Resistance against the potato cyst nematode *Globodera pallida* systemically induced by the rhizobacteria *Agrobacterium radiobacter* (G12) and *Bacillus sphaericus* (B43)

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Accepted for publication 20 February 1998.

Summary – *Bacillus sphaericus* strain B43 and *Agrobacterium radiobacter* strain G12, selected from the potato rhizosphere, significantly reduced *Globodera pallida* juvenile penetration into potato roots. To better understand the basis of antagonism, the mode-of-action of the bacterial antagonists was investigated. The ability of the rhizobacteria to stimulate induced systemic resistance against the nematode was demonstrated in split-root-trials, where the root system of a single potato plant was spatially divided into two separate parts. Induced systemic resistance in the split-root system was caused by live and heat-killed bacterial cells of both bacteria strains. Culture filtrates of B43 had the same effect but G12-culture filtrates did not. Therefore, it was not possible to demonstrate the presence on the leaf surface of a basipetal systemic mechanism affecting the root system. © Orstom/Elsevier, Paris

Résumé – ***Résistance au nématode à kyste de la pomme de terre* Globodera pallida *induite de façon systémique par les rhizobactéries* Agrobacterium radiobacter *(G12) et* Bacillus sphaericus *(B43)*** – *Bacillus sphaericus* souche B43 et *Agrobacterium radiobacter* souche G12 provenant de la rhizosphère de pomme de terre diminuent significativement la pénétration des juvéniles de *Globodera pallida* dans les racines de pomme de terre. Pour mieux comprendre les bases de cet antagonisme, le mode d'action de ces bactéries antagonistes a été étudié. La capacité des rhizobactéries à stimuler une résistance induite au nématode a été démontrée grâce à un dispositif de division du système radiculaire dans lequel la masse radiculaire d'un seul plant de pomme de terre est séparée physiquement en deux parties. La résistance induite de façon systémique dans un tel dispositif est provoquée par l'une et l'autre bactéries, tant vivantes que tuées par la chaleur. Les filtrats de culture de B43 provoquent le même phénomène, mais non ceux de G12. L'existence d'un mécanisme systémique affectant basipétalement le système radiculaire à partir des feuilles n'a pu être démontrée. © Orstom/Elsevier, Paris

Keywords : *Agrobacterium radiobacter*, antagonistic rhizobacteria, *Bacillus sphaericus, Globodera pallida,* systemic resistance, nematodes, split-root system.

Public concern over pesticide use and limited availability of such products have heightened interest in biological control of plant parasitic nematodes. Since the rhizosphere provides the first line of defence for roots against nematode attack, it is generally considered that rhizosphere bacteria are ideal biocontrol agents. Their ability to multiply and spread in the rhizosphere environment, to colonize potential infection-sites on the root and possibly to act by direct contact with the parasites are characteristics that make them useful agents for nematode management. Initial investigations on antagonistic rhizobacteria against plant-parasitic nematodes include works by Zavaleta-Meija and Van Gundy (1982), Oostendorp and Sikora (1986), and Racke and Sikora (1992). Rhizobacteria with antagonistic potential against potato and sugarbeet cyst nematodes and root knot nematodes were selected, which reduce early infestation processes. The pale potato cyst nematode *Globodera pallida* is of particular interest to nematology as a target for biocontrol, because of a lack of useful crop resistance and acceptable chemical control methods.

Two bacterial strains, *Agrobacterium radiobacter* (G12) and *Bacillus sphaericus* (B43), were shown to reduce penetration of the potato cyst nematode *G. pallida* in greenhouse and field experiments by up to 30% - 40% (Racke & Sikora, 1992). Similar results were obtained by Hackenberg (1993). To understand and improve the effectiveness of this biological control system, it is important to determine the underlying mode-of-action. Competition for nutrients supplied by root exudates probably occurs in most interactions between bacteria and pathogens on the root surface (Elad & Baker, 1985; Elad & Chet, 1987). This factor is involved to some (small) degree in the biocontrol of fungal pathogens by bacteria. In the pathosystem rhizobacteria/plant parasitic nematode, completely different mechanisms are at play. Many rhizobacteria produce antibiotics, siderophores, HCN, and other toxic compounds which could be involved in biologi-

cal control. The ability of bacteria to envelop or bind to root-surface lectins possibly interfere with nematode-host-recognition and, therefore, penetration (Oostendorp & Sikora, 1990). In addition, these authors also demonstrated a reduction or alteration of root exudate hatch stimulation after incubation with several bacterial isolates.

