Impact of 1-Methylcyclopropene and Methyl Jasmonate on Apple Volatile Production

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Climacteric Fuji apples were treated with 10 μL·L^{-1} MCP (1-methylcyclopropene), 2 mmol·L^{-1} MJ (methyl jasmonate), or a combination of 10 μL·L^{-1} MCP and 2 mmol·L^{-1} MJ. Fruit were kept at 20 °C for 15 days after treatment. Production of ethylene and other volatile compounds was measured prior to and 3, 7, 11, and 15 days after treatment. Ethylene production decreased 3 days following MJ treatment and then increased. MCP treatment alone or in combination with MJ inhibited ethylene production. MJ and MCP inhibited production of many volatile alcohols and esters. The production of individual alcohols and esters appears to be differentially inhibited by MJ or MCP. MJ and MCP inhibited not only production of alcohols but also formation of esters from alcohols.

Keywords: *Apples; ethylene; 1-methylcyclopropene; methyl jasmonate; volatile compounds*

Apple fruit ripening is associated with dramatically changed volatile compound production. Most volatile compounds produced by apple fruit are esters, alcohols, aldehydes, acids, ketones, and terpenes. The largest change in volatile compound production during apple fruit ripening is an increase in ester production (Brown et al., 1966). The increase in ester production is responsible, in part, for development of characteristic flavor and aroma of apple fruit during ripening. Ethylene is believed to be involved in the regulation of ester production. Oeller et al. (1991) demonstrated that tomato fruit produced by plants transformed with a 1-aminocyclopropane-1-carboxylic acid oxidase antisense gene failed to produce climacteric ethylene. The authors mentioned that the fruits did not develop an aroma characteristic of ripe fruit, although no data were presented. Compounds such as methyl jasmonate (MJ) that modulate ethylene production also enhance ester production in preclimacteric apple fruits (Fan et al., 1997). Apples treated with the ethylene synthesis inhibitor aminoethyoxyvinylglycine (AVG) have reduced production of ethylene and volatiles contributing to aroma (Halder-Doll and Bangerth, 1987).

The ethylene action inhibitor, diazocyclopentadiene (DACP), inhibits production of ethylene and some volatile compounds in climacteric apple fruit (Fan et al., 1998a), indicating that continuous ethylene action is required for production of some ripening related volatiles. DACP, however, does not totally block ethylene synthesis and may not completely inhibit ethylene action. Another ethylene action inhibitor, 1-methylcyclopropene (MCP), is a much stronger ethylene action inhibitor (Sisler and Serek, 1997) and can totally inhibit ethylene production in apple fruit (Fan and Mattheis, 1999). Volatile production has been shown to be inhibited by MCP in banana (Golding et al., 1998) and plum (Abdi et al., 1998) fruits, although it is unclear whether production of all volatile compounds was inhibited to the same degree.

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Jasmonates (jasmonic acid and MJ) are plant growth regulators that modulate a wide range of plant responses (Creelman and Mullet, 1997; Sembdner and Parthier, 1993) and may have a role in modulation of climacteric fruit ripening (Fan et al., 1998b). MJ treatment promotes production of volatile alcohols and esters by preclimacteric apples (Fan et al., 1997) but inhibits volatile ester production by apples previously stored in controlled atmosphere conditions (Olias et al., 1992). Jasmonate treatment can also promote or inhibit ethylene production depending on fruit developmental stage (Saniewski and Czapski, 1985; Saniewski et al., 1987). It is unknown whether the effects of jasmonates on volatile production require ethylene action or whether all esters are affected similarly following jasmonate treatment of fruit after storage. The objectives of this study were to examine the effects of MCP and MJ, as well as interaction of MJ and MCP on production of volatile compounds by apple fruit.

MATERIALS AND METHODS

Fuji apples (*Malus domestica* Borkh.) were harvested from a commercial orchard near Orondo, WA. The fruit were stored in air at 0 °C for 2 weeks and warmed to 20 °C overnight prior to treatment. The internal ethylene concentration (IEC) of individual fruit was measured according to Williams and Patterson (1962). A 0.5 mL gas sample withdrawn through a hypodermic needle inserted into the core cavity was injected into a gas chromatograph (HP5880A; Hewlett-Packard, Avondale, PA) fitted with a 30-cm glass column (3.2-mm i.d.) packed with Porapak Q (80/100 mesh). Gas flows for N_2, H_2, and air were 30, 30, and 300 mL·min^{-1}, respectively. Oven, injector, and FID temperatures were held at 60, 60, and 100 °C, respectively. The apples had a mean IEC of 32.5 μL·L^{-1} (range 10.1−67.9, indicating the onset of the ethylene climacteric had occurred) when dipped into 0.02% (v/v) Tween 20 and 1% (v/v) ethanol in water for 2 min (control), 2.0 mmol·L^{-1} MJ (Bedoukian Research, Danbury, CN) in 0.02% (v/v) Tween 20 and 1% (v/v) ethanol for 2 min, 10 μL·L^{-1} MCP (BioTechnology for Horticulture Inc., Burr Ridge, IL) in air for 12 h, or 12 h 10 μL·L^{-1} MCP followed by 2 min 2 mmol·L^{-1} MJ. Treatment protocols were as described previously (Fan and Mattheis, 1999). For MCP treatment, each replicate group of apples was

