

# Inhibitory Action of Auxin on Root Elongation Not Mediated by Ethylene

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## ABSTRACT

The inhibitory effects of indole-3-acetic acid (IAA) and 1-aminocyclopropane-1-carboxylic acid (ACC) on elongation growth of pea (*Pisum sativum* L.) seedling roots were investigated in relation to the effects of these compounds on ethylene production by the root tips. When added to the growth solution both compounds caused a progressively increasing inhibition of growth within the concentration range of 0.01 to 1 micromolar. However, only ACC increased ethylene production in root tips excised from the treated seedlings after 24 hours. High auxin concentrations caused a transitory increase of ethylene production during a few hours in the beginning of the treatment period, but even in 1 micromolar IAA this increase was too low to have any appreciable effect on growth. ACC, but not IAA, caused growth curvatures, typical of ethylene treatment, in the root tips. IAA caused conspicuous swelling of the root tips while ACC did not. Cobalt and silver ions reversed the growth inhibitory effects induced by ACC but did not counteract the inhibition of elongation or swelling caused by IAA. The growth effects caused by the ACC treatments were obviously due to ethylene production. We found no evidence to indicate that the growth inhibition or swelling caused by IAA is mediated by ethylene. It is concluded that the inhibitory action of IAA on root growth is caused by this auxin *per se*.

A wealth of evidence indicates that the endogenous auxin, IAA, plays an important role in the regulation of root growth. IAA moves into the root tips from the shoots (29) or, in the case of seedlings, from the endosperm (22). Growing root tips of intact plants contain conspicuously high IAA concentrations (15, 24). Although low auxin concentrations applied to ambient growth solution may stimulate elongation growth in roots if ethylene is not present in inhibitory concentrations (23), the typical response of roots to exogenous auxin is inhibited elongation. Åberg (3) reported that concentrations down to 1 nM IAA in the solution surrounding the roots of wheat and flax seedlings inhibited root growth.

Ethylene, another regulator of root growth, has stimulatory as well as inhibitory effects on elongation. Growing root tips normally produce ethylene, and low ethylene concentrations may stimulate root growth (19). The more commonly demonstrated effect of applied ethylene is the inhibition of root elongation (1). Moreover, endogenously produced ethylene can easily reach inhibitory concentrations. Mulkey *et al.* (23) found that inhibitors of ethylene biosynthesis applied to maize roots stimulated root elongation by about 50% compared with control roots, and light increased ethylene production to clearly inhibitory levels (13). Impaired diffusion of gas from

the roots, *e.g.*, associated with flooding or hydroponic growing conditions, may also cause ethylene to increase to inhibitory levels within roots (18).

Auxin treatments at concentrations higher than 1  $\mu\text{M}$  increase the production of ethylene from roots as well as from most other plant parts (1, 2, 21). Chadwick and Burg (10) advanced the hypothesis that the inhibitory action of auxin on root growth is mediated by ethylene. Although other investigators (4, 8, 12, 26) could find little or no support for this hypothesis, it seems to have been widely accepted. It was strongly advocated by Lieberman (21) and recently discussed in relation to the supposed role of IAA in root gravitropism by Pickard (25). Mulkey *et al.* (23) used this hypothesis to explain their results regarding the response of maize roots to IAA in the presence of ethylene synthesis inhibitors, although their finding that IAA also inhibited growth at concentrations of 0.1  $\mu\text{M}$  and higher in the presence of these inhibitors is not consistent with the hypothesis. Stenlid (27) found that the inhibition of root elongation caused by auxins and cytokinins could be counteracted by various compounds that decrease ethylene production and concluded that the inhibitory action of these regulators is related to the synthesis and action of ethylene.

We have investigated whether growth-inhibitory auxin concentrations added to the growth solution of intact pea seedlings exert their effect by increased ethylene production or some other mechanism. Our approach was to compare the effects of IAA on root growth and ethylene production to those of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC)<sup>1</sup>. We have already shown that application of ACC to the growth solution increased ethylene production by pea seedling roots and inhibited elongation (13). The inhibition caused by ACC was mediated by the increase in ethylene production. If the inhibitory effect of IAA is mediated by ethylene, this compound should be expected to stimulate ethylene production to the same extent as ACC at a concentration giving the same degree of inhibition as IAA. Furthermore, earlier work has shown that the conversion of ACC into ethylene is inhibited by cobalt ions (20), and the action of ethylene is blocked by silver ions (6). If these inhibitors are effective in reversing the inhibitory effect of ACC on root elongation they should also reverse the effects of other agents that cause inhibition by increasing ethylene production.

