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# Effects of Methyl Jasmonate on Ethylene Production in Tomato (*Lycopersicon esculentum* Mill.) Hypocotyl Segments and Fruits

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**Effects of methyl jasmonate (MeJA) on ethylene production in tomato (*Lycopersicon esculentum* Mill.) hypocotyl segments and fruits were studied. Ethylene production in tomato hypocotyl segments was inhibited by the increasing concentrations of MeJA, and 450 μM of MeJA showed 50% inhibitory effect. Time course data indicate that this inhibitory effect of MeJA appeared after 3 h of incubation period and continued until 24 h. Inhibition of ethylene production by MeJA was due to the decrease in 1-aminocyclopropane-1-carboxylic acid (ACC) synthase activity. However, MeJA treatment had no effect on ACC oxidase activity and the accumulation of ACC oxidase mRNAs. MeJA also inhibited auxin-induced ethylene production by decreasing in ACC synthase activity. In contrast, MeJA stimulated ethylene production in tomato fruits. When 30 μL/mL MeJA was treated in a gaseous state, ethylene production doubled and this stimulating effect continued until 4 days. To investigate the mechanisms of MeJA on ethylene production, ACC synthase and ACC oxidase activities were examined after MeJA treatment. MeJA increased the activities of both ACC synthase and ACC oxidase, and induced ACC oxidase mRNA accumulation. These data suggest that MeJA plays distinct roles in the ethylene production in different tomato tissues. It is possible that MeJA affects differently the mechanisms of signal transduction leading to the ethylene biosynthesis.**

*Keywords*: methyl jasmonate, ACC synthase, ACC oxidase, auxin, ethylene

Jasmonic acid (JA) and its methyl ester, methyl jasmonate (MeJA), are naturally occuring growth regulators found in higher plants (Meyer *et al.*, 1984; Anderson, 1989). JA and MeJA affect plant growth and development. Among the many observed effects of exogenously applied jasmonate are the promotion of senescence, petiole abscission, root formation, tendril coiling, ethylene synthesis and β-carotene synthesis (Sembdner and Parthier, 1993). On the other hand, jasmonate has been reported to inhibit seed germination, callus growth, root growth, chlorophyll production, and pollen germination (Sembdner and Parthier, 1993).

Recently, jasmonates have been proposed to be stress-related compounds (Farmer and Ryan, 1990; Parthier, 1991). MeJA, in particular, is a signal molecule that is released in plants in response to various stresses, such as wounding or pathogen attack (Creelman *et al.*, 1992), or subjection of tissues to osmotica or desiccation (Parthier *et al.*, 1992). Because MeJA is a volatile compound, it is able to traverse the atmosphere and thus can reach neighboring plants, in which characteristic defense reactions may be induced (Farmer and Ryan, 1990). All of the different plant responses to jasmonates, whether applied externally or released internally, appear to be correlated with alterations in gene expression. It has been identified that the synthesis of several proteins is either induced or repressed by jasmonate treatment (Reinbothe *et al.*, 1994). Jasmonates induce novel abundant polypeptides, designated jasmonate-induced

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proteins (JIPs). On the other hand, genes that encode proteins involved in photosynthetic carbon assimilation are negatively regulated by MeJA (Reinbothe *et al.*, 1994).

An important mediator of the defense response is the plant hormone ethylene. Ethylene regulates many aspects of plant growth and development, is synthesized in response to a wide range of stimuli, such as wounding, anaerobiosis, ripening, or auxin treatment (Yang and Hoffman, 1984). The ethylene biosynthetic pathway is methionine (Met) → S-adenosylmethionine (SAM) → 1-aminocyclopropane-1-carboxylic acid (ACC) → ethylene. In this pathway, the conversion of SAM to ACC catalized by ACC synthase, is generally regarded as a rate limiting step (Yang and Hoffman, 1984). Several groups have reported partial purification of the enzyme (Kende, 1993), and recently cDNA clones for ACC synthase have been isolated from various plant species including zucchini squash, winter squash, tomato, apple, and carnation (Kende, 1993). In several species, the evidence has been presented indicating that ACC synthase is encoded by multi-gene family (Huang *et al.*, 1991; Olson *et al.*, 1991). Not surprisingly, given the diverse stimuli leading to induction of ACC synthase, differential regulation of genes encoding this enzyme has been reported (Huang *et al.*, 1991).

