Effect of Methyl Jasmonate on *in Vitro* Strawberry Ripening

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Strawberry fruits (*Fragaria* × *ananassa* Duch.), cultivar Camarosa, were harvested at green inmature stages and grown *in vitro* in sucrose-containing solutions. The effect of exogenously added methyl jasmonate (JAMe, 50 μM) on *in vitro* development and ripening of strawberry was evaluated through different parameters. A significant increase in respiratory activity and ethylene production was determined in white and pink strawberries treated with JAMe, while different responses were elicited from ripe and overripe fruits. A higher growth rate was found in JAMe-treated fruits, with a 55% weight gain against 33% for control fruits. A significant effect of JAMe treatment on strawberry color evolution was also observed by a stimulation of anthocyanin biosynthesis after 2 days of treatment and an accelerated degradation of chlorophyll *a*, chlorophyll *b*, and, to a lesser extent, β-carotene and lutein.

Keywords: *Strawberry fruit; ripening; methyl jasmonate*

INTRODUCTION

Jasmonic acid (JA), a product of 13-hydroperoxy-9,11,15-octadecatrienoic acid metabolism, and its volatile methyl ester, methyl jasmonate (JAMe), are regarded as endogenous plant growth regulators with a wide range of physiological functions not yet fully elucidated.

Although early research focused primarily on jasmonates' potential role in plant growth and development, after jasmonates were shown to increase the expression of genes involved in plant defense, there was a surge in activity aimed at clarifying this function as signaling molecules rather than its physiological role during plant development and senescence (Staswick, 1995). Thus, jasmonate-induced proteins (JIPs) have been demonstrated in all plant species tested so far and different hypotheses for the JAMe role in the plant defense mechanism against wounding have been proposed (Peña-Cortés et al., 1996). More recently, due to its potential importance as a signaling molecule in plants, Meir et al. (1996) have suggested that JAMe might also mediate the plant's natural response to chilling stress and that its application could reduce injuries in chilling-sensitive comodities.

Jasmonate's main activities as plant growth regulators include inhibition of seed germination and callus growth and promotion of leaf and fruit senescence, root formation, and petiole abscission. The induced promotion of senescence is characterized by chlorophyll degradation, inhibition of lycopene accumulation (Saniewsky and Czapsky, 1985), and increase in respiration and enzymatic activities such as protease and peroxidase, lipoxygenase and hydroperoxide-lyase (Avdiusko et al., 1995). Ethylene, known to enhance senescence, is suggested to regulate parts of this syndrome other than JAMe. Stimulating effects of JAMe on ethylene formation have been found in ripening tomato and apple fruits (Saniesky et al., 1987). The role of JAMe, via ethylene, in fruit ripening, especially of the nonclimacteric type, needs further study. In fact, details on the induction and regulation of ripening have been derived largely from studies with climacteric fruits.

Strawberry is classified as a nonclimacteric fruit on the basis of a lack of increased respiration and ethylene production as the fruit changes color, texture, and flavor (Abeles and Takeda, 1990). Direct study of nonclimacteric fruits such as strawberries has been limited because ripening generally does not continue normally following detachment. In this sense, Perkins-Veazie and Huber (1992) provided an *in vitro* system to study nonclimacteric fruit development that permits introduction of hormones and substances that inhibit or promote fruit ripening.

Although hormonal regulation of strawberry ripening is not fully understood, auxins produced by the achenes are probably the key hormones in strawberry development and ripening. It was first reported (Nistsch, 1950) that auxins were necessary for the growth of the receptacle, and more recently it has been shown that decline in auxin content during achene maturation triggers the fruit ripening (Given et al., 1988; Manning, 1994). Others hormones, such as gibberellic acid, have also an inhibitory effect on strawberry ripening (Martínez et al., 1994, 1996), while the role of the main ripening hormone, ethylene, remains unclear in strawberry with contradictory results from different studies (Basioumy, 1989; Abeles and Takeda, 1991; Luo and Liu, 1994; Wills and Kim, 1995). The best approach to study the role of a hormonal compound in the ripening process is to investigate its effect on the main factors associated with fruit ripening such as changes in respiratory activity, texture, flavor, and color development.

