Responses of Apples to Postharvest Jasmonate Treatments

Xuetong Fan and James P. Mattheis¹

U.S. Department of Agriculture, Agricultural Research Service, Tree Fruit Research Laboratory, 1104 North Western Avenue, Wenatchee WA 98801

John K. Fellman

Department of Horticulture and Landscape Architecture, Washington State University, Pullman, WA 99164-6414

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ABSTRACT. The effect of exogenous methyl jasmonate (MJ) and jasmonic acid (JA) compared with the effect of ethephon on surface color and quality of 'Golden Delicious' and 'Fuji' apples (*Malus × domestica* Borkh.) was studied. Treatments were applied by dipping fruit in water solutions of JA, MJ, or ethephon or by exposing fruit to MJ vapors. Response to MJ vapor treatment depended on fruit developmental stage, with the maximum effect occurring as fruit began to produce ethylene. MJ promoted color changes more effectively than JA. The promotive effect of JA increased with JA concentration. A minimum concentration of 0.1 mmol·L⁻¹ JA was needed to promote significant color change within 15 d at 20 °C. JA at 1 or 10 mmol·L⁻¹ promoted color change more effectively than 0.35 or 3.5 mmol·L⁻¹ ethephon. The magnitude of JA-promoted responses decreased at lower temperatures. Treatments with 10 mmol·L⁻¹ JA or 3.5 mmol·L⁻¹ ethephon were phytotoxic. Treatments using JA at 1 or 10 mmol·L⁻¹ in water promoted loss of fruit titratable acidity compared to controls. Firmness and soluble solids content were relatively unresponsive to JA treatments. Based on these results, using JA and MJ to promote degreening of apple fruit with minimal loss of other quality attributes appears feasible.

As apples mature, chlorophyll degradation and carotenoid synthesis cause peel ground color to change from green to yellow. Some late maturing apple cultivars, such as 'Fuji', fail to change color in some seasons (Fan, 1992), resulting in loss of commercial value. Postharvest degreening may be one method to minimize the problem. The degreening of leaves and fruit is a well-known effect of ethylene (Abeles et al., 1992), and ethylene is used commercially to promote degreening of bananas and tomatoes before sale in the retail market.

Jasmonates [jasmonic acid (JA) and its methyl ester, methyl jasmonate (MJ)] (Fig. 1) are a class of oxylipins derived from lipoxygenase-dependent oxidation of fatty acid. They modulate a wide variety of plant responses (Koda, 1992; Semblender and Parthier, 1993), including promotion of chlorophyll degradation in oat leaves (Ueda and Kato, 1980; Ueda et al., 1981). Other studies have supported the idea that jasmonates are senescence-promoting substances that accelerate chlorophyll degradation (Emery and Reid, 1996; Miersch et al., 1986; Yeh et al., 1995). We have previously shown that endogenous jasmonate concentration is high in senescing apples and tomatoes (Fan et al., 1998). Exogenous MJ promotes chlorophyll degradation and β -carotene accumulation in tomatoes (Saniewski and Czapski, 1983; Saniewski et al., 1987b) and apples (Perez et al., 1993). Despite these studies, there have been few reports on the effects of jasmonate dose, fruit developmental stages, or use of JA as a fruit degreening agent.

Jasmonates promote ethylene production in apples and tomatoes (Fan et al., 1997; Saniewski et al., 1987a, 1987b); however, carotenoid accumulation can be inhibited by ethylene (Kang and Burg, 1972) and jasmonates (Miersch et al., 1986). It is unclear whether fruit jasmonate responses occur via enhanced ethylene action and/or production. The objectives of this study were to determine the effect of fruit developmental stage on jasmonate-promoted color change, to compare jasmonate and ethephon for promoting color change, and to evaluate treatment effects on fruit firmness, soluble solids content (SSC), and titratable acidity (TA).

