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The effect of selected plant hormones on *in vitro* proliferation of hyphae of *Glomus fistulosum*

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Abstract

Effects of N^6-benzyladenine, kinetin, zeatin, N^6-benzyladenosine, kinetin riboside, zeatin riboside, jasmonic acid, indole-3-acetic acid, indole-3-butyric acid, indole-3-propionic acid, abscisic acid and gibberellic acid on proliferation of hyphae of arbuscular mycorrhizal (AM) fungus *Glomus fistulosum* were studied under axenic conditions *in vitro*. The growth of intraradical hyphae of *G. fistulosum* was fully suppressed by 30 μM indole-3-acetic acid, but a perceptible decrease in the proliferation of the hyphae was observed already at 3 μM. Because such concentration is near the concentrations common in root tissues *in vivo*, the effect may be biologically significant. Similar effect was also observed for *Glomus mosseae*. Inhibitory effects of abscisic acid and cytokinins occurred only at very high, non-physiological concentrations. Ribosylated cytokinins showed stronger inhibition effects than their non-ribosylated counterparts. No stimulation of proliferation of hyphae by any plant hormone tested was observed.

Additional key words: abscisic acid, N^6-benzyladenosine, gibberellic acid, indole-3-acetic acid, indole-3-butyric acid, jasmonic acid, kinetin riboside, maize, *Zea mays*, zeatin riboside.

Introduction

Plant hormones are present in all plants. These compounds, mainly indole-3-acetic acid (IAA), are found also in root exudates (Murofushi *et al.* 1983, Torrey 1976), in cultures of some soil bacteria (Přikryl *et al.* 1985) and in soil itself (Sarwar *et al.* 1993).

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Abbreviations: AM - arbuscular mycorrhiza(l); BEG - La Banque Européenne des Glomales; GH - growth of proliferating hyphae, IAA - indole-3-acetic acid, PAR - photosynthetically active radiation, P% - percentage of root segments bearing proliferating hyphae, RH - relative air humidity.

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It is known that cell-free preparations of some bacteria containing plant hormones support the development of arbuscular mycorrhizal (AM) infection in host roots (Azcon *et al.* 1978). The invasion of a mycorrhizal fungus into the root tissue is accompanied by accumulation of plant hormones such as cytokinins (Allen *et al.* 1980, Baas and Kuiper 1989, Drüge and Schönbeck 1992) or abscisic acid (Danneberg *et al.* 1992). Other plant hormone, jasmonic acid, is supposed to play a signaling role during the response of plants to pathogens (Gundlach *et al.* 1992). This compound was reported to affect AM fungi in pot culture (Regvar *et al.* 1996), perhaps by modulating the plant defense mechanisms. Strong effects of jasmonic acid on the growth of ectomycorrhizal fungi has already been reported (Regvar *et al.* 1997).

The above facts give rise to the question whether there is a particular growth response of AM fungi to plant hormones or growth regulators. If so, the plant hormones might serve as chemical signals between the two partners in the symbiosis.

It is not possible to cultivate AM fungi in axenic culture enabling direct observations of the response of the vegetative mycelium of AM fungi to an effector molecule. We used, in our recent experiments, the technique of measuring the growth of proliferating intraradical hyphae of the symbiotic fungus. This technique, which minimizes the effects of the host plant, enabled us to observe the effect of the tested compounds on the limited growth of AM fungal hyphae under axenic conditions.

Materials and methods

Maize (*Zea mays* L., cv. CE 240) plants, as a source of mycorrhizal roots, were grown in a hydroponic culture based on Perlite-steamed soil (5:1) substrate at constant conditions (day/night 16/8, temperature 23/18 °C, RH 60 %, PAR 330 μmol m^{-2} s^{-1}). Pregerminated seeds were inoculated with 10 g of a soil inoculum containing mycorrhizal leek root segments, hyphae and 400 spores of *Glomus fistulosum* Skou and Jakobsen (isolate BEG 23). The only exception was the experiment exploring the effect of IAA on proliferation of *Glomus mosseae* (Nicol. and Gerd.) Gerdemann and Trappe (isolate BEG 76), in which each plant received 200 spores. The plants were cultivated in plastic tubes (180 mm in height and 50 mm in diameter), covered with canvas at the bottom to keep the substrate inside the tube. Each tube was placed in a separate black vessel and supplied with distilled water for the first two weeks of growth. After this two-week period, 400 cm^3 of a mineral nutrient solution P2N3 (Gryndler *et al.* 1992) was added to each vessel and renewed once a week. The plants were harvested after 4 weeks.