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placed in a 20-L glass jar and MCP was injected into the jar through a rubber septum in the lid. After 12 h, fruit were removed from the jar and dipped into 0.02% (v/v) Tween 20 and 1% (v/v) ethanol in water for 2 min. For the combination MCP + MJ treatment, fruit were dipped in 2 mmol·L^{-1} MJ with 1% (v/v) ethanol and 0.02% (v/v) Tween 20 for 2 min after the MCP treatment. Control and MJ-treated fruit were enclosed in 20-L jars for 12 h prior to dipping in 0.02% (v/v) Tween 20 and 1% (v/v) ethanol with or without MJ. MCP-treated fruit was also dipped in 0.02% (v/v) Tween 20 and 1% (v/v) ethanol for 2 min. There were four replicates (5 apples each) per treatment. The fruit were stored at 20 °C after treatment. Production of ethylene (Fan et al., 1998c) and other volatile compounds (Mattheis et al., 1991) were measured initially and 3, 7, 11, and 15 days after treatment in a flow-through system. Purified compressed air flowed at 6 L·h^{-1} through the 4-L jars containing apple fruit. A 0.5 mL gas sample was collected from the outlet of the jars, and ethylene was analyzed using the same gas chromatograph described previously. Volatile compounds in the outlet gas (25−100 mL depending on the amount of volatiles generated by the fruit) were adsorbed onto 50 mg of 30−50 mesh Tenax (Alltech Associates, Deerfield, IL) packed in glass tubing (17.5 cm × 0.4 cm i.d). Volatile compounds on the Tenax traps were desorbed at 250 °C for 3 min using a Tekmar 6000 aero trap desorber (Tekmar Co., Cincinnati, OH). After the desorbed sample compounds were condensed at −120 °C, the cryofocusing module was flash heated to 250 °C under a stream of He carrier gas which carried the analytes into a Hewlett-Packard 5890A/5971A GC-MSD equipped with a DB-Wax column (J&W Scientific, 60 m × 0.25 mm i.d., 0.25 μm film thickness). Compound identification was made by comparison of spectra of sample compounds with those contained in the Wiley-NBS library and by comparing retention indices of sample compounds and standards. Quantification was performed using selected ion monitoring for base peaks, and quantitative values were calculated using response factors generated with standards. Volatile compounds measured included esters, alcohols, aldehydes, acids, plus α-farnesene and 6-methyl-5-hepten-2-one. Volatile esters were grouped by alcohol moiety: methyl esters, ethyl esters, propyl esters, 2-methylpropyl esters, butyl esters, 2-methylbutyl esters, pentyl esters, hexyl esters.

The data were subjected to analysis of variance using SAS release 6.12 (SAS Institute, Cary, NC). Treatment differences were identified using Fisher's least significant difference (LSD), and unless indicated, only significant differences ($P < 0.05$) are discussed. To simplify the figures, mean standard deviations are indicated. Differences between means that exceed the mean standard deviations were always significant when analyzed using the LSD procedure.

RESULTS

Ethylene production by control fruit increased between days 0 and 3 after treatment and was then relatively stable through day 15 (Figure 1A). MJ treatment delayed the increase in ethylene production until 7 days after treatment. Ethylene production by MCP-treated fruit was undetectable through 15 days after treatment. Ethylene production was detectable 15 days after the combined MCP−MJ treatment.

Alcohol production by MJ-treated fruit was lower than that of the controls through 15 days after treatment (Figure 1B). Alcohol production by MCP-treated fruit was lower compared to that of the controls 7, 11, and 15 days after treatment. Alcohol production following the combined treatment of MCP and MJ was similar to the treatment with MCP alone.

Production of esters was inhibited by MJ treatment throughout the 15 day period following treatment (Figure 1C). Ester production decreased during the first 3 days after MJ treatment and then increased slightly.

