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Effect of Silver Ions on Ethylene Biosynthesis by Tomato Fruit Tissue[1]

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ABSTRACT

Mature-green tomato fruit (*Lycopersicon esculentum* Mill.) were treated asymmetrically with 2 millimolar silver thiosulfate (STS) through a cut portion of the peduncle while still attached to the plant. One-half of the fruit received silver and remained green while the other half ripened normally and was silver-free (less than 0.01 parts per billion). Harvested mature-green fruit were also treated with STS through the cut pedicel. Green tissue from silver-treated fruit had levels of 1-aminocyclopropane-1-carboxylic acid (ACC, the immediate ethylene precursor) slightly less or similar to that of turning or red-ripe tissue from the same fruit, and similar to that of mature-green tissue from control fruit. Ethylene production was higher in green tissue from silver-treated fruit than from either red tissue from the same fruit, or mature-green tissue from control fruit. By inhibiting ACC synthesis with aminoethoxyvinyl glycine, and by applying ACC ± silver to excised disks of pericarp tissue from control or silver-treated tomatoes, we showed that short-term silver treatment did not affect the biological conversion of ACC to ethylene, while long-term treatment stimulated both the conversion of ACC to ethylene and the synthesis of ACC.

Respiration and ethylene synthesis increase during the climacteric phase of tomato fruit ripening and elevated endogenous ethylene levels are required for normal ripening (9). Ripening can be either stimulated by applying ethylene to mature-green fruit (5, 15), or inhibited by applying inhibitors of ethylene biosynthesis (5) or action (13), or by increasing ethylene diffusion from the fruit under low pressure storage (4, 15). Silver appears unique among heavy metals as an inhibitor of ethylene action (3), and thereby, fruit ripening (8, 13). For example, soaking excised pericarp disks of breaker fruit for 2 min in 0.3 to 5 mM silver nitrate, an inhibitor of ethylene action (3), significantly reduced endogenous ethylene production, softening, and lycopene synthesis (13). This treatment also prevented exogenously applied ethylene from promoting ripening. Silver can also inhibit ripening of whole fruit attached to the plant when a mobile silver thiosulfate complex is introduced into the vascular system of the fruit through a sliver of peduncle tissue (7). Application of AVG,[2] an inhibitor of ethylene biosynthesis (9), to excised disks of tomato pericarp tissue reduced ethylene production and ripening (5). In contrast to the response of silver treated tissue, exposure of AVG treated pericarp disks to ethylene promoted lycopene synthesis and softening (5).

The biosynthetic pathway for ethylene production in vascular plants progresses from the amino acid MET through SAM to ACC, and finally to ethylene (1, 18). In this scheme, the controlling step is thought to be the conversion of SAM to ACC. At appropriate concentrations, AVG inhibits the conversion of SAM to ACC and reduces ethylene production by about 90% (18). Exogenously applied ACC can therefore be used to study the activity of ACC conversion to ethylene in tissue previously treated with AVG.

Attached and detached whole fruit and excised disks of tomato pericarp tissue were used to study the effect of silver ion on the biosynthesis of ethylene.

MATERIALS AND METHODS

Treating Attached Whole Fruit with Silver. Whole fruit still attached to the plant were asymmetrically treated with STS using a modification of a procedure described by Hobson *et al.* (7). The peduncles of mature-green tomato fruit (*Lycopersicon esculentum* Mill.) still attached to the plant were cut in half lengthwise to expose an approximately 3-cm long sliver of tissue. The free end of this sliver was inserted into a 5 × 1 cm diameter plastic tube containing 2 ml of 2 mM STS, prepared immediately before treatment as previously described (2, 16). The STS complex was used because it has much greater mobility in plant tissue than uncomplexed silver ion (16). The fruit half receiving STS remained firm and green, while the other half started to soften and turn red after 12 to 15 d. Ethylene production by the silver-free and silver-treated sides was measured on the plant as described below. Fruit were harvested when the silver-free side reached either the turning or red-ripe stage, and the fruit were used whole, or 1-cm pericarp disks were excised as described below. This experiment was replicated five times with red and green tissue coming from the same fruit.