Recent studies have shown that some rhizobacteria are also able to induce systemic resistance in plant to microbial pathogens (Wei *et al.*, 1991). Induced resistance can be triggered by different inductors. Various cell structures, abiotic compounds such as isonicotinic acid, salicylic acid and their derivatives, and extracellular structures of micro-organisms and their metabolites are known as elicitors of induced resistance in different systems (White, 1979; Smith & Metreaux, 1991; Schönbeck *et al.*, 1993; Kessmann *et al.*, 1994). The purpose of this study was to determine, whether the rhizobacteria strain *A. radiobacter* G12 and *B. sphaericus* B43 or their metabolites are able to incite systemically induced resistance in potato plants toward the potato cyst nematode *G. pallida*.

Material and methods

General techniques

Nematodes

G. pallida was originally obtained from a field population and was maintained continually on potato plants. Nematodes for inoculum production were multiplied in 3 dm^3 pots in the greenhouse on the potato cv. Hansa in infested soil containing 1500 eggs and juveniles/100 g soil. After 3 months, shoots of the plants were discarded and the soil, containing newly formed cysts, was stored for at least 9 months to overcome diapause. Cysts were extracted by a wet sieve decantation technique (modified by Ayoub, 1980) and separated from organic material by $MgSO_4$-flotation procedures. Suspensions of eggs and juveniles were separated from the cyst wall debris in a tissue homogenizer.

Bacteria

Both rhizobacteria strains, *A. radiobacter* (G12) and *B. sphaericus* (B43) were maintained for long-term storage at -80°C in Microbank (Pro-Lab Diagnostic). Cultures to be used for testing were transferred to liquid culture media. *B. sphaericus* was cultured in Tryptic Soy Broth (3%, pH 7.2), *A. radiobacter* in King's B Medium (pH 5.8) (King *et al.*, 1954) on a rotary shaker at 24°C for 24 h in an incubator. After incubation the bacterial suspension was centrifuged at 5400 *g* and the pelleted bacterial cells resuspended in sterile 25% concentrated Ringer-solution (Merck). Optical cell density of the bacterial suspensions was adjusted with a spectral photometer to $OD_{560} = 2.0$, which corresponds to 1.8×10^{10} cfu ml^{-1} (B43) and 1.2×10^{10} cfu ml^{-1} (G12). Potato roots were inoculated by pipetting 2.5 ml of a bacterial suspension onto the soil surface. Controls were treated with Ringer-solution.

Rifampicin-resistant mutants of both strains were selected by streaking *B. sphaericus* on Tryptic Soy Agar (TSA) and *A. radiobacter* on King's B Agar (KB) supplemented with 100 and 200 ppm Rifampicin, respectively. Then, mutants were multiplied in 100 or 200 ppm Rifampicin supplemented liquid media. The inoculum preparation and inoculation techniques were the same as for the wild strains outlined above.

Culture filtrates used for inducing experiments were obtained from the liquid culture media after removal of bacteria cell by filtration through a series of nitrocellulose filters down to a final pore size of 0.2 µm. Heat-killed bacteria cells were produced by autoclaving bacteria 20 min at 120°C at 1.2×10^5 Pa pressure.

Experimental evaluation

Nematode penetration was determined 21 days after nematode inoculation when the nematodes have reached the J3 or J4 developmental stage. Both parts of the split-root system were cut off separately and rinsed with tap water. Fresh root weight was determined after blotting off free water. Nematode penetration rates were determined by boiling roots in 0.1% lactic acid fuchsin. Stained roots were then homogenized in an Ultra-Turax (IKA-Werk) and the number of juveniles in the roots were counted under a stereomicroscope.

