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Volume 84, numéro 3, décembre 2003

URI : <https://id.erudit.org/iderudit/008492ar>

DOI : <https://doi.org/10.7202/008492ar>

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Éditeur(s)

Société de protection des plantes du Québec (SPPQ)

ISSN

0031-9511 (imprimé)

1710-1603 (numérique)

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Citer cet article

Fernández-Falcón, M., Borges, A. A. & Borges-Pérez, A. (2003). Induced resistance to *Fusarium* wilt of banana by exogenous applications of indoleacetic acid. *Phytoprotection*, 84(3), 149–153. <https://doi.org/10.7202/008492ar>

Résumé de l'article

La maladie de Panama du bananier, causée par *Fusarium oxysporum* f.sp. *cubense*, est une maladie systémique qui obstrue le système vasculaire de l'hôte. Nous présentons ici deux expériences sur l'induction de la résistance chez le bananier (cv. Dwarf Cavendish) effectuées en serre avec différents traitements d'acide indole-acétique capables d'augmenter la résistance à la maladie de Panama. Les résultats obtenus dans ces expériences suggèrent que l'application exogène d'acide indole-acétique aux bananiers augmente la résistance à la maladie de Panama et que l'induction de résistance est plus efficace lorsque les doses d'acide indole-acétique employées sont faibles et que les applications sont fréquentes. Ce travail semble confirmer le rôle joué par l'acide indole-acétique selon les modèles de Beckman, comme un des facteurs de défense principaux de la plante hôte face aux maladies de flétrissement vasculaire.

Induced resistance to *Fusarium* wilt of banana by exogenous applications of indoleacetic acid

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Received 2003-04-02; accepted 2003-11-28

PHYTOPROTECTION 84 : 149-153

Fusarium wilt of banana (Panama disease), caused by *Fusarium oxysporum* f.sp. *cubense*, is a soilborne systemic disease which occludes host vascular system. We report here two experiments on resistance induction with banana plants (cv. Dwarf Cavendish) carried out in glass greenhouse with different indoleacetic acid treatments, which are capable of inducing resistance to Panama disease. The results obtained in these experiments suggest that the exogenous application of indoleacetic acid to banana plants induce resistance to Panama disease and that the resistance induction is more effective when performed using low doses and frequent applications. This work seems to confirm the role played by indoleacetic acid according to Beckman's models as, one of the major defence factors of the host plant in vascular wilt diseases.

[Résistance induite à la fusariose vasculaire de la banane]

La maladie de Panama du bananier, causée par *Fusarium oxysporum* f.sp. *cubense*, est une maladie systémique qui obstrue le système vasculaire de l'hôte. Nous présentons ici deux expériences sur l'induction de la résistance chez le bananier (cv. Dwarf Cavendish) effectuées en serre avec différents traitements d'acide indole-acétique capables d'augmenter la résistance à la maladie de Panama. Les résultats obtenus dans ces expériences suggèrent que l'application exogène d'acide indole-acétique aux bananiers augmente la résistance à la maladie de Panama et que l'induction de résistance est plus efficace lorsque les doses d'acide indole-acétique employées sont faibles et que les applications sont fréquentes. Ce travail semble confirmer le rôle joué par l'acide indole-acétique selon les modèles de Beckman, comme un des facteurs de défense principaux de la plante hôte face aux maladies de flétrissement vasculaire.

INTRODUCTION

Fusarium wilt of banana (Panama disease), caused by *Fusarium oxysporum* f.sp. *cubense* (E.F. Smith) Snyder &

Hans. (FOC), is a soilborne, systemic disease which occludes host vascular system. Important dessert and cooking bananas are affected throughout the subtropics. *Fusarium* wilt also affects

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locally import cultivars in regions in which bananas are an important source of foods. Effective fungicides do not exist for this fatal disease. The highly susceptible cultivar Gros Michel, used by the export trades until about 1960, was replaced by clones of Cavendish subgroup. Although Cavendish cultivars are resistant to Race 1 (FOC-1) and Race 2 (FOC-2), the Race 4 of the pathogen (FOC-4) damages these cultivars in subtropical banana-growing regions. The continued use of the Cavendish cultivars is now threatened in these regions and producers in the tropics, mindful of disastrous epidemics which occurred in 'Gros Michel', are concerned that Race 4 or similar one, might develop in their areas (Ploetz 1990).