<sup>1</sup> Abbreviation: ACC, 1-aminocyclopropane-1-carboxylic acid.

## MATERIALS AND METHODS

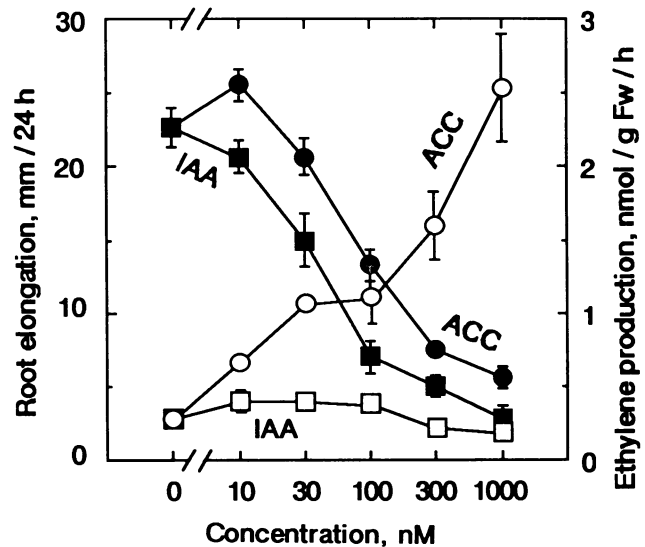
Seeds of *Pisum sativum* L., cv Weibulls Marma, were imbibed in tap water for 6 h and germinated for about 45 h in moist vermiculite in the dark at 24°C. Seedlings with 35- to 40-mm long roots were selected, measured under green safelight and placed on styrofoam holders in pots with one litre of well-aerated solution, as described earlier (13). Ten seedlings were grown in each pot in the dark for 24 or 48 h at 24°C and a RH of about 50%. The growth solution contained 1 mM KPO<sub>4</sub> buffer, pH 6.0, 1 mM Ca(NO<sub>3</sub>)<sub>2</sub> (or 1 mM CaCl<sub>2</sub> as specified) and 1 μM H<sub>3</sub>BO<sub>3</sub>. In the treatments, IAA, ACC, CoCl<sub>2</sub> or Ag(S<sub>2</sub>O<sub>3</sub>)<sub>2</sub><sup>3-</sup> (prepared according to Veen [30]) were added to this solution alone or in combinations as indicated.

Increase in root length was usually measured after 24 h. Ethylene production was measured in root tips excised after treatment for 24 h. Five root tips, all 10-mm long except for in one experiment, where they were 30-mm long, were placed in a 5.5 mL test tube on a filter-paper strip moistened with the solution in which the roots had grown. The tubes were sealed with rubber serum stoppers and stored in a dark room for 2 h. Gas samples (1.0 mL) were withdrawn with a syringe and injected in a Shimadzu GC-15A gas chromatograph equipped with a packed alumina (60/80 mesh) column (1.6 m × 2.6 mm) and a flame ionization detector. Carrier gas (N<sub>2</sub>) flow was 42 mL min<sup>-1</sup>, and injector, column and detector temperatures were 120°C, 75°C, and 150°C, respectively. Under these conditions, the limit of sensitivity was 1 pmol ethylene/mL. The root tips were weighed, and the fresh weight was used to calculate the rate of ethylene production and to measure swelling. The ethylene measurements were made in duplicates for each treatment, and the experiments were repeated at least twice.

## RESULTS

Root elongation was inhibited by IAA and ACC in a concentration-dependent manner (Fig. 1). However root tips treated with IAA or ACC looked different. In the IAA treatments the roots grew straight and showed strict positive gravitropism. In addition swelling of the root tips was more pronounced in IAA than in ACC (Table I). In ACC the root tips exhibited diagravitropism. After exposure to the two highest concentrations (0.3 and 1 μM ACC) they bent to an almost horizontal direction, as described earlier for ethylene and ACC treatments (13, 14). No appreciable change in the degree of inhibition occurred during the first day after treatment (Fig. 2). Later a recovery of growth was observed as also reported by Burström (9).

