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SHORT COMMUNICATION

Effect of indole-acetic acid (IAA) on the development of symptoms caused by *Pythium ultimum* on tomato plants

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Abstract The effect of indole-acetic acid (IAA) on the development of symptoms caused by *Pythium ultimum* on tomato plants was investigated using different bioassays. Application of IAA (5 μg ml^{-1}) on tomato seedlings inoculated with *P. ultimum* did not affect their emergence suggesting that IAA did not affect the severity of Pythium damping-off. However, IAA was shown to influence the development of *P. ultimum* symptoms on tomato plantlets. Low concentrations of IAA (0–0.1 μg ml^{-1}) within the rhizosphere of plantlets increased the severity of the symptoms caused by *P. ultimum*, while higher concentrations (10 μg ml^{-1}), applied either by drenching to the growing medium or by spraying on the shoot, reduced the symptoms caused by this pathogen. In addition, the study demonstrated that *P. ultimum* produces IAA in liquid culture amended with L-tryptophan, tryptamine or tryptophol (200 μg ml^{-1}) and in unamended culture.

Keywords Damping-off · Plant growth regulator · *Pythium ultimum* · Root rot · Systemic response · Tomato

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Over the last few years, diseases caused by *Pythium ultimum* have become problematic in greenhouse tomato (*Lycopersicon esculentum*) production, especially under hydroponic conditions. Pythium damping-off, affecting young seedlings, and Pythium root rot, causing an early degeneration (reduction in development and elongation) of the root system of mature tomato plants, result in important losses. In order to have a better understanding of the development of these diseases, previous studies have focused on the infection process of roots by *P. ultimum* (Chérif et al. 1991; Désilets and Bélanger 1991). Typical symptoms of *P. ultimum* infection have been associated with the production of toxins and hydrolytic enzymes, which cause cell death prior to penetration by the pathogen (Désilets et al. 1994; Rey et al. 2001).

Indole-acetic acid (IAA) is the most common natural auxin found in plants. IAA is involved in physiological processes such as cell elongation and tissue differentiation (Taiz and Zeiger 1991) and has also been associated with the plant growth-promoting effect of numerous rhizospheric microorganisms (Patten and Glick 2002; Persello-Cartieaux et al. 2003; Vessey 2003). In addition to its key role in the growth of plants, IAA plays an important role in numerous plant–pathogen interactions (Yamada 1993; Jameson 2000). Symptoms caused by tumorigenic bacteria and the expression of genes involved in the virulence of these bacteria have been associated with the effect of IAA (Yamada 1993). Of

particular interest, auxins seem to be involved in the infection process of root pathogens, such as *Pythium* spp. (Shimada et al. 1999; Rey et al. 2001; Le Floch et al. 2003a). In the case of *P. ultimum*, IAA through the alteration of the morphology of the root tissues, could facilitate the infection process by this pathogen (Désilets and Bélanger 1991; Rey et al. 2001).

In the present study, the objective was to evaluate the effect of IAA on the development of the symptoms caused by *P. ultimum*. The capacity of *P. ultimum* to produce IAA was also investigated.

A virulent strain of *P. ultimum* isolated from infected tomato roots was provided by the Laboratory of Dr. Richard Bélanger (Université Laval, Québec, QC, Canada). The pathogen was grown on potato dextrose agar (PDA; Difco Laboratories, Becton Dickinson, Sparks, MD, USA) at 24°C. PDA disks colonized with *P. ultimum* mycelium suspended in sterile distilled water (SDW) at 24°C served as stock cultures.