Several investigators have isolated ACC oxidase cDNA clone from ripening avocado, apple, peach, and melon fruits, senescent carnation and orchid flowers, and pea and mungbean seedlings. These clones share about 80% homology at the amino acid level, and the levels of these transcripts increased greatly during fruit ripening or flower senescence (Kim and Yang, 1994).

On the basis that jasmonates and ethylene play similar roles in plant cells, there are some investigations on the effects of jasmonates on ethylene production. MeJA stimulates ethylene production in tomato (Saniewski *et al.*, 1987). MeJA was found to stimulate ACC-dependent ethylene production in detached rice leaves (Chou and Kao, 1992). On the other hand, the conversion of ACC to ethylene by hypocotyl segments sunflower (*Helianthus annuus* L.) seedlings was inhibited by MeJA (Bailly *et al.*, 1992).

In this report, we showed that ethylene production and activities of ACC synthase and ACC oxidase were changed by MeJA in tomato hypocotyls and fruits, and the effects of MeJA were different according to plant tissues and developmental stages. We attempted to estimate a possible mechanisms of MeJA action.

## MATERIALS AND METHODS

### Plant material and incubations

Seeds of tomato (*Lycopersicon esculentum* Mill.) were germinated and grown in vermiculite for 6 d in darkness at 26± 1℃. 1-cm-long hypocotyl segments were cut at 0.5-1 cm below the hook, incubated in 2 mL of a medium consisting of 2% (w/v) sucrose, 50 μg/mL chloramphenicol, 10 mM Mes/Tris buffer (pH 6.8), and various concentrations of indole-3-acetic acid (IAA) or MeJA.

Tomato fruits were purchased from a local market. Intact tomato fruits were put in a desiccator containing various concentrations of MeJA in a gaseous state and incubated at 26± 1℃.

### Determinations of ethylene and ACC

A 1-mL gas sample was withdrawn from the vial with a hypodermic syringe, and ethylene was assayed on a gas chromatograph (Shimadzu GC-9A, Flame Ionization Detector, Porapark Q Column 100-200 mesh, 90℃).

Approximately 0.5 g of tissue was extracted twice at 80℃ in 2 mL 80% ethanol for 2 h. The extracts were then concentrated in *vacuo* at 40℃ and adjusted with water to 1 mL. ACC was determined by the method of Lizada and Yang (1979), based on the conversion of ACC to $C_2H_4$ with NaOCl reagent. The amount of $C_2H_4$ liberated was determined by GC. The efficiency of the conversion of ACC to $C_2H_4$ was estimated by adding a known amount of authentic ACC as internal standard to a separate sample, which then was degraded to $C_2H_4$ by the same method.

### Assay of ACC synthase and ACC oxidase

The homogenization and extraction of plant tissues for ACC synthase activity assay were performed as described by Yip *et al.* (1991). Tissue was homogenized in 100 mM Hepes-KOH buffer, pH 8.5, con-

taining 4 mM DTT, 0.5 μM pyridoxal phosphate (PLP), 10 mM EDTA, 0.1 mM PMSF, 2 M NaOH using a pestle in a mortar. Homogenization buffer was used at a ratio of 1 mL/g fresh weight of tissue. The homogenate was centrifuged at 25,000 *g* for 15 min. The supernatant was applied to a Sephadex G-25 column (2×11 cm, bed volume, 30 mL) previously equilibrated with 2 mM Hepes buffer, pH 8.5, containing 0.5 mM DTT, 0.5 μM PLP, 1 mM EDTA, and the active enzyme fractions were pooled. Appropriate aliquots of enzyme were incubated at 30℃ in 50 mM Hepes buffer, pH 8.5, containing 0.5 μM PLP, and 10 μM SAM. The amount of ACC formed was determined by chemical conversion of ACC to ethylene followed by gas chromatographic quantitation. One unit of enzyme converts 1 nmol of SAM to ACC per h at 30℃.