Ethylene production, as measured in excised root tips after treatment of the intact seedlings for 24 h, was increased at most 25% by the IAA treatments, whereas ACC caused a manifold increase (Fig. 1). A number of other experiments with other auxins such as indolebutyric acid and 2,4-D gave similar results (data not shown). Ethylene production was lower when 30 mm long tips were used (Table II), indicating that mature root tissues produced less ethylene than growing root tips. A similar result was obtained when ethylene pro-



**Figure 1.** Effect of IAA (□,■) or ACC (○,●) on the ethylene production (open symbols) and the root elongation (filled symbols) of pea seedlings. The seedlings were grown in a well aerated phosphate buffer solution with boron and calcium [as Ca(NO<sub>3</sub>)<sub>2</sub> or CaCl<sub>2</sub>] plus growth regulators as indicated. Elongation, ethylene production and weight of the root tips were measured after 24 h. Each treatment of 10 seedlings was repeated at least three times. Values are means ± SE.

**Table I.** Effect of IAA and ACC on Swelling of Pea Root Tips, Measured as Fresh Weight of 10-mm Long Root Tips

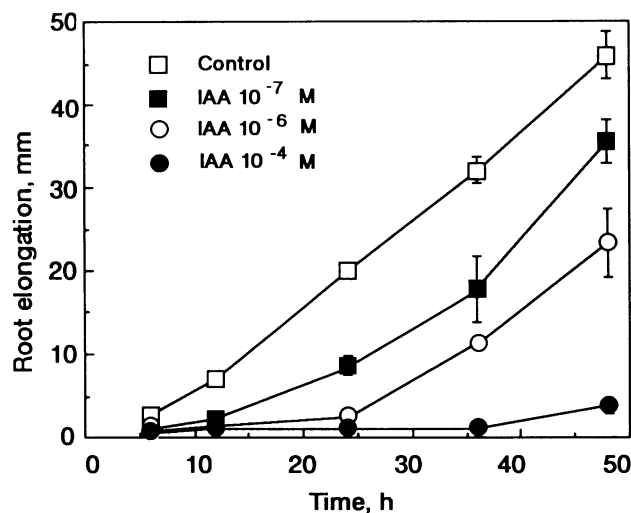
Sets of 10 seedlings were grown for 24 h in the dark in a well aerated phosphate buffer solution with boron and calcium [as Ca(NO<sub>3</sub>)<sub>2</sub> or CaCl<sub>2</sub>] plus growth regulators as indicated. The root tips were excised and weighed. Values for fresh weight are means of at least three experiments ± SE.

Concentration	IAA	ACC
nM	mg · (root tip) <sup>-1</sup>	
0	6.5 ± 0.2	6.5 ± 0.2
10	7.5 ± 0.3	5.9 ± 0.4
30	8.0 ± 0.2	5.4 ± 0.4
100	11.2 ± 0.4	7.0 ± 0.3
300	13.9 ± 0.9	8.9 ± 1.1
1000	12.0 ± 0.5	10.9 ± 0.2

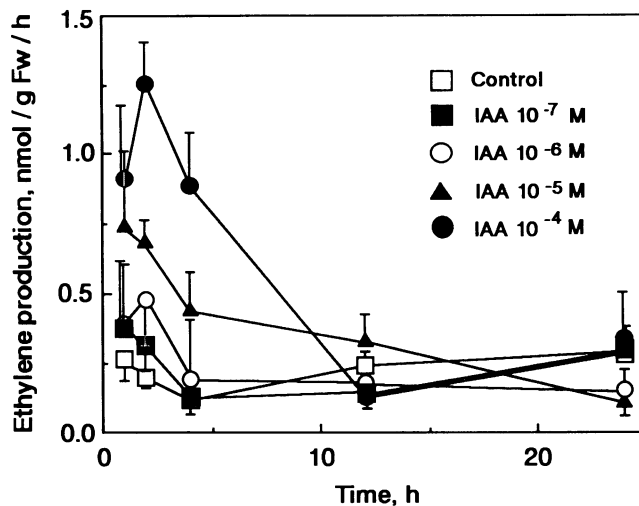
duction in 10 mm long root tips was directly compared to production in excised, older parts of the root (data not shown).