Experimental design

Split-root system

Potato plants were grown in a three-pot-system with each pot measuring 8 cm in diameter (Fig.1). The potato seed was put in the upper pot and its roots grew through two openings in the bottom of the upper pot and spread to the lower two pots. This system makes it easy to separate the root system into two fractions. Our goal was to prevent movement of inoculated bacteria from one root fraction into the other. The efficacy of the system for preventing bacteria movement from one root fraction to the other was tested using antibiotic-resistant mutants of both bacteria strains.

There were six or seven replications for each experiment. Potatoes cv. Hansa were grown in sterile fine quartz sand. Plants were 2 to 4 weeks old at the onset of the experiments. Depending on the time of year, the plants were cultivated either in climatic chambers at 21°C or in the greenhouse.

Rifampicin resistant mutants of *B. sphaericus* and *A. radiobacter* (10^{10} cfu) were applied onto one side of the split-root-system. After 3 and 16 days of incuba-

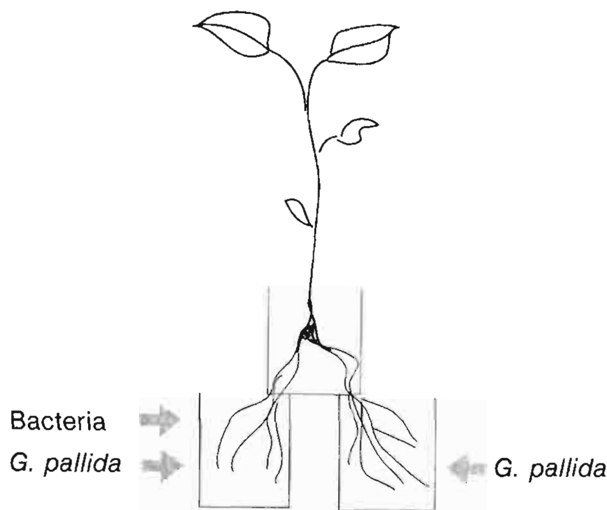

Fig. 1. *Potato plant grown in a three-pot split-root system where roots are separated in two fractions (Bacteria were applied to one root fraction; after 24 h incubation, nematodes were inoculated to both sides of the root system to examine systemic induced effects of the bacteria against* Globodera pallida*).*

tion at 21°C in the climate chamber or the greenhouse, the presence of the mutants in the rhizosphere and rhizoplane was determined in both segments of the root system. The roots in each lower pot were cut and sand particles were carefully washed away with tap water. The roots were then thoroughly washed in saline buffer. The resulting solution was spread over TSA containing 100 ppm Rifampicin for *B. sphaericus* and KB Agar with 200 ppm Rifampicin for *A. radiobacter.* No movement of bacteria to the untreated section of the root system was detected in repeated tests.

Resistance induction – roots

In the first experiment, both sides of the root system were inoculated with juveniles to determine whether control occurred when *i*) the nematodes were in direct contact with the bacteria and *ii*) on the bacteria-free fraction of the root system, which would indicate induced resistance.

A 2.5 ml solution of viable bacteria cells containing either 1.8×10^{10} *B. sphaericus*/ml or 1.2×10^{10} *A. radiobacter*/ml was applied to one side of the split-root system. After 24 h incubation, a suspension containing 1500 nematode eggs and juveniles was inoculated to both sides of the root system. The nematode inoculum was pipetted onto the sand near the roots in the lower pots. Control plants were treated with 25% concentrated Ringer-solution, which was also used to resuspend the bacteria. Previous experiments have demonstrated that there was no difference between water- and Ringer-treatment concerning the penetration of nematodes into the roots. Plants were incubated in the growth chamber or the greenhouse at 22°C with 16 h illumination until evaluation.

In the second experiment, the bacteria were applied to one side of the root system. After 24 h incubation, a suspension containing 1500 nematode eggs and juveniles was applied only to the bacteria-free side of the split-root system. The experiment was designed to exclude bacteria from possibly entering the root through wounds produced by nematode penetration.

