Methyl Jasmonates in Developing Strawberry Fruit (*Fragaria ananassa* Duch. Cv. Kent)

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Two isomeric methyl jasmonates were isolated from extracts of strawberry fruit (*Fragaria ananassa* Duch. cv. Kent) by means of micropreparative gas chromatography. Enantiomeric separation and comparison with reference compounds allowed the determination of their absolute configuration as (3*R*,7*S*)-(+)-methyl *epi*-jasmonate and (3*R*,7*R*)-(−)-methyl jasmonate, respectively. Their genuine content in fruit was monitored throughout the ripening period from 7 days after anthesis (DAA) to the overripe stage (36 DAA). On a per weight basis, the sum of both isomers had a maximum concentration of 277.5 μg kg^{-1} in immature fruits and then steadily decreased. The levels of methyl jasmonates in strawberry may affect aroma formation and further events during fruit development.

Keywords: *Strawberry; Fragaria ananassa; methyl jasmonates; multidimensional preparative GC; enantiomeric separation; flavor; plant growth regulator*

INTRODUCTION

The methyl esters of jasmonic acid and 7-*iso*-jasmonic acid (*epi*-jasmonic acid, Figure 1) occur widely in the plant kingdom (reviewed by Hamberg and Gardner, 1992). Because of their volatility, methyl jasmonates may be involved in interplant communication (Farmer and Ryan, 1990). Several researchers reported on other remarkable biological activities, such as promotion of senescence (Ueda and Kato, 1980) or induction of tendril coiling (Falkenstein et al., 1991; reviewed by Hamberg and Gardner 1992; Sembdner and Parthier, 1993). Most of those studies have been carried out with a commercial, synthetic mixture that contains at least six different methyl jasmonates (Müller and Brodschelm, 1994), but there is increasing evidence that the absolute configuration is of decisive importance for their physiological effects (Koda et al., 1992). The same holds for their odor activity toward humans: (3*R*,7*S*)-Methyl jasmonate displays a strong and the 3*R*,7*R* isomer a weak lemon-like odor (detection thresholds 3 and >70 μg L^{-1}, respectively), while the other isomers are odorless (Acree et al., 1985). Several reports on the direct enantiomeric resolution using HPLC (Okamoto and Nakazawa, 1992) or capillary GC on cyclodextrin phases (König et al., 1992; Wang et al., 1996) have been published. On a preparative scale, racemic methyl jasmonates have been resolved using HPLC (Okamoto and Nakazawa, 1992; Kramell et al., 1996).

This paper reports on the rapid isolation of pure methyl jasmonate isomers from strawberry extracts by micropreparative gas chromatography, their subsequent enantiomeric separation, and their concentrations during the development of strawberry fruit.

EXPERIMENTAL PROCEDURES

Fruits. The strawberries were from regional cultivation of 2-year-old plants and were of the same batch as the ones investigated earlier (Latza et al., 1996). Anthesis was defined as the point of time at which 60% of the buds were in full bloom. Fresh fruits were processed within 12 h after picking.

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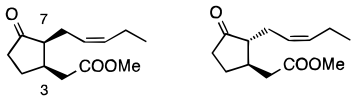

Figure 1. (3*R*,7*S*)-(+)-Methyl *epi*-jasmonate (left) and (3*R*,7*R*)-(−)-methyl jasmonate.

Preparation of Extracts. After careful washing and removal of the leaves and the calyx, the strawberries (150 g) were immediately blended with 600 mL of a 80:20 (v/v) mixture of methanol and 0.15 M phosphate-citrate buffer pH 5.5. MeOH served to inhibit enzymatic degradation processes, while buffering to pH 5.5 was favorable to prevent epimerization of *epi*-jasmonates (Müller and Brodschelm, 1994). Thereafter, internal standards (126.4 μg of methyl nonanoate and 115.7 μg of 2-methyl-1-pentanol in MeOH) were added, and the mixture was homogenized in a Rotor blender (Rotor AG, Uetendorf, Switzerland) for 5 min (14 000 rpm) at ambient temperature. The homogenate was then centrifuged for 20 min (2900*g*, 4 °C). The supernatant was diluted with 1 L of a 5% NaCl solution and extracted in a continuous liquid−liquid extractor for 8 h according to Drawert and Rapp (1968). The extraction medium was 250 mL of pentane−dichloromethane (2:1, v/v), the bath temperature 40 °C, and the condenser temperature −20 °C. After the mixture was dried over sodium sulfate, the organic layer was evaporated to about 1 mL on a Vigreux column (40 °C). This concentrate was used for the following steps.

