Research Note

Methyl Jasmonate and 1-Aminocyclopropane-1-Carboxylic Acid Interact to Promote Grape Berry Abscission

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Abstract: The application of methyl jasmonate (MeJA) or ethephon, an ethylene-releasing agent, to Thompson Seedless grapes can reduce fruit detachment force (FDF) and promote the development of dry stem scars on berries, possibly improving the quality of machine-harvested grapes. However, the amount of MeJA or ethephon needed to stimulate abscission may be prohibitively expensive and result in excessive residues. Thus, experiments were conducted to determine whether MeJA might interact with 1-aminocyclopropane-1-carboxylic acid (ACC), a natural biochemical precursor of ethylene, to promote abscission-related processes and possibly reduce the amount of MeJA needed. In a preliminary trial, MeJA (672 and 1,344 mg/L) interacted with ACC (500 and 1,000 mg/L) to reduce FDF by 25 to 70% compared with untreated grapes. However, MeJA and ACC did not interact to affect preharvest fruit drop, although treatment with 672 or 1,344 mg/L MeJA caused 16 to 23% drop by 3 days after treatment (DAT). In a second trial, grapes treated with MeJA, singly, or with ACC, produced ethylene which peaked at 1 DAT, remained elevated at 2 DAT, and declined rapidly thereafter, whereas grapes treated only with ACC maintained moderately elevated ethylene production throughout the 10-day study. Treatment with ACC or MeJA reduced FDF within 1 or 2 DAT, respectively. By 2 DAT, berries began to abscise from MeJA-treated clusters, regardless of whether they were also treated with ACC, but on 3, 4, and 10 DAT, ACC and MeJA interacted to greatly promote preharvest fruit drop. Moreover, the combination of ACC and MeJA also promoted dry stem scar development. Thus, coapplication of MeJA and ACC is more effective at stimulating grape abscission-related processes than either compound applied singly.

Key words: abscission, mechanical harvesting, plant growth regulators, *Vitis vinifera* L.

Mature grape (*Vitis vinifera* L.) berries do not normally abscise, but they can be induced to do so with the application of certain plant growth regulators, including methyl jasmonate (MeJA) (Fidelibus and Cathline 2010, Fidelibus et al. 2007) and ethephon (Ferrara et al. 2010, Hedberg and Goodwin 1980). The stimulation of grape berry abscission results in some potentially beneficial effects, including a reduction in fruit detachment force (FDF) and an increase in the proportion of berries with dry stem scars, effects that could improve the quality of machine-harvested fruit (Fidelibus et al. 2007, González-Herranz et al. 2009, Hedberg and Goodwin 1980, Uzquiza et al. 2013a, 2013b). However, MeJA and ethephon are only effective grape abscission agents at relatively high concentrations (Fidelibus and Cathline 2010, Gonzalez-Herranz et al. 2009, Uzquiza et al. 2013a, 2013b). Therefore, the high cost of MeJA and the potential for excessive residues, particularly of ethephon, could preclude their potential commercial use as grape abscission agents.

One strategy for improving the efficacy of abscission agents, and thereby potentially decreasing their required application rates, is to use them in combination (Holm and Wilson 1977, Kender et al. 2001, Uzquiza et al. 2013a, 2013b). The coapplication of MeJA and 5-chloro-3-methyl-4-nitro-1H-pyrazole (CMN-pyrazole) increased internal ethylene content and decreased FDF of oranges (*Citrus sinensis* L. [Osb.]) to a greater extent than was achieved by applying either agent singly (Holm and Wilson 1977, Kender et al. 2001). The effects that combinations of abscission agents may have on grape have been less studied, although combinations of ethephon (1,000 mg/L) and MeJA (4,480 or 8,960 mg/L) were generally more effective at reducing FDF and promoting dry stem scars on Verdejo grapes than either compound applied singly (Uzquiza et al. 2013a). Even so, Verdejo was not nearly as responsive to abscission agents as some other grape cultivars such as Thompson Seedless (Fidelibus et al. 2007), so additional testing is needed to determine the potential benefit of combined treatments on responsive cultivars.

Exogenous application of jasmonates stimulates ethylene production in several fruits, including orange (Hartmond et al.