Treating Detached Whole Fruit with Silver. Mature-green fruit were harvested by cutting the pedicel 2 cm behind the node. In the laboratory, the pedicel was recut at the node and a short length of amber rubber tubing was used to make a watertight connection between it and the end of a 5-ml plastic tube. One ml of STS was transferred immediately after preparation into the tube. The sodium thiosulfate solution used to make the STS solution was used as the control. Ethylene and CO_2 production were determined periodically for 11 d. One-ml gas samples were taken after 1 h incubation in a closed glass jar, and analyzed as previously described (12). This experiment was repeated five times.

Measuring ACC Levels in Attached STS Treated Fruit. Two

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[2] Abbreviations: AVG, aminoethoxyvinyl glycine; ACC, 1-aminocyclopropane-1-carboxylic acid; MET, methionine; SAM, *S*-adenosylmethionine; STS, silver thiosulfate; ppb, parts per billion.

g frozen tissue were homogenized in 10 ml 0.2 M TCA with a mortar and pestle (a little washed silica sand was used to assist the grinding). The mixture was centrifuged at 7000*g* for 10 min and the supernatant decanted. Aliquots were assayed for ACC with a modified version of the procedure used by Lizada and Yang (10). Each assay was repeated with similar results.

Measuring Ethylene in Attached Whole Fruit. Two red rubber serum stoppers (15 × 25 mm diameter; about 3 ml volume) were placed on opposite sides of normal or silver-treated attached fruit near the equatorial plane. The stoppers were held in place by rubber bands around the fruit. Silicone stopcock grease was used to seal the outer edge of the stopper to the epidermis. One-ml gas samples were removed after varying lengths of time and analyzed for ethylene (12). For time course experiments, the top of the serum stopper was cut away and the barrel of a 6-ml plastic syringe inserted through the hole. The syringe was set to 6 ml. The plunger was advanced 1 ml when taking each 1-ml gas sample. In this way many gas samples could be taken without having to flush the stopper with ethylene-free air between samples. Ethylene accumulation in the serum stopper was followed over time. Equilibrium between ethylene concentration in the fruit and in the serum stopper was considered to have been reached when the levels of ethylene in consecutive samples were not significantly different from one another.

Silver Ion Determination. Two g frozen pericarp tissue were homogenized in 10 ml of 16 mM sodium thiosulfate. The mixture was centrifuged at 7000*g* for 10 min, and the supernatant decanted for silver determination using atomic absorption at a wave length of 328.1 nm. Silver standards confirmed that this method could detect as little as 0.01 ppb silver.

Excised Pericarp Disks. Fruit at the mature-green, pink, and overripe stage of maturity were surface sterilized by washing with 80% ethanol. Disks of pericarp tissue were excised with a 1-cm diameter cork borer, trimmed of excess material, and randomly distributed among treatments. Four disks were placed epidermal surface down into sterile 100 × 15 mm plastic Petri dishes which were divided into 4 cavities by raised dividers (5, 6).

After distributing the disks among the treatments, solutions were applied to the locular surface of each disk with a 1-ml plastic syringe fitted with an 18 gauge × 3.8 cm needle and a 20 μm filter. The filter ensured that the applied solutions were sterile. All procedures were performed under aseptic conditions in a laminar flow hood (5, 6). Disks were held in a humid, ethylene-free atmosphere during the course of these experiments (5).

In one series of experiments, 20 μl of water or 10 mM AVG were applied 2 h after excision. Three d after excision, 20 μl of water ± 2 mM STS, or 20 μl of 300 μM ACC ± 2 mM STS were applied to the disks. Solutions containing STS were not applied to disks excised from STS treated, attached fruit. The disks were transferred to 10-ml syringes after waiting 2 h for the solutions to be absorbed.

The order of treatment applications were varied in another series of experiments. Two h after excision, 30 μl of water or 10 mM STS were applied to the locular surface of each disk. One d after excision, 30 μl of water or 10 mM AVG were applied to the disks. Two d after excision, 30 μl of water or 300 μM ACC were applied and the disks were transferred to 10-ml syringes after waiting 2 h for the solutions to be absorbed.