The unexpected decrease in ethylene production caused by the two highest IAA concentrations (Fig. 1) prompted us to investigate the time course of ethylene release in the presence of IAA and also to include higher auxin concentrations (10 and 100 μM) known to cause an appreciable increase in ethylene production (10). This experiment showed that the increase in ethylene was transitory in all auxin concentrations tested (Fig. 3). In 1 μM IAA ethylene production was at or below the control value during most of the 24 h growth period.

Effects of the most active concentrations of silver and cobaltous ions on root elongation are shown in Figure 4. Both treatments counteracted the inhibitory effect of ACC but did not affect the inhibition caused by IAA. Similarly the swelling



**Figure 2.** Effect of IAA on time course of root elongation during 48 h. Pea seedlings were grown as described in Figure 1 for 48 h with IAA added to the solution as indicated. Sets of 10 seedlings were removed and the length of their roots was measured after 6, 12, 24, 36, and 48 h. Values are means of two replicates  $\pm$  SE.



**Figure 3.** Effect of IAA on time course of ethylene production in root tips during 24 h. Pea seedlings were grown as described in Figure 1. Ten-mm long root tips were excised after 1, 2, 4, 12, and 24 h and their ethylene production was measured as described in Table II. Values are means of four replicates  $\pm$  SE.

**Table II.** Effects of IAA and ACC on Ethylene Production by 10- or 30-mm Long Root Tips of Pea Seedlings

Sets of ten seedlings were grown as described in Table I in the absence of growth regulator or in the presence of either 0.1  $\mu$ M IAA or 0.1  $\mu$ M ACC. Five root tips, 10 or 30 mm long, were excised after 24 h and placed on a moistened filter paper in a sealed test tube. After 2 h incubation in the dark the ethylene production was measured. Values are means of at least four replicates  $\pm$  SE.

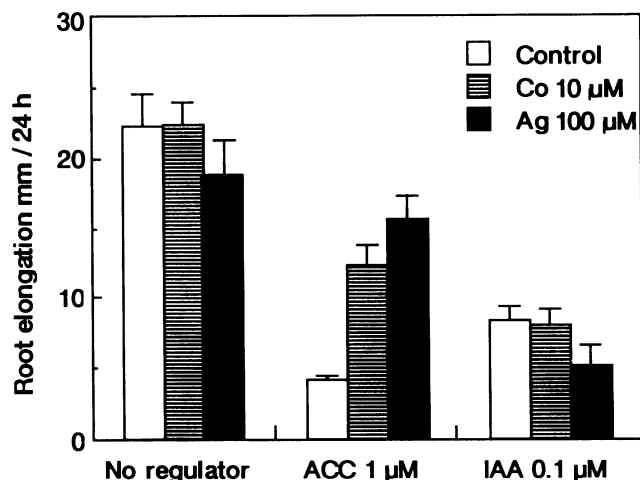
Treatment	Ethylene Production	
	10-mm root tip	30-mm root tip
	<i>pmol · g Fw<sup>-1</sup> · h<sup>-1</sup></i>	
Control	280 $\pm$ 27	171 $\pm$ 39
IAA, 0.1 $\mu$ M	374 $\pm$ 35	158 $\pm$ 49
ACC, 0.1 $\mu$ M	1116 $\pm$ 205	562 $\pm$ 118

of the root tips (Table III) and curvatures (data not shown) caused by ACC were reversed by these agents, whereas the swelling caused by IAA (Table III) was not affected. Ethylene production was increased by the silver treatment but decreased by the treatment with cobaltous ions (Table IV).

## DISCUSSION

Our results confirm the conclusion of a number of investigators (4, 8, 12), that the inhibition of root elongation caused by the exogenous application of auxin is not mediated by auxin-induced ethylene synthesis. Although complex interactions may occur between auxin and ethylene in plant tissues (1, 21) our evidence is that IAA and ethylene inhibit root elongation by separate mechanisms independently of each other.