Analytical Gas Chromatography. GC was carried out on a HRGC Fractovap 4160 chromatograph (Carlo Erba, Rodano, Italy) equipped with a cool on-column inlet, a flame-ionization detector, a deactivated FS-CW precolumn 3 m × 0.32 mm i.d. (CS, Langerwehe, Germany), and a DB-Wax fused silica column, 30 m × 0.32 mm i.d.; film thickness 0.4 μm (J&W, Folsom, CA). Operating conditions were as follows: carrier gas H_2 at 3.5 mL min^{-1}, detector 260 °C, injection volume 1 μL). The column was held at 40 °C for 3 min, programmed at 3 °C min^{-1} to 230 °C, and held there for 20 min. Concentrations of methyl jasmonates were calculated relative to the internal standard methyl nonanoate. The response factor was assumed to be 1.

GC−Olfactometry (GC−O). A Satochrom GC (Fisons, Rodano, Italy) equipped with a cool on-column inlet and a Satowax fused silica column (30 m × 0.32 mm i.d., film thickness of carbowax phase 0.45 μm) was employed. The end of the column was split (by a ratio of about 1:1) to a flame-ionization detector and a heated sniffing port. Other parameters were as described for analytical GC.

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GC−MS. A Fisons 8060 GC coupled to a Fisons MD 800 MS (Fisons, Mainz, Germany) was used. Gas chromatographic conditions were the same as for analytical GC, except that the carrier gas was He. Other parameters were as follows: interface temperature 230 °C, ion source 200 °C, ionization energy 70 eV, scan range 33−300 amu.

Preparative GC. A MCS Gerstel Series II instrument (Gerstel, Mülheim/Ruhr, Germany) with a HP 7673 autosampler, a Gerstel KAS-3 cold injection sytem, a Gerstel PFS fraction collector, and a Gerstel MCS 1.15 control and data acquisition system was employed. An OV 1 fused silica column (3 m × 0.53 μm i.d., 2 μm film thickness, Leupold, Fahrenzhausen-Weng, Germany) was connected to a BC CW 20 M fused silica capillary column (25 m × 0.53 μm i.d., film thickness of carbowax phase 1 μm, Leupold, Fahrenzhausen-Weng, Germany). Conditions were as follows. KAS: 45 °C for 10 s, then raised by 10 °C s^{-1} up to 250 °C, held there for 60 s. Oven: 100 °C for 3 min, then raised by 5 °C min^{-1} up to 195 °C, then held for 2 min. PFS: supply pipe and distributor 250 °C, trap cooling 0 °C. FIDs: 250 °C. Gases: carrier gas H_2 at 5.0 mL min^{-1}, auxiliary gas H_2 at 1.0 mL min^{-1}, counter gas H_2 at 10.0 mL min^{-1}. Transfer of compounds from the KAS to the first column was allowed from 10 to 45 s after injection; from the first column to the second column from 15.75 to 17.50 min; from the second column to trap 1 from 21.00 to 21.60 min (*trans*-isomers, relative to the cyclopentanone ring); and from the second column to trap 2 from 21.90 to 22.30 min (*cis*-isomers); injection volume 10 μL.

Enantioselective GC. The trapped methyl jasmonates were separated in a Fisons 8180 instrument (Fisons, Mainz, Germany) equipped with a cool on-column inlet, a flame-ionization detector, and an Octakis (6-*O*-methyl-2,3-di-*O*-pentyl-γ-cyclodextrin; 50% in polysiloxan PS 086) column (25 × 0.25 mm i.d.; 0.125 μm film thickness; W. A. König, Institut für Organische Chemie, Hamburg, Germany) with a 3 m × 0.32 mm i.d. deactivated FS-CW precolumn (CS, Langerwehe, Germany). Parameters: carrier gas H_2 at 2.0 mL min^{-1}; detector temperature 160 °C; oven 50 min at 90 °C, raised by 0.2 °C min^{-1} up to 105 °C.

Reference Compounds. A mixture of synthetic (racemic) methyl jasmonates was purchased from Aldrich (Steinheim, Germany). Enantiomerically pure compounds were kindly donated by M. J. Müller and M. H. Zenk, Lehrstuhl für Pharmazeutische Biologie, Universität München, Germany.

RESULTS AND DISCUSSION

Aroma extracts from unripe Kent strawberries exhibited a green, grassy odor (mainly due to 3(*Z*)-hexenal) with a pronounced citrus-like note. Using GC−O the citrus-like odor impression could be assigned to two peaks (first eluting, weak; second, strong) in the chromatogram. Comparison of retention time and mass spectra with those of authentic reference compounds revealed their identity as methyl jasmonate isomers.

Considering the retention behavior, the first-eluting isomer should be *trans*- and the second one *cis*-configurated relative to the cyclopentanone ring (Nishida and Acree, 1984). Since the biosynthesis of jasmonic acid from linolenic acid has been elucidated (Vick and Zimmermann, 1984), the absolute stereochemistry should be 3*R*,7*R* ((−)-methyl jasmonate) and 3*R*,7*S* ((+)-methyl *epi*-jasmonate), respectively. This is in good agreement with the intensities of the perceived odor impressions as (−)-methyl jasmonate is a rather weak, while (+)-methyl *epi*-jasmonate is a potent odorant (Acree et al., 1985).