Materials and Methods

EFFECT OF FRUIT DEVELOPMENTAL STAGE ON MJ-MEDIATED COLOR CHANGES. 'Golden Delicious' apples were harvested 129, 157, and 185 d after full bloom (DAFB) from the Washington State Univ. Tukey orchard, Pullman, Wash. Fruit were treated with MJ vapor on the day of harvest (Fan et al., 1997). There were four replications (three apples each) per treatment. Each replication was placed in a 4-L glass jar along with a filter paper wetted with 25 mg of MJ (Bedoukian Research, Danbury, Conn.). The jars were tightly sealed for 12 h at 22 °C, and fruit were stored at 22 °C after treatment. Peel ground color, internal ethylene concentration (IEC), and ethylene production were measured 0, 3, 6, 9, 12, and 15 d after treatment. Fruit color was recorded as CIE L*, a*, b* with a

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¹E-mail: mattheis@trfl.ars.usda.gov.

Fig. 1. Chemical structure of jasmonic acid and methyl jasmonate.

chromameter (model CR-200; Minolta, Japan) using CIE illuminant C and an 8-mm measuring aperture. The chromameter was calibrated with a standard white plate (CR-A43) and d/0 was the illuminant/viewing geometry. Hue and chroma values were calculated from a^* and b^* (McGuire, 1992). Ethylene production was measured by sealing fruit in 4-L glass jars for 1 h, after which a 0.5-mL headspace gas sample was removed using a syringe inserted into the jar through a rubber septum in the jar lid. To determine IEC, a 0.5-mL internal gas sample was removed through a needle inserted into the fruit core. Ethylene concentrations in the gas samples were analyzed using a gas chromatograph (model 427; Pachard Instrument, Downers Grove, Ill.) equipped with a flame ionization detector (FID) and a 30-cm stainless-steel column (2-mm ID) packed with Porapak QS (80/100 mesh; Millipore Co., Milford, Mass.) (Fan et al., 1997).

EFFECTS OF JA CONCENTRATION ON PROMOTING COLOR CHANGE. 'Fuji' apples with an IEC of 0.25 (0.08 to 0.55) $\mu\text{L}\cdot\text{L}^{-1}$ were harvested from the Columbia View Experimental Plots near Wenatchee, Wash. Twenty fruit per treatment were dipped into 0 (control), 0.01, 0.1, 1, or 10 $\text{mmol}\cdot\text{L}^{-1}$ JA in deionized water containing 0.02% (v/v) Tween 20 for 2 min and then air dried. Fruit were stored at 20 °C after treatment. Ethylene, respiration rate, and peel ground color were measured at 0, 3, 6, 9, 12, and 15 d after treatment. To measure ethylene and respiration rate, fruit (four in each jar) were placed in 4-L glass jars and the jars were sealed using Teflon lids with two gas ports. Compressed air, free of ethylene and CO_2 , flowed through the jars at $6\text{ L}\cdot\text{h}^{-1}$ for 3 h before sampling. A 0.5-mL sample was withdrawn from the jar outlet, and ethylene in the sample was determined using a gas chromatograph (HP 5880A; Hewlett Packard, Avondale, Pa.) fitted with a 30-cm glass column (3.2-mm ID) packed with Porapak Q (80/100 mesh). Gas flows for N_2 , H_2 , and air were 30, 30, and 300 $\text{mL}\cdot\text{min}^{-1}$, respectively. Oven, injector, and FID temperatures were 50, 50, and 200 °C, respectively. Concentration of CO_2 in the outlet flow was determined using an HP 5890 gas chromatograph equipped with a methanizer (John T. Booker, Austin, Texas) and a 60-cm stainless-steel column (2-mm ID) packed with Porapak Q (80/100 mesh). Gas flows for N_2 , H_2 , and air were 65, 30, and 300 $\text{mL}\cdot\text{min}^{-1}$, respectively. Oven, injector, and FID temperatures were 30, 50, and 200 °C, respectively. Color was measured as described earlier.

COMPARISON OF MJ AND JA FOR PROMOTING COLOR CHANGE. 'Golden Delicious' apples with an IEC of 0.25 (0.06 to 0.51) $\mu\text{L}\cdot\text{L}^{-1}$ were harvested from the Columbia View Experimental Plots and dipped into deionized water (control), 10 $\text{mmol}\cdot\text{L}^{-1}$ JA, or 10 $\text{mmol}\cdot\text{L}^{-1}$ MJ for 2 min. All treatments included 0.02% (v/v) Tween 20. Fruit were then air dried and stored at 22 °C after treatment. There were four replications with four apples for each replication. Ground color and ethylene production were measured at 0, 2, 4, and 6 d after treatment as described previously.