In previous studies done in apple, we have evaluated the effect of exogenous applied JAMe vapors on ripening parameters, such as ethylene production (Olías et al., 1991), aroma development (Olías et al., 1992), and pigment changes (Pérez et al., 1993). In this work, inmature green strawberries were grown *in vitro* in JAMe (50 μM) containing solutions, and several parameters such as weight gain, firmness, color, pigment composition, ethylene and CO_2 production, and sugar and acid contents were determined during fruit development and ripening. The main objective of the present

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S0021-8561(97)00356-7 CCC: $14.00

study was to characterize the effects of JAMe on development and ripening of a nonclimacteric fruit.

EXPERIMENTAL PROCEDURES

Materials. Strawberry fruits (*Fragaria* × *ananassa* Duch.), cultivar Camarosa, were grown in field plantings in Torreagro (San Bartolomé de la Torre, Huelva, Spain). Inmature, green strawberries were harvested with intact peduncles, placed in plastic bags, and transported on ice to the laboratory. Fruits were carefully matched according to color and weight. Fully green fruits with an average initial weight 8.3 ± 1.3 g were selected. Ten fruits were randomly sampled and used for day 0 determinations, and others were immediately prepared for the *in vitro* growth experiments.

***In Vitro* Growth Experiments.** The *in vitro* growth experiments were carried out using the system developed by Perkins-Veazie and Huber (1992). Fruit peduncles were trimmed to a uniform length of 60 mm and immersed in an autoclaved headspace vial (20 mL, 23 × 75 mm) containing 18 mL of standard growth solution. Each fruit was accommodated on a perforated rubber stopper that closed the vial. The standard solution consisted of autoclaved distilled water containing 1 mM hydroxyquinoline hemisulfate (HQS) and 88 mM sucrose. Control fruits were grown with this standard solution, while 50 μM JAMe was added to the growth solution of the JAMe-treated strawberries. Forty fruits were used for each treatment. All fruits were grown in a growth chamber, temperature 25/15 °C day/night, 16 h photoperiod, 300 μE m^{-2} s^{-1} light, and 85% relative humidity. On days 2, 4, 7, and 9, fruit peduncles were recut (1−2 mm) and fresh weight and surface color of all strawberries were measured. On each of these days, five fruits per treatment were sampled. Strawberries were cut symmetrically in eight portions, and five portions of five different fruits were used for each analytical determination.

Color. Strawberry skin color was evaluated using a Minolta CR-200 portable tristimulus colorimeter (Minolta, Ramsey, NY) and expresed as *L*, *a**, *b** values. Two opposite zones were measured for each fruit.

Firmness. Firmness was measured as penetration force with a Zwick 3303 penetrometer, using a 5 mm plunger tip, and expresed as newtons (N). Three measures per fruit were done.

CO_2 and Ethylene Production. Four fruits per treatment were sampled each day for CO_2 and ethylene production. Strawberries were maintained in their respective treatment solutions and placed in 650 mL jars. Jars were sealed and maintained at 25 °C for 90 min. Gas samples (1 mL) were withdrawn from the headspace using gastight syringes and analyzed by GC. CO_2 was analyzed by a HP-5890 gas chromatograph equipped with a thermal conductivity detector on a stainless steel Carbosieve S-II (3 m × 3 mm i.d.) column and helium as carrier gas. Ethylene was analyzed by GC using an activated alumina column and a FID (Sanz et al., 1993). CO_2 and ethylene were determined in four replicated samples per treatment.

Total Anthocyanin Content. Strawberry tissue (2 g) was ground with 20 mL of methanol, 1% HCl, using an Omni-mixer (Sorvall, Newton, CT), and centrifuged at 2000*g* for 15 min at 4 °C. Anthocyanin concentration was determined as pelargonidin 3-glucoside in a Beckman DU 640 spectrophotometer, at 510 nm, using a molar absorptivity coefficient of 36 000.