After cutting off the shoots, the root systems were washed with tap water and yellow-coloured roots - mycorrhizae - were carefully selected. In all experiments, the selected roots were shaken 5 times in sterile 0.1 % $MgSO_4 . 7 H_2O$ in distilled water for 2 min to remove retained particles of the hydroponic substrate, and subsequently kept for 4 h in a volume of 100 cm^3 of a solution containing 1 drop of Tween 80, streptomycin, polymyxin B, penicillin G and neomycin, all at concentrations of 500 mg dm^{-3}, and rolitetracycline at a concentration of 250 mg dm^{-3}. The roots were

then immersed in a 1:50 solution of sodium hypochlorite (*Savo*) containing 1 drop of Tween 80 for 4 min and washed with 500 cm^3 of distilled water. The washed roots were transferred to the sterile solution of 0.1 % $MgSO_4 . 7 H_2O$, cut with sterile surgical scissors into segments 1 - 2 mm long and washed 10× in the same solution (for more details see Gryndler *et al.* 1997).

In all experiments, the root segments were incubated in 0.03 cm^3 drops of a medium containing a buffering mixture of 1 mM BIS-TRIS and 0.9 mM MES, pH 6.3. The medium contained minerals [mg dm^{-3}]: KNO_3, 19.3; $Ca(NO_3)_2 . 4 H_2O$, 292.2; $CaCl_2 . 2 H_2O$, 97.2; $MgSO_4 . 7 H_2O$, 195.7; KH_2PO_4, 0.6; K_2HPO_4, 4.5; Na_2SO_4, 70.4; K_2SO_4, 38.4; NH_4NO_3, 2.5; FeNaEDTA, 1.6; $MnCl_2 . 4 H_2O$, 0.8; H_3BO_3, 0.8; KI, 0.04; $CuSO_4 . 5 H_2O$, 0.088; $ZnSO_4 . 7 H_2O$, 0.116 and $(NH_4)_6Mo_7O_{24} . 4 H_2O$, 0.012. Vitamins were added at concentrations [mg dm^{-3}]: Thiamin, 10; biotin, 0.01; pyridoxin, 3; riboflavin, 0.03; panthothenic acid, 1; nicotinic acid, 1; folic acid, 0.3; cyanocobalamin, 0.3 and myo-inositol, 5. Anhydrous glucose was present at a concentration of 5 g dm^{-3}.

In each experiment, this medium was supplied with various concentrations of plant hormones or growth regulators. The compounds were dissolved in the incubation medium and diluted to reach the concentration needed. Slowly soluble compounds were suspended in the medium, sonicated for 15 min and diluted.

In one experiment, the concentrations of zeatin of 0.05 - 5000 nM were used. Effects of all plant hormones except IAA were further studied in a series of 11 experiments, each compound being tested in a separate experiment. All cytokinins (N^6-benzyladenine, kinetin, zeatin, N^6-benzyladenosine, kinetin riboside, zeatin riboside) and jasmonic acid were used at concentrations 0.1 - 100 μM. Jasmonic acid was first dissolved in ethanol and then added into the medium. In this case, the incubation medium contained the same final concentration of ethanol (5 mM) in all treatments. Abscisic acid was dissolved to reach the final concentrations 0.01 - 100 μM. The effect of gibberellic acid (gibberellin GA_3) was studied at concentrations 0.005 - 50 μM. Indole-3-propionic acid and indole-3-butyric acid were tested at concentrations 0.03 - 100 μM.

Effects of IAA were investigated in a total of 4 experiments: 1 separate experiment for each of the 2 lots of the compound (lot 1: *Sigma I-1250/84F-0345*, lot 2: *Sigma I-2886/106H1053*) at concentrations 0.01 - 30 μM, 1 factorial experiment focused on interaction of effects of IAA and fusicoccin (see below), and one experiment verifying the effect of IAA on other AM fungus (*G. mosseae*) at concentrations 0.1 - 100 μM.