The production of IAA and IAA-related compounds by *P. ultimum* was evaluated spectrophotometrically. Briefly, liquid cultures were prepared in 250-ml flasks containing 100 ml of half-strength tryptic soy broth (TSB; Sigma-Aldrich, Mississauga, ON, Canada) supplemented with 200 μg ml^{-1} of either L-tryptophan, tryptamine or tryptophol (Sigma-Aldrich) or not supplemented (control). The culture medium was inoculated with three PDA disks colonized with actively growing mycelium of *P. ultimum*. Blanks consisted of uninoculated culture media amended or not with the three precursors. Flasks in eight replicates were incubated on a rotary shaker (150 rev min^{-1}, 24°C) for 1 week after which the mycelium was removed by filtration. One ml of each culture filtrate was mixed vigorously with 2 ml of Salkowski's reagent (150 ml of H_3PO_4, 250 ml of distilled water and 7.5 ml of 0.5M $FeCl_3.6H_2O$) (Gordon and Weber 1951). The mixture was incubated at room temperature for 20 min and the absorbance was measured at 535 nm. The concentration of IAA and IAA-related compounds was evaluated by comparison with a standard curve prepared using serial dilutions of a 50 μg ml^{-1} IAA (Sigma-Aldrich) solution in half-strength TSB. The results showed that *P. ultimum* produced IAA in all the culture media tested (Table 1). The highest amount of IAA (7.6 μg of IAA equivalent ml^{-1}) was produced when L-tryptophan was added to the culture medium whereas the smallest amount of IAA (3.1 μg of IAA equivalent ml^{-1}) was produced when tryptophol was added (Table 1). In addition, the production of IAA was not further stimulated by an increase up to 800 μg ml^{-1} in the concentration of L-tryptophan in the growth medium (data not shown).

Table 1 Production of indole-acetic acid (IAA) and IAA-related compounds by *Pythium ultimum* in liquid culture amended with either L-tryptophan, tryptophol or tryptamine

Precursors (200 μg ml^{-1})	IAA (μg of IAA equivalent ml^{-1})
Control[a]	5.5 ± 0.4 (0.60)[b]
L-Tryptophan	7.6 ± 1.2 (0.60)
Tryptophol	3.1 ± 0.9 (0.61)
Tryptamine	4.9 ± 1.0 (0.59)

Values are a mean of 8 replicates ± standard deviation

[a] Control medium consisted of half-strength TSB not amended with any precursor

[b] Values between brackets represent the TLC R_f values for IAA extracted from each culture

The production of IAA was confirmed with thin-layer chromatography (TLC) using the method described by Hasan (2002). Fifty ml of each culture filtrate were adjusted to pH 2.0 with 1M HCl and subsequently extracted with an equal volume of ethyl acetate. The ethyl acetate layer was recovered and evaporated with a Rotavapor R-200 (Büchi Analytical inc., New Castle, DE, USA). The residue was taken up in methanol and developed on TLC plates using isopropanol/ammonia/water (10/1/1; v/v/v) as a solvent. The plates were sprayed with a reagent (3% H_2SO_4 in methanol containing 50 mg $FeCl_3$) and heated until colour development. IAA appeared as a red colour under visible light and orange colour under UV light. In all cases, the production of IAA was confirmed by TLC analysis. Compounds with R_f values close to 0.60 (pure IAA) were considered as IAA (Table 1). Other unidentified IAA-related compounds but with different R_f values were also observed on the TLC plates indicating that other auxinic compounds were also produced by *P. ultimum.*

In order to evaluate the effect of IAA on damping-off, tomato seeds (cv. Vita Gold; Pike Seeds, Brandon, MB, Canada) were surface-sterilized and soaked for 15 min in either a 5 μg ml^{-1} solution of IAA or SDW (control). Seeds were subsequently sown in multicellular blocks of rockwool, received

1 ml of a suspension (1×10^6 propagules ml^{-1}) of *P. ultimum* or SDW (control), were covered with vermiculite and placed in a growth chamber (24°C, 80% RH and 16 h photoperiod). Every three days, germinating seeds received 1 ml of either SDW (control) or a 5 μg ml^{-1} solution of IAA. Damping-off was evaluated as the lack of emergence of the seedlings after 2 weeks of incubation in a growth chamber. This experiment, performed as a complete randomized design (five replicates) with an experimental unit consisting of 20 rockwool plugs each containing one seed, showed that *P. ultimum*-inoculated seeds treated (rate of emergence of 18%) or not with IAA (rate of emergence of 16%) had a significantly lower rate of emergence as compared to the control (rate of emergence of 99%) (Table 2). The application of IAA on non-inoculated seeds did not affect their emergence (rate of emergence of 97%) as compared to the control.