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2000, Kender et al. 2001), apple (*Malus* x *domestica* Borkh.) (Fan et al. 1998, Saniewski et al. 1987a), tomato (*Lycopersicon esculentum*) (Saniewski et al. 1987b), and strawberry (*Fragaria* x *ananassa* Duch) (Mukkun and Singh 2009). Most of those studies focused on the physiology of fruit ripening with the exception of the work on oranges (Hartmond et al. 2000, Kender et al. 2001), which showed that the application of MeJA stimulated ethylene production by the fruit, which was followed by fruit abscission. Malladi et al. (2012) provided indirect evidence that MeJA stimulates abscission of blueberry (*Vaccinium* spp.) fruits at least partly via ethylene action, as the coapplication of MeJA with aminoethoxyvinylglycine (AVG), an ethylene biosynthesis inhibitor, attenuated MeJA effects on abscission. However, MeJA still induced some abscission of blueberry, even when coapplied with AVG, which could suggest that MeJA may initiate some abscission processes independently of ethylene. This finding agrees with recently reported work showing that ethylene and jasmonic acid promote floral organ abscission via independent pathways in *Arabidopsis thaliana* (Kim et al. 2013).

To our knowledge, the physiology of MeJA-induced berry abscission has not been studied in grape, although such knowledge is needed to advance progress toward developing effective grape abscission agents. If MeJA stimulates grape abscission indirectly, via ethylene, then the coapplication of MeJA and 1-aminocyclopropane-1-carboxylic acid (ACC), the biochemical precursor of ethylene, might be expected to interact to promote abscission-related processes. To test this hypothesis, Thompson Seedless grape berries were subjected to applications of MeJA and ACC to determine whether those compounds, applied individually and in combination, affected berry ethylene production, detachment force, preharvest abscission, and the development of dry stem scars.

Materials and Methods

Location and vineyard characteristics. The experiments were conducted at the University of California Kearney Agricultural Center, Parlier, CA, with own-rooted *Vitis vinifera* cv. Thompson Seedless grapevines supported by an overhead arbor trellis. The vines, planted in 1995, were quadrilateral cordon trained and cane-pruned, leaving ~6 canes per vine and 15 nodes per cane. Vines were spaced ~1.83 m within rows and 3.65 m between rows, which were oriented east to west. All vines were subjected to cultural practices considered normal and ordinary for dry-on-vine raisin grapes in the San Joaquin Valley (Christensen 2000), except that the canes were not severed and raisins were not made.

Experiment I. In 2010, a preliminary study was conducted. Four vines, each surrounded within and between rows by guard vines, were selected based on their uniformity of appearance and crop load. Nine clusters of similar size and appearance were selected on each vine and randomly assigned to one of nine possible treatment combinations of MeJA: 0, 672, or 1,344 mg/L (Bedoukian Research, Inc., Danbury, CT) and ACC: 0, 500, or 1,000 mg/L (Valent BioSciences, Libertyville, IL). Each treatment solution also included 0.05% Latron-B 1956 spreader-sticker (Loveland Industries, Inc., Greeley, CO). A factorial treatment structure in a randomized complete block design (RCBD) was employed, with individual vines considered blocks and individual clusters considered experimental units, so each treatment combination was applied to a cluster on each vine, and all treatment combinations were replicated on each of the four vines.

On 20 Sep 2010, when berries had accumulated ~22 Brix, handheld sprayers were used to apply the solutions directly to the appropriate clusters until run off (~0.06 L/cluster), and polyethylene shields were used to prevent overspray from contacting other clusters. After the clusters had dried, they were enclosed in polypropylene mesh bags to catch any berries that might abscise. The bags had a resealable flap at the bottom, from which berries were collected and counted at harvest (González-Herranz et al. 2009).

On 23 Sep, the peduncle of each cluster was severed with shears and the clusters, still enclosed within mesh bags, were carefully transported to a laboratory where FDF measurements were made. The clusters were gently removed from their bags, and small shears were used to sever 10 berries from the top, middle, and bottom part of each cluster, retaining the pedicel and a short section of rachis with each berry. Each berry was then placed in a jig attached to a force gauge (DPS-11; Imada, Northbrook, IL), force parallel to the fruit axis was applied to the rachis until it detached from the berry, and peak force was recorded (González-Herranz et al. 2009).