Chlorophyll and Carotenoid Analysis. Strawberry tissue (2 g) was ground with 20 mL of acetone at −20 °C. The extracts were placed in 25 mL vials, sealed and kept overnight at 4 °C in the dark. The extracts were filtered through a 45 μm nylon microfilter, and triplicate samples were analyzed by HPLC on a Beckman System Gold Programmable Solvent Module 126 coupled to a diode array detector Module 168, according to the method of Pérez et al. (1993).

Sugar and Acid Analysis. *Preparation and Fractionation of Fruit Extracts for HPLC Analysis.* Five pieces from five fruits were blended in the dark with 95% ethanol for 3−5 min, with an Omni-mixer (Sorvall). The homogenate was vacuum-filtered through Whatman No. 1 filter paper and the residue washed twice with 80% ethanol. The filtrates were combined and adjusted to 5 mL/g; 10 mL of this extract was evaporated in the dark to dryness at 50 °C. The dry residue was redissolved in 1 mL of 0.2 N H_2SO_4, 0.05% EDTA, loaded onto a Sep-Pak C_{18} cartridge (Lida, Kenosha, WI), and eluted with up to 4 mL of the same solution. These extracts containing sugars and organic acids were filtered through 0.45 μm nylon filters before HPLC analysis.

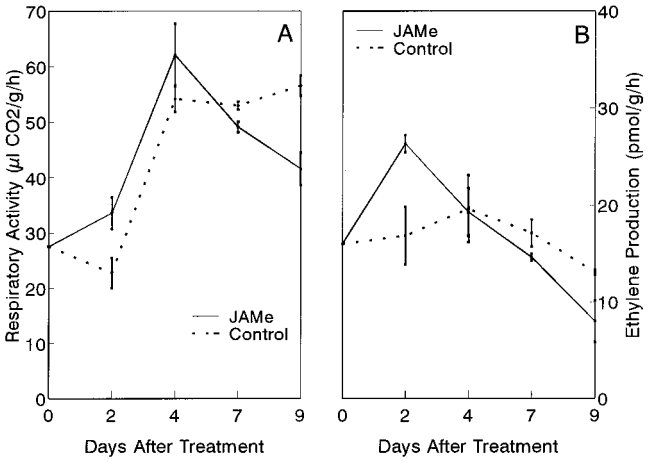

Figure 1. Effect of JAMe on ethylene production and respiratory activity during *in vitro* development and ripening of Camarosa strawberries. Green fruits were placed in solutions containing 88 mM sucrose and 1 mM HQS, with or without 50 μM JAMe. Vertical bars indicate ± SD.

HPLC Analysis. Sugars and organic acids were analyzed in a Hewlett-Packard 1090 liquid chromatograph equipped with a photodiode array detector and a Waters 410 differential refractometer (Millipore) connected in series. Data were processed by means of a Hewlett-Packard 85-B computing system and a Beckman Analogue Interface Module 406 and a Gold V.711 software, respectively. Isocratic separations of the compounds were made on a stainless steel Ion-300 (300 mm × 7.8 mm, 10 μm) column, containing a cation-exchange polymer in the ionic hydrogen form, with an IonGuard GC-801 guard column (Interaction, San Jose, CA), and thermostated at 23 °C. The mobile phase utilized for the elution consisted of a filtered (0.22 μm nylon) and degassed solution of 0.0085 N H_2SO_4 and a flow rate of 0.4 mL/min. UV detection was at 195 and 245 nm, the refractive index detector was used at a sensitivity of 16×, and the injection volume was 20 μL.

Analysis of Results. The data were statistically evaluated using CoStat statistical sofware (CoHort Software, 1995; CoStat, Minneapolis, MN). Analysis of variance (ANOVA) was used, and comparison of means was done by the Student−Newman−Keuls/Duncan test, at a significance level of 0.05.