Resistance induction – leaves

Induced systemic resistance in plants has been demonstrated in many plant-pathogen systems. Very often elicitor-induced resistance appeared after leaf inoculation (Guedes *et al.*, 1980). In the present case, leaf inoculation with bacteria would be easier to use than root inoculation for field experiments. To determine whether *B. sphaericus* or *A. radiobacter* have the ability to induce resistance in roots after leaf application, bacterial suspensions or bacteria culture filtrates were spread onto the upper and lower side of the leaves of potato plants with a fine paint brush. To promote dispersion and adhesion of the bacteria to the leaf surface, 0.1% methylcellulose was added to the bacterial suspension. Control plants were treated with sterile water or Ringer solution. After application of bacteria onto the leaves, transparent polyethylene bags were placed over the plants to maintain high humidity and improve conditions for micro-organism survival. Two days later, 30 cysts of *G. pallida* were inserted into the soil by placing the cysts between 100 µm mesh gauze sandwiched in a slide frame. Cysts were chosen as the inoculum because they provide a higher rate of penetration than egg and juvenile suspensions.

Inducing agents

An attempt was made to determine which bacterial component can or cannot elicit resistance. Viable cells, heat-killed cells and culture filtrates of both bacteria strains were examined for their ability to induce systemic resistance toward *G. pallida.*

A 2.5 ml solution of each component was applied in separate treatments to one side of a split root. One day later, 30 cysts of *G. pallida* in slide frames were inserted into the soil on the untreated side of the root system.

Results

RESISTANCE INDUCTION – ROOTS

Experiment 1

• *B. sphaericus* : The application of the bacterial strain to one side of a split-root system followed by

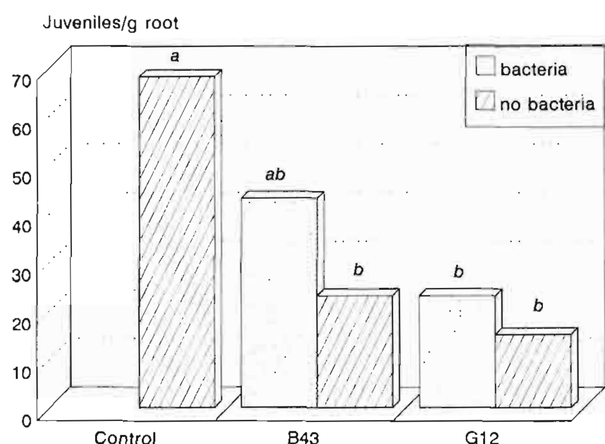

Fig. 2. *Penetration of* Globodera pallida *into the bacteria treated and into the untreated root section in a split root system. The bacteria used were* Bacillus sphaericus *(B43) and* Agrobacterium radiobacter *(G12) (Mean values with different letters are significantly different; Duncan's Multiple Range Test; $P \leq 0.05$; $n = 7$).*

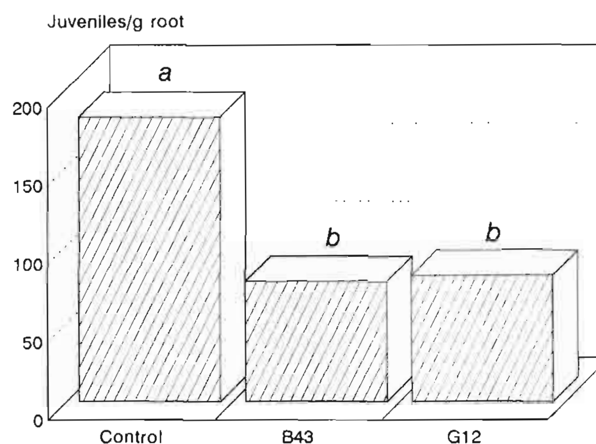

Fig. 3. *Number of juveniles of* Globodera pallida *which had invaded the roots of the untreated side of a split root system. The other side was inoculated with* Bacillus sphaericus *(B43) and* Agrobacterium radiobacter *(G12). (Mean values with different letters are significantly different; Duncan's Multiple Range Test; $P \leq 0.01$; $n = 7$).*

inoculation of *G. pallida* to both parts of the split-root system resulted in significant reductions of nematode penetration into both root sections (Fig. 2). Nematode penetration was reduced by about 37% on the side of the root system where both *B. sphaericus* and *G. pallida* were present. It was reduced by 67% in the bacteria-free side of the split-root system.