Experiment II. In 2013, a second trial with more measurement times and response variables was conducted. A factorial treatment structure in a RCBD was again employed. This trial included five plots (replicates), each composed of six adjacent vines in a row. Within each plot, 28 clusters were randomly selected from among all the clusters available on the six vines in each plot, and the clusters were assigned to receive one of four possible combinations of MeJA (0 or 1,344 mg/L) and ACC (0 or 1,000 mg/LACC), with 0.05% Latron-B 1956. Seven clusters per plot received the same treatment combination so that a cluster subjected to each treatment could be harvested from each of the five plots on each of seven observation dates: the day of treatment and 1, 2, 3, 4, 5, and 10 days after treatment (DAT).

On 25 Aug 2013, when grapes had amassed 21 Brix, one cluster per treatment per block was harvested. The remaining clusters were then treated with the appropriate solution and, when dry, were enclosed in mesh bags as in the 2010 experiment. On 1, 2, 3, 4, 5, and 10 DAT, the number of berries that had abscised before harvest from a cluster of each treatment and block was counted to determine the % abscission. The clusters were then harvested and FDF was measured on 10 berries, as in 2010. After each of the ten berries was detached, the stem-end condition of each detached berry was observed and assigned to one of three classes: wet, dry, or with the pedicel attached. Approximately 100 other berries from the same clusters were also clipped from their clusters, retaining their pedicels, and used to determine ethylene production rate. The berries were weighed and placed in airtight 473 mL glass mason jars (Kerr Glass Manufacturing, Lancaster, PA), filling the jars by approximately half. The jars were then sealed and held for 1 hr at 20°C. At that time, a sample of headspace gas was taken with a gas-tight syringe passed through silicone septa installed in the jar lids and injected into a gas chromatograph (series 400 AGC 211-2; EG&G Chandler, Broken Arrow, OK) equipped with two 8% NaCl on alumina F-1 columns (0.32 × 122 cm and 0.32 × 30 cm, 80/100 mesh) and one molecular sieve 5A column (0.32 × 91 cm, 80/100 mesh) and a flame ionization detector. Separations were performed at 70°C and a flow rate of 60 mL/min using a flow gas mixture consisting of hydrogen (220 kPa), compressed air (83 kPa), and helium (248 kPa) and a sample injection volume of 2.0 mL. Quantification of ethylene was accomplished by comparing sample and standard peak heights. The measurements were expressed in nL/g fresh wt/hr.

Data analysis. All data were subjected to analysis of variance (PROC GLM) by date, using SAS statistical software (SAS Inst., Cary, NC). When appropriate, treatment means were separated by Tukey–Kramer adjusted *t* test ($p = 0.05$).

Results

In experiment I, MeJA interacted with ACC ($p = 0.02$) to reduce FDF at 3 DAT, the only observation date that year (Table 1). Without ACC, MeJA did not reduce FDF, and without MeJA, neither did ACC. The FDF of grapes treated with ≥500 mg/L ACC and ≥672 mg/L MeJA was 25 to 30% lower than the FDF of grapes treated with MeJA but not ACC. Treatment with a combination of 1,344 mg/L MeJA and 500 or 1,000 mg/L ACC reduced FDF by more than 50% compared to treatment with 1,344 mg/L MeJA alone.

The primary and interaction effects of MeJA and ACC on FDF differed from those on berry abscission. MeJA stimulated grape berry abscission ($p = 0.002$) but ACC did not ($p = 0.07$), and MeJA and ACC did not interact to affect abscission ($p = 0.38$). Grapes did not abscise from clusters unless they were treated with MeJA, and a similar percent berry abscission, 16 to 23%, was noted from clusters treated with 672 or 1,344 mg/L MeJA.

