

# Inhibition of Ethylene Synthesis in Tomato Plants Subjected to Anaerobic Root Stress<sup>1</sup>

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## ABSTRACT

Enhanced ethylene production and leaf epinasty are characteristic responses of tomato (*Lycopersicon esculentum* Mill.) to waterlogging. It has been proposed (Bradford, Yang 1980 Plant Physiol 65: 322–326) that this results from the synthesis of the immediate precursor of ethylene, 1-aminocyclopropane-1-carboxylic acid (ACC), in the waterlogged roots, its export in the transpiration stream to the shoot, and its rapid conversion to ethylene. Inhibitors of the ethylene biosynthetic pathway are available for further testing of this ACC transport hypothesis: aminoxyacetic acid (AOA) or aminoethoxyvinylglycine (AVG) block the synthesis of ACC, whereas  $\text{Co}^{2+}$  prevents its conversion to ethylene. AOA and AVG, supplied in the nutrient solution, were found to inhibit the synthesis and export of ACC from anaerobic roots, whereas  $\text{Co}^{2+}$  had no effect, as predicted from their respective sites of action. Transport of the inhibitors to the shoot was demonstrated by their ability to block wound ethylene synthesis in excised petioles. All three inhibitors reduced petiolar ethylene production and epinasty in anaerobically stressed tomato plants. With AOA and AVG, this was due to the prevention of ACC import from the roots as well as inhibition of ACC synthesis in the petioles. With  $\text{Co}^{2+}$ , conversion of both root- and petiole-synthesized ACC to ethylene was blocked. Collectively, these data support the hypothesis that the export of ACC from low  $\text{O}_2$  roots to the shoot is an important factor in the ethylene physiology of waterlogged tomato plants.

Ethylene is an important endogenous regulator of plant responses to waterlogging (7, 14). Under the low  $\text{O}_2$  conditions in the soil during flooding, tomato roots synthesize ACC,<sup>3</sup> the immediate precursor of ethylene, and transport it in the xylem to the shoot, where it is rapidly converted to ethylene (8, 9). This increase in the ethylene content of the shoot tissues results in petiole epinasty, aerenchyma formation, and other anatomical and morphological responses associated with waterlogging (6, 11, 14).

The sites of inhibition in the biosynthetic pathway of ethylene are now known for several inhibitors. Application of these inhibitors allows further tests of the role of root-synthesized ACC in shoot responses to waterlogging. AOA and AVG effectively prevent the conversion of SAM to ACC, both *in vivo* (1, 22, 23) and with isolated ACC synthase (4, 21), but do not interfere with the

conversion of ACC to ethylene.  $\text{Co}^{2+}$  on the other hand, has no effect on ACC synthesis but inhibits the formation of ethylene from ACC (23). These compounds, therefore, permit inhibition of ethylene biosynthesis at specific steps in the pathway (see 18, 19, for reviews). In waterlogged plants, the locations of stress-induced ACC synthesis and its conversion to ethylene are separated spatially, with the formation of ACC from SAM occurring in the roots and conversion of ACC to ethylene occurring in the shoot. Thus, the effects of application of AOA, AVG, or  $\text{Co}^{2+}$  to anaerobic roots should reflect their differing sites of action. In this study, these inhibitors were used to further characterize the role of root-synthesized ACC in the responses of tomato plants to root anaerobic stress.