Measuring Ethylene Production from Disks. The syringes were set to 10 ml and plugged with rubber serum stoppers. One-ml gas samples were withdrawn after 1 h and assayed for ethylene as previously described (12). The syringes were flushed with ethylene-free air between 1-h accumulations to study ethylene production over time.

RESULTS AND DISCUSSION

Ethylene Production by Silver-Treated Attached Fruit. Pericarp disks excised from the green, silver-containing side of fruit treated asymmetrically with silver through the peduncle while attached to the plant contained around 2.0 ppb silver, while disks excised from the ripening, silver-free side of the same fruit contained less than 0.01 ppb silver. Disks excised from green, silver-containing tissue had higher rates of ethylene production than disks excised from red, silver-free tissue from the same fruit (Fig. 1). This difference was statistically significant 1 h after excision (5% level), and the difference increased as ethylene evolution increased with time after excision for both the red and green pericarp disks. The general rise in ethylene production in silver-free and silver-containing tissues over the 5 h of the experiment may have been caused by excision. To see if excision was differentially influencing ethylene production by the red and green tissue, a method was used to sample ethylene production from fruit still attached to the plant.

Serum stoppers were attached to the green side and the ripening side of fruit treated with silver while attached to the plant. Differences in the rate of ethylene evolution from tissue could result from either differences in the epidermal resistance to gas diffusion, or differences in the actual concentration of ethylene within the tissue. The accumulation periods were varied to differentiate between these possibilities. Short-term accumulation would be influenced by epidermal resistance to gas diffusion, while longer accumulation times would not be influenced by epidermal resistance since equilibrium would be reached. This kinetic study showed that ethylene concentrations within tissue immediately below the serum stopper and within the serum stopper reached equilibrium after 16 h (*i.e.* no statistical change in concentration during the next four samples taken over 12 h). Measurement of the ethylene concentration at equilibrium showed that the green, silver-containing side of the fruit had a higher ethylene concentration than the red, silver-free side (4.6 μl/L *versus* 2.2 μl/L, respectively). This difference was evident even before equilibrium was established (*e.g.* 1.5 *versus* 0.95 μl/L, respectively after 2 h).

Effect of Silver on ACC Levels in Attached Fruit. Green, silver-containing tissue excised from asymmetrically treated attached fruit that had reached the turning stage of maturity, contained significantly less ACC (1.8 nmol/g fresh weight) than ripening, silver-free tissue from the same fruit (2.6 nmol/g fresh weight). When the silver-free side reached the red-ripe stage, the green, silver-treated tissue contained about the same level of ACC as did the red-ripe tissue (9.0 *versus* 9.2 nmol/g fresh weight, respectively). In comparison, mature-green and red-ripe

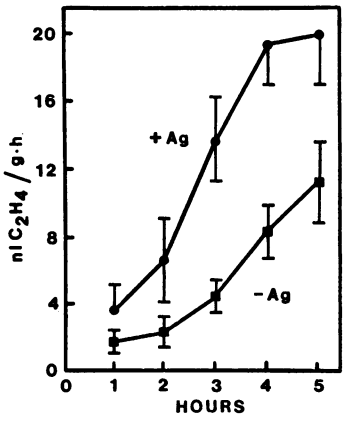

FIG. 1. Ethylene production by disks of red, silver-free, and green, silver-containing pericarp tissue excised from tomato fruit previously treated asymmetrically with silver.

Table I. *Effect of Treating Disks of Pericarp Tissue Excised from Different Maturity Fruit with AVG 2 d Before Application of ACC on the Rate of Ethylene Production 2 h after ACC Application*

Fruit had previously been treated asymmetrically with silver while attached to the plant. Means within each maturity followed by the same letter are not statistically different at the 5% level.