In experiment II, MeJA plus ACC markedly and rapidly increased grape berry ethylene production (Figure 1). At 1 DAT, grapes treated with both MeJA and ACC produced 19 times more ethylene than untreated fruit, whereas grapes treated with ACC singly produced ~5 times more ethylene than untreated berries. Ethylene production from grapes treated with MeJA, with or without ACC, began to decline 2 DAT, though berries treated with ACC still produced 10 times more ethylene than untreated berries, and berries treated with MeJA and ACC produced nearly 30 times more ethylene than controls. Ethylene production from berries treated with MeJA plus ACC further declined at 3 DAT, though it was still greater than that of any other treatment. By 4 DAT, grapes treated with the combination of MeJA and ACC produced similar amounts of ethylene as grapes treated with ACC only, but grapes subjected to either of those two treatments still produced more ethylene than grapes subjected to other treatments. By 5 and 10 DAT, grapes treated with ACC produced more ethylene than other grapes, though by 10 DAT most of the berries from clusters treated with MeJA and ACC had abscised, either before or immediately after harvest, so there were no longer enough nonabscised grapes to use for ethylene measurements. Grapes treated with ACC only had a different pattern of ethylene evolution production than those treated with MeJA, either singly or in combination with ACC: grapes treated only with ACC had a steady, relatively moderate, elevated production of ethylene throughout the study period.

In 2013, ACC reduced FDF on 1 DAT, and almost every day thereafter; MeJA also reduced FDF, starting at 2 DAT, then every day thereafter (Table 2). At 3 and 4 DAT, ACC and MeJA interacted to affect FDF as they did in 2010 (interaction $p = 0.02$), and the combination of ACC and MeJA reduced FDF to half of that observed in the other treatments.

No berries abscised until 2 DAT, regardless of treatment, so berry abscission data from 1 DAT is not shown. By 2 DAT, berries began to abscise from clusters treated with MeJA, regardless of whether they were also treated with ACC (Table 3). At 3, 4, and 10 DAT, ACC and MeJA interacted to promote

Table 1 Effect of 1-aminocyclopropane-1-carboxylic (ACC) and methyl jasmonate (MeJA) on fruit detachment force of Thompson Seedless grapes three days after treatment in 2010.

	Fruit detachment force (N)		
	MeJA (mg/L)		
ACC (mg/L)	0	672	1,344
0	1.176 a A[a]	0.884 a A	0.962 a A
500	1.190 a A	0.649 ab A	0.342 b B
1,000	1.242 a A	0.623 b A	0.439 b B

[a] Values are treatment means, n = 4. Within rows, values are significantly different if followed by a different lower case letter. Within columns, values are significantly different if followed by a different upper case letter ($p = 0.05$).

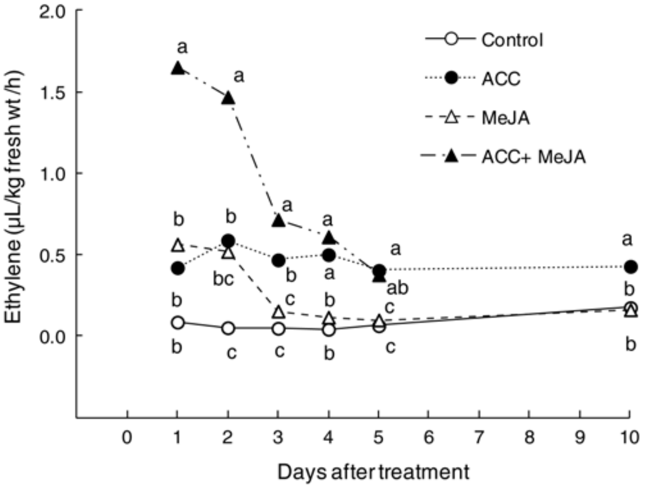

Figure 1 Effect of treatments of 1,000 mg/L 1-aminocyclopropane-1-carboxylic (ACC), 1,344 mg/L methyl jasmonate (MeJA), and their combination on ethylene production by Thompson Seedless grapes on several days after treatment in 2013. Means (n = 5) followed by a different letter on each day are significantly different ($p = 0.05$). Due to berry abscission during handling, there were not enough berries with pedicels attached to measure ethylene production at 10 DAT in the ACC + MeJA treatment.

berry abscission, with the combination of ACC and MeJA inducing much greater abscission than MeJA alone, which in turn stimulated more abscission than ACC alone or untreated clusters.