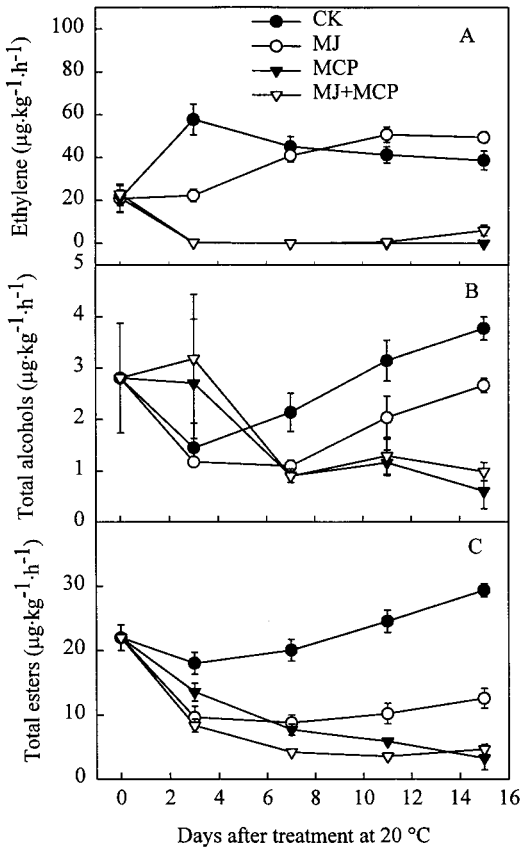

Figure 1. Production of ethylene (A), total alcohol (B), and total esters (C) of Fuji apples. Fruit were treated with water (CK), 2 mmol·L^{-1} MJ, 10 μL·L^{-1} MCP, and a combination of 2 mmol·L^{-1} MJ and 10 μL·L^{-1} MCP and kept at 20 °C. Vertical bars represent mean standard deviation.

MCP also inhibited ester production, and ester production gradually decreased throughout the experiment. The ester production by MCP-treated fruit was 11% of that by control fruit 15 days after treatment. Similar to fruit treated with MJ alone, ester production by fruit treated with MCP and then MJ was reduced 3 days after treatment and ester production continued to decrease through the end of the 15 day posttreatment period. Aldehyde production following MCP treatment alone or in combination with MJ was lower than that of the controls 15 days after treatment (data not shown). Volatile acid production was not affected by any of the treatments (data not shown).

No treatment effects were observed on the production of 6-methyl-5-hepten-2-one 3, 7, or 11 days after treatment (Figure 2A). MCP alone or in combination with MJ inhibited 6-methyl-5-hepten-2-one production 15 days after treatment. Production of α-farnesene was not affected by MJ treatment (Figure 2B). MCP alone or in combination with MJ reduced production of α-farnesene, particularly 11 and 15 days after treatment.

Ethanol production decreased relative to the controls 7, 11, and 15 days after MJ treatment (Figure 3A). Compared to the controls, ethanol production of fruit treated with MCP alone or in combination with MJ was higher 3 days after treatment but lower thereafter. Production of ethyl esters (ethyl acetate, ethyl propanoate, ethyl butyrate, ethyl 2-methyl butyrate, ethyl pentanoate, ethyl hexanoate, and ethyl octanoate) by control fruit increased during the 15 days at 20 °C (Figure 3B). MJ treatment inhibited the increase in ethyl ester production. Production of ethyl esters by MJ-

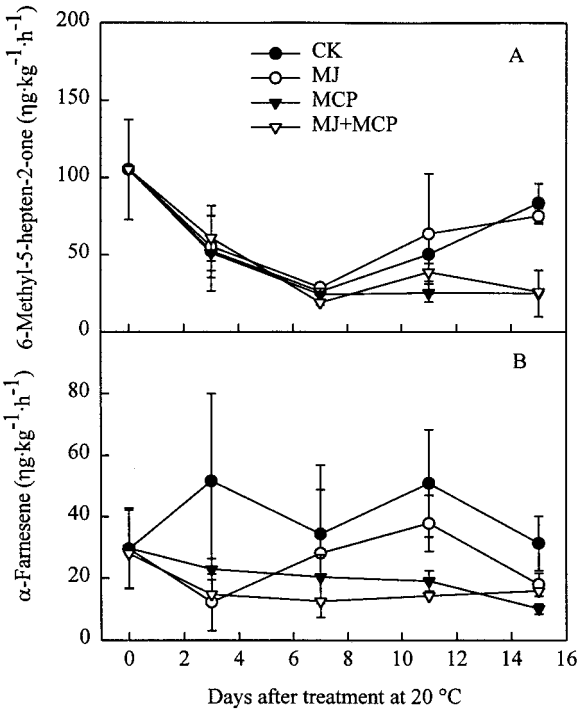

Figure 2. Production of 6-methyl-5-hepten-2-one (A) and α-farnesene (B) of Fuji apples. Fruit were treated with water (CK), 2 mmol·L^{-1} MJ, 10 μL·L^{-1} MCP, and a combination of 2 mmol·L^{-1} MJ and 10 μL·L^{-1} MCP and kept at 20 °C. Vertical bars represent mean standard deviation.