• *A. radiobacter* : The application of *A. radiobacter* to one half of the split-root system caused a significant decrease of 67% in nematode penetration (compared to control) on the side of the root system where both the bacteria and the nematodes were present. Penetration on the bacteria-free side of the split-root system was reduced by about 78% when compared to absolute control.

Experiment 2

The *Bacillus sphaericus* treatment caused a 58% decrease in nematode penetration in the bacteria-free side. *A. radiobacter* caused a 55% decrease (Fig. 3). No effects on fresh root weights were detected in either experiments.

Resistance induction - leaves

The bacteria strains and their culture filtrates exhibited no basipetal activity in inducing resistance to nematode root infestation after inoculation onto the leaf surface. On the contrary, leaf treatment with culture filtrates of both bacteria led to nonsignificant increases in nematode penetration (Table 1).

Inducing agents

The treatment of split-root systems with living or dead bacteria cells and culture filtrates of *B. sphaericus* and *A. radiobacter* led to different induced resistance reactions toward *G. pallida*. Inoculation of viable cells of *B. sphaericus* or *A. radiobacter* resulted in a significant reduction in nematode penetration: 77% with *B. sphaericus* and 59 % with *A. radiobacter*. With both bacteria, heat-killed cells produced the same effect as living cells (Fig. 4).

The culture filtrate of the two bacteria had very different effects on the expression of induced resistance. The culture filtrate of *B. sphaericus* applied to one side of the split-root system induced an 84% reduction in nematode penetration per gram of root in the untreated side. In contrast, culture filtrates of *A. radiobacter* did not cause any systemic induced resistance against the nematodes in the split-root tests.

Discussion

Previous studies have shown that specific rhizosphere bacteria have an antagonistic activity against various species of plant-parasitic nematodes. Oostendorp and Sikora (1990) isolated a *Pseudomonas fluorescens* strain with antagonistic activity against the sugar beet cyst nematode *Heterodera schachtii*. Sikora (1992) reported on the antagonistic behaviour of a *Bacillus subtilis* isolate to *Meloidogyne incognita* on a number of crops. Racke and Sikora (1992) isolated two strains of

Table 1. *Effects of a leaf inoculation with* Bacillus sphaericus *(B43) and* Agrobacterium radiobacter *(G12) on the penetration of* Globodera pallida *into potato roots.*

Leaf treatment	Penetrated juveniles / root
Control H_2O + 0.1% methylcellulose	78 *ab*
Control Ringer + 0.1% methylcellulose	47 *b*
B43 + 0.1% methylcellulose	80 *a*
G12 + 0.1% methylcellulose	81 *a*

Mean values with different letters are significantly different (Duncan's Multiple Range Test; $P \leq 0,05$; n = 6).

rhizobacteria with antagonistic effects against the potato cyst nematode *G. pallida*. Little is known on the mode-of-action of such bacterial/nematode relationship (Sikora & Hoffmann-Hergarten, 1993). In the present study, two bacteria, *B. sphaericus* B43 and *A. radiobacter* G12 were tested for their ability to induce systemic resistance against *G. pallida*. In repeated tests, both bacteria caused large reductions in nematode penetration that were clearly systemically induced.

Systemic induced resistance has been reported in several host-pathogen systems (Kuc, 1990) and is defined as the process of active resistance dependent on physical or chemical barriers of the host plant, activated by biotic or abiotic inducing agents (Kloepper *et al.*, 1992). In earlier studies systemic resistance was usually induced against leaf pathogens. However, induced systemic resistance against root pathogens by root and stem induction has been reported by Gessler and Kuc (1982). Knowledge concerning induced resistance toward plant parasitic nematodes is scarce. Kiyohara (1986) obtained resistance against the pine wilt nematode *Bursaphelenchus xylophilus* after preimmunisation with an avirulent strain of the same nematode. Decker and Dowe (1989) reported induced tolerance in tomatoes against *Globodera rostochiensis* after infestation with *Heterodera schachtii*, which they speculated to be due to changes in plant physiology. Whether these results are based on real induced resistance or on competition or occupation of the same niche for survival is questionable. Glazer and Orion (1985) observed a 70-80% reduction in female development of *Meloidogyne javanica* after soil treatment with hydroxyurea. They attributed the effect to induced resistance. In the present study, bacteria inoculation onto leaf surfaces did not affect nematode penetration into roots. Therefore, it was not possible to demonstrate the presence on the leaf surface of a basipetal systemic mechanism affecting the root system. This could be explained by the origin of the bacteria strains used, as they were isolated from rhizosphere soil and, therefore, not adapted to leaf surface conditions.