For assay of ACC oxidase *in vivo*, 0.5 g of tomato hypocotyl was incubated in 2 mL of a medium containing 2% (v/v) sucrose, 1 mM $CaCl_2$, 50 mM Mes (pH 6.2) and 2 mM ACC for 1 h, and the ethylene produced was measured (Fernandez-Maculet and Yang, 1992).

### RNA isolation and northern blot analysis

Total RNAs of tomato hypocotyls and fruits were obtained by a method adapted from the established protocols by Nakajima *et al.* (1988, 1990) and Kim *et al.* (1992). Frozen tissue was pulverized in liquid nitrogen with a mortar and pestle, and homogenized with 10 mL of extraction buffer (0.1 M Tris-HCl, pH 9.0, 0.1 M NaCl, 1% SDS) and an equal volume of phenol/chloroform/isoamyl alcohol (25 : 24 : 1, v/v). RNA was precipitated by adding 2.5 volume ethanol at −20℃, collected and dissolved in a minimum amount of water. To the aqueous solution, 1/3 volume of 10 M LiCl was added to precipitate RNA. RNA was again dissolved in water, adjusted to 250 mM NaCl, and added 2.5 volumes of ethanol. Precipitated high molecular weight RNA was collected by centrifugation, rinsed with 70% ethanol and dissolved in water. Total RNA was electrophoresed on 1% agarose gel (20 μg per lane) in presence of 1.9% formaldehyde, blotted onto nitrocellulose membrane, and RNA was fixed by UV radiation. Hybridization was carried out in 5X SSPE (0.75 M NaCl and 6 mM EDTA in 45 mM phosphate buffer, pH 7.4), 5X Denhardt's solution, 100 μg/mL denatured salmon sperm DNA ,and 0.1% SDS at 52℃. The membrane was washed with 2X SSPE and 0.1% SDS at 52℃. The blots were visualized by autoradiography at −80℃.

## RESULTS AND DISCUSSION

It has been recently proposed that JA and MeJA may serve as a signal transducer in stress-induced plant responses (Gundlach *et al.*, 1992). There are some investigations on the effects of jasmonates in ethylene production. Saniewski *et al.* (1987) reported that MeJA stimulates ethylene production and the synthesis or activity of the ACC oxidase in tomato. Chou and Kao (1992) reported that MeJA is capable of stimulating the ACC-dependent synthesis of ethylene in detached rice leaves. Bailly *et al.* (1992), however, observed that MeJA inhibits the ACC-dependent production of ethylene in sunflower seedlings. Thus, despite numerous studies, contradictory hypothesis exist regarding the effect of MeJA on ethylene production.

To study the possible mechanism of MeJA in ethylene production in more detail, we incubated excised hypocotyls for 18 h in the presence of various concentrations of MeJA, and ethylene was assayed on a gas chromatograph. Ethylene production in tomato hypocotyl segments was inhibited by the increasing concentrations of MeJA, and 350 μM of MeJA showed about 50% inhibitory effect (Fig. 1). All the following experiments were performed by incubating hypocotyl segments with 450 μM MeJA. Fig. 2 shows the time courses of the ethylene synthesis rate of tomato hypocotyls in the presence or absence of 450 μM MeJA. In the absence of 450 μM MeJA, the ethylene production rate was continuously increased, reaching about 37 nL/g at 24 h incubation. In the presence of MeJA, however, the inhibitory effect of MeJA appeared after 3 h of incubation period and continued until 24 h. The ethylene production rate decrease by 30% at 3 h and 50-60% after 6 h incubation.