RESULTS AND DISCUSSION

Respiratory Activity and Ethylene Production. Rate of respiratory activity is associated with rate of ripening. In this work, the respiratory activity and the ethylene production of *in vitro* grown strawberries were evaluated during 9 days (Figure 1). JAMe treatment caused a higher respiratory activity in white and pink strawberries (days 2 and 4), while a decrease in CO_2 production was observed on days 7 and 9 (red ripe and dark-red overripe fruits, respectively). Statistically significant differences ($p < 0.001$) were found in CO_2 production for interaction treatment × time. A similar profile was found when ethylene production was analyzed. Ethylene emission in JAMe strawberries reached a peak 2 days after treatment, and then a steady decrease was observed with significative lower levels ($p < 0.05$) in JAMe-treated strawberries on days 7 and 9. Ethylene values determined in this study are in a range (0.01−0.03 nmol g^{-1} h^{-1}) similar to those described for

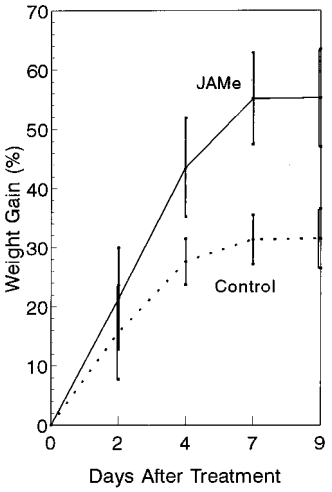

Figure 2. Effect of JAMe on cumulative growth of Camarosa strawberries *in vitro*. Green fruits were placed in solutions containing 88 mM sucrose and 1 mM HQS, with or without 50 μM JAMe. Vertical bars indicate ± SD.

Pajaro strawberries by Perkins-Veazie et al. (1995). Results obtained on days 7 and 9 (ripe and overripe strawberries) could be compared to previous data obtained with harvested strawberry fruits (Pérez et al., 1996). In those experiments the effect of JAMe on postharvest life of strawberries was evaluated, and lower CO_2 and ethylene production was found in JAMe-treated fruits. Saniewsky et al. (1987) reported JAMe promotion of ethylene production in preclimacteric apples but inhibition of ethylene production by postclimacteric apples. In a recent publication (Fan et al., 1997) on the effect of JAMe on ethylene and volatile biosynthesis by Summered apples, responses to JAMe treatment were also found to be associated with the stage of fruit development. In our opinon, the increase in CO_2 and ethylene production in white and pink strawberries and the decrease in ripe and overripe fruits shown in Figure 1 could be also due to a distinct activity of JAMe along fruit development and ripening.

Flavor. In relation to flavor development, sugar and acid content of *in vitro* grown strawberries was studied. Sucrose is the major assimilate translocated to strawberry fruit (Forney and Breen, 1985). In our experiment, fruits harvested at the green stage and provided with sucrose demonstrated normal growth and ripening response. Fruit growth, expressed as cumulative weight gain (grams per initial gram × 100) of control and JAMe-treated strawberries is shown in Figure 2. After 4 days a significative ($p < 0.001$) higher growth rate was found in JAMe-treated fruits, so that at day 7, JAMe-treated strawberries reached a weight gain of 55% while control fruits had only 33%. These values are equivalent to the *in vitro* growth rate of Pajaro green strawberries and clearly higher than that exhibited by the Douglas variety (Perkins-Veazie and Huber, 1992). To the best of our knowledge, no previous data on JAMe inducing growth or fruit weight gain have been reported. Furthermore, an inhibitory effect of jasmonic acid on the auxin-induced elongation of oat coleoptile, by interfering with some aspects of sugar metabolism, had been shown (Ueda et al., 1994). On the other hand, strawberry growth and development have been related to increasing accumulation of sugars and abscisic acid (ABA) by fruits from middevelopment to ripening (Archbold and Dennis, 1984). More recently, John and Yamaki (1994) reported that treating strawberries with ABA increased size and weight of the fruit at maturity, due to stimulatory effect on accumulation of sugars in strawberry flesh. In this sense, the described effect of JAMe on strawberry growth could be new evidence of similarity between ABA and JAMe physiological properties and activities (Staswick, 1995).