## MATERIALS AND METHODS

**Plant Material.** Tomato plants (*Lycopersicon esculentum* Mill.) of two cultivars, VFN8 and UC82, were germinated in vermiculite for 12 to 14 d. The seedlings were then transplanted into 1.75-l plastic boxes containing full-strength nutrient solution [ $\text{K}^+$ , 4 mM;  $\text{NO}_3^-$ , 12 mM;  $\text{Ca}^{2+}$ , 5 mM;  $\text{Mg}^{2+}$ ,  $\text{SO}_4^{2-}$ ,  $\text{PO}_4^{3-}$ , 2 mM; Fe-chelate (sodium ferric ethylenediamine di-(*o*-hydroxyphenylacetate)), 0.04  $\mu\text{M}$ ; micronutrients as for full-strength Hoagland solution]. Two seedlings were planted per box. The solutions were continuously aerated at a rate of 250 ml  $\text{min}^{-1}$ . The pH was initially adjusted to 6.0, and the solutions were replenished with distilled  $\text{H}_2\text{O}$  as needed. Two weeks after transplanting (five to seven leaf stage), the nutrient solutions were replaced and stress treatments were begun on the next day. The environmental conditions in the growth chamber were: light, 500  $\mu\text{E m}^{-2} \text{s}^{-1}$  PAR; temperature, 27°C; photoperiod, 16 h; RH, 40%.

**Inhibitor and Stress Treatments.** Solutions of AOA, AVG, or  $\text{CoCl}_2$  were added to the nutrient solutions to give the final concentrations indicated. Due to the large quantities of the inhibitors required, most experiments used AOA rather than AVG. AOA was purchased from Sigma, and AVG was a gift from J. P. Scannel (Hoffman-LaRoche). After 4 h of aerobic uptake, root anaerobiosis was imposed by bubbling  $\text{N}_2$  through the solutions at 250 ml  $\text{min}^{-1}$ . Measurements with an oxygen electrode indicated that deoxygenation was complete after 1 h. Twenty-four hours after the start of the anaerobic treatment, both plants from a box were sampled for ethylene and epinasty measurements and xylem sap was collected from one plant, as described below. Three or four replicate boxes were used for each treatment.

**Epinasty, Ethylene, and ACC Measurements.** Epinasty was measured with a transparent protractor as the adaxial angle between the third oldest petiole and the stem. The increase in petiole angle over 24 h is plotted in the figures. Ethylene production from 3-cm proximal petiole sections was measured by placing the sections in 4.1 ml test tubes fitted with serum caps and determining the ethylene content of the air in the tube by GC after 0.5 h (9). Xylem sap was collected and analyzed for ACC as described

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<sup>3</sup> Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; AOA, aminoxyacetic acid; AVG, aminoethoxyvinylglycine [L-2-amino-4-(2-aminoethoxy)-*trans*-3-butenic acid]; NAA, naphthyl-1-acetic acid; SAM, S-adenosylmethionine.

previously (9), except that a suction of 0.5 rather than 0.9 bar was applied during sap collection. (HCl addition to the collected sap to stabilize the ACC was found to be unnecessary and, therefore, was omitted in these experiments.) The data are expressed as a flux rate ( $\text{nmol h}^{-1}$ ) by multiplying the ACC concentration in the sap by the rate of sap collection. Root ACC content was determined as before (9), except that the extract was directly used for ACC assay without passing through an ion exchange column.

The data were analyzed by analysis of variance procedures. Error bars indicating  $\pm 1$  SE are shown in the figures as an indication of experimental variance. All experiments except that shown in Table I were performed at least twice with similar results.

## RESULTS

**Inhibitor Effects on Excised Petioles.** To ensure that AOA and  $\text{Co}^{2+}$  act to inhibit ethylene synthesis in tomato as they do in other plant systems, excised petioles were pretreated in various concentrations of the inhibitors for 3 h, then exposed to either IAA or ACC (Fig. 1). The stimulation of ethylene production by IAA was inhibited 80% by  $10 \mu\text{M}$  AOA and completely blocked at  $100 \mu\text{M}$ . Conversion of ACC to ethylene, however, was unaffected at the lower concentrations and perhaps slightly reduced at  $100 \mu\text{M}$  AOA. These results are expected since IAA stimulates ethylene production by inducing the synthesis of ACC synthase (23), which is subject to inhibition by AOA or AVG (4, 21). The conversion of ACC to ethylene is not affected by inhibitors of ACC synthase (1, 15, 22). The present observations are in agreement with the report of Amrhein and Schneebeck (2), who found that AOA was effective in preventing NAA-induced ethylene production and epinasty in tomato plants but was ineffective in blocking ACC-dependent ethylene production and epinasty.  $\text{Co}^{2+}$  inhibited both