It is well known that IAA stimulates ethylene production by promoting the conversion of SAM to ACC in various plant tissues (Yang and Hoffman, 1984; Kim *et al.*, 1992). To study the effect of MeJA on IAA-induced ethylene production, hypocotyl seg-

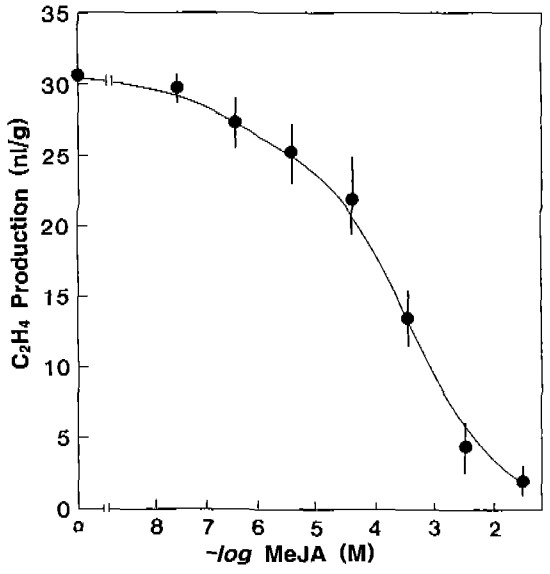


**Fig. 1.** Effect of various concentrations of MeJA on ethylene production in tomato hypocotyl segments. Ethylene production was measured at the end of a 18 h incubation period.

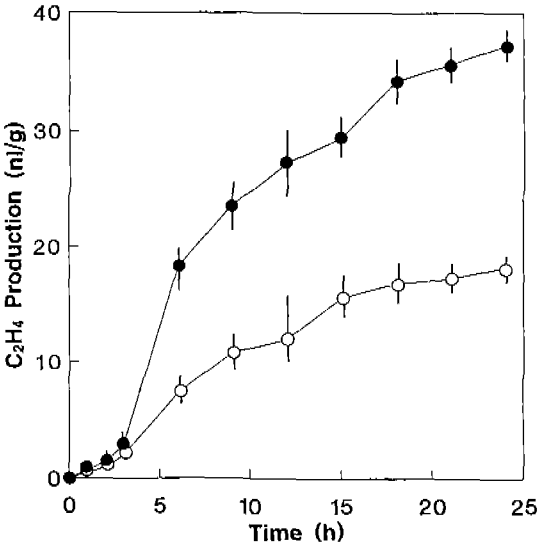


**Fig. 2.** Time courses of ethylene production in tomato hypocotyl segments. Open circles (○) denote ethylene production in the presence of 450 μM MeJA and closed circles (●) denote ethylene production in the absence of MeJA.

ments was incubated in the presence of various concentrations of MeJA and IAA. Fig. 3 shows the effects of various concentrations of MeJA and IAA on ethylene production. In the presence of IAA and MeJA, the ethylene production rate of tomato hypocotyls gradually declined by increasing concentrations of MeJA as compared with IAA-treated tissue