The experiments with ACC show that increased ethylene production by roots caused an inhibition of root elongation. However, to obtain an appreciable degree of inhibition, ethylene production had to be increased 5-fold (Fig. 1). This



**Figure 4.** Effect of cobaltous and silver ions on the inhibition of root elongation caused by IAA or ACC. Seedlings were grown in phosphate buffer, boron and calcium [ $\text{Ca}(\text{NO}_3)_2$ ]. IAA, ACC, cobalt (as  $\text{CoCl}_2$ ) and/or silver [as  $\text{Ag}(\text{SO}_3)_2^{3-}$ ] were added to the growth solution. Root length was measured at the start and after 24 h. Each experiment included 10 seedlings and was repeated twice. Values are means  $\pm$  SE.

agrees with our earlier results (13) although the use of root tips with a length of 10 mm rather than 30 mm in this investigation caused some unexpected irregularities in the relation between applied ACC concentration and ethylene production measured in excised root tips after a treatment period of 24 h. The reason for these irregularities may be that the amount of ACC taken up and stored in 10-mm root tips was limiting ethylene production after excision of the roots. Figure 1 shows that there was little correlation between IAA-induced inhibition of root growth and ethylene production. With these pea roots the lowest level of ethylene production after 24 h was obtained from strongly IAA-inhibited root tips

**Table III.** Effect of Cobalt and Silver on Swelling of Pea Roots Treated with IAA or ACC

Seedlings were grown for 24 h in the dark in phosphate buffer, boron and calcium nitrate with or without 0.1  $\mu\text{M}$  IAA or 1  $\mu\text{M}$  ACC, silver [as  $\text{Ag}(\text{S}_2\text{O}_3)_2^{3-}$ ] or cobalt (as  $\text{Co}^{2+}$ ) was added to the growth solution. Swelling was measured as fresh weight of 10-mm long root tips. Values are means for at least 20 roots  $\pm$  SE.

Treatment	No Regulator	IAA, 0.1 $\mu\text{M}$	ACC, 1 $\mu\text{M}$
	<i>mg · (root tip)<sup>-1</sup></i>		
Control	6.5 $\pm$ 0.2	12.2 $\pm$ 0.2	10.5 $\pm$ 0.8
$\text{Ag}^+$ , 100 $\mu\text{M}$	6.5 $\pm$ 0.3	13.5 $\pm$ 0.3	6.9 $\pm$ 0.7
$\text{Co}^{2+}$ , 10 $\mu\text{M}$	6.4 $\pm$ 0.2	11.1 $\pm$ 0.3	6.0 $\pm$ 0.7

**Table IV.** Effect of Silver and Cobalt on Ethylene Production Resulting from Treatment with IAA or ACC

Seedlings were grown as described in Table III for 24 h in the dark, and the ethylene production of five 10-mm long root tips was measured. Values are means of at least four replicates  $\pm$  SE.

Treatment	Ethylene production by 10-mm Root Tips		
	No regulator	IAA, 0.1 $\mu\text{M}$	ACC, 1 $\mu\text{M}$
	<i>pmol · g fresh wt<sup>-1</sup> · h<sup>-1</sup></i>		
Control	279 $\pm$ 51	255 $\pm$ 13	2441 $\pm$ 536
$\text{Ag}^+$ , 100 $\mu\text{M}$	1974 $\pm$ 554	786 $\pm$ 408	5867 $\pm$ 58
$\text{Co}^{2+}$ , 10 $\mu\text{M}$	45 $\pm$ 16	50 $\pm$ 6	397 $\pm$ 83

(Fig. 1). Determination of the time course of ethylene production in the presence of IAA showed that the IAA-induced increase in ethylene production in the root tips is transitory and followed by a decrease of ethylene production below the control value (Fig. 3). However, in 1  $\mu\text{M}$  and lower concentrations of IAA the initial increase in ethylene production is too small to have any appreciable effect on root growth. In earlier investigations small increases in ethylene production have been reported where 0.1 to 1  $\mu\text{M}$  IAA has been applied to excised root tips (8, 10, 11, 17) or to intact seedlings (28), but no proof that such small increases affect root growth has been provided.

Ethylene inhibition of root elongation is associated with pronounced curvatures of the root tips (14). Such curvatures are also obtained when ethylene is produced from ACC added to the growth solution (13), and they were observed in the present experiments when ACC was present in the solution at 0.1  $\mu\text{M}$  or higher concentrations. Similar curvatures were not observed when root growth was inhibited by IAA, as would have been expected if ethylene is an important mediator of IAA inhibition.