IAA- and ACC-dependent ethylene production (Fig. 1). This is consistent with the proposal that  $\text{Co}^{2+}$  blocks the conversion of ACC to ethylene (23). The relatively small stimulation of ethylene production by IAA in these experiments (Fig. 1; note difference in scales) is probably due to the short 3-h exposure to the auxin and to poor penetration into the petioles, as a much greater effect was seen in 3 h when IAA was supplied to petioles via the transpiration stream (8). Similarly, the lack of complete inhibition of IAA-stimulated ethylene production by  $\text{Co}^{2+}$  (Fig. 1) could be due to poor uptake and uneven distribution within the sections of  $\text{Co}^{2+}$  relative to IAA. It is clear, however, that the inhibitors are effective in tomato petioles and act in the predicted fashion.

**Effects of AOA and AVG Supplied to the Roots.** Since AOA prevents the synthesis of ACC, feeding AOA to tomato roots should block the appearance of ACC in the sap of stem xylem during flooding or root anaerobiosis. If export of ACC from roots is responsible for elevated ethylene synthesis and epinasty in the petioles, these responses should also be prevented when AOA is supplied to the roots. The presence of AOA in the nutrient solution greatly reduced the ACC transported in the xylem stream following a 24-h anaerobic treatment (Fig. 2). Concomitant with the decline in ACC transport, ethylene production by the petioles decreased and petiole epinasty was inhibited (Fig. 2). Similar results were obtained with a second tomato variety, UC82 (data not shown). As expected, if the shoots of the anaerobic, AOA-treated plants were excised and supplied with ACC via the transpiration stream, they rapidly became epinastic (data not shown).

In contrast to the appearance of the plants receiving the anaerobic AOA treatments, those supplied with AOA under aerobic conditions showed marked signs of toxicity. Severe wilting of VFN8 shoots occurred if the aerobic roots received 30 or  $100 \mu\text{M}$  AOA, precluding measurements of epinasty (Fig. 2). No xylem