In the present study, systemic resistance toward *G. pallida* was elicited by living as well as heat-killed cells of *B. sphaericus*. In addition, culture filtrates induced the same reaction against the nematodes, but to an even stronger degree. The resistance inducing activity of bacterial metabolites to diseases has been described in literature. Schönbeck *et al.* (1980) isolated a *Bacillus subtilis* strain whose metabolites are able to induce systemic resistance against powdery mildew on barley. Culture filtrates of several fungi and bacteria protected beans against bean rust *Uromyces phaseoli*. In our study, the weaker inducing activity of viable and dead cells could possibly be related to the lower content of active metabolites in cells than in culture filtrates.

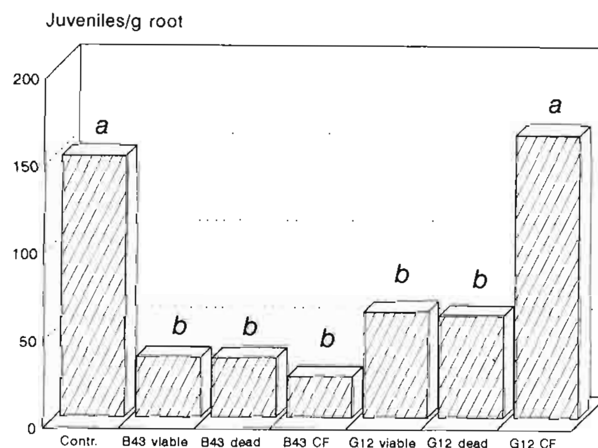

Fig. 4. *The number of juveniles of* Globodera pallida *which had invaded the bacteria-free side of a split-root system. The other side was inoculated with either viable bacteria, heat-killed bacteria or culture filtrates (CF) of* Bacillus sphaericus *(B4) and* Agrobacterium radiobacter *(G12). (Mean values with different letters are significantly different; Duncan's Multiple Range Test;* $P \leq 0.01$*; n = 6).*

Viable and heat-killed cells of *A. radiobacter* also led to a significant systemic reduction of nematode pene-

tration, whereas the culture filtrate of the bacteria showed no effect. Obviously, the mode of action of *A. radiobacter* differs from that of *B. sphaericus* and *A. radiobacter* metabolites are unable to elicit resistance. *A. radiobacter* is known to express exopolysaccarides (EPS) and lipopolysaccharides (LPS) on its surface (Sutherland, 1985). These surface structures of bacterial cell walls adhere specifically and strongly to cell wall structures of the plant (Costerton *et al.*, 1987) and are important virulence factors of plant pathogenic bacteria (Mansfield & Brown, 1986). They are also considered to affect physiological reactions in plants. EPS and LPS were found in living and in dead cells of the present G12 isolate, but not in culture filtrates (unpubl.). This could explain the activity of cells and the lack of activity of the bacterial metabolites. It is quite clear that the two bacteria strains examined in the present study have similar activity but different modes of action.

Before elucidating the exact mode of action of the induced resistance demonstrated here, a number of questions still need to be answered. Because the potato cyst nematode hatches only in the presence of a hatching factor produced by the host plant, the systemic induced effects may be due to alteration in exudates or the respective amounts of these factors in the exudates (Perry & Clarke, 1981). Secondly, specific exudates on the root surface are used by the cyst nematodes for host recognition (Zuckermann & Jansson, 1984). These components of the root exudates could be altered by the rhizobacteria inducing resistance. Thirdly, secreta in the root could be produced that repel the nematode from the root due to adverse environmental conditions as in resistant green manures. Fourthly, death of the juveniles may occur after penetration, caused by activity related to giant cell formation. These possibilities remain to be investigated. In conclusion, the results obtained here demonstrate for the first time that rhizobacteria have the ability to induce systemic resistance against cyst nematodes within the root system.

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