Following vascular infection by any of a variety of organisms, including *F. oxysporum*, the phenolic-storing cells that occur regularly in many plants, including banana and tomato (Mace 1963) can release the stored phenolics and diffuse out their cellular compartments into the vascular elements. According to Beckman (2000), there is substantial correlative evidence, that these phenolic-storing cells, produced during normal differentiation and strategically located and kinetically poised in xylem parenchyma tissues, serve as a sensing and defence-triggering system. In the event of injury or infection, these cells collapse, triggering chemical oxidation of the phenolics, which serves to lignify and/or suberize the immediate site of disturbance and, in the process, shifts the indoleacetic acid/ethylene/cytokinin balance. These hormonal reactions sound the alarm and mobilize a periderm-like defence in depth, including induced secondary metabolism, for several centimeters beyond the point of immediate danger. This sequence of responses, when successfully carried out, serves to seal off the endangered vessels longitudinally for some distance. Above this zone of response, the vessels again become functional by means of anastomosis with unaffected vessels.

Beckman (1987, 1990, 2000) added indoleacetic acid (IAA) to the list of host factors in his time-space model of host-

parasite interactions in an infected vascular element and the surrounding contact parenchyma cells, since a reasonable and timely role in defense process has been established for this hormone.

Tylose are occlusions in xylem vessels and considered to be a resistance factor against the attack of *Fusarium* races in resistant banana cultivars due to an inhibition of the upward spread of the fungus (Beckman 1987, 1990, 2000). Tylose formation has been successfully found, 2 d after inoculation of a resistant banana cultivar with Race 1 of *Fusarium oxysporum* f.sp. *cubense* (Vander-Molen *et al.* 1987).

By other hand, Borges-Pérez *et al.* (1983, 1991) and Gutiérrez-Jerez *et al.* (1983) hypothesized about the role played by the Zn nutrition on the tylose formation in the xylem of infected banana roots. Zn is likely to play a role in IAA biosynthesis (Marschner 1995) that is known to control xylem differentiation.

We report here two independent experiments carried out in order to investigate whether exogenous applications of IAA could induce resistance to *Fusarium* wilt (Panama disease) of banana plants under optimal conditions of Zn nutrition.

MATERIALS AND METHODS

Experiment 1 was carried out in a glasshouse in a random block experimental design using 192 banana plants (96 plants per treatment) from tissue culture of cv. Dwarf Cavendish (30 cm high). The temperature during the experiments was 12-35°C and relative humidity 40-95% (minimum and maximum respectively). The plants (1 plant per pot) were grown in pots each containing 6 kg soil surface level at the onset of the experiment. The soil contained in each pot was inoculated with the same amount of spores (4500 spores g⁻¹ soil) of *Fusarium oxysporum* f.sp. *cubense* FOC-4 (VCG-0120, Canary Islands isolate). The treatment consisted in thoroughly wetting the aerial part of the plant until run off with an aqueous solution of 10 mg

L⁻¹ IAA (Sigma Chemical Co., St Louis, MO, USA). The control plants were foliar spray treated with water only. The aerial spray solution was added 40% alkylphenyl polyglycolic ether as adjuvant. The treatments were begun on the date of inoculation of the soil, and were repeated every 15 d. After 44 wk (21 sprays), the plants were removed from pots and rhizomes were dissected to determine the severity of disease (infection index) in each case. The infection index used to evaluate the damage caused by the disease varied from zero for healthy rhizome to 10 for a 100% damaged rhizome. Both treated and control plants were fertilized with macro and micronutrients, according to the requirements of plants, by applications of 2 g per plant every wk of a commercial fertilizer containing (wt/wt): N 18%, P₂O₅ 18%, K₂O 18%, Fe 0.10%, Mn 0.05%, Zn 0.015%, B 0.02%, Cu 0.011%, Mo 0.007%.