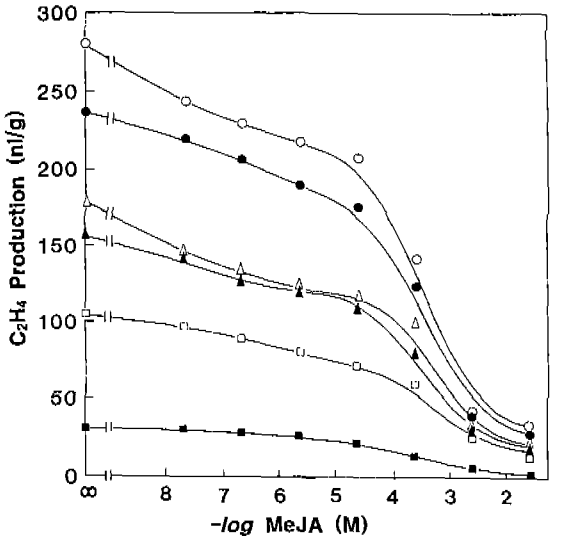


**Fig. 3.** Effects of various concentrations of MeJA and IAA on ethylene production in tomato hypocotyl segments. Ethylene production was measured at the end of a 18 h incubation period. The concentrations of IAA were $10^{-3}$ M (▲), $10^{-4}$ M (○), $10^{-5}$ M (●), $10^{-6}$ M (△), $10^{-7}$ M (□), 0 M (■).

**Table 1.** Effects of MeJA and IAA on ACC synthase activity, endogenous ACC content, and *in vivo* ACC oxidase activity in tomato hypocotyl segments. After 18 h incubation, the ACC synthase activity was assayed using 10 μM SAM as substrate

| Treatment | ACC synthase activity[a] (unit/mg) | ACC content (M) | ACC oxidase activity (nL/g) |
|---|---|---|---|
| Control | 1.03 | $9.5\times10^{-7}$ | 108.4 |
| MeJA[b] | 0.73 | $6.6\times10^{-7}$ | 119.7 |
| IAA[c] | 3.50 | $6.1\times10^{-6}$ | 143.8 |
| IAA1MeJA | 1.97 | $2.0\times10^{-6}$ | 150.3 |

[a]1 Unit of ACC synthase=1 nmol ACC produced per h at 30℃, [b]The concentration of MeJA was 450 μM, [c]The concentration of IAA was 100 μM.

and 100 M of IAA showed the maximum ethylene production at the same MeJA concentration. These data show that MeJA has inhibitory effect on the IAA-induced ethylene production.

To assess the roles of ACC synthase and ACC oxidase in the regulation of ethylene biosynthesis in MeJA-treated tomato hypocotyls, the activities of these enzymes and the level of ACC were determined (Table 1). Before the MeJA treatment, ACC synthase activity was 1.03 unit/mg and ACC content

**Table 2.** Effect of MeJA on *in vitro* ACC synthase activity in tomato hypocotyl segments. The ACC synthase activity was assayed with or without 450 μM of MeJA in the reaction mixture

| SAM (μM) | Specific activity (unit/mg)[a] | | Ratio (MeJA/control×100) |
|---|---|---|---|
| | Control | MeJA[b] | |
| 1 | 0.96 | 0.93 | 96.9 |
| 3 | 1.86 | 1.87 | 100.5 |
| 5 | 2.09 | 2.13 | 101.9 |
| 10 | 2.41 | 2.36 | 97.9 |

[a]1 Unit of ACC synthase=1 nmol ACC produced per h at 30℃. [b]The concentration of MeJA was 450 μM.

was $9.5\times10^{-7}$ M. With MeJA treatment, ACC synthase activity and ACC content decreased by 30% and 39%, respectively. ACC oxidase activity, however, did not decreased by MeJA and substantially maintained. Therefore, we could conclude that the inhibition of ethylene production by MeJA was due to the decrease in ACC synthase activity. In the same way, when IAA was added to the incubation medium with or without MeJA, ACC content and ACC synthase activity decreased, and ACC oxidase activity was maintained in MeJA treated tissues. Thus, MeJA also inhibited the auxin-induced ethylene production by decreasing ACC synthase activity. To examine if the decrease of ACC synthase activity was a result that MeJA directly affected the enzyme, *in vitro* ACC synthase activity was assayed with or without MeJA (Table 2). When MeJA was treated to the crude enzyme solution, ACC synthase activity was similar to that of control. Thus, MeJA may regulate ACC synthase activity before the step of protein action, such as transcriptional, posttranscriptional, and/or translational control.