A definite proof of the suggested stereochemistry came from the enantioselective GC. The complexity and the number of high-boiling compounds in the crude extract necessitated a preseparation prior to injection into an enantioselective column. As for previous applications (Gansser et al., 1995), micro-prep-GC of the crude extract proved to be a powerful tool for the efficient and rapid isolation of pure compounds from complex mixtures. Subsequent analysis of the trapped isomers on an Octakis (6-*O*-methyl-2,3-di-*O*-pentyl-γ-cyclodextrin; 50% in polysiloxan PS 086) column and cochromatography with authentic reference compounds clearly showed the first-eluting isomer to represent (3*R*,7*R*)-(−)-methyl jasmonate (peak 3 in Figure 2), while the second isomer was (3*R*,7*S*)-(+)-methyl *epi*-jasmonate (peak 6 in Figure 2).

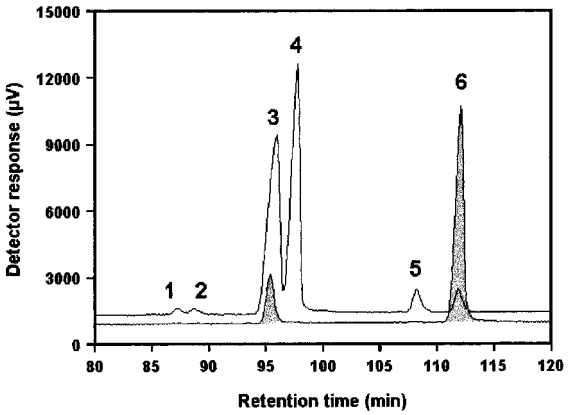

Figure 2. Chromatographic separation of methyl jasmonate isomers (1, 9*E*-3*R*,7*R*; 2, 9*E*-3*S*,7*S*; 3, 9*Z*-3*R*,7*R*; 4, 9*Z*-3*S*,7*S*; 5, 9*Z*-3*S*,7*R*; 6, 9*Z*-3*R*,7*S*). Upper: commercial mixture. Lower: partially epimerized methyl *epi*-jasmonate (**6**) isolated from strawberry extracts by micro-prep-GC.

The two isomers were isolated in almost pure form. Trapped (−)-methyl jasmonate displayed a purity of >95%. Partial isomerization (about 16%) of methyl *epi*-jasmonate (*cis*-configurated with respect to the cyclopentanone ring) to the thermodynamically more stable methyl jasmonate (*trans*; Nishida et al., 1985) was detected (Figure 2). Since the monitor−detector of the micro-prep-GC indicated pure compounds, the epimerization is most likely to occur, after methyl *epi*-jasmonate has passed the monitor−detector split, in the transfer line and the distributor prior to condensation in the cold trap.

Sembdner and Parthier (1993) speculated that methyl jasmonates could arise during isolation by artifact formation from endogenous jasmonic acid conjugates (e.g. amino acid conjugates; Brückner et al., 1986, 1988). When the general enzyme inhibitor MeOH was replaced by EtOH in our extraction procedure, no ethyl jasmonates were detected, and the methyl jasmonate levels were the same as for the MeOH workup. Therefore, at least (+)-methyl *epi*-jasmonate (accounting for up to 96% of the total determined methyl jasmonates) can be considered as a genuine constituent of the investigated strawberries. This agreed also with the odor impression perceived from homogenates of fresh, green fruits. The small amount of (−)-methyl jasmonate may have been formed by epimerization of the less stable methyl *epi*-jasmonate during the sample preparation.

In 1990, Knöfel et al., using a radioimmunoassay, reported on the determination of 38.3 μg kg^{-1} jasmonic acid in immature Senga Sengana strawberries. They also found more polar jasmonic acid-like compounds, while methyl jasmonates seemed to be absent. In the present investigation, high concentrations (a sum of up to almost 280 μg kg^{-1} fresh weight) of methyl jasmonates were determined in immature Kent strawberries, which steadily decreased during fruit development to about 3.3 μg kg^{-1} in overripe fruits (Figure 3).

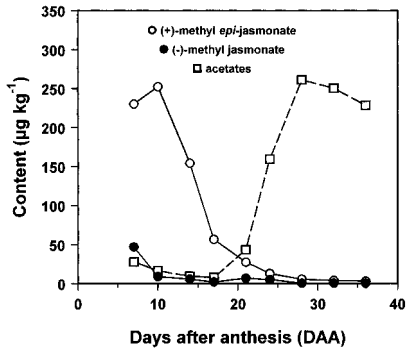

Figure 3. Content of methyl jasmonates and acetates in strawberry fruit (μg kg^{-1}) as a function of time. Acetates are the sum of butyl-, 3-methylbutyl-, hexyl-, 3(*Z*)-hexenyl-, 2(*E*)-hexenyl-, and benzylacetate.