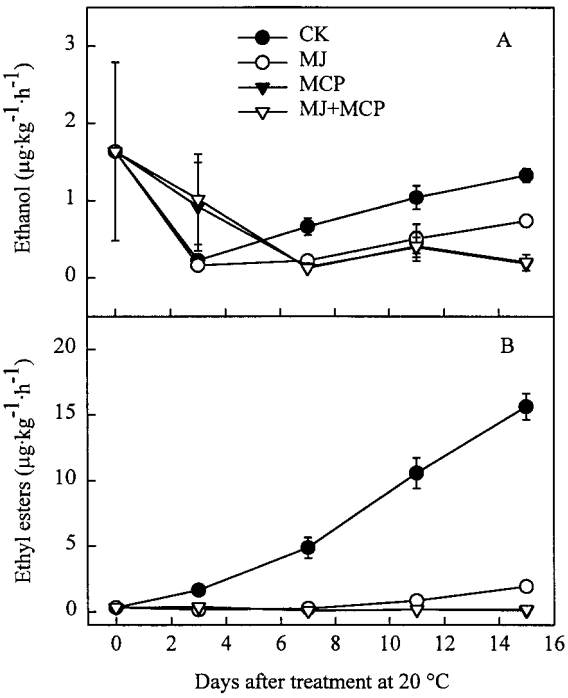

Figure 3. Production of ethanol (A) and ethyl esters (B) of Fuji apples. Fruit were treated with water (CK), 2 mmol·L^{-1} MJ, 10 μL·L^{-1} MCP, and a combination of 2 mmol·L^{-1} MJ and 10 μL·L^{-1} MCP and kept at 20 °C. Vertical bars represent mean standard deviation.

treated fruit was 13% of that of the controls 15 days after treatment. Treatment with MCP alone or in combination with MJ prevented the increase in ethyl ester production during the entire 15 day period after treatment. Similar results were observed for methyl esters (data not shown).

Production of butanol decreased over time for all fruit (Figure 4A). MJ treatment did not affect production of butanol. MCP and the combined MCP−MJ treatment inhibited the decrease in butanol production detected 3 days after treatment for control and MJ-treated fruit, but butanol production decreased 7, 11, and 15 days after treatment. Production of butyl esters (butyl acetate, butyl propanoate, butyl butyrate, butyl 2-methyl butyrate, and butyl hexanoate) by control fruit decreased during the 15 day period after treatment (Figure 4B). MJ treatment resulted in reduced butyl ester production relative to control fruit 3 and 7 days after treatment but not 11 or 15 days after treatment. Butyl ester production following MCP treatment was inhibited throughout the 15 day period. The combination of MCP and MJ treatment further reduced butyl ester production 3, 7, and 11 days after treatment.

None of the treatments affected hexanol production, but levels of hexyl esters decreased over time in all treatments (Figure 4C). Production of hexyl esters (hexyl acetate, hexyl propanoate, hexyl butyrate, and hexyl 2-methylbutyrate) by control fruit decreased over time (Figure 4D). MJ treatment did not affect hexyl ester production; however, MCP treatment alone or in combination with MJ inhibited synthesis of hexyl esters.

The change in production of propanol was similar to that of propyl esters (propyl acetate, propyl propanoate, and propyl hexanoate) (Figure 5A,B). Production of both propanol and propyl esters in control fruit increased over time. Although MJ treatment reduced the production of propanol and propyl esters during the 15 day posttreatment period compared to that of the controls, the production of these volatiles in MJ-treated fruit increased, although at a slower rate compared to that of the control fruit. MCP did not affect the production of propanol and propyl esters 3 days after treatment, but production was lower 7, 11, and 15 days after treatment. The production of propanol and propyl esters in fruit treated with the combination of MCP and MJ was low throughout the investigation period.

Production of pentanol was not significantly altered by any of treatments (Figure 5C). The amount of pentyl esters (pentyl acetate and pentyl butyrate) produced by control fruit decreased during the 15 days at 20 °C (Figure 5D). Production by MJ- and MCP-treated fruit was lower than that of the controls, and the combined MCP−MJ treatment resulted in the lowest production 3, 7, and 11 days after treatment.

Production of 2-methyl-1-propanol by MJ-treated fruit was higher compared to that of the control fruit 3 days after treatment but similar for the rest of the posttreatment period (Figure 6A). MCP treatment alone or when followed by MJ inhibited 2-methyl-1-propanol production 7, 11, and 15 days after treatment. Production of 2-methylpropyl acetate in control fruit decreased slightly over 15 days (Figure 6B). MJ and MCP treatments inhibited production of 2-methylpropyl acetate, but the lowest production was by fruit treated with MCP followed by MJ.