To evaluate the effect of low concentrations of IAA on the development of *P. ultimum*-inoculated tomato plantlets, seeds (cv. Vita Gold; Pike seeds) were surface-sterilized as described previously and placed in individual growth pouches containing 20 ml of a sterile solution of 0, 0.0001, 0.001, 0.01 or 0.1 μg ml^{-1} of IAA. Pouches, wrapped in aluminium foil, were placed in a growth chamber at 25°C for 5 days after which the seedlings were inoculated with a 5 ml suspension (1×10^6 propagules ml^{-1}) of *P. ultimum* or SDW (control). The seedlings were grown for two weeks following inoculation with the pathogen after which the weight of the roots and shoots, and shoot-length were measured. This experiment, conducted according to a complete randomized design (five replicates) with an experimental unit consisting of a growth pouch in which two seedlings were grown, showed that the length of the shoot and the fresh weight of the roots of non-inoculated seedlings (control) were not affected significantly by application of IAA. Concentrations of 0.001, 0.01, and 0.1 μg ml^{-1} of IAA significantly reduced the fresh weight of the shoot (Fig. 1). Application of increasing concentrations of IAA on *P. ultimum*-inoculated seedlings generally resulted in a significant decrease of the fresh weight of both the roots and the shoot (Fig. 1). The results obtained also showed that, for each concentration of IAA tested, fresh weight of the shoot and of the roots were significantly lower when seedlings were inoculated with *P. ultimum* (Fig. 1). This was not observed for the length of the shoot.

Table 2 Effect of indole-acetic acid (IAA) on Pythium damping-off of tomato seedlings in rockwool

Treatments	Emergence (%)
Control[a]	99 a
IAA[b]	97 a
IAA-*P. ultimum*[c]	18 b
P. ultimum[d]	16 b

[a] Seeds were treated with sterile distilled water

[b] Seeds were treated with 5 μg ml^{-1} IAA

[c] Seeds were inoculated with *P. ultimum* and treated with 5 μg ml^{-1} IAA

[d] Seeds were inoculated with *P. ultimum*

Each value represents the mean of 5 replicates. Analysis of variance (ANOVA) was performed with SAS (SAS Institute, Cary, NC, USA), using the general linear models procedure. Values followed by the same letter are not significantly different according to Fisher protected LSD test ($P < 0.05$)

To determine the effect of IAA on *P. ultimum* symptoms severity, surface-sterilized tomato seeds (cv. Vita Gold; Pike Seeds) were sown in 10-cm pots containing industrial quartz (0.65 mm; Unimin Canada ltd, St-Canut, Québec, QC, Canada) which were then placed in a growth chamber (temperatures of 20°C (day) and 24°C (night), 80% RH and 16 h photoperiod). Two separate experiments were conducted. For the first experiment, once the plants had reached the second leaf stage, they were drenched with 10 ml of a 10 μg ml^{-1} solution of IAA. Five hours later, they were inoculated by drenching 10 ml suspension (1×10^6 propagules ml^{-1}) of *P. ultimum*. Plants were treated with IAA a second time seven days later in the same way. For the second experiment, plants (stem and leaves) at the second leaf stage were sprayed with 10 ml of a 10 μg ml^{-1} solution of IAA and were then inoculated with *P. ultimum* as described previously. Plants were treated a second time with IAA after seven days. For both experiments, plants were grown for a total of 30 days after which *Pythium* root rot severity was evaluated. For both experiments, controls were not inoculated with *P. ultimum* and were not treated with IAA. The level of infection was evaluated through binocular observations as the number of infection points on five roots, including root hairs, sampled randomly from each plant. The development of the