Although total sugar content per fruit is higher in JAMe-treated strawberries, concentration of sugars [expressed as milligrams per gram of fresh weight (FW)] is lower in JAMe-treated fruits due to the higher weight of strawberries grown in the presence of JAMe (Table 1). The increased uptake of sucrose atributed to JAMe was not reflected in an exaggerated sucrose accumulation in treated fruits. Forney and Breen (1986) concluded from studies of sugar uptake by strawberry fruit tissue that sucrose was hydrolyzed by a cell wall bound invertase prior to uptake into fruit tissue. In this sense, differences in sucrose content on day 2, with 5.89 ± 0.30 mg/g of FW in JAMe strawberries and 7.30 ± 037 mg/g of FW in control fruits, could be explained by a more rapid hydrolysis of sucrose in treated fruits, which would be consistent with a higher respiratory activity (47%) and ethylene production (60%). The levels of sucrose, glucose, and fructose determined in this work are very low compared to values found in Camarosa fruits grown in the plant. Ripe greenhouse-grown Camarosa strawberries showed sugar values of 17.97 ± 0.86 mg/g of FW of sucrose, 21.63 ± 0.44 mg/g of FW of glucose, and 26.01 ± 0.33 mg/g of FW of fructose.

Organic acid content was also analyzed in developing strawberries (Table 1). No significant differences ($p < 0.05$) were found for citric acid content, and significant lower levels ($p < 0.05$) of malic acid were determined in JAMe-treated strawberries, except for day 9, on which malic acid content in JAMe strawberries remained constant and higher than in control fruits. Sugar and acid distributions found in *in vitro* grown fruits, although below habitual physiological levels, follow the same pattern found during strawberry development and ripening in the plant, with increasing glucose, fructose, and ascorbic acid levels and decreasing amounts of sucrose, citric, and malic acids.

Texture. Camarosa strawberries are characterized by very high values of firmness. Along development and ripening, firmness decreased following a sigmoidal curve with values around 60 N at the onset of ripening (Table 2). No significative differences ($p < 0.05$) were found due to JAMe treatment, although slightly lower values were determined for JAMe-treated strawberries from day 4.

Color. Color development is an important event in fruit ripening, and it is frequently used as a maturity index. Fruit color changes, during development and ripening, were assessed by physical and chemical analytical methods. Strawberry skin color was measured using a colorimeter and expressed as L, a^*, and b^* parameters (Table 2). No significant differences were found when surface color of treated and control fruits was evaluated. A steady decrease of L (brightness) and b^* (blue-yellow color) was determined along fruit ripening, and a more dramatic increase was observed in a^* values, ranging from −10 (green fruits) to +25 (full-red fruits). Strawberry color depends mainly on two different groups of pigments: chlorophylls and anthocyanins. To investigate the effect of JAMe on these pigments, they were analyzed separately.

The accumulation of anthocyanins has been proposed as a useful marker of strawberry ripening (Given et al., 1988). Pelargonidin 3-glucoside is the major anthocya-

Table 1. Effect of JAMe on Sugar and Organic Acid Content (Milligrams per Gram of Fresh Weight) of *in Vitro* Grown Strawberries

