to delay preharvest fruit drop while maintaining fruit quality may provide apple growers with flexibility to harvest their apples with high quality.

1-MCP counteracts ethylene action through blocking ethylene receptors (Blankenship and Dole, 2003). In this study, sprayable 1-MCP effectively inhibited fruit ethylene production, delayed fruit softening, and more effectively delayed preharvest fruit drop than AVG or NAA alone in 'Bisbee Delicious' apples. This is consistent with previous reports in 'Golden Delicious' apples (McArtney et al., 2008; Yuan and Carbaugh, 2007). There was no difference in fruit ethylene production, fruit firmness, and fruit drop control between one and two applications of 1-MCP, indicating that the frequency of application of 1-MCP does not affect the effectiveness of 1-MCP. The concentration of 1-MCP did not affect the efficacy of 1-MCP when applied 15 DBAH, but the high concentration of 1-MCP more effectively delayed preharvest fruit drop than a low concentration of 1-MCP when applied 7 DBAH. A low concentration of 1-MCP applied at 7 DBAH did not affect prehavest fruit drop in the first 7 d after treatment. These suggest that more ethylene receptors are produced in apple fruit and higher concentration of

Table 8. Effects of sprayable 1-MCP, AVG, and NAA on starch of Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate ($mg \cdot L^{-1}$)	Starch (1 to 8)					
			21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.
Control	—	—	5.1 b[y]	6.1 b	6.8 b	7.0 b	7.3 bc	7.8 a
1-MCP	15 and 7	160	3.4 d	4.3 f	5.1 de	6.0 c	6.5 d	7.8 a
1-MCP	15 and 7	320	3.9 bcd	4.6 f	5.4 de	6.4 c	6.8 cd	7.7 ab
AVG	15 and 7	125	5.1 b	5.5 bcd	5.4 de	6.0 c	6.4 d	7.3 bc
1-MCP	15	160	3.8 cd	4.3 f	5.4 de	5.9 c	6.8 cd	7.7 ab
AVG	15	125	4.2 bcd	5.0 def	5.3 de	5.9 c	6.5 d	7.2 c
1-MCP	7	160	4.6 bc	4.6 f	5.4 de	5.9 c	6.4 d	7.3 bc
1-MCP	7	320	4.3 bcd	4.7 ef	5.1 e	6.3 c	6.6 d	7.7 ab
AVG	7	125	5.0 b	5.3 cde	5.9 cd	6.1 c	6.8 cd	7.1 cd
NAA	15 and 7	20	6.8 a	7.6 a	7.8 a	8.0 a	8.0 a	8.0 a
AVG +	15	125	4.9 bc	5.5 bcd	5.8 cde	6.1 c	6.7 d	6.8 d
NAA	15 and 7	20						

[z]Days before anticipated harvest date, which was 21 Sept. 2006.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

Table 9. Effects of sprayable 1-MCP, AVG, and NAA on water core of Bisbee Delicious apples (2006).

Treatment	Application time (DBAH[z])	Rate ($mg \cdot L^{-1}$)	Water core (%)					
			21 Sept.	28 Sept.	4 Oct.	11 Oct.	18 Oct.	26 Oct.
Control	—	—	15.0 ab[y]	40.0 ab	55.0 b	90.0 a	100.0 a	97.5 a
1-MCP	15 and 7	160	0.0 b	0.0 c	0.0 d	22.5 c	97.5 a	87.5 a
1-MCP	15 and 7	320	0.0 b	0.0 c	2.5 d	17.5 c	100.0 a	100.0 a
AVG	15 and 7	125	0.0 b	0.0 c	5.0 cd	50.0 b	92.5 ab	90.0 a
1-MCP	15	160	0.0 b	0.0 c	0.0 d	50.0 b	90.0 ab	97.5 a
AVG	15	125	2.5 b	2.5 c	0.0 d	40.0 bc	87.5 ab	92.5 a
1-MCP	7	160	2.5 b	5.0 c	0.0 d	30.0 bc	92.5 ab	97.5 a
1-MCP	7	320	0.0 b	0.0 c	0.0 d	17.5 c	82.5 b	92.5 a
AVG	7	125	17.5 ab	2.5 c	17.5 c	52.5 b	90.0 ab	92.5 a
NAA	15 and 7	20	22.5 a	57.5 a	77.5 a	87.5 a	92.5 ab	97.5 a
AVG +	15	125	0.0 b	0.0 c	2.5 d	32.5 bc	80.0 b	85.0 a
NAA	15 and 7	20						