To observe a possible interaction (in terms of their effect on proliferation of AM fungus) of IAA with fusicoccin, a fungal toxin showing some anti-auxin effects on plant physiology, we performed a simple two-factorial experiment involving 3 concentrations of fusicoccin (0, 0.3 and 3 μM, first factor) and two concentrations of IAA (0 and 5 μM, second factor). Fusicoccin was dissolved in ethanol and then added into the incubation medium. The medium contained 5 mM of ethanol in all treatments.

Drops of the filter-sterilized incubation medium were placed on the inside bottom of the cover of a polystyrene Petri dish. The dishes, each containing 16 hanging drops of the medium, were incubated in the dark in a humid chamber for 5 d at 25 °C.

After the incubation, the root segments placed in the drops of the incubation medium were observed under a microscope (magnification 63×) with an eyepiece equipped with a grid net focal plate. Only the root segments non-contaminated by bacteria or saprophytic microfungi were taken into account. The intersections of grid net lines with the mycorrhizal mycelium were counted as a measure of hyphal growth. The data were expressed as a mean total length of hyphae per root segment. One intersection corresponded to a hyphal length of 59 μm.

The data were analyzed by a second-order polynomial regression analysis. Only the significant results are shown in Tables 1 and 2. In the case of the factorial experiment (fusicoccin × IAA), two-way *ANOVA* with Duncan's multiple range test ($P \leq 0.05$) were used.

Results

No significant effects of gibberellic acid, jasmonic acid, kinetin and zeatin on proliferation of *G. fistulosum* hyphae were observed in the concentration range used. The only significant effect of non-ribosylated cytokinins on proliferation obtained in

Table 1. Effects of cytokinins on the percentage of root segments bearing proliferating intraradical hyphae (P%) and on the growth of proliferating hyphae (GH) [mm root segment^{-1}] of *Glomus fistulosum*. Regression $y = a + bx + cx^2$, 7 replicates, *, **, *** - significant at $P \leq 0.05$, 0.01 or 0.001, respectively; n.s. - not significant.

Concentration [μM]	Zeatin riboside		Kinetin riboside		^{6}N-benzyl adenine	^{6}N-benzyl adenosine
	P%	GH	P%	GH	P%	P%
0	27.6	1.26	32.9	0.92	29.6	17.6
0.1	24.2	1.95	35.2	1.26	26.6	9.6
0.3	19.1	1.55	30.6	0.83	30.1	9.9
1.0	22.8	1.72	38.1	1.42	22.2	12.9
3.0	23.8	1.51	26.8	1.05	29.5	15.4
10.0	18.4	1.46	27.2	1.06	23.4	13.2
30.0	20.4	0.96	14.9	0.77	18.6	1.9
100.0	12.8	0.77	9.6	0.42	8.3	0.0
a	23.2	1.63	33.6	1.11	27.7	13.8
b	-0.16 **	-0.027 **	-0.78 **	-0.012 *	-0.36 **	-0.43 ***
c	0.000 n.s.	0.000 n.s.	0.005 n.s.	0.000 n.s.	0.002 n.s.	0.003 *
F	4.41	4.67	10.81	3.49	4.94	13.97
r^2	0.143	0.150	0.290	0.121	0.157	0.345
P	0.017	0.014	0.000	0.038	0.011	0.000

our experiments was the decrease in the percentage of root segments bearing proliferating hyphae (P%) by N^6-benzyladenine (Table 1). All ribosylated cytokinins (kinetin riboside, zeatin riboside and N^6-benzyladenosine) caused a decrease in P% and N^6-benzyladenosine was the only ribosylated cytokinin causing no inhibition of hyphal growth (GH) at high concentrations.

Table 2. Significant effects of auxins and abscisic acid on the percentage of root segments bearing proliferating intraradical hyphae (P%) and on growth of hyphae of *Glomus fistulosum* (GH) [mm root segment^{-1}]. Regression $y = a + bx + cx^2$, 7 replicates, *, **, *** - significant at $P \leq 0.05$, 0.01 or 0.001, respectively; n.s. - not significant, n.d. - not determined.