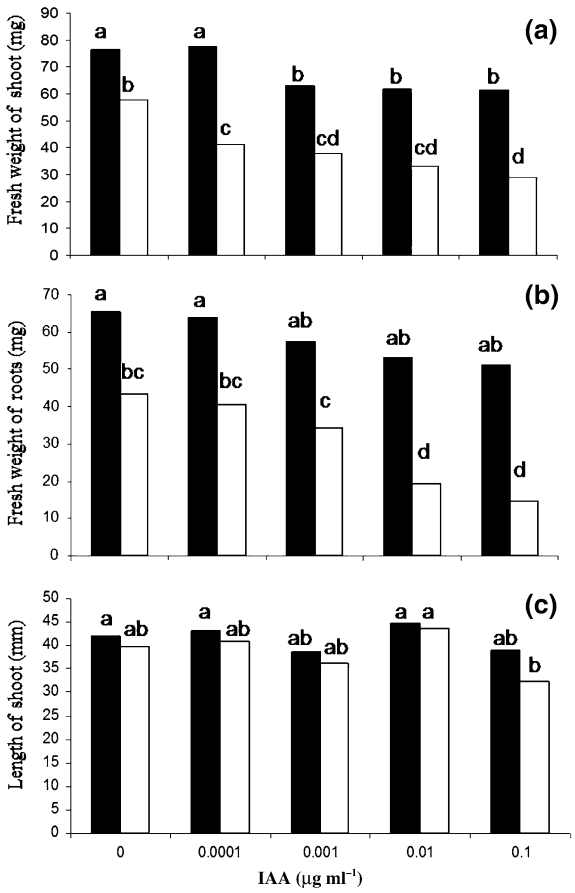

Fig. 1 Effect of low concentrations of indole-acetic acid (IAA) on fresh weight of the shoot (**a**) and of roots (**b**) as well as on length of the shoot (**c**) of *Pythium ultimum*-inoculated (□) and non-inoculated (control; ■) tomato seedlings grown in pouches. Each value represents the mean of 5 replicates. Analysis of variance (ANOVA) was performed with SAS (SAS Institute, Cary, NC, USA), using the general linear models procedure. Bars with a same letter are not significantly different according to Fisher protected LSD test ($P < 0.05$)

symptoms on the root surface was also rated according to a disease index of 0–4. The stem length and the fresh weight of the shoot and the roots were measured. These experiments, conducted as complete randomized designs with six replicates, showed that the application of 10 µg ml^{-1} of IAA by drenching on non-inoculated plants significantly reduced their overall growth. Indeed, the length of the stem and the fresh weight of both shoot and roots of non-inoculated plants treated with IAA were significantly lower compared to the control (Table 3). As for *P. ultimum*-inoculated plants, the length of the stem and the fresh weight of the roots were significantly increased when treated with IAA. Applied on the shoot, IAA did not significantly affect the growth of both non-inoculated and *P. ultimum*-inoculated plants as compared to the control (Table 3). However, the application of IAA to the stem allowed for a significant increase in the length of the stem and the fresh weight of both shoot and roots of *P. ultimum*-inoculated plants. Applied either by drenching or by spraying the stem, IAA reduced significantly the disease index and the number of infection points on *P. ultimum*-inoculated plants (Table 3).

This study showed that, applied at low concentrations (0–0.1 µg ml^{-1}), IAA did not have a marked detrimental effect on the development of the root system of healthy seedlings grown under axenic conditions but increased the overall negative effect of *P. ultimum* on plant development. Considering that *Pythium* spp. mainly infect juvenile or succulent tissues, such as feeder roots, root tips and root hairs (Hendrix and Campbell 1973) and that IAA stimulates, among other things, the proliferation of root hairs (Scott 1972), it could be hypothesized that IAA increased damage caused by *P. ultimum* by increasing areas susceptible to the pathogen. On the other hand, the production of auxin compounds by another *Pythium* sp., the antagonist *Pythium oligandrum*, has been associated with an increased plant growth (Le Floch et al. 2003a, b).

IAA applied by drenching to the roots of young tomato plants inoculated with *P. ultimum*, at a relatively high concentration (10 µg ml^{-1}), caused a significant reduction in disease severity and a significant improvement in the growth of the plant. However, the development of the tomato plant was severely affected by the treatment with IAA regardless of the presence of the pathogen. Foliar application of 10 µg ml^{-1} IAA on young *P. ultimum*-inoculated tomato plants was also shown to reduce the infection by *P. ultimum* and improved the overall development of the plant. Moreover, it did not adversely affect the growth of non-inoculated plants. The repressive effect of IAA application on disease development was previously reported. Indeed, Fernández-Falcón et al. (2003) reported on the reduction of the infection of banana rhizomes by *Fusarium oxysporum* f. sp. *cubense* following foliar application of IAA. The repressive effect of IAA on post-harvest diseases, such as dry rot (*Gibberella pulicaris*) of potato (Slininger et al. 2004), or foliar pathogens,

Table 3 Effect of indole-acetic acid (IAA) on symptoms severity caused by *Pythium ultimum* on tomato plants