days of treatment	sucrose	glucose	fructose	malic	citric	ascorbic
0	10.07 ± 0.22[a]	6.92 ± 0.18	6.68 ± 0.20	1.66 ± 0.26	10.60 ± 0.48	0.31 ± 0.04
2, control	7.30 ± 0.37	8.44 ± 0.38	8.86 ± 0.20	1.35 ± 0.08	9.26 ± 0.40	0.27 ± 0.01
2, JAMe	5.89 ± 0.30	7.70 ± 0.71	8.16 ± 0.68	1.21 ± 0.14	8.33 ± 0.72	0.22 ± 0.01
4, control	5.85 ± 0.14	7.62 ± 0.33	9.68 ± 0.48	1.13 ± 0.04	7.74 ± 0.31	0.28 ± 0.01
4, JAMe	5.66 ± 0.16	7.46 ± 0.16	9.24 ± 0.37	1.09 ± 0.03	8.21 ± 0.19	0.26 ± 0.01
7, control	4.61 ± 0.76	7.59 ± 0.26	10.28 ± 0.59	0.79 ± 0.08	7.80 ± 0.51	0.33 ± 0.07
7, JAMe	4.60 ± 0.35	8.66 ± 0.90	10.48 ± 0.39	0.54 ± 0.07	8.10 ± 0.73	0.35 ± 0.06
9, control	4.36 ± 0.24	8.60 ± 0.60	11.95 ± 0.89	0.28 ± 0.05	8.90 ± 0.89	0.35 ± 0.01
9, JAMe	4.38 ± 0.09	8.06 ± 0.66	11.02 ± 0.65	0.46 ± 0.08	8.37 ± 0.16	0.44 ± 0.02

[a] Values represent the mean and standard deviation of four analyses.

Table 2. Effect of JAMe on Firmness and Surface Color (*L*, *a, *b** Values) of *in Vitro* Grown Strawberries**

		color		
days of treatment	firmness (N)	*L*	*a**	*b**
0	85.94 ± 7.60[a]	56.43 ± 4.02[b]	−11.06 ± 2.26	37.01 ± 1.53
2, control	79.17 ± 6.59	58.44 ± 3.70	−8.01 ± 8.84	35.93 ± 1.77
2, JAMe	85.94 ± 8.92	57.48 ± 4.32	−4.16 ± 11.20	34.64 ± 2.01
4, control	60.55 ± 7.57	37.01 ± 6.15	25.08 ± 6.04	24.64 ± 6.30
4, JAMe	58.06 ± 7.04	41.17 ± 9.25	23.07 ± 12.70	26.12 ± 5.63
7, control	49.88 ± 8.97	29.85 ± 2.73	26.81 ± 2.06	15.51 ± 3.98
7, JAMe	45.70 ± 11.73	31.19 ± 2.25	27.51 ± 2.46	17.16 ± 3.74
9, control	47.45 ± 6.99	27.78 ± 2.14	23.15 ± 2.50	11.13 ± 2.82
9, JAMe	47.80 ± 6.57	29.14 ± 2.78	24.37 ± 3.35	13.33 ± 4.09

[a] Values represent mean and standard deviation of 15 analyses. [b] Values represent mean and standard deviation of 30 analyses.

Table 3. Effect of JAMe on Pigment Composition of *in Vitro* Grown Strawberries

days of treatment	anthocyanins (nmol/g of FW)	chlorophyll *a* (μg/g of FW)	chlorophyll *b* (μg/g of FW)	lutein (ng/g of FW)	β-carotene (ng/g of FW)
0	19.10 ± 1.22[a]	11.07 ± 1.62	2.47 ± 0.200	47.91 ± 10.81	970.85 ± 39.42
2, control	27.40 ± 2.00	1.94 ± 0.21	0.47 ± 0.020	224.10 ± 26.82	1113.01 ± 170.35
2, JAMe	40.44 ± 1.74	1.55 ± 0.11	0.28 ± 0.004	218.92 ± 29.42	899.41 ± 49.70
4, control	430.20 ± 23.60	1.20 ± 0.11	0.47 ± 0.015	195.95 ± 17.54	612.12 ± 93.25
4, JAMe	301.73 ± 53.10	0.42 ± 0.06	0.19 ± 0.004	128.23 ± 5.82	516.87 ± 18.16
7, control	1001.96 ± 33.20	1.21 ± 0.06	0.45 ± 0.031	97.79 ± 3.66	231.78 ± 16.32
7, JAMe	982.30 ± 74.21	1.00 ± 0.07	0.08 ± 0.006	72.89 ± 16.52	121.12 ± 10.51
9, control	1379.63 ± 99.55	0.11 ± 0.02	0.04 ± 0.003	60.73 ± 8.90	102.14 ± 8.36
9, JAMe	1255.96 ± 11.60	0.71 ± 0.12	0.03 ± 0.002	47.52 ± 12.33	118.07 ± 6.15