The conversion of ACC into ethylene by ethylene-forming enzyme is inhibited by cobalt (20). In our experiments cobaltous ions were also found to reverse the inhibitory effect of ACC but not those of IAA. Similarly, silver ions known to inhibit the ethylene action (6), were also found to counteract the inhibitory effect of ACC but not IAA on root growth. The inhibition of root elongation by IAA was associated with swelling of the root tips. This 2-fold increase in diameter was not affected by cobalt or silver ions, indicating that the swelling as well as the inhibition of root elongation are caused by IAA *per se*. On the other hand, ACC induced swelling was

reversed by cobalt and silver ions. Similar results with silver ions were recently reported by Häggquist *et al.* (16) from experiments in which the root growth of oat seedlings was inhibited with IAA as well as the ethylene-releasing compound 2-chloroethylphosphonic acid. The inhibition caused by IAA in their experiments was not influenced by silver, whereas the effect of the ethylene-releasing compound was.

The evidence for an ethylene-mediated response of root growth to IAA presented by Chadwick and Burg (10, 11) was obtained with excised root tips. As the high IAA concentrations in the growing tips and stele of roots (7) is probably maintained by acropetal transport from the seed or shoot tissues, endogenous levels of auxins may decrease rapidly after excision (15). Excision is known to reduce the growth of root tips (26). The growth rate of the excised root tips used by Chadwick and Burg (10, 11) was about 0.3 mm h<sup>-1</sup> as compared with 0.9 mm h<sup>-1</sup> in our intact seedlings. This difference may at least partly explain the considerable difference in sensitivity to the inhibitory action of IAA between their excised root tips and our intact roots. Whereas 0.1  $\mu\text{M}$  IAA inhibited elongation by 67% compared with the control in our experiments, 1  $\mu\text{M}$  IAA had only a marginal effect in the experiments of Chadwick and Burg (10, 11). Consequently they had to use 10 or 100  $\mu\text{M}$  IAA to obtain appreciable growth inhibition. There is no doubt that such high IAA concentrations cause a considerable increase in the rate of ethylene synthesis in short-term experiments with excised root tips. However, experiments of this type cannot prove that auxin-induced ethylene production is necessary for the inhibition caused by the auxin. In fact, in similar experiments with excised lentil root tips Dubucq *et al.* (12) showed that ethylene production but not the growth inhibition caused by 10  $\mu\text{M}$  IAA could be reversed by an inhibitor of ACC synthesis.

Chadwick and Burg (11) also refer to certain experiments with intact seedlings in which pots with seedlings growing in vermiculite were immersed in IAA solutions for a few minutes. With this experimental technique most of the IAA retained in the pots may have been adsorbed by the vermiculite. Thus it is difficult to see how experiments of this kind can support their claim that inhibition of intact roots after IAA treatment is the result of IAA-dependent ethylene production.

According to our results the endogenous production of ethylene in root tips can be varied within certain limits with little or no effect on root growth. For instance, similar rates of root elongation were found in the control (ethylene production rate = 0.3 nmol g<sup>-1</sup> · h<sup>-1</sup>), in 10  $\mu\text{M}$   $\text{CoCl}_2$  (0.05 nmol g<sup>-1</sup> · h<sup>-1</sup>) and in 0.01  $\mu\text{M}$  ACC (0.7 nmol g<sup>-1</sup> · h<sup>-1</sup>). Only when ethylene production was increased to levels several times higher than those in the controls, did appreciable growth inhibition occur, as also shown earlier (13). Hence moderate increases in ethylene production after treatment with growth regulators may be unrelated to the observed growth inhibition. For roots growing submerged in water solutions, entrapment of ethylene, due to its slow diffusion through water, may increase endogenous concentrations of this gas considerably (18). In our experiments we have noticed that efficient aeration is necessary to obtain rapid and reproducible root elongation. A number of other factors, including oxygen supply

(5, 18) and illumination (13) affect endogenous levels of ethylene in roots, and there is no doubt that inhibitory ethylene levels may occur in roots under certain growth conditions. For example Mulkey *et al.* (23) found that maize roots treated with a combination of ethylene synthesis inhibitors (cobaltous ions + aminoethoxyvinylglycine) exhibited a 50% increase in their elongation rate. Although low IAA concentrations (0.1–10 nM) stimulated root elongation, higher concentrations (0.1–1  $\mu$ M) had an inhibitory effect, even in the presence of the ethylene synthesis inhibitors. These results are in agreement with our conclusion that the inhibitory effect of IAA is caused by IAA *per se*.

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