Concentration [μM]	IAA (lot 1) P%	IAA (lot 2) P%	IBA P%	Abscisic acid GH
0	21.2	17.6	28.0	1.42
0.01	20.3	6.4	n.d.	1.48
0.03	26.1	22.9	24.2	0.87
0.1	22.4	14.1	33.2	1.47
0.3	30.3	17.0	19.9	1.15
1.0	16.3	11.8	32.3	0.98
3.0	5.4	7.6	16.2	0.94
10.0	0.9	1.3	26.9	0.41
30.0	n.d.	0.0	13.3	0.48
100.0	n.d.	n.d.	10.9	0.30
a	24.4	15.2	26.6	1.20
b	-7.70***	-1.98***	-0.51***	-0.043 *
c	0.53*	0.049*	0.004 n.s.	0.000 n.s.
F	16.1	9.29	9.74	4.53
r^2	0.378	0.236	0.245	0.139
P	0.0000	0.0003	0.0002	0.015

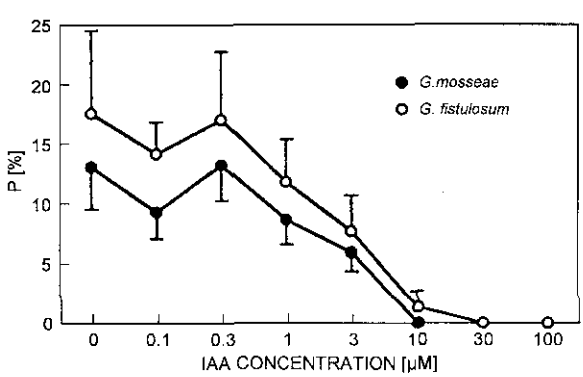

Fig. 1. Effect of concentration of IAA (lot 2) on proliferation of *Glomus fistulosum* and *Glomus mosseae*. P% - percentage of root segments bearing proliferating hyphae. Vertical lines indicate standard error of the mean.

Increased concentrations of indole-3-butyric acid resulted in a slight decrease in P% (Table 2). Indole-propionic acid showed no significant effect on proliferation. The strong, highly statistically significant effect of IAA on P% was observed consistently in two independent experiments using two different lots of the compound. A concentration of 30 μM was fully suppressive. In both experiments, P% was obviously decreased even at a concentration of 3 μM. When IAA was used at a concentration of 5 μM in the factorial experiment with fusicoccin (Table 3), the effect was not reversed and no significant interaction between the effects of IAA and fusicoccin was observed. A significant decrease in P% was observed when the concentration of 3 μM fusicoccin was used. When the effect of IAA on *Glomus mosseae* was studied, the suppression of proliferation was also found, at the concentration of 10 μM (Fig. 1).

Table 3. Effect of IAA and fusicoccin on the percentage of root segments bearing proliferating hyphae (P%) and on growth of hyphae of *Glomus fistulosum* (GH) [mm root segment^{-1}]. Mean values followed by the same letter do not differ according to Duncan's multiple range test at $P \leq 0.05$ in two-way experimental design.

Hormone	Concentration [μM]	P%	GH
Fusicoccin	0	23.8 a	1.94 a
	0.3	19.8 a	2.01 a
	3.0	6.7 b	0.99 a
IAA	0	23.8 a	2.38 a
	5.0	9.8 b	1.00 b
Effect of fusicoccin	*F*	25.94	1.11
	P	0.0000	0.344
Effect of IAA	*F*	47.42	6.51
	P	0.0000	0.017
Interaction	*F*	2.62	1.38
	P	0.087	0.268

Abscisic acid significantly inhibited the growth of hyphae of *G. fistulosum* at concentrations higher than 3 μM (Table 2).

Discussion

Cytokinins may stimulate the growth of some saprophytic fungi. Botz and Hilgenberg (1987) observed an increase in growth and enzyme activity of *Phycomyces blakesleeanus* caused by several cytokinins. The results of our experiments do not confirm this finding in the case of *G. fistulosum*.