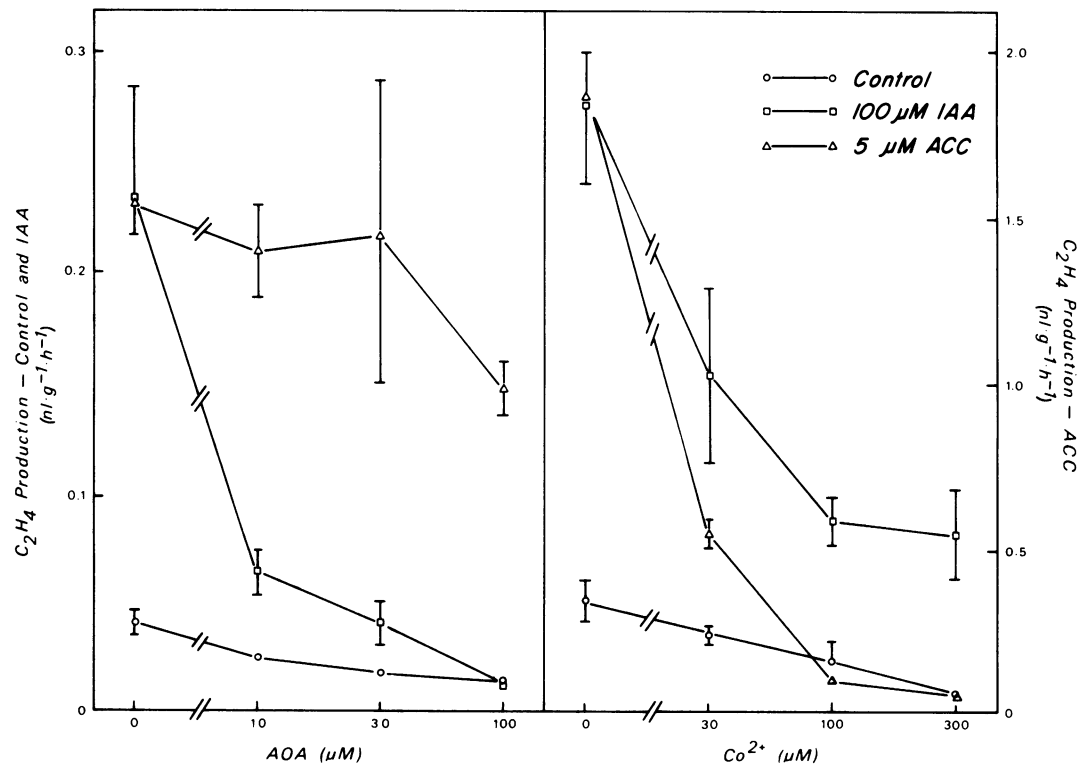


FIG. 1. Effects of AOA and  $\text{Co}^{2+}$  on endogenous, IAA-, and ACC-dependent ethylene production in excised tomato petioles. Proximal 3-cm sections, from third or fourth leaves of VFN8 plants grown in a greenhouse, were floated for 3 h in aerated solutions (50 ml/15 sections) containing 2% (w/v) sucrose,  $5 \mu\text{g ml}^{-1}$  chloramphenicol, 50 mM Mes buffer (pH 6.1), and varying concentrations of inhibitors. Sections were then transferred to similar solutions (25 ml/five sections) which also contained either  $5 \mu\text{M}$  ACC or  $100 \mu\text{M}$  IAA for an additional 3 h. Individual sections were then enclosed in test tubes and ethylene produced was determined after 1 h. Data are plotted on different scales (control and IAA on left, ACC on right) due to marked elevation of ethylene production when ACC was fed. Error bars indicate  $\pm 1$  SE in this and all subsequent figures.

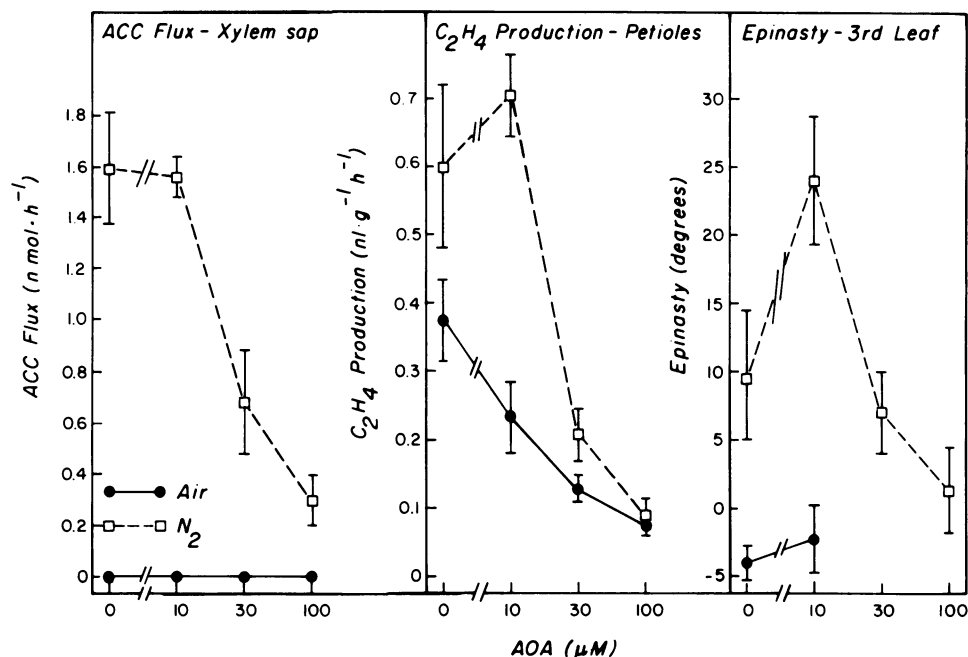


FIG. 2. ACC flux in stem xylem, petiolar ethylene production, and leaf epinasty of VFN8 plants as affected by root aeration and AOA concentration. Samples or measurements were taken after 24 h of air or N<sub>2</sub> treatment of roots. Epinasty at 30 and 100 μM AOA in the aerobic treatment was not measurable due to wilting (see "Results").