[z]Days before anticipated harvest date, which was 21 Sept. 2006.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

Table 10. Effects of sprayable 1-MCP, AVG, and NAA on preharvest fruit drop of Bisbee Delicious apples (2007).

Treatment ($mg \cdot L^{-1}$)	Application time (DBAH[z])	Rate ($mg \cdot L^{-1}$)	Cumulative fruit drop (%)						
			5 Sept.	12 Sept.	19 Sept.	25 Sept.	2 Oct.	9 Oct.	16 Oct.
Control	—		0 a[y]	3.2 ab	8.7 a	15.4 a	27.3 a	58.0 a	70.8 a
1-MCP	14	80	0 a	1.6 b	2.9 ab	6.7 c	14.5 b	24.0 c	45.1 b
1-MCP	14	160	0 a	0.0 c	1.8 bc	6.8 c	12.1 b	23.1 c	40.1 bc
1-MCP	7	80	0 a	5.5 a	9.4 a	15.6 a	21.4 a	33.4 b	41.6 b
1-MCP	7	160	0 a	0.0 c	1.9 b	8.5 bc	13.6 b	18.9 c	30.9 cd
AVG	28	125	0 a	2.5 ab	5.0 a	12.2 ab	21.6 a	29.8 bc	38.6 bc
NAA	14	10	0 a	0.7 bc	2.9 ab	7.6 bc	12.8 b	19.0 c	24.7 d
AVG +	14	125	0 a	0.0 c	0.5 c	4.4 d	8.3 c	18.4 c	24.7 d
NAA	14	10							

[z]Commercial harvest date was 19 Sept. 2007.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

1-MCP are required to block ethylene receptors at 7 DBAH than 15 DBAH. Our results also showed that the effect of 1-MCP on fruit ethylene production, fruit firmness, and fruit drop sustained ≈5 weeks in 'Bisbee Delicious' apples, which is similar to previous report in 'Golden Delicious' apples (Yuan and Carbaugh, 2007). Therefore, to effectively delay preharvest fruit drop, maintain fruit quality, and save the cost for 1-MCP, 1-MCP should be applied 15 DBAH instead of 7 DBAH in 'Delicious' apples.

It has been reported that the conversions of S-adenosyl methionine to 1-aminocyclopropane-1-carboxylate and ACC to ethylene are the rate-limiting steps in ethylene biosynthesis and catalyzed by ACC synthase and ACC oxidase, respectively (Alexander and Grierson, 2002). In this study, AVG or 1-MCP only inhibited the expression of *MdACS1* and *MdACO1* but not *MdACS5A* in fruit cortex. These results indicate that *MdACS1* and *MdACO1* in fruit cortex are associated with climacteric ethylene production in apple fruit. In the fruit abscission zones, both AVG and 1-MCP inhibited the expression of *MdACS5A* and *MdACO1* but not *MdACS1*. This suggests that both AVG and 1-MCP inhibit apple fruit drop by inhibiting expression of *MdACS5A* and *MdACO1*. On the other hand, NAA increases apple fruit ethylene production by increasing expression of *MdACS1* and *MdACO1* in fruit cortex (Li and Yuan, 2008). AVG and 1-MCP also decreased expression of *MdPG1* and *MdPG2* in fruit cortex. Our previous results showed that NAA increased expression of *MdPG1* but decreased expression of *MdPG2* in fruit cortex (Li and Yuan, 2008). These indicate that *MdPG1* but not *MdPG2* in fruit cortex is related to fruit softening. Both AVG and 1-MCP also inhibited expression of *MdPG1* and *MdPG2* in fruit abscission zones. However, our previous results showed that expression of *MdPG1* in fruit abscission zones was effectively suppressed by 1-MCP and NAA although 1-MCP and NAA had no more effect on fruit ethylene production and fruit abscission (Li and Yuan, 2008). These results suggest that expression of *MdPG2* but not *MdPG1* in fruit abscission zones is related to fruit abscission. In addition, 1-MCP more effectively inhibited expression of *MdPG2* in