In order to know the effects of MeJA in the different part of tomato plants, we also examined ethylene production in tomato fruits. Tomato fruit tissues were incubated in a desiccator containing the various concentrations of MeJA for the various time period, and ethylene production was measured (Fig. 4). In contrast to the hypocotyl tissues, MeJA stimulated ethylene production at various concentrations in tomato fruits. When 30 μL/mL MeJA was treated in a gaseous state, the highest stimulation of ethylene production occured. In this case, ethylene production doubled and this stimulating effect continued until 4 day (Fig. 4).

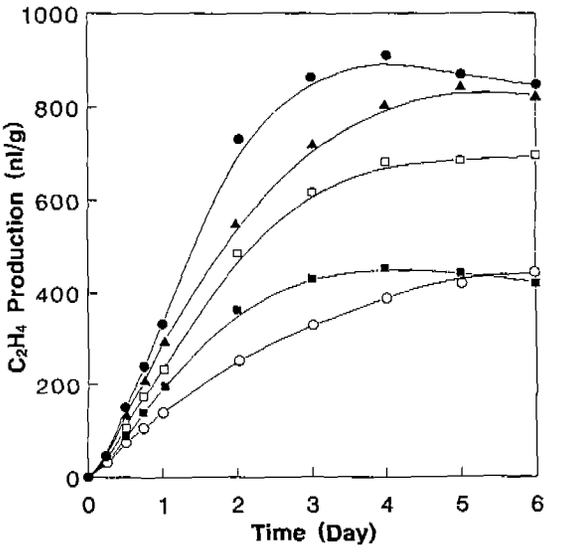


**Fig. 4.** Effect of various concentrations of MeJA on ethylene production in unripen tomatoes. Open circles (○) indicate ethylene production in the absence of MeJA. The concentrations of MeJA were 3 Ml/ml (■), 30 μL/mL (●), 60 μL/mL (▲), 90 μL/mL (□).

**Table 3.** Effects of MeJA on ACC synthase activity, endogenous ACC content, and *in vivo* ACC oxidase activity in tomato fruits. Tissues were incubated with or without 30 μL/mL MeJA for 4 days. After the incubation, the ACC synthase activity was assayed using 10 μM SAM as substrate

| Treatment | ACC synthase activity[a] (unit/mg) | ACC content (M) | ACC oxidase activity (nL/g) |
|---|---|---|---|
| Control | 1.88 | $2.56\times10^{-7}$ | 44.2 |
| MeJA[b] | 3.34 | $6.09\times10^{-7}$ | 360.9 |

[a]1 Unit of ACC synthase=1 nmol ACC produced per h at 30℃. [b]The concentration of MeJA was 30 μL/mL.

To investigate of the modes of MeJA on ethylene production in tomato fruit tissue, ACC synthase and ACC oxidase activities were examined after MeJA treatment. These data are summarized in Table 3. The ACC synthase activity showed a 78% increase and ACC content also doubled. Furthermore, MeJA caused a marked increase in ACC oxidase activity. Thus, MeJA stimulates ethylene production in fruit tissue by increasing the activities of both ACC synthase and ACC oxidase.

The expression of the ACC oxidase gene in diffe-

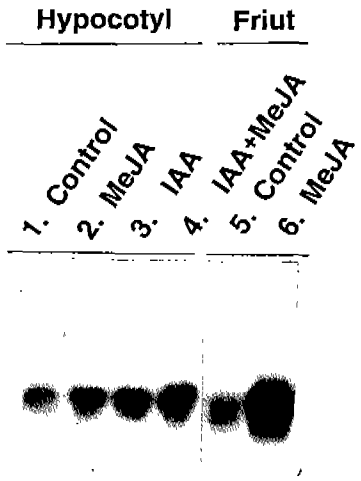


**Fig. 5.** The accumulation of ACC oxidase mRNA in hypocotyl segments and friuts. The tissues were incubated under various treatments and total RNA was isolated. Each lane contains 40 μg total RNA. Lane 1-4, hypocotyl segments for 18 h incubation; 1, control; 2, MeJA (450 μM); 3, IAA ($10^{-4}$ M); 4, IAA ($10^{-4}$ M)+MeJA (450 μM); lane 5-6, friut tissues for 4 days incubation; 5, control; 6, MeJA (30 μL/mL).