	Length of stem (mm)	Fresh weight		Disease index[a]	Number of infection points[b]
		Shoot (g)	Roots (g)		
IAA on root system[c]					
Control[d]	84.0 a	3.65 a	3.76 a	0 a	0 a
IAA[e]	53.0 b	1.58 b	1.82 b	0 a	0 a
IAA-*P. ultimum*[f]	40.4 c	0.87 bc	1.60 b	2.0 b	8.6 b
P. ultimum[g]	22.4 d	0.56 c	0.34 c	4.0 c	46.0 c
IAA on shoot[h]					
Control	100.6 a	5.26 ab	5.40 a	0 a	0 a
IAA	100.4 a	5.56 a	5.24 a	0 a	0 a
IAA-*P. ultimum*	94.4 a	4.67 b	4.88 a	1.4 b	11.1 b
P. ultimum	75.4 b	3.54 c	3.61 b	3.6 c	47.9 c

[a] Disease index: 0: no symptoms; 1: 1–25% of root surface showing symptoms; 2: 26–50%; 3: 51–75%; 4: 76–100%

[b] Number of infection points on roots (including root hairs)

[c] Roots were treated (drenching) twice with 10 ml of 10 μg ml^{-1} IAA

[d] Plants were treated with sterile distilled water

[e] Plants were treated with 10 μg ml^{-1} IAA

[f] Plants were inoculated with *P. ultimum* and treated with 10 μg ml^{-1} IAA

[g] Plants were inoculated with *P. ultimum*

[h] Stem and leaves were treated (spraying) twice with 10 ml of 10 μg ml^{-1} IAA

Each value represents the mean of 6 replicates. Analysis of variance (ANOVA) was performed with SAS (SAS Institute, Cary, NC, USA), using the general linear models procedure. For each experiment, values within a column followed by a same letter are not significantly different according to Fisher protected LSD test ($P < 0.05$)

such as *Magnaporthe grisea* on rice (Ueno et al. 2004) has also been reported. Of particular interest is the reported repressive effect of IAA against *Phytophthora infestans*, an oomycete which causes late blight on potato (Martínez Noël et al. 2001). However, to the best of our knowledge, this is the first report of the repressive activity of IAA on the development of *P. ultimum* symptoms. The mechanisms involved in the disease repression observed in this study have not yet been identified. However, the results suggest that this effect of IAA could be related to the induction of plant defence mechanisms rather than through a direct impact on the pathogen. Previous studies have reported that IAA is involved in the induction of plant defence reactions. Martínez Noël et al. (2001) showed that exogenous IAA regulates β-1,3-glucanase and chitinase accumulation in potato leaves following inoculation with *P. infestans*. Furthermore, the regulation of the enzymatic activity of the glutathione *S*-transferase in potato by IAA and the possible effect of such a regulation on the induction of plant defence mechanisms have also been reported (Hahn and Strittmatter 1994). Ueno et al. (2004) also describe IAA as an activator of plant resistance causing an enhanced activity of enzymes such as phenylalanine ammonia-lyase and peroxidase. Although IAA was shown to affect the development of *P. ultimum* symptoms on young tomato plantlets, IAA, at the concentration tested, had no effect on the emergence of tomato seedlings inoculated with *P. ultimum* suggesting that its application did not repress damping-off.

In regard to IAA production by *P. ultimum*, the results of this study are in agreement with a previous report showing the production of this plant growth regulator by *P. ultimum* (Rey et al. 2001). Indeed, IAA and IAA-related compounds were produced by *P. ultimum* in all the media tested. Moreover, the TLC analysis detected the presence of IAA in all the media tested, although previous studies reported that *P. ultimum* is unable to produce IAA in a tryptophan-amended medium (Furukawa et al. 1996; Rey et al. 2001). In addition, it was shown that the amount of IAA and IAA-related compounds produced in the

culture medium amended with tryptophol or tryptamine was lower than the amount produced in the unamended culture medium, suggesting that the pathways involving those two precursors were not active under the conditions tested. However, the existence of the tryptamine pathway in *Pythium* spp. and their capacity to synthesize tryptophol have previously been reported (Rey et al. 2001; Le Floch et al. 2003a). As is the case with most microorganisms, more than one pathway is most likely involved in the synthesis of IAA by *P. ultimum*.

This study suggests that IAA influences the development of the symptoms caused by *P. ultimum* on tomato seedlings. It also suggests that the effect (repressive or stimulating) of IAA on the development of the symptoms varies according to the concentration used. Although this study showed that *P. ultimum* is able to secrete IAA, further work is needed to investigate the impact of IAA produced by the pathogen in the rhizosphere on symptom development.

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