Solution Applied on		Stage of Ripeness			
		+Ag	−Ag		
Day 1	Day 3	Green	Green	Pink	Red-ripe
		nl ethylene/g fresh wt h			
Water	Water	155.2 a	49.4 a	45.6 a	28.3 a
AVG, 10 mM	Water	8.8 c	4.3 c	7.9 c	1.1 c
AVG, 10 mM	ACC, 300 μM	73.2 b	16.8 b	20.3 b	4.0 b

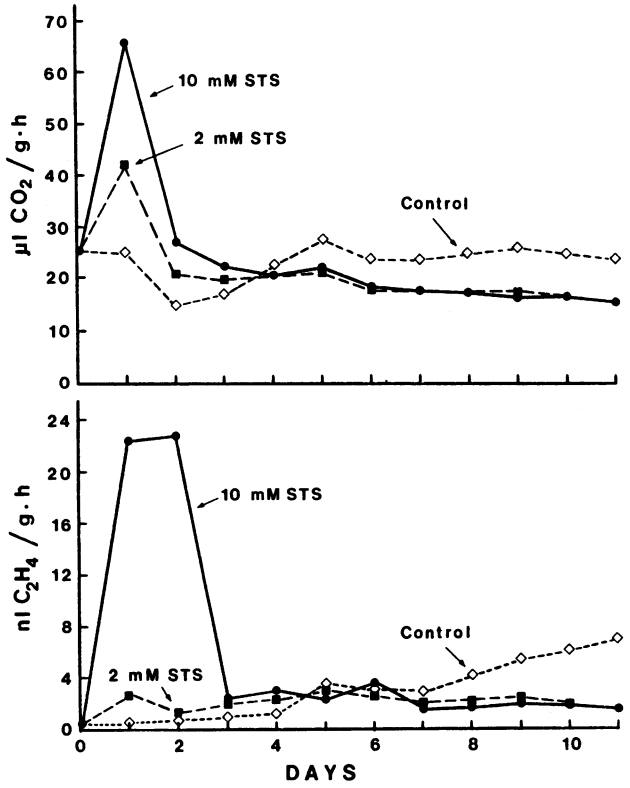

FIG. 2. Ethylene and CO_2 production by detached whole mature-green fruit treated with STS through the pedicel.

Table II. *Effect of Treating Disks of Pericarp Tissue Excised from Breaker Fruit with AVG, and then with ACC and Silver 2 d Later on the Rate of Ethylene Production 2 h after ACC and Silver Application*

Means followed by the same letter are not statistically different at the 5% level. The AVG was 10 mM and the ACC was 300 μM.

Solutions Applied		Ethylene Production
Day 1	Day 3	
	nl ethylene/g fresh wt h	
Water	Water	59.2 b
Water	Ag	86.8 a
AVG	Water	9.9 d
AVG	Ag	6.3 d
AVG	ACC	27.5 c
AVG	ACC + Ag	34.9 c

tissue from fruit not treated with STS contained 1.4 and 10 nmol ACC/g fresh weight, respectively. These results showed that STS did not increase ACC levels over the controls in mature-green (1.8 *versus* 1.4 nmol/g fresh weight, respectively) or in red-ripe tissue (9.0 *versus* 10.0 nmol/g fresh weight, respectively). They also showed that ACC levels in green, silver-containing tissue were less, or similar to ACC levels in silver-free tissue at the turning or red-ripe stage (1.8 *versus* 2.6 and 9.0 *versus* 9.2 nmol/g fresh weight, respectively). It should also be noted that the green side of tomato fruit in which the silver-free tissue was red-ripe contained over six times as much ACC (9.0 nmol/g fresh weight) as did mature green tissue not treated with silver (1.4 nmol/g fresh weight).

Ethylene Biosynthesis in Silver-Treated Attached Fruit. Although ACC levels were never greater in silver-containing tissue than in silver-free tissue, ethylene production was twice as high from silver-containing tissue than from silver-free tissue. Increased activity of the ethylene producing biosynthetic pathway in silver-containing tissue could account for this. To test this idea, AVG was used to inhibit the conversion of endogenous SAM to ACC in disks of pericarp tissue excised from silver-treated fruit. Addition of ACC would allow measurement of the ethylene forming enzyme activity.