Table I. Effects of AVG on ACC Synthesis, Petiolar Ethylene Production, and Epinasty of VFN8 Tomato Plants Subjected to Anaerobic Root Stress

AVG was supplied to the roots in the nutrient solution, and measurements were taken 24 h after the start of the anaerobic root treatment.

AVG	Aerating Gas	Epinasty	Ethylene Production	ACC Flux	Root ACC Content
μM		degrees	nl g <sup>-1</sup> h <sup>-1</sup>	nmol h <sup>-1</sup>	nmol g <sup>-1</sup>
0	Air	-2.5 a <sup>a</sup>	0.34 a	0.05 a	0.14 a
0	N <sub>2</sub>	10.7 b	0.50 b	3.6 b	12.4 b
10	Air	-2.3 a	0.04 c	0.04 a	0.10 a
10	N <sub>2</sub>	-0.7 a	0.07 c	0.11 a	0.28 a

<sup>a</sup> Mean values in the same column followed by the same letter are not significantly different at P < 0.05.

sap could be collected from the roots, even with the application of 0.5-bar suction. When the wilted shoots were excised and placed in vials of 5 μM ACC solution, they quickly rehydrated and eventually became epinastic. The major toxic effect, therefore, seems to be a severe reduction in root permeability to water. The root tips were discolored, an effect not seen in the anaerobic roots regardless of whether AOA was present. In the cultivar UC82, root permeability was reduced by AOA, but less severely than in VFN8, and wilting was not observed. Instead, 30 and 100 μM AOA caused epinasty (data not shown). This might have been caused by a slight loss of turgidity and subsequent drooping of the petioles, but pressure bomb measurements failed to detect a difference in water potential between treatments.

Since AOA is a general inhibitor of pyridoxal phosphate-dependent enzymes (12), a toxic effect at high concentrations is not unexpected. Another inhibitor of ACC formation, AVG, can also have toxic effects at concentrations above 100 μM (17), but is effective in inhibiting ethylene production in vegetative tissues at concentrations as low as 10 μM (22). When AVG was fed to the anaerobic roots of VFN8 plants, 10 μM (the lowest concentration applied) completely blocked ACC flux in the xylem, petiolar ethylene production, and epinasty (Table I). Concentrations up to 100 μM had no additional effect in anaerobic plants, but slight

wilting was observed at 100 μM in the aerobic plants. Thus, there is a wider separation between effective and toxic concentrations of AVG than of AOA, as would be expected from the generally more specific action of AVG on ethylene production (16, 21). The wilting observed in aerobic plants at high AVG concentrations also confirms that both AVG and AOA can have nonspecific effects on root metabolism. Under anaerobic conditions, the inhibitors are much less toxic. It is unlikely that the difference in toxicity is due to less uptake of the inhibitor during anaerobiosis, because the inhibition of wound ethylene production by AOA was not greater in aerobic plants than in anaerobic plants (see below). Anaerobiosis caused increases in both ACC flux and root ACC content of similar magnitudes relative to the aerobic values (Table I). AVG effectively blocked the increases.