EFFECTS OF JA, ETHEPHON, AND STORAGE TEMPERATURE ON FRUIT QUALITY. 'Fuji' apples with an IEC of 0.57 (0.02 to 1.92) $\mu\text{L}\cdot\text{L}^{-1}$ were harvested from the Columbia View Experimental Plots and dipped into deionized water (control), 0.35 or 3.5 $\text{mmol}\cdot\text{L}^{-1}$ ethephon, or 1 or 10 $\text{mmol}\cdot\text{L}^{-1}$ JA in water for 2 min and then air dried. Ethrel, which contains 21.7% (w/v) ethephon, was used as an ethylene-releasing agent. All treatments included 0.02% (v/v) Tween 20. After treatment, fruit were stored at 20 °C for 24 h, then transferred to 0, 4, or 20 °C. Fruit ground color, firmness, SSC, TA, and ethylene production were measured initially and after storage at 0 °C for 84 d, 4 °C for 80 d, and 20 °C for 7 d. Firmness was measured using a penetrometer fitted with a 1.1-cm tip (EPT-1 pressure tester; Lake City Technical Products, Kelowna, B.C., Canada). TA was measured by titrating a 5-mL aliquot of juice to pH 8.1 using an autotitrator (Radiometer America Inc., Cleveland, Ohio). SSC was measured with an N1 refractometer (Atago Co, Tokyo).

STATISTICAL ANALYSIS. Analyses of variance and the LSD procedure were performed using the Statistical Analysis System program (SAS Inst., Raleigh, N.C.). Unless otherwise mentioned, only results significant at $P < 0.05$ are discussed.

Results and Discussion

EFFECT OF FRUIT DEVELOPMENTAL STAGE ON MJ-MEDIATED COLOR CHANGES. During 'Golden Delicious' apple fruit ripening, L^* , a^* , and b^* values increased resulting in decreased hue values, increased chroma values, and a visual color change from green to yellow. Apples from three harvests (129, 157, and 185 DAFB) were treated, representing three stages of fruit development (pre-climacteric, onset of climacteric, and postclimacteric) having

Table 1. Changes in color of fruit peel during ripening of 'Golden Delicious' apples. Apples harvested 129, 157, 185 d after full bloom (DAFB) were treated with methyl jasmonate (MJ) vapor for 12 h and then held at 22 °C for 15 d after treatment. Control fruit [checks (CK)] were placed in jars without MJ. Color was measured at 3, 6, 9, 12, and 15 d after treatment. The changes in L^* , chroma, and hue values were calculated by subtracting initial value. Initial color value are indicated in the footnotes.

Days after treatment	Treatment	Harvest time (DAFB)								
		129	157	185	129	157	185	129	157	185
		L^* difference ^a			Chroma difference ^b			Hue difference ^c		
3	CK	-0.60 a ^w	0.23 a	0.72 a	0.22 a	1.01 a	6.98 a	0.23 a	-0.03 a	-3.30 a
	MJ	-0.11 b	0.51 a	1.16 a	1.27 b	2.76 b	7.61 a	-0.04 a	-2.12 b	-4.85 b
6	CK	-0.78 a	0.21 a	1.47 a	1.09 a	2.38 a	9.60 a	0.13 a	-1.17 a	-5.95 a
	MJ	-0.14 a	2.15 b	0.91 a	2.16 b	7.07 b	11.22 b	-0.24 a	-7.69 b	-6.95 b
9	CK	-1.55 a	0.25 a	1.72 a	1.04 a	3.71 a	12.17 a	-0.09 a	-2.67 a	-8.23 a
	MJ	-0.75 b	3.14 b	0.94 a	2.46 b	9.49 b	13.97 b	-0.62 b	-11.12 b	-8.78 a
12	CK	-1.75 a	0.98 a	1.87 a	1.18 a	6.03 a	13.02 a	-0.29 a	-4.79 a	-10.29 a
	MJ	-1.09 b	4.00 b	0.95 a	3.00 b	11.86 b	15.15 a	-1.09 b	-13.91 b	-9.79 a
15	CK	-2.32 a	1.99 a	1.29 a	1.56 a	9.16 a	13.19 a	-0.83 a	-7.65 a	-11.90 a
	MJ	-1.44 b	4.66 b	0.76 a	3.72 b	14.12 b	15.82 b	-1.88 b	-16.16 b	-10.77 a

^aInitial L^* value was 70.51 at 129 DAFB, 72.83 at 157 DAFB, and 77.81 at 85 DAFB.