rent parts of tomato plants was examined by Northern blot analysis. Total RNAs were isolated from tomato hypocotyls after 18 h and tomato fruits after 4 day of MeJA treatments, when their ethylene synthesis rate reached the maximum. Hybridization was carried out under the low stringency conditions using mung bean hypocotyl ACC oxidase cDNA, pACO1 as probe (Kim and Yang, 1994). As shown in Fig. 5, the level of the ACC oxidase transcript was greatly increased by MeJA in tomato fruits, but not in tomato hypocotyls. These data indicate that the increase in ACC oxidase activity by MeJA was due to the induction of its transcripts in tomato hypocotyls, the expression of ACC oxidase transcript was slightly increased by auxin treatment.

While MeJA inhibited ethylene production in tomato hypocotyls by decreasing in ACC synthase activity, it stimulated ethylene production in tomato fruits by increasing the activities of ACC synthase and ACC oxidase. One data also show that the increase in ACC oxidase activity in fruit tissue is due to the accumulation of ACC oxidase transcript. These results indicate that MeJA exerts its effect on ethylene production through the regulation of expression of genes encoding ethylene biosynthetic enzymes. Our data also show that MeJA plays the distinct roles in the ethylene production in different tomato tissues. However, the modes of action of MeJA in inhibiting or stimulating the activities of both ACC synthase and ACC oxidase in different tomato tissues are not known. More detail investigations are required to define the mechanisms of MeJA signal transduction which leads to the change of ethylene biosynthesis in different tissues. It is possible that MeJA might induce the de novo synthesis or increase the stability of distinct transcription factors that regulate transcription of MeJA responsive genes, including ACC oxidase.

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# Methyl jasmonate가 토마토(*Lycopersicon esculentum* Mill.) 하배축 절편과 열매에서 에틸렌 생성에 미치는 영향

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## 적 요

Methyl jasmonate(MeJA)가 토마토(*Lycopersicon esculentum* Mill.) 하배축과 과일조직에서 에틸렌 생성에 미치는 영향을 조사하였다. 토마토 하배축에서는 MeJA 농도가 증가함에 따라 에틸렌 생성이 억제되었으며 450 μM에서 약 50% 억제되었다. 시간에 따른 에틸렌 생합성량을 측정한 결과 MeJA의 억제율은 3시간 이후부터 50%로 나타나서 24시간까지 거의 같은 정도의 비율로 지속되었다. 하배축의 MeJA에 의한 에틸렌 합성감소는 ACC synthase의 효소활성 감소에 기인하였으며 ACC oxidase의 효소활성과 mRNA 축적에는 영향을 주지 않았다. MeJA는 IAA와 함께 작용한 경우에도 ACC synthase의 활성을 감소시킴으로써 에틸렌생성을 억제시켰다. 과일조직에서는 하배축과는 반대로 MeJA가 에틸렌 생성을 촉진시켰다. 30 μL/mL의 농도로 MeJA를 기체상태로 처리했을 때 에틸렌 합성이 100% 정도 증가하였으며 그 촉진효과는 12시간 이후부터 나타나기 시작하여 4일째되는 날까지 계속되었다. 과일조직에서의 MeJA에 의한 에틸렌의 합성증가는 ACC synthase와 ACC oxidase의 활성증가에 기인하였으며, ACC oxidase mRNA의 축적도 유도되었다. 따라서 MeJA는 토마토의 서로 다른 조직에서 에틸렌 합성에 대해 상반된 효과를 나타내었다. 이것은 MeJA가 에틸렌 생성의 신호전달경로에서 다르게 작용하기 때문이라고 생각해 볼 수 있다.

주요어 : methyl jasmonate, ACC synthase, ACC oxidase, IAA, 에틸렌

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