Wounding stimulates ethylene production after a 20- to 30-min lag period by inducing synthesis of ACC from SAM and consequently is sensitive to inhibition by AVG (24). Wound ethylene synthesis reflects the activity of ACC synthase within the petiole itself, in contrast to ethylene production from ACC imported from roots, which is insensitive to AOA or AVG. Increasing concentrations of AOA applied to roots progressively inhibit the production of wound ethylene in excised petioles (Fig. 3), indicating that the inhibitor has been transported to the petioles. In anaerobic plants, 30 μM was completely effective, but 100 μM was required to eliminate the response in aerobic plants. As mentioned above, this indicates that uptake and transport of AOA was not prevented by anaerobic root stress. Transport of AVG to petioles is indicated in Table I and by inhibition of wound ethylene synthesis (data not shown).

**Effects of Co<sup>2+</sup> Supplied to the Roots.** As Co<sup>2+</sup> does not interfere with the synthesis of ACC, supplying Co<sup>2+</sup> to anaerobic roots should not affect the ACC flux in the xylem. Up to 30 μM, this was the case for both VFN8 (Fig. 4) and UC82 (data not shown). At 100 μM, ACC flux was somewhat inhibited but was still quite high. Ethylene production and epinasty declined progressively as the concentration of Co<sup>2+</sup> increased, regardless of the ACC flux rate (Fig. 4), indicating that the inhibitor was transported to the petioles. Ethylene production was also inhibited in the aerobic plants (Fig. 4). Transport of Co<sup>2+</sup> to the shoot was

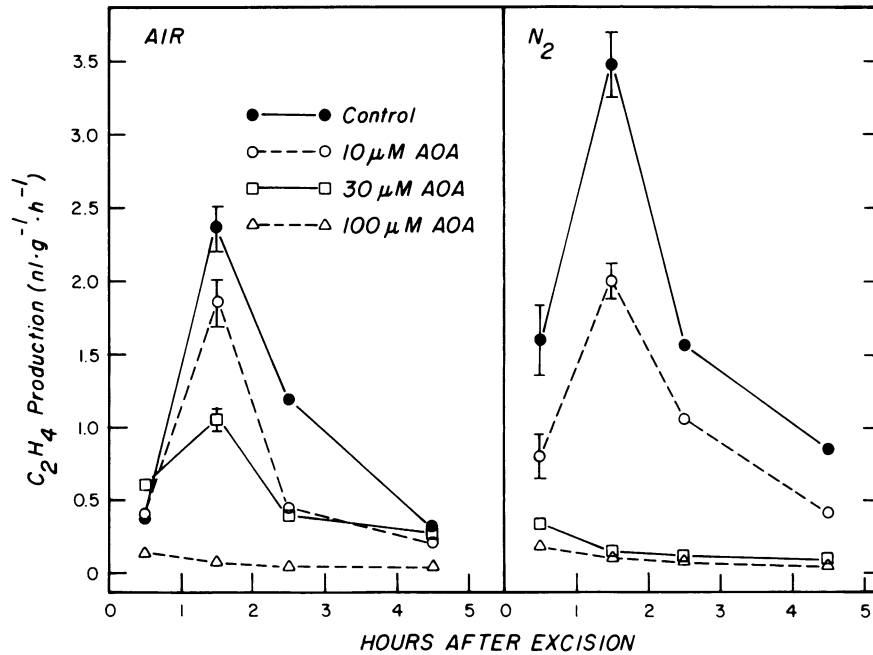


FIG. 3. Effects of AOA supplied for 28 h to roots of UC82 plants on wound ethylene synthesis by petioles following excision. 'Air' and 'N<sub>2</sub>' indicate treatment applied to roots for 24 h prior to ethylene measurement. Initial 0.5-h ethylene determination was followed by accumulation periods of 1, 1, and 2 h.