MJ did not affect production of 2-methyl-1-butanol. Production of 2-methyl-1-butanol by control and MJ-treated fruit increased during the 15 day posttreatment period (Figure 6C). MCP treatment prevented the increase in production. The amount of 2-methyl-1-butanol produced by fruit treated with the combination of MCP then MJ was less than that of MJ-treated fruit and greater than that of MCP-treated fruit. MJ, MCP, or the combination of MCP then MJ (Figure 6D)

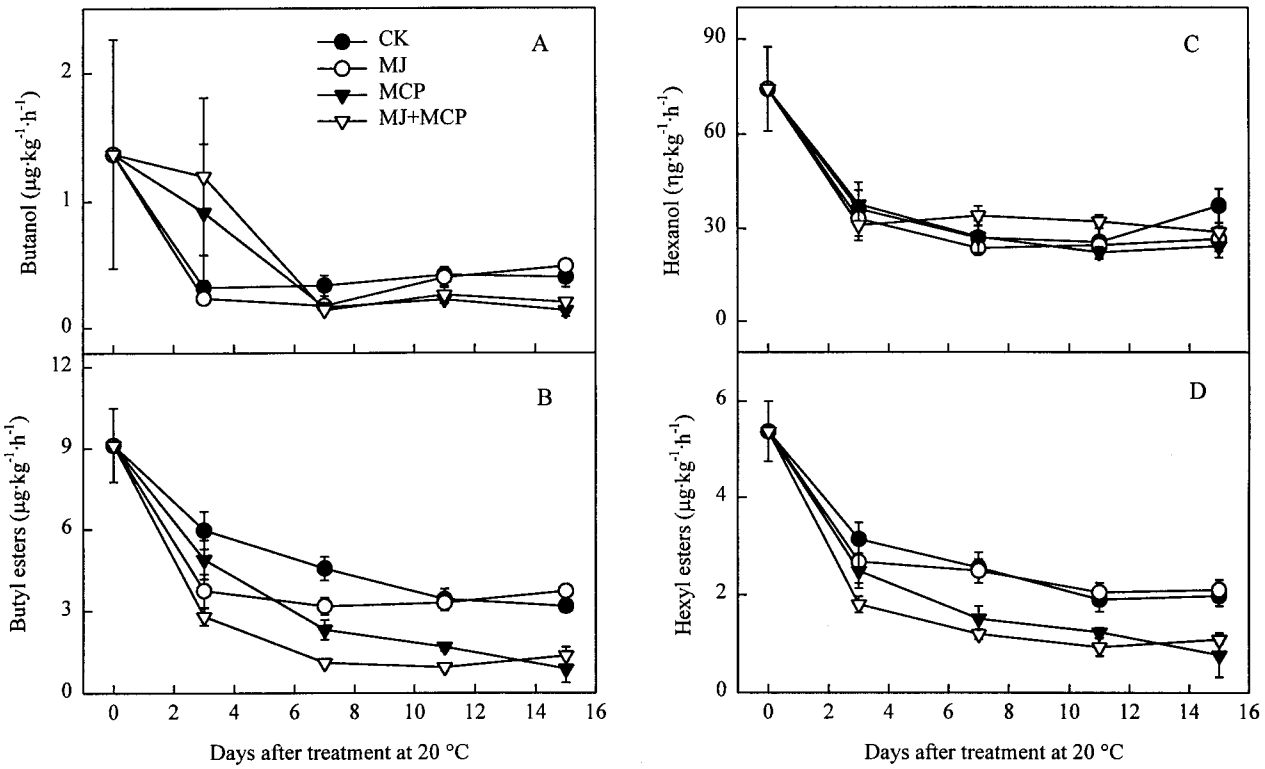

Figure 4. Production of butanol (A), butyl esters (B), hexanol (C), and hexyl esters (D) of Fuji apples. Fruit were treated with water (CK), 2 mmol·L^{-1} MJ, 10 μL·L^{-1} MCP, and a combination of 2 mmol·L^{-1} MJ and 10 μL·L^{-1} MCP and kept at 20 °C. Vertical bars represent mean standard deviation.

inhibited production of 2-methylbutyl esters (2-methylbutyl acetate and 2-methylbutyl 2-methyl butyrate).