Methyl esters of jasmonic acid have previously been identified only in a limited number of ripe fruits. Considerably high concentrations have been found in lemon peels (a sum of 75 μg in the peel of one lemon; Nishida and Acree, 1984), whereas only small amounts have been determined in black currants (Latrasse et al., 1982).

There are few reports on physiological effects of exogenously applied methyl jasmonates on fruits. In tomato fruits, Czapski and Saniewski (1992, and references therein) observed various effects of exogenously applied methyl jasmonates, e.g. a great stimulation of so-called ethene-forming enzyme (which should be 1-aminocyclopropane-1-carboxylic acid [ACC] oxidase). Methyl jasmonate, by its influence on ethene production, could therefore appear as a determinant of fruit ripening.

Very recently, Fan et al. (1997) reported on the effect of endogenous methyl jasmonates on ethene and volatile production in Summerred apples. In preclimacteric fruits methyl jasmonate stimulated ethene, ester, alcohol, and acetic acid production, while in postclimacteric fruits little or no response was observed. The authors concluded that methyl jasmonate participates in modulating initial events in apple ripening. This supports the view that the high concentration of endogenous methyl jasmonates in unripe Kent strawberries contributes to the initiation and modulation of ripening processes.

Exposure of ripe intact apples to vapors of methyl jasmonate resulted in decreased concentrations of volatile esters (Olías et al., 1992). This indicates an inhibitory effect of methyl jasmonates on the esterifying system of apples. Especially the formation of hexyl esters, which are important flavor constituents of apples, and of acetic acid esters was considerably reduced (Olías et al., 1992). With the exception of hexyl acetate, hexyl esters qualitatively and quantitatively appeared to be of minor importance for the strawberries under investigation (data not shown). The concentration of acetates in the developing fruits was negatively correlated to the content of methyl jasmonates (Figure 3). According to the results of Olías et al. this finding could reflect an inhibitory effect of methyl jasmonates on the esterifying system in strawberries. Another possible interpretation can be deduced from results of Pérez et al. (1996). They reported on the alcohol acyltransferase (AAT) activity in developing strawberries. The activity profile of AAT, which is thought to play a main role in ester formation in fruits, was very similar to that of the measured concentration of acetates in the present study. Since the determination of AAT activities was made in a crude extract without separation from potential inhibitors, the observed apparent increase in enzyme activity could involve effects caused by the decrease of an endogenous inhibitor. It is subject to further studies as to whether these observations are due to an increase in AAT protein, an increase in AAT specific activity, and/or a decrease in inhibitor concentrations.

In leaves of tobacco (*Nicotiana tabacum* L.) and cucumber (*Cucumis sativa* L.), methyl jasmonate induced additional lipoxygenase and hydroperoxide lyase activities (Avdiushko et al., 1995). The increased enzyme activities were persistent for at least 7 days after termination of methyl jasmonate exposure. Since the cooperation of both enzymes leads to odor-active six-carbon volatiles, such as 3(*Z*)-hexenal, the concentrations of these compounds significantly increased. The concentration of six-carbon volatiles in Kent strawberries was high in green fruits and began to decrease sharply after 24 DAA (data not shown), whereas the concentration of methyl jasmonates did after 10 DAA. These observations may be attributable to effects similar to those reported by Avdiushko et al. (1995): Higher concentrations of methyl jasmonate induce enzyme activities which are maintained for several days.

In soybean (*Glycine max*) cell suspension cultures, methyl jasmonate induced *de novo* transcription of genes, such as phenylalanine ammonia lyase (PAL; Gundlach et al, 1992). PAL is a key enzyme that links the primary metabolism with the phenylpropanoid pathway (Heller and Forkmann, 1994). It catalyzes the first-step reaction in the biosynthesis of a large range of secondary products in plants such as flavonoids, lignins, plant hormones, and UV protectants (Hanson and Havir, 1981). Cheng and Breen (1991) monitored PAL activity in developing Tillikum strawberries. The reported time course of enzyme acitivity paralleled that of methyl jasmonate concentration in the present study.

Methyl jasmonates are a prime example of aroma compounds that are also highly potent phytoeffectors. In the present study, parallels have been discovered between the time course of their endogenous levels in developing strawberries and other events during development. One could imagine that endogenous methyl jasmonates directly influence these events. However, their respective phytoeffector-like actions have previously been investigated by an exogenous addition, mostly of a mixture of synthetic isomers. Further studies will be necessary as to whether results obtained by an exogenous application can be transferred to endogenous methyl jasmonate stereoisomers.

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