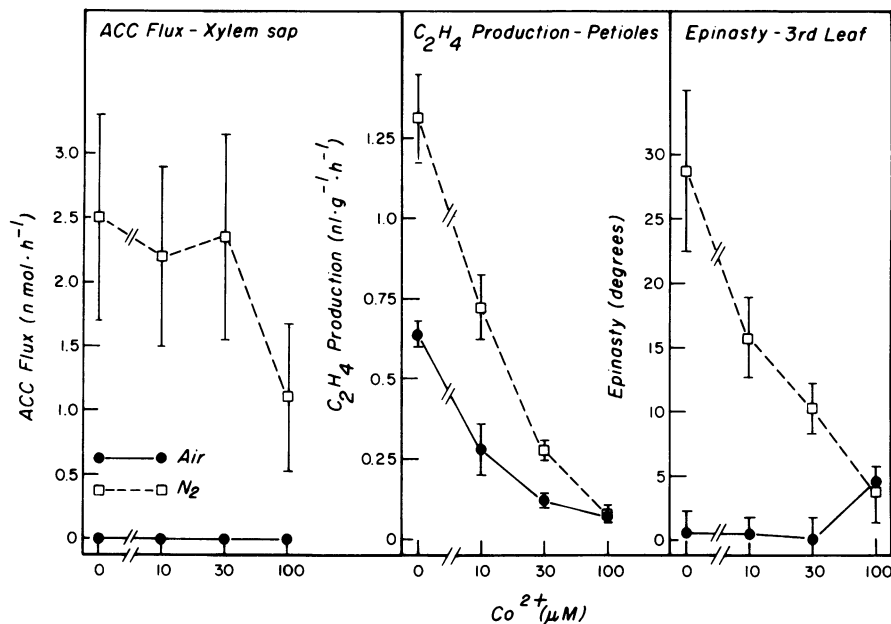


FIG. 4. Xylem ACC flux, petiolar ethylene production, and epinasty of VFN8 plants as affected by root aeration and Co<sup>2+</sup> concentration. Other conditions are as in Figure 2.

also indicated by the inhibition of wound ethylene production in excised petioles of both aerobic and anaerobic plants (Fig. 5). No toxic effects were apparent in either aerobic or anaerobic treatments even at the highest Co<sup>2+</sup> concentration.

## DISCUSSION

The hypothesis (8, 9) that ACC transport from low O<sub>2</sub> roots is responsible for the elevated ethylene production and epinasty in the shoots received further support from the present work. Since ACC synthesis and its subsequent conversion to ethylene occur in separate plant organs in this situation, it was predicted that different inhibitors of ethylene biosynthesis would have contrast-

ing effects dependent on their sites of action. In agreement with results from other systems (13, 15, 21-23), AOA and AVG inhibited the synthesis of ACC but had little effect on the conversion of ACC to ethylene (Fig. 1, Table I). Co<sup>2+</sup>, on the other hand, prevented the conversion of ACC to ethylene with little effect on the synthesis of ACC (Figs. 1 and 4). When these inhibitors were applied to tomato roots, AOA and AVG prevented the anaerobic stimulation of ACC export, whereas Co<sup>2+</sup> had no effect, as predicted (Figs. 2 and 4; Table I). Thus, within both the petioles and the roots the inhibitors act as would be expected from their respective sites of inhibition of the ethylene biosynthetic pathway.

If the inhibitors were not transported from the roots to the shoot, the consequences for shoot ethylene synthesis would be