DISCUSSION

Esters produced by apple fruit are synthesized enzymatically by coupling the respective acid and alcohol (Salunkhe and Do, 1976; Knee and Hatfield, 1981; Bartley et al., 1985; Fellman et al., 1993). The process is detectable at all stages of apple fruit development and may be limited by alcohol availability (Knee and Hatfield, 1981). Treatment with MCP or MJ inhibits the conversion of some alcohols to esters as well as production of some alcohols. For example, ethyl ester production was inhibited more than ethanol production following MCP or MJ treatment (Figure 3). Ethanol production was higher than the controls 3 days after MCP treatment, production of acids was not affected by any treatment, yet ethyl esters were not detected from MCP-treated fruit. Fruit treated with MCP or the combined MCP−MJ-treated fruit had higher butanol production than the control 3 days after treatment; however, production of butyl esters by MCP and MCP−MJ-treated fruit was lower than that of the controls during the same time frame (Figure 4A,B). MCP or MJ did not affect the production of hexanol, but hexyl ester production was reduced. These results indicate the availability of alcohols may not be the only factor limiting apple ester production when ethylene action is inhibited by MCP or following treatment with MJ.

Production of methyl and ethyl esters (Figure 3B) by control fruit increased during 15 days at 20 °C. MJ and (more notably) MCP inhibited the increase in production of methyl or ethyl esters. Of all the esters produced by Fuji apples in these studies, production of methyl and ethyl esters was most affected by MJ and MCP relative to initial production rates.

Apple fruit can produce straight-chain alcohols by β-oxidation of long-chain fatty acids (Bartley, 1985) and branched-chain alcohols from amino acid degradation (Tressl and Albrecht, 1986; Hansen and Poll, 1993). MCP and MJ reduced production of most esters and alcohols, suggesting MCP and MJ impact both pathways. The effects of MJ and MCP on production of 2-methyl-1-propanol and 2-methyl-1-butanol were similar (Figure 6), indicating production of these compounds may be regulated in a like manner.

MCP substantially inhibited ester volatile production in the climacteric fruit used in this experiment, indicating that a high rate of ester volatile production requires continuous ethylene action (Fan et al., 1998a). Ethylene production was not detectable following MCP treatment. In the absence of detectable ethylene production by MCP-treated fruit during the 15 day period after treatment, ester production continued albeit at a reduced rate. To sustain production of these esters at a low rate, continuous ethylene action may not be necessary. Alternatively, MCP may not totally inhibit ethylene action and a low, nondetectable ethylene production rate and subsequent binding may be enough to stimulate synthesis of some esters.

The inhibition of ester production by MJ does not appear to be closely associated with inhibition of ethylene production. Although ethylene production was inhibited 3 days after MJ treatment, the rate of production was still indicative of climacteric apples. MJ-treated fruit had higher ethylene production 11 and 15 days after treatment compared to the controls, yet MJ treatment inhibited ester production during the 15 day period after treatment (Figure 1C). This suggests a differential effect of MJ on ethylene and ester volatile production, possibly via a MJ-induced alteration in ethylene sensitivity (Dathe, 1992).