^bInitial chroma value was 47.15 at 129 DAFB, 47.75 at 157 DAFB, and 51.20 at 85 DAFB.

^cInitial hue value was 115.72 at 129 DAFB, 113.47 at 157 DAFB, and 103.88 at 85 DAFB.

^wValues have same letter within columns for each color parameter for each time after treatment are not significantly different (LSD test, $P < 0.05$).

Fig. 2. Effect of jasmonic acid (JA) on chroma (A) and hue (B) values of 'Fuji' apples. The fruit were treated with 0 (check), 0.01, 0.1, 1, and 10 mmol·L⁻¹ JA and held at 20 °C for 15 d. Initial chroma and hue values were 34.91 and 104.43, respectively. Vertical bars represent SE of mean.

mean IEC values of 0.00, 0.14 (0.01 to 0.54), and 80.40 (6.86 to 276.43) $\mu\text{L}\cdot\text{L}^{-1}$ respectively. During 15 d of ripening at 22 °C after treatment, MJ-treated fruit harvested 129 and 157 DAFB had higher L* values than controls (Table 1). The largest effect was observed in fruit just beginning to produce ethylene (harvested 157 DAFB). Postclimacteric

(185 DAFB) 'Golden Delicious' apples failed to lighten significantly in response to MJ. The MJ effect on chroma was similar to L*, except that MJ promoted the increase in chroma even in postclimacteric fruit (Table 1). MJ decreased hue values at all stages of development (Table 1), but the largest effect occurred in apples harvested 157 DAFB. MJ promoted ethylene production only in fruit beginning to produce ethylene at 15 d after treatment (data not shown). For all parameters (L*, chroma, hue, and ethylene production), the largest MJ effects occurred in fruit where ethylene biosynthesis had just been initiated (157 DAFB). Apples became less sensitive to exogenous MJ as development progressed when larger amounts of ethylene were produced. These results indicate that the effect of exogenous jasmonates on color change depends on fruit developmental stage and suggest that the jasmonate effect occurs in part via interaction with ethylene. The effect of jasmonates on ethylene and volatile production has previously been shown to depend on developmental stage (Fan et al., 1997). MJ promoted changes in L*, chroma, and hue even on fruit without detectable ethylene production, indicating that some degree of MJ response occurs independently of ethylene. Abeles et al. (1989) reported that MJ is as effective as ethylene in inducing chlorophyll degradation in excised cucumber cotyledons. The effect of MJ on chlorophyll degradation does not require ethylene action, as inhibition of ethylene action by silver thiosulfate (STS) does not affect the ability of MJ to promote chlorophyll degradation (Emery and Reid, 1996). Hung and Kao (1996), however, observed that STS inhibited MJ-promoted chlorophyll degradation in detached maize leaves and concluded that MJ-promoted chlorophyll degradation is mediated through increased ethylene sensitivity. In addition to enhanced chlorophyll degradation, jasmonates also promote β -carotene synthesis in apples (Perez et al., 1993). Our results indicate that jasmonates may modulate color changes in two ways: one acting with ethylene and another independent of ethylene.

EFFECT OF JA CONCENTRATION ON PROMOTING COLOR CHANGES. The effect of JA concentration on color changes was studied using 'Fuji' apples with an average IEC of 0.25 $\mu\text{L}\cdot\text{L}^{-1}$. JA treatment did not induce significant changes in L* values (data not shown). The promotive effect on changes in chroma and hue values increased

with JA concentrations of 0.01 to 10 mmol·L⁻¹ compared to controls (Fig. 2). Effects on chroma and hue values were induced by 1, 10, and sometimes 0.1 mmol·L⁻¹ during 15 d at 20 °C. A lower JA concentration (0.01 mmol·L⁻¹) did not promote significant color change within 15 d at 20 °C. These results indicate that the effect of JA on color changes is dose-dependent. JA also increased ethylene production rate in a dose-dependent fashion (Fig. 3A). Respiration rate was increased by 10 mmol·L⁻¹ JA only at 9 d after treatment (Fig. 3B). JA at 0.01 mmol·L⁻¹ decreased respiration at 12 d after treatment.