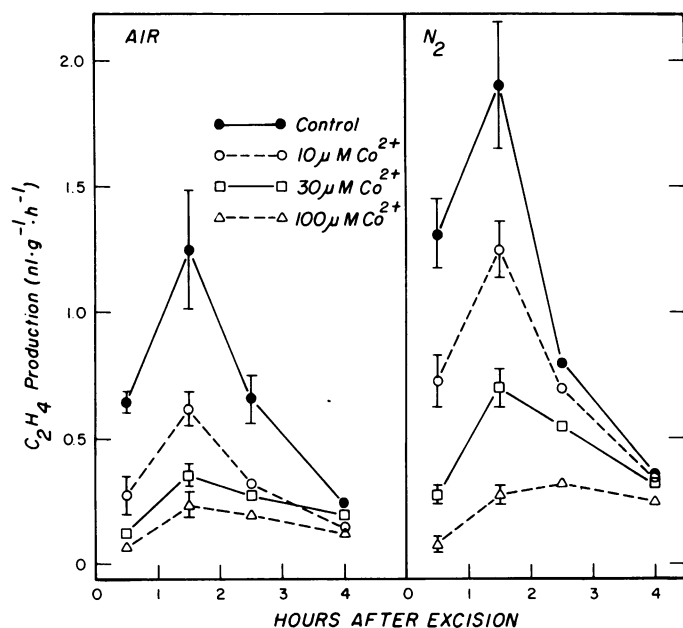


FIG. 5. Effects of  $\text{Co}^{2+}$  supplied to roots of VFN8 plants on wound ethylene synthesis by petioles following excision. 'Air' and ' $\text{N}_2$ ' indicate treatment applied to roots for 24 h prior to ethylene measurement. Initial 0.5-h ethylene determination was followed by accumulation periods of 1, 1, and 1.5 h.

straightforward: AOA would reduce ethylene synthesis by blocking ACC export, whereas  $\text{Co}^{2+}$  would have no effect. However, the patterns of wound ethylene production clearly indicate that both inhibitors were carried into the petioles (Fig. 3 and Ref. 5). In the case of  $\text{Co}^{2+}$ , this caused inhibition of ethylene production even though ACC flux remained high (Fig. 4). With AOA, ethylene production declined due to the reduction in ACC flux and the simultaneous inhibition of endogenous ACC synthesis in the petioles. A number of attempts were made to apply the inhibitors only to the shoot as a further test of the hypothesis. AOA present only in the shoot should inhibit ACC synthesis in the petioles, but not the synthesis of ethylene from ACC transported from the roots.  $\text{Co}^{2+}$  would inhibit ethylene production from both sources. However, experiments with spray applications of the inhibitors were inconclusive due to problems of foliage uptake and of transport to the roots (5).

Both  $\text{Co}^{2+}$  and low  $\text{O}_2$  are known to prevent the conversion of ACC to ethylene (1, 23). If the effect of anaerobiosis in tomato roots simply is to block this final step, then high concentrations of  $\text{Co}^{2+}$  applied to aerobic roots should bring about an effect similar to anaerobiosis. Namely, in the presence of  $\text{Co}^{2+}$ , ACC should appear in the xylem at a rate reflecting the normal endogenous rate of ACC synthesis in the aerobic roots. However, ACC is not detected in the xylem sap of aerobic plants regardless of whether  $\text{Co}^{2+}$  is present (Fig. 4). This indicates that the rate of ACC formation in aerobic roots is quite low, in agreement with *in situ* rates of root ethylene production (6). These data are consistent with the conclusion that anaerobiosis not only blocks the conversion of ACC to ethylene, but also stimulates the formation of ACC in the roots (8, 9). Physical, chemical, or water stresses apparently promote ethylene production by inducing the synthesis of ACC synthase (3, 24). Flooding stress may also induce the synthesis of this enzyme. It is pertinent to note that in an IAA-dependent ethylene production system, ACC-synthesizing activity can be induced under oxygen levels which are too low to allow

the conversion of ACC to ethylene (10, 20). Our preliminary attempts to isolate ACC synthase from anaerobic tomato roots have been unsuccessful, and others have experienced similar difficulties in extracting the enzyme from other vegetative tissues (13, 21). Confirmation of this hypothesis, therefore, awaits the perfection of techniques for extracting and assaying ACC synthase from tomato roots.

In conjunction with previous results (8, 9), the data presented here support the hypothesis that ACC export from low  $\text{O}_2$  roots plays an important role in the ethylene physiology of waterlogged tomato plants. This is of interest because a precursor of a plant growth regulator (ACC) is synthesized in one plant organ, transported to a site of action, and converted into an active form (ethylene). Such mechanisms of interorgan communication contribute to the coordination of whole plant responses to environmental stress.

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