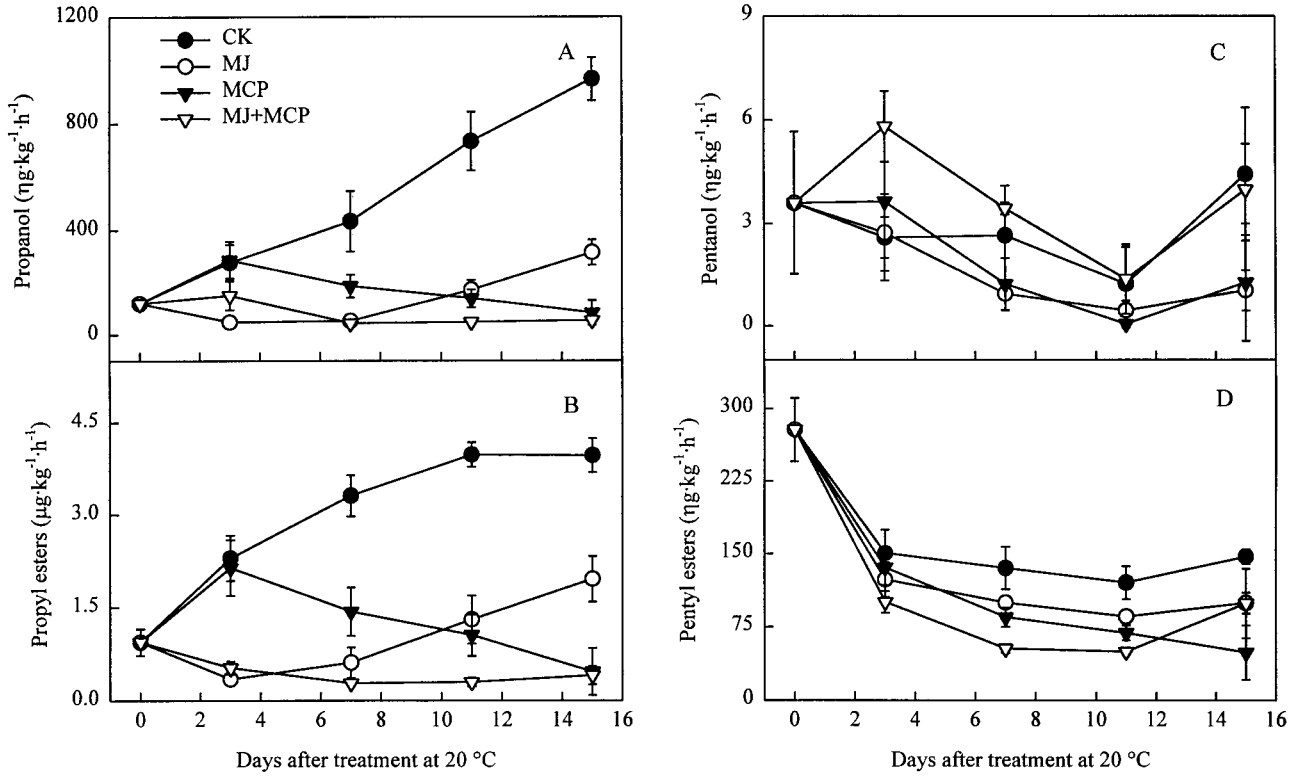

Figure 5. Production of propanol (A), propyl esters (B), pentanol (C), and pentyl esters (D) of Fuji apples. Fruit were treated with water (CK), 2 mmol·L^{-1} MJ, 10 μL·L^{-1} MCP, and a combination of 2 mmol·L^{-1} MJ and 10 μL·L^{-1} MCP and kept at 20 °C. Vertical bars represent mean standard deviation.