COMPARISON OF MJ AND JA FOR PROMOTING COLOR CHANGES. Based on the results demonstrating that the effect of jasmonates on promoting color change was maximal during onset of the climacteric, 'Golden Delicious' apples with an average IEC of 0.25 $\mu\text{L}\cdot\text{L}^{-1}$ were treated to compare the efficiency of MJ and JA. MJ decreased L* values 6 d after treatment, while JA did not have any effect (Fig. 4A). JA and MJ promoted an increase in chroma and a decrease in hue values (Fig. 4 B and C). MJ was more effective than JA in promoting changes in L*, chroma, and hue values. The difference between JA and MJ may be due to the fact that MJ is more volatile and not ionized, properties that enhance its incorporation into plant tissue (Staswick, 1992).

EFFECT OF JA, ETHEPHON, AND STORAGE TEMPERATURE ON APPLE QUALITY. High concentrations of JA enhanced ethylene production and respiration rate (Fig. 3). To determine if the increased ethylene production and respiration had any adverse effect on fruit quality, apples treated with JA or ethephon were evaluated after storage at 20, 4, and 0 °C for changes in firmness, SSC, TA, color, and IEC. After storage at 20 °C for 8 d, 4 °C for 80 d, or 0 °C for 84 d, fruit treated with 0.35 or 3.5 mmol·L⁻¹ ethephon or 1 or 10 mmol·L⁻¹ JA had lower hue values and higher chroma values (Table 2) than the control. The effect decreased with storage temperature. Fruit treated with 1 or 10 mmol·L⁻¹ JA generally had higher chroma and lower hue values than those treated with 0.35 or 3.5 mmol·L⁻¹ ethephon, although the differences between JA and ethephon treatment were not always significant. These results indicate that JA has a more pronounced effect on color change than ethylene supplied via ethephon, again suggesting that jasmonates may

modulate color change in addition to affecting ethylene synthesis.

After 2 weeks at 20 °C or 80 d at 4 °C, there was no difference in firmness between controls and JA- or ethephon-treated fruit (Table 3), but fruit treated with 10 mmol·L⁻¹ JA and previously stored at 0 °C showed higher firmness over other treatments. Apples treated with 10 mmol·L⁻¹ JA had higher

Fig. 3. Effect of jasmonic acid (JA) on ethylene production (A) and respiration rate (B) of 'Fuji' apples. Fruit were treated with 0 (check), 0.01, 0.1, 1, and 10 mmol·L⁻¹ JA and held at 20 °C for 15 d. Vertical bars represent SE of mean.

Fig. 4. Changes in L* (A), chroma (B), and hue (C) values of 'Golden Delicious' apples. Apples were treated with 0 (check) and 10 mmol·L⁻¹ jasmonic acid (JA) and 10 mmol·L⁻¹ methyl jasmonate (MJ) and then held at 22 °C. Initial values for L*, chroma, and hue values were 72.27, 46.40, and 111.26, respectively. *Significant difference compared with control (LSD, *P* < 0.05). **Significant difference between JA and MJ treatments (LSD, *P* < 0.05).

firmness than those treated with 1 mmol·L⁻¹ JA after 2 weeks at 20 °C. Compared to the control, SSC was higher in fruit treated with 0.35 mmol·L⁻¹ ethephon 4 °C and fruit treated with 10 mmol·L⁻¹ JA or 0.35 mmol·L⁻¹ ethephon at 20 °C. Fruit treated with JA had generally lower TA than controls or ethephon-treated fruit. JA- and ethephon-treated fruit had a lower IEC than controls after 14 d at 20 °C, although fruit from all treatments produced large amounts of ethylene. The lower IEC in JA-treated fruit may indicate an advanced developmental stage (postclimacteric) as JA pro-

moted fruit ripening. MJ at 1% (w/w) can inhibit ethylene production in postclimacteric apples (Saniewski et al., 1987a). The lower IEC in ethephon-treated fruit may reflect the negative feedback of ethylene biosynthesis (Yang and Hoffman, 1984).