Table 11. Effects of 1-MCP, AVG at 125 $mg \cdot L^{-1}$, and NAA at 20 $mg \cdot L^{-1}$ on fruit quality and maturity in Bisbee Delicious apples[z] (year 2007).

Treatment	Application time (DBAH[z])	Rate ($mg \cdot L^{-1}$)	Fruit ethylene ($\mu L \cdot kg^{-1}$/fresh weight/h^{-1})		Flesh firmness (N)		Starch (0 to 8)		Fruit color (%)		Soluble solids (%)	
			19 Sept.	3 Oct.	19 Sept.	3 Oct.	19 Sept.	3 Oct.	19 Sept.	3 Oct.	19 Sept.	3 Oct.
Control	—		0.153 a[y]	17.993 a	71.6 c	64.5 b	4.5 ab	6.8 a	93.6 a	95.9 ab	13.3 abc	15.2 ab
1-MCP	14	80	0.000 b	3.074 b	73.4 bc	70.7 a	2.8 f	5.8 cde	91.9 a	95.8 ab	12.4 d	14.6 bc
1-MCP	14	160	0.000 b	4.060 b	74.3 abc	69.0 a	3.0 ef	5.5 e	92.0 a	95.7 ab	12.8 cd	14.0 c
1-MCP	7	80	0.000 b	2.634 b	73.0 c	69.0 a	3.8 bcd	5.8 cde	91.2 a	95.5 ab	13.1 bc	14.2 c
1-MCP	7	160	0.000 b	0.881 c	76.5 a	70.3 a	3.7 cde	5.7 cde	91.1 a	94.3 b	13.4 abc	13.8 c
AVG	28	125	0.000 b	0.446 c	75.2 ab	68.5 a	3.3 def	5.7 de	93.1 a	94.8 ab	12.9 cd	14.6 bc
NAA	14	10	0.055 a	11.504 a	72.1 c	62.3 c	4.7 a	7.1 a	92.3 a	97.4 a	13.9 a	15.5 a
AVG +	14	125	0.000 b	0.236 c	74.3 abc	69.0 a	4.2 abc	6.4 bc	90.7 a	96.9 ab	13.6 ab	14.2 c
NAA	14	10										

[z]Commercial harvest date was 19 Sept. 2007.
[y]Mean separation within columns by Duncan's multiple range test ($P = 0.05$).
1-MCP = 1-methylcyclopropene; AVG = aminoethoxyvinylglycine; NAA = naphthaleneacetic acid.

fruit abscission zones than did AVG. This may be related to the stronger inhibitory effect of 1-MCP on fruit abscission than when AVG was used alone in 'Bisbee Delicious' apples. Similarly, the expression of *MdPG2* in fruit abscission zones was more effectively inhibited by NAA + AVG than by AVG or NAA alone (Li and Yuan, 2008). This has been attributed to the stronger inhibitory effect of NAA + AVG on fruit abscission than when AVG or NAA was used alone in 'Bisbee Delicious' apples (Li and Yuan, 2008).

In conclusion, our results showed that 1-MCP or NAA + AVG was more effective than NAA or AVG alone in reducing preharvest fruit drop and extending the harvest season while maintaining fruit quality. 1-MCP applied 15 DBAH more effectively delayed preharvest fruit drop than when applied 7 DBAH in 'Delicious' apples. 1-MCP more effectively inhibited expression of *MdPG2* in fruit abscission zones than AVG alone.

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