By 1 DAT, dry stem scars became much more common on berries detached from clusters treated with MeJA than on berries detached from clusters that were not treated with MeJA, regardless of whether those clusters were also treated with ACC (Figure 2). However, the combination of ACC and MeJA especially promoted the development of dry stem scars; >80% of the berries from clusters treated with both compounds had dry stem scars on most observation dates (Figure 2B). The application of ACC alone had little effect on dry stem scar incidence except at 10 DAT, when clusters treated with ACC alone had a similar proportion of berries with a dry stem scar as those treated with MeJA and ACC.

Discussion

The results of experiment I suggested a potential benefit in combining MeJA and ACC, a finding that agrees with Uzquiza et al. (2013a, 2013b), who showed that combinations of MeJA with ethephon, an ethylene-releasing agent, were more effective at reducing FDF of Verdejo and increasing abscission of Sauvignon blanc grapes than single applications of either compound. However, the studies on Verdejo and Sauvignon blanc tested much more concentrated applications of MeJA, up to 8,960 mg/L, and observed less loosening and abscission than occured with Thompson Seedless subjected to far lower concentrations of MeJA. For example, the data reported here suggest that 672 to 1,344 mg/L MeJA combined with 500 to 1,000 mg/L ACC stimulates considerable abscission of Thompson Seedless grapes. Striking differences among cultivars in responsiveness to abscission agents has been previously reported in grape (Fidelibus et al. 2007) and blueberry (Malladi et al. 2012), though the physiological basis for such differences is unclear.

Treatments had different effects on FDF and abscission, probably because a decline in FDF precedes abscission, but also due to the fact that grapes with very low FDF generally abscise before FDF measurements can be made (González-Herranz et al. 2009). To confirm the interactive effects of MeJA and ACC on grape berry abscission, to develop a better understanding of the time course of these treatment effects, and to determine how these treatments may affect ethylene production by berries, a variable that is critical in orange fruit abscission (Kender et al. 2001), a similar study was conducted in 2013, with more observation times and response variables measured.

Experiment II confirmed that MeJA and ACC stimulated ethylene production by the grapes and that ethylene production preceded, or occurred along with, other abscission-related responses, as was observed with MeJA in oranges (Hartmond et al. 2000, Kender et al. 2001). Moreover, coapplication of MeJA and ACC stimulated grapes to produce far more ethylene than grapes treated with either compound singly, and the combined treatment was also far more effective at stimulating berry abscission. However, our data suggest that MeJA effects on grape berry abscission might not be solely via ethylene production. For example, in the first 2 DAT, berries treated with MeJA or ACC alone produced similar concentrations of ethylene, but for the remainder of the study, berries treated with MeJA alone produced less ethylene than berries treated with ACC alone, even though the MeJA-treated grapes generally had lower FDF, greater abscission, and a higher proportion of dry stem scars than the grapes treated with ACC.

Table 3 Effect of methyl jasmonate (MeJA) and 1-aminocyclopropane-1-carboxylic (ACC) on berry abscission of Thompson Seedless grapes in 2013.

MeJA (mg/L)	ACC (mg/L)	Abscised berries (%): days after treatment				
		2	3	4	5	10
0	0	0.0 a[a]	0.0 a	0.0 a	0.3 a	0.0 a
	1000	0.0 a	0.0 a	0.16 a	0.1 a	0.2 a
1,344	0	2.7 a	0.0 b	1.8 b	16.3 a	3.6 b
	1000	5.3 a	6.9 a	21.6 a	21.3 a	36.0 a
Signif.	ACC	0.49	0.03	0.03	0.57	<0.01
	MeJA	0.05	0.03	0.02	<0.01	<0.01
	ACC x MeJA	0.49	0.03	0.04	0.55	<0.01

[a] Values are treatment means, n = 5. Within each column and concentration of MeJA, means followed by a different letter are significantly different ($p = 0.05$).

Table 2 Effect of 1-aminocyclopropane-1-carboxylic (ACC) and methyl jasmonate (MeJA) on fruit detachment force of Thompson Seedless grapes at different intervals following treatment in 2013.