[a] Values represent the mean and standard deviation of four analyses.

nin described in strawberry fruits (Hong and Wrolstad, 1990). Total anthocyanin content expressed as pelargonidin 3-glucoside was determined during *in vitro* ripening of Camarosa strawberries. Significative differences ($p < 0.01$) in total anthocyanins content were found among treated and nontreated fruits (Table 3). JAMe-treated fruits exhibited a higher content of anthocyanin (40.44 ± 1.74 nmol/g of FW) than control strawberries (27.4 ± 2.0 nmol/g of FW) at day 2, which could be explained by a stimulatory effect of JAMe on anthocyanin biosynthesis. After day 2, a dramatic increase in anthocyanin accumulation was observed, up to 1300 nmol/g of FW on day 9, with slightly lower levels in JAMe-treated strawberries. A similar effect had been found in a recent study on petunia flowers grown *in vitro* and incubated with JAMe for 48 h (Tamary et al., 1995), in which the observed increase of anthocyanins was explained as a rapid and transient induction of flavonoid biosynthesis by JAMe.

Carotenoids, lutein and β-carotene, and chlorophylls *a* and *b* were also analyzed during *in vitro* development and ripening of strawberries. Table 3 shows the effects of JAMe on these four pigments. Carotenoids and chlorphylls are present at higher levels in green strawberries, and their biosyntheses decrease along fruit ripening (Woodward, 1972). The rate of loss was accelerated in all cases by the JAMe treatment. Most significant differences were found in chlorophyll degradation. Chlorophyll *a* in control fruits decreased from 11.07 to 0.11 μg/g of FW in overripe strawberries (day 9). On days 2, 4, and 7, significant ($p < 0.01$) lower amounts of chlorophyll *a*, the major green pigment, were determined for JAMe-treated strawberries, with maximum differences on day 4 with 70% less chlorophyll *a* in JAMe-treated than in control fruits. There appears to be a recovery of chlorophyll synthesis after 7 days of JAMe treatment. A similar result was found in a previous study on JAMe effects in apple peel pigments (Pérez et al., 1993). Thus, the effect of JAMe treatment on chlorophyll biosynthesis could be only transitory, similar to that of anthocyanins. In both cases, the effect of JAMe treatment on anthocyanin biosynthesis and chlorophyll degradation could be masked by a dilution effect due to the faster growth rate observed in JAMe-treated strawberries.

Most of the effects associated with JAMe treatment reported in this paper, such as an increase in respiratory activity and ethylene production in immature strawberries and the observed transitory induction of anthocyanin biosynthesis and chlorophyll degradation, support a role for JAMe as inducer of ripening in strawberry, a nonclimacteric fruit, as has been described for climacteric fruits (Sanieswki and Czapski, 1985; Sanieswki et al., 1987; Olías et al., 1991; Pérez et al., 1993; Fan et al., 1996). However, whether JAMe may modulate some of these changes associated with strawberry ripening, directly or via ethylene, remains to be elucidated.

ACKNOWLEDGMENT

We are indebted to D. Pedro Marín for the generous supply of strawberries from his fields at San Bartolomé de la Torre, Huelva.

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Received for review April 30, 1997. Accepted July 10, 1997.[⊗] This work was supported by Proyecto de Investigación ALI 738/94 from Plan Nacional de Ciencia y Tecnología de Alimentos, and R.O. is recipient of a grant from MEC.

JF9703563

[⊗] Abstract published in *Advance ACS Abstracts,* September 1, 1997.