Treatment with AVG reduced ethylene production by 94% in green, silver-containing tissue, while in silver-free tissue, ethylene production was reduced by 91% in green tissue, 83% in pink tissue, and 96% in red-ripe tissue (Table I). Although AVG caused the same level of reduction in ethylene synthesis among these tissues (around 91%), the rate of ethylene production by silver-containing tissue was always significantly higher than from silver-free tissue. The rate averaged around 4-fold higher in control and ACC treated tissue. Ethylene production from AVG treated tissue was variable. Pink, silver-free tissue produced almost the same as the silver-containing green tissue, while green tissue produced about half and red-ripe tissue produced an eighth. These data indicate that pink and silver-containing tissue had roughly comparable ACC forming activity, while green, silver-free and red-ripe tissue had less ACC forming activity.

The addition of ACC stimulated subsequent ethylene production 8.3-fold in green, silver-containing tissue, while in silver-free tissue there was a stimulation of 3.9-fold in green tissue, 2.6-fold in pink tissue, and 3.6-fold in red-ripe tissue. The greater stimulation of ethylene production by ACC in silver-containing tissue indicates that this tissue had a more active ethylene forming enzyme system than tissue free of silver. Since the red (silver-free) and green (silver-containing) sides of fruit treated asymmetrically with silver had similar concentrations of ACC, but the green side produced much more ethylene, it appears that the rate of ACC turnover must be much higher in the green side. A high turnover rate suggests increased ACC synthase activity in the silver-treated green side. These data imply that long-term treatment with silver stimulated both ACC forming activity and

Table III. *Effect of Treating Different Maturity Pericarp Disks with Silver, AVG, and ACC on the Rate of Ethylene Production 2 h after ACC Application*

Solutions Applied on			Stage of Ripeness		
Day 1	Day 2	Day 3	Mature-green	Pink	Red-ripe
			nl ethylene/g fresh wt h		
Water	Water	Water	49.4 a	120.6 a	33.8 a
Ag	Water	Water	11.0 b	46.8 b	7.5 b
Water	AVG	Water	4.3 c	15.1 c	4.0 c
Ag	AVG	Water	5.3 c	13.7 c	4.4 c
Water	AVG	ACC	16.8 b	16.6 c	9.4 b
Ag	AVG	ACC	13.0 b	14.1 c	9.4 b

ethylene production from ACC.

Ethylene and CO_2 Production by Silver-Treated Detached Fruit. Whole fruit were treated with silver through the pedicel to study the short-term effect of STS on respiration and ethylene production. This treatment caused a transient increase in ethylene and CO_2 production similar to that reported by Hobson *et al.* (8). Treatment with 10 mM STS caused an initial 50-fold stimulation of ethylene production that lasted 2 d (Fig. 2). It was followed by a swift decline to a level 5-fold higher than the control. Two mM STS had a much smaller effect. It stimulated ethylene production 5-fold for 1 d. After 3 d, both STS treatments had the same level of ethylene production. The control level of ethylene production increased after 5 d to equal both STS treatments, and surpassed both STS treatments after 7 d.

Production of CO_2 was stimulated 2.6-fold by 10 mM STS, and 1.7-fold by 2 mM STS (Fig. 2). Both increases lasted for 1 d, before declining to near control levels. Apart from the 1-d stimulation by STS, all tissue produced CO_2 at roughly the same rate.

Ethylene Biosynthesis by Silver-Treated Pericarp Disks. Excised pericarp disks from turning fruit were treated with silver or ACC ± silver 2 d after inhibiting the conversion of SAM to ACC with AVG (Table II). Silver alone stimulated ethylene production 47%, but did not significantly increase the rate of ethylene production either in the presence of AVG or added ACC. AVG caused a 83% reduction in ethylene production by silver-free tissue and a 93% reduction by silver-treated tissue. ACC caused a 3.9-fold increase in ethylene production by all tissue. This implies that silver had no direct effect on the conversion of ACC to ethylene, but did stimulate SAM conversion to ACC.