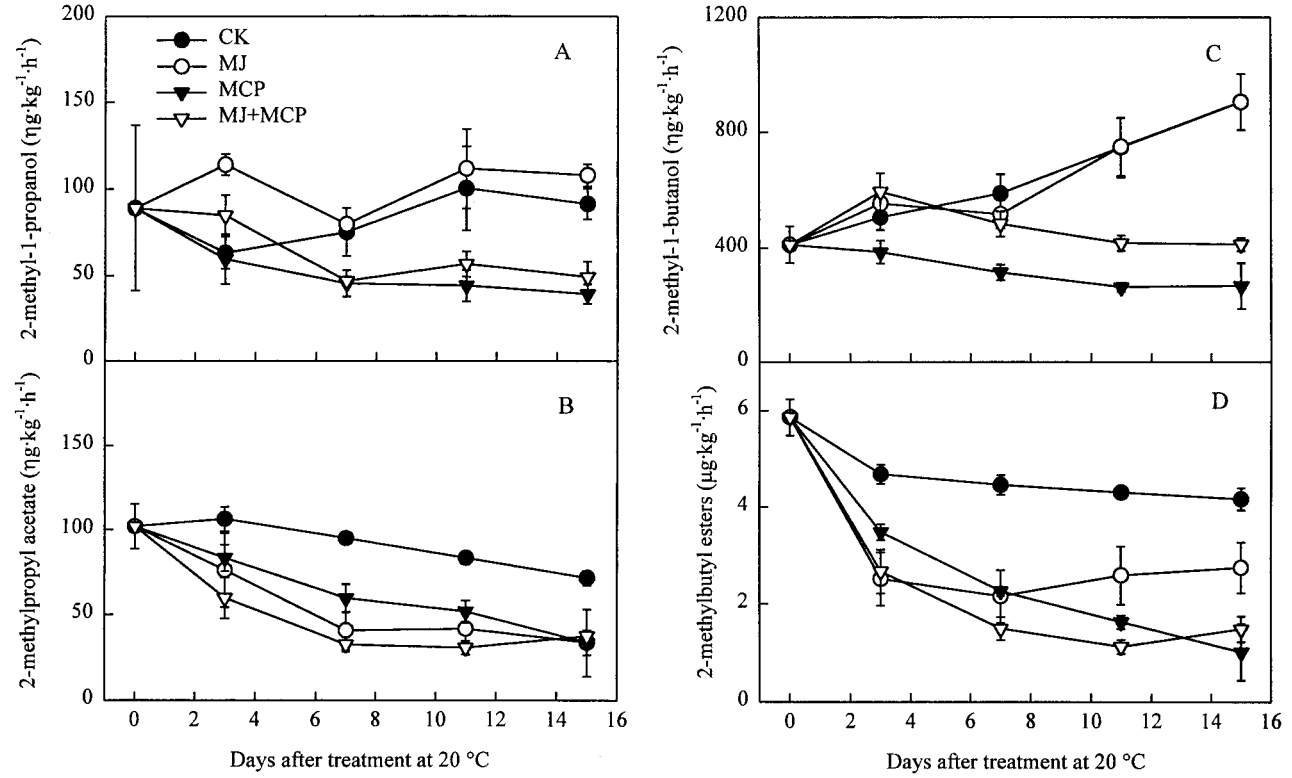

Figure 6. Production of 2-methylpropanol (A), 2-methylpropyl acetate (B), 2-methylbutanol (C), and 2-methylbutyl esters (D) of Fuji apples. Fruit were treated with water (CK), 2 mmol·L^{-1} MJ, 10 μL·L^{-1} MCP, and a combination of 2 mmol·L^{-1} MJ and 10 μL·L^{-1} MCP and kept at 20 °C. Vertical bars represent mean standard deviation.

MJ can either promote or inhibit volatile production depending on the physiological stage of development when apple fruit are treated. MJ does not reduce ester production in climacteric fruit when fruit are ripened on the tree (Fan et al., 1997). MJ, however, inhibits volatile ester production by fruit after long-term controlled atmosphere storage (Olias et al., 1992). The apple fruit used in the current study had been stored at 0 °C

for 2 weeks before treatment. Storage conditions, tree factors, or cultivars are possible factors determining the effect of MJ on volatile production. A period of chilling after harvest also enhances ethylene production in Fuji apples (Fan, 1992; Jobling and McGlasson, 1995).

The toxicity of α-farnesene oxidation products is considered a primary factor in the development of the apple disorder superficial scald (Huelin and Murray, 1966; Huelin and Coggiola, 1968). One of the major oxidative products of α-farnesene is 6-methyl-5-hepten-2-one (Anet, 1972), a compound that has been proposed to be involved in the induction of injury leading to superficial scald (Mir et al., 1999). MCP alone or in combination with MJ inhibits production of both of these compounds, although production of α-farnesene is more sensitive to MCP (Figure 2A,B). Synthesis of α-farnesene and development of superficial scald in preclimacteric fruit requires ethylene action (Fan et al., 1999b). The fruit used in this experiment were at the climacteric stage of development, and production of α-farnesene was inhibited by MCP even though α-farnesene was being produced when the fruit were treated. MCP did not totally inhibit α-farnesene production, indicating that once initiated, production of α-farnesene may be partially independent of ethylene action. α-Farnesene is a sesquiterpene located in apple fruit primarily in the waxy cuticle (Huelin and Coggiola, 1970). Even if α-farnesene production in the apple fruit is completely inhibited following MCP treatment, there still may be a significant reservoir concentration of α-farnesene in the cuticle, which may slowly deplete. In this case, the α-farnesene emitted from MCP-treated fruit may overestimate the actual synthesis of α-farnesene occurring during the 15 day posttreatment period.

Decreased production of α-farnesene and its oxidation products following treatment with MCP is correlated to superficial scald reduction during storage (Fan et al., 1999b). MCP is an ethylene action inhibitor (Sisler and Serek, 1997), and inhibition of ethylene action slows the ripening process. Indeed, MCP retarded the loss in firmness, acidity, and greenness of apple fruit during storage and ripening (Fan et al., 1999a; Fan and Mattheis, 1999). Volatile ester production is a major component of apple fruit flavor; therefore, the reduced volatile production by MCP- and MJ-treated fruit may have a negative impact on flavor development.

There are similarities as well as differences between the effects of MJ and MCP on apple fruit ripening. MCP treatment can reduce ethylene production to undetectable levels, while MJ can reduce or promote ethylene production depending on the physiological stage when fruit are treated. MJ can overcome some of the inhibitory effects of MCP on ethylene production (Figure 1A) when MJ is applied after MCP treatment. Although both MJ and MCP inhibit production of most esters, MJ treatment after MCP application can further inhibit production of some esters. Production of some volatile compounds was inhibited by MJ but not by MCP, while production of other volatile compounds was promoted by MCP but not MJ, although the effects were transient. For example, production of propanol and propyl esters was not affected by MCP but was inhibited by MJ 3 days after treatment (Figure 5A,B). MCP-treated fruit had higher ethanol and butanol production rates compared to control fruit 3 days after treatment, but MJ did not affect production of ethanol or butanol during the same period (Figures 3A and 4A). MJ can overcome MCP effects on production of some volatiles when the two are used together, indicating the effect of MJ may not occur via changes in ethylene action or that MJ and MCP act on different points in the volatile synthesis pathways. Other results indicate that some effects of MJ on fruit ripening do not require ethylene action (Fan and Mattheis, 1999). While MCP effects on apple volatile production appear to result from inhibition of ethylene action, the mode of MJ action remains to be identified.

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