Experiment 2 was carried out in a glasshouse in a random block experimental design using 40 banana plants (20 plants per treatment) from tissue culture of cv. Dwarf Cavendish (30 cm high). The temperature during the experiences was 12-35°C and relative humidity 40-95% (minimum and maximum respectively). The plants (1 plant per pot) were grown in pots each containing 6 kg soil surface level at the onset of the experiment. The soil contained in each pot was inoculated with the same amount of spores (10 000 spores g⁻¹ soil) of *Fusarium oxysporum* f.sp. *cubense* FOC-4 (VCG-0120, Canary Islands isolate). The treatment consisted in thoroughly wetting the aerial part of the plant until run off with an aqueous solution of 100 mg L⁻¹ IAA (Sigma Chemical Co., St Louis, MO, USA). The control plants were foliar spray treated with water only. The aerial spray solution was added 40% alkylphenyl polyglycolic ether as adjuvant. The treatments were begun on the date of inoculation of the soil, and were repeated every 90 d (13 wk). After 24 wk (two applications of IAA), the plants were removed from pots and rhizomes were dissected to determine the severity of disease (infection index) in each case. The infection index used to evaluate the damage caused by the dis-

ease varied from zero for healthy rhizome to 10 for a 100% damaged rhizome. Both treated and control plants were fertilized with the same amount and frequency of application of the fertilizer used in *experiment 1*.

RESULTS AND DISCUSSION

The results obtained in the first experiment (Table 1) show that the percentage of diseased plants with a high severity of disease (Index >5) in untreated plants (control) and in IAA treated plants was 35.4 and 13.5%, respectively (2.6-fold increase). The average of rhizome infection index in untreated plants (control) was significantly higher (1.7-fold increase) than in IAA treated plants (3.2 and 1.5, respectively), these values being statistically different ($P = 0.01$). Treatment with IAA (10 ppm) implied an induced resistance of 53.1% as compared to untreated plants (control).

In the second experiment (Table 2), a similar tendency is observed. The percentage of plants with a high severity of disease index (Index >5) in untreated plants (control) and in IAA treated plants was 50 and 30%, respectively. Thus, the average of the rhizome infection index in untreated plants (control) as compared to IAA treated plants was 3.7 and 2.1, respectively but in this case no statistical differences were found between both values ($P = 0.01$).

Treatment with exogenous IAA of the banana plants apparently does slightly increase the level of endogenous free IAA. This could involve a better availability of endogenous free IAA in the plant and a quicker defence response when infected by the fungus. We suggest that the over-expression of IAA according to Beckman's models (1987, 1990, 2000) could act positively on other defence factors of the host plant such as the phenolic infusion, enzyme synthesis such as glucanase, gel formation, phytoalexin synthesis and tylose formation, which may result in a significant increase of resistance of banana plants to *Fusarium* wilt.

Table 1. Comparative study between IAA treated and untreated banana plants inoculated with low dose (10 mg L⁻¹) and frequent applications of *Fusarium oxysporum* f.sp. *cabense*, Race 4

Treatment	Rhizome infection index ^{a,b} (44 weeks after inoculation)	Diseased plants (%) (Index > 5)	Induced resistance ^c (%)
IAA 10 mg L ⁻¹	1.5 a	13.5	53.1
Control	3.2 b	35.4	–

^a Calculated as described in Materials and Methods.

^b Mean of 96 replicates; within the same column, values followed by different letters are significantly different at $P = 0.01$ according to one-way analysis of variance (ANOVA) statistical procedure.

^c Induced resistance (IR) calculated as described by Davis (1967); IR (%) = $100(C-B)/C$ where C = rhizome disease index of the untreated plants (control), and B = rhizome disease index of the IAA treatment.

Table 2. Comparative study between IAA treated and untreated banana plants inoculated with high dose (100 mg L⁻¹) of *Fusarium oxysporum* f.sp. *cabense*, Race 4

Treatment	Rhizome infection index ^{a,b} (24 weeks after inoculation)	Diseased plants (%) (Index > 5)
IAA 100 mg L ⁻¹	2.1 a	30
Control	3.7 a	50

^a Calculated as described in Materials and Methods.

^b Mean of 20 replicates; within the same column, values followed by the same letters are not significantly different at $P = 0.01$ according to one-way analysis of variance (ANOVA) statistical procedure.

The results shown here suggest that the exogenous IAA treatments to banana plants induce resistance to Panama disease. Moreover, the resistance induction seems more effective when it is performed using lower doses and more frequent applications. This work seems to confirm the role played by IAA according to Beckman's models as one of the major defence factors of the host plant in vascular wilt diseases.

ACKNOWLEDGEMENTS

The authors would like to thank J.M. Hernández Hernández from the Departamento de Patología Vegetal, Instituto Canario de Investigaciones Agrarias (ICIA), for kindly providing FOC-4 inoculum. We also acknowledge Mrs. Pauline Agnew who endeavoured to edit the English translation of this paper.

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