	Fruit detachment force (N): days after treatment						
	0	1	2	3	4	5	10
ACC (mg/L)							
0	1.716[a]	1.254	1.093	1.143	1.139	1.105	1.099
1,000	1.616	0.956	0.756	0.894	0.813	0.966	0.740
MeJA (mg/L)							
0	1.566	1.225	1.078	1.224	1.215	1.373	1.147
1,344	1.766	0.984	0.771	0.813	0.737	0.699	0.687
Significance							
ACC	0.56	0.03	<0.01	0.02	<0.01	0.15	<0.01
MeJA	0.26	0.07	<0.01	<0.01	<0.01	<0.01	<0.01
ACC x MeJA	0.30	0.96	0.10	0.05	<0.01	0.58	0.34

[a] Values are treatment means, n = 10.

These data support those of Malladi et al. (2012), who indirectly showed that the abscission activity of MeJA on blueberries may not depend entirely on ethylene, as the coapplication of MeJA and AVG, an ethylene biosynthesis inhibitor, reduced but did not eliminate MeJA-induced abscission.

The FDF and berry abscission data presented may suggest the combination of MeJA and ACC was less effective than it actually was because abscised berries were counted immediately before harvesting the clusters of grapes, but harvest and sample preparation invariably detached many of the most loosely-attached berries before FDF measurements could be made. As previously noted, so many berries abscised from clusters treated with MeJA and ACC due to handling during harvest and sampling of the clusters that there were not enough berries with pedicels attached to measure ethylene production at 10 DAT. Preharvest fruit drop is undesirable, so harvest would need to occur after FDF was reduced, but before considerable abscission begins: within 2 or 3 DAT, as suggested by previous studies (Fidelibus and Cathline 2010, Gonzalez-Herranz et al. 2009).

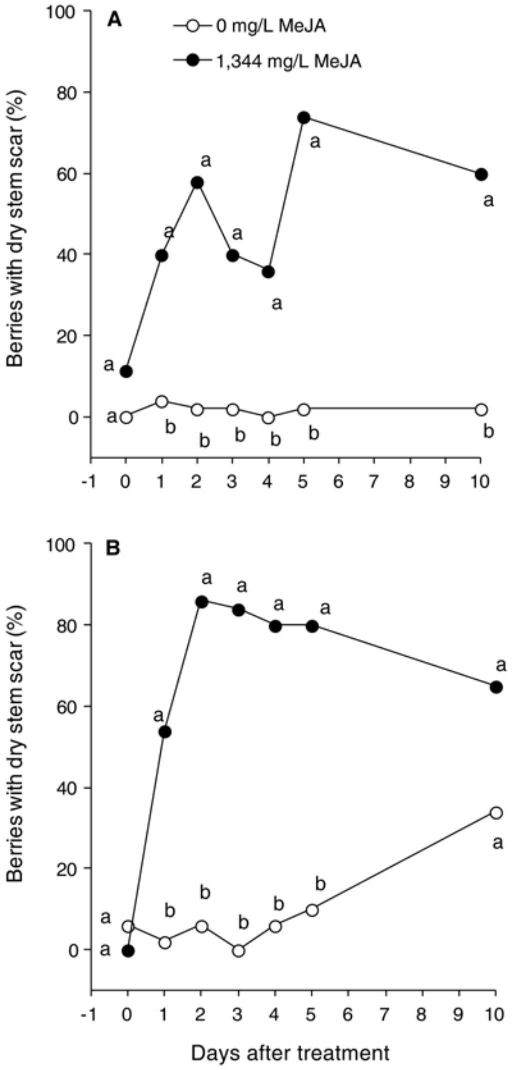

Figure 2 Effect of 1-aminocyclopropane-1-carboxylic (ACC) and methyl jasmonate (MeJA) on the percentage of Thompson Seedless grape berries with dry stem scars after detachment on several days after treatment in 2013. **(A)** The effect of MeJA on grapes with 0 mg/L ACC, and **(B)** the effect of MeJA on grapes with 1000 mg/L ACC. Values are treatment means, n = 5. Means with a different letter on each day are significantly different (*p* = 0.05).

Conclusion

The coapplication of MeJA and ACC strongly promotes the production of ethylene by grape berries and is more effective at stimulating abscission-related processes than either compound applied singly. Additional research is needed to better understand how MeJA and ethylene interact to affect the abscission-related physiology of grape berries.

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