The natural concentrations of cytokinins in roots rise when the root tissue is colonized by the symbiotic fungus (Allen *et al.* 1980, Drüge and Schönbeck 1992, Baas and Kuiper 1989) and it may reach 31 pmol g^{-1}(f. m.) of mycorrhizal root tissue of maize (Danneberg *et al.* 1992). Such a concentration is near to the lower limit of

the concentration range used in our experiments with cytokinins. In our experience, the concentrations of the cytokinins necessary to show the inhibitory effect were so high (>10 μM) that we cannot assume a direct inhibition of AM *in vivo*. Thus, the increased concentration of cytokinins in mycorrhizal roots, evoking a signal function, is probably the result of changed physiology of the root and it does not act as a direct chemical signal for the AM fungus. Nevertheless, the apparent distinction between the effects of ribosylated and non-ribosylated cytokinins is interesting and was not reported before.

In the case of IAA, the critical concentration 3 μM could be compared with its natural concentrations in root tissues to evaluate its potential role in the plant-microbe interaction. Pilet and Saugy (1987) measured the amount of IAA in maize root elongation zone. According to their data, the internal concentration of IAA could be estimated to approx. 2.1 (or less) μmol dm^{-3} of the root volume. Danneberg *et al.* (1992) measured the concentration of IAA in mycorrhizal and non-mycorrhizal maize root systems. The mean concentration of IAA was approximately the same in control and mycorrhizal roots and reached 3.0 - 6.6 nmol g^{-1} (root f. m.), which approx. corresponds to 3 - 7 μmol dm^{-3} of the root volume. Such a concentration of IAA already significantly decreased the growth of the hyphae, as documented by our results.

The IAA, besides its effects in the root tissue, may influence extraradical hyphae of AM fungi. Maize root exudates support the production of auxins by some soil bacteria (Martinez-Toledo *et al.* 1988, Přikryl *et al.* 1985) and, at the same time, humic-like substances may protect IAA against decomposition by soil microrganisms (Mato 1975). The hormone may thus accumulate in the soil and reach the level which affects the development of the extraradical mycelium of AM fungi in the rhizosphere. Some of the effects of IAA on plant tissue physiology are modulated by fusicoccin, *e.g.*, Böttger and Hilgendorf (1988) and Miller and Gow (1989) reported opposite effects of fusicoccin and IAA on proton secretion from maize roots. We have not found any significant interaction between the effects of these two compounds on proliferation of hyphae of *G. fistulosum*. It is thus unlikely that the proliferation of hyphae of *G. fistulosum* is controlled indirectly by IAA/fusicoccin modulated ion transport through plant plasmalemma.

Like the concentration of some cytokinins, the mean concentration of abscisic acid is consistently increased in mycorrhizal roots (Danneberg *et al.* 1992). Esch *et al.* (1994) found abscisic acid also in the *Glomus* sp. spores and hyphae, however, our results do not suggest a possible role of abscisic acid in symbiosis as a plant-released inhibitory signal.

Allen *et al.* (1982) reported a decreased gibberellin activity in mycorrhizal roots but the biological significance of the lower activity remains unexplained. El-Ghachtouli *et al.* (1996) reported the suppression of mycorrhizal infection by gibberellic acid. Our results with gibberellic acid do not confirm this finding and do not show a direct effect of gibberellic acid on the proliferation of the AM fungus *G. fistulosum*. The same results with jasmonic acid do not support the notion of a direct regulation of the development of AM fungi by this modulator of the plant defense response.

As a conclusion, it is obvious that the majority of plant hormones studied, at physiological concentrations or at concentrations which are used, *e.g.*, for *in vitro* plant cultures, do not affect directly the proliferation of intraradical hyphae of *G. fistulosum*. They probably do not act as a particular signal molecules in the symbiosis. The only exception found is IAA which strongly inhibits the proliferation of intraradical hyphae at concentrations near these usually found in the root. Thus, this effect may be biologically significant. Hence, if AM fungi would be managed in dual cultures together with host plant tissues, the concentration of IAA should be kept at a minimum or it should be replaced by other auxins, *e.g.*, indole-3-butyric acid.

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