The 10-mmol·L⁻¹ JA, 10-mmol·L⁻¹ MJ, and 3.5-mmol·L⁻¹ ethephon treatments injured apple peel tissue. JA injury was manifested as round brown spots mostly near the calyx end of the fruit. Ethephon injury also occurred near the calyx end. Small cracks in the calyx and shrivel were observed. The injuries may be due to high residual JA or ethephon accumulation near the calyx, as fruit were placed on the calyx end during the air-drying period after treatments were completed. The 1-mmol·L⁻¹ JA treatment induced noticeable color change with little fruit injury, and its effect was generally more effective than 0.35- or 3.5-mmol·L⁻¹ ethephon treatments.

The volatility of MJ allows treatments to be applied without immersing fruit in water. While MJ has a pleasant aroma, its chemical properties result in surface binding to polymeric materials, which may prolong MJ's presence in storage rooms or fumigation chambers. JA is more soluble in water, allowing its use in solution as a drench or dip. Under the conditions of these experiments, however, JA was less effective at promoting color change than MJ when treatments were applied in water (Fig. 4).

Similar to our earlier observation (Fan et al., 1997) on ethylene and volatile compound production, the effect of jasmonates on promoting color changes of apples depended on dose and developmental stage. The largest effect was observed during onset of climacteric ethylene production, although jasmonates can enhance color changes at all stages of ripening. JA at 1 mmol·L⁻¹ can be used effectively while avoiding phytotoxicity and excessive loss of firmness, SSC, or TA. It is possible that a combination of jasmonate and ethephon could be used to promote commercially desirable color changes in apples while minimizing adverse effects on other fruit quality attributes.

Table 2. Effect of jasmonic acid (JA) and ethephon on chroma and hue values of 'Fuji' apples. Fruit were held at 20 °C for 24 h after treatment, then stored 1 week at 20 °C, 80 d at 4 °C, or 84 d at 0 °C.

Treatment	Chroma			Hue		
	Temp (°C)					
	0	4	20	0	4	20
Control	44.2 b ²	47.2 b	43.2 c	105.0 a	104.1 a	107.5 a
Ethephon, 0.35 mmol·L ⁻¹	45.8 ab	47.3 b	45.5 bc	103.8 a	103.1 ab	103.4 b
Ethephon, 3.5 mmol·L ⁻¹	46.2 ab	47.5 b	46.9 b	104.1 a	100.6 bc	103.5 b
JA, 1 mmol·L ⁻¹	46.3 a	49.3 b	46.7 b	100.2 b	98.5 c	101.0 b
JA, 10 mmol·L ⁻¹	46.3 a	52.0 a	50.8 a	99.2 b	97.4 c	97.3 c

²Values having the same letter in each column are not significantly different (LSD test, *P* < 0.05).

Table 3. Effect of jasmonic acid (JA) and ethephon on firmness, soluble solids content (SSC), titratable acidity (TA), and internal ethylene concentration (IEC) of 'Fuji' apples. Fruit were held at 20 °C for 24 h after treatment, then stored 1 week at 20 °C, 80 d at 4 °C, or 84 d at 0 °C. After storage, fruit were ripened at 20 °C for 1 week.

Treatment	Firmness (N)			SSC (%)			TA (%)			IEC (μL·L ⁻¹)		
	Temp (°C)											
	0	4	20	0	4	20	0	4	20	0	4	20
Control	67 b ²	62 a	68 ab	13.2 a	13.1 b	12.8 b	0.257 a	0.260 b	0.310 a	241 a	454 a	166 a
Ethephon, 0.35 mmol·L ⁻¹	65 b	65 a	70 ab	13.1 a	13.5 a	13.3 a	0.262 a	0.265 b	0.306 a	211 ab	392 a	62 c
Ethephon, 3.5 mmol·L ⁻¹	65 b	62 a	71 ab	12.9 a	13.0 b	13.5 a	0.234 bc	0.290 a	0.304 a	206 ab	515 a	97 b
JA, 1 mmol·L ⁻¹	65 b	63 a	67 b	13.2 a	12.9 b	13.2 ab	0.237 b	0.250 b	0.280 b	155 b	356 a	62 c
JA, 10 mmol·L ⁻¹	71 a	65 a	72 a	13.3 a	12.7 b	13.6 a	0.219 c	0.231 c	0.312 a	177 ab	512 a	91 bc

²Values having same letter in each column are not significantly different (LSD test, *P* < 0.05).

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