An experiment was conducted to investigate the effect of silver on ethylene synthesis after the initial 2 d wound response, as indicated by peaks in ethylene and CO_2 production, had subsided (Fig. 2). Disks were treated with ±STS on d 1, with ±AVG on d 2, and with ±ACC on d 3. Silver reduced ethylene production from mature-green tissue by 78%, from pink by 61%, and from red-ripe by 78% (Table III), while reducing CO_2 production from mature-green tissue by 34%, from pink by 36%, and from red-ripe by 33% (data not shown). AVG and ACC had no statistically significant effect on CO_2 production.

Treatment with AVG caused an additional 50% reduction in ethylene production below that of silver-treated tissue, and eliminated the significant difference in ethylene production between silver-treated and control tissue at all maturities (Table III). AVG application reduced ethylene production from mature-green control tissue by 90%, from pink by 88%, and from red-ripe by 88%. Addition of ACC stimulated ethylene production 3.1-fold by mature-green AVG treated tissue, 1.1-fold by pink, and 2.2-fold by red-ripe AVG treated tissue. AVG eliminated any significant effect of silver on ethylene production by ACC treated tissue. The observation that AVG, an inhibitor of ACC synthesis, reduced ethylene synthesis, as did silver, and that ACC promoted ethylene synthesis equally in both silver-treated and free tissues implies that short-term silver treatments reduce the biosynthesis of ACC, but have no effect on the conversion of ACC to ethylene.

Silver and Ethylene Biosynthesis. In short-term experiments, silver applied to pericarp disks did not affect conversion of ACC to ethylene, but did affect ACC synthesis. Silver either stimulated ACC synthesis when applied 2 h before sampling, or inhibited ACC synthesis when applied 3 d before sampling. If the rate of ACC conversion to ethylene had been affected by silver, then the response of the ± silver-treated tissue to AVG and to ACC would have been different from one another; however, they were the same for all tissue maturities and times of application.

During long-term exposures on the plant, silver not only stimulated SAM conversion to ACC but also stimulated the conversion of ACC to ethylene. This was shown by enhanced ethylene production by the green (silver-containing) *versus* ripening (silver-free) side and the greater stimulation in ethylene production by ACC treatment of AVG treated tissue (Table I). The stimulation of ethylene production by silver-treated pericarp disks (Table II) probably resulted from this short-term effect since ethylene measurements were taken only a few hours after silver application. In contrast, the increased rate of ethylene production in silver-containing tissue from asymmetrically treated fruit probably resulted from an induction of both the conversion of SAM to ACC and ACC to ethylene.

Effect of Silver on the Control of Ethylene Synthesis. Silver could have this effect on ethylene production either through its injurious effect as a heavy metal, which has been shown to stimulate the conversion of SAM to ACC (16), or through its effect on ethylene perception by the tissue. Lack of lycopene synthesis in silver-containing tissue showed that silver was preventing ethylene perception by the tissue (5,13). If the rate of ethylene synthesis is governed by positive and negative feedback from endogenous ethylene levels (18), then inhibiting ethylene perception could either stimulate or inhibit the rate of ethylene synthesis.

Autoinhibition of ethylene synthesis has been reported in citrus peel (11), etiolated pea stems (14), banana fruit (17), and nonripening stages of figs (19). The inhibitory effect of ethylene was rapid and reversible upon removal of ethylene (11, 14, 17, 19). In wounded etiolated pea stems and wounded flavedo tissue, ethylene production was stimulated many-fold by a decrease in endogenous ethylene (11, 14). Silver may have blocked the negative feedback of endogenous ethylene on ethylene synthesis in these tissues, inhibited the perception of ethylene by the tissue, and thereby promoted the observed increase in ethylene production (Table II).

Ripening climacteric tissue have a positive feedback system in which internal ethylene levels promote ethylene synthesis (18). In these tissues, silver may be effectively reducing the perceived internal level of ethylene and thereby reducing ethylene synthesis. Additional research is needed to distinguish between the possible modes of action of silver in tomato tissue.

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