Recent and Up-Coming Strategies to Counter Plant-Parasitic Nematodes in Banana Cropping Systems of the French West Indies

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Abstract

In the French West Indies, the productivity of export banana plantations is adversely affected by plant-parasitic nematodes (PPNs) including the endoparasitic species *Radopholus similis* (Pratylenchidae). In the last decades, control of PPNs was mainly based upon repeated applications of carbamate or organophosphate nematocides that are potentially toxic for human health and the environment. This paper describes a prophylaxis-based strategy, combining soil and plant sanitation that was developed in recent years to reduce dependence on chemical nematocides. Soil sanitation was implemented through a cleansing system based on glyphosate injection of banana plants before up-rooting. In addition, as a decision support tool, soil cleansing assessment biotests were developed to evaluate the effectiveness of the method before planting new banana crops. Crops were initiated using tissue culture-derived plants of 'Grande Naine' (AAA, Cavendish subgroup). In association with soil sanitation, this resulted in a reduction of 60% in nematocide use. The plant sanitation system is being modified by i) selecting *R. similis* non-host rotational crops, such as perennial soybean (*Neonotonia wightii*), siratro (*Macroptilium atropurpureum*) and forage grasses like *Digitaria decumbens* and *Brachiaria humidicola*, ii) exploiting the existing variation in susceptibility to *R. similis* within Cavendish clones, and iii) identifying *R. similis*-resistant or weakly susceptible clones among improved banana hybrids developed by the CIRAD breeding programme. New initiatives to further enhance the PPN control method are also discussed. They include the promotion of techniques designed for improving management of crop residues, the identification of nematotoxic plants showing allelopathic effects against *R. similis* and the benefits from the preservation of soil biodiversity in banana cropping systems. Most of these approaches are being carried out in the framework of a European Commission-funded network of excellence known as ENDURE.

INTRODUCTION

Plant-parasitic nematodes (PPNs) have long been recognised as being among the most detrimental soil-borne pathogens of banana (Gowen and Quénéhervé, 1990). They occur as communities that vary with geographic and climatic conditions, soil type and cropping sequences. The burrowing nematode *Radopholus similis* (Tylenchida, Pratylenchidae) is the most damaging member of these parasitic communities (Sarah, 2000). From the 1980s until recently, the application of chemical nematocides (mainly carbamates or organophosphates) was the main method of controlling PPNs in banana. However, their use has been increasingly restricted because of their hazardous effects on human health and on the environment. As an alternative, land was used as fallow in the French West Indies (FWI) (Ternisien and Melin, 1989). However, even combined with

the use of plantlets derived from in vitro culture, recontamination occurred early in the first cropping cycle. Chabrier and Quénéhervé (2003) significantly improved the efficiency of the fallow period by injecting glyphosate into old banana plants to be destroyed before fallowing. Only 12% of the plants became infected in the following growing cycle of banana, compared with 76% with classical mechanical destruction. Nevertheless, in practice, as the duration needed for the fallow period to be fully efficient had not yet been defined, many attempts to satisfactorily complete fallows failed. At this time, growers were also asking for cover crops that could help to reduce populations of PPNs in the soil. Thus, there was an urgent need to design innovative cropping practices to control PPNs in banana that were also compatible with the need for sustainability.

The objectives of this paper were (i) to describe the prophylaxis-based strategy that was developed in the FWI in recent years to rationally reduce PPN populations in soils and (ii) to briefly present other approaches that are currently under study. How fallows coupled with the injection of banana plants with glyphosate were improved by a better knowledge of residual populations of *R. similis* in roots and soil after glyphosate injection is described firstly. How sanitation was implemented by selecting *R. similis* non-host rotational crops, exploiting variation in susceptibility to *R. similis* within Cavendish clones and identifying clones among improved banana hybrids that are resistant or less susceptible to PPNs is described secondly. Finally, approaches that are currently being developed in FWI to promote integrated crop protection against banana PPNs (Ferron and Deguine, 2005) are reviewed. Most of this work is being implemented in the framework of the European Network for Durable Exploitation of Crop Protection Strategies (ENDURE), a European Commission-funded network.

MATERIALS AND METHODS

All experiments described below were conducted in Guadeloupe. Similar experiments were also carried out in Martinique, with similar results.

Determination of Residual Populations of *Radopholus similis* in Roots and Soil after Glyphosate Injection

An old PPN-infested banana crop grown on an andosol soil (FAO-ISRIC-ISSS, 1998) was selected for the trial. Four glyphosate treatments injections were compared: T1: injection of 2 ml of commercial product (c.p.) titrating at 360 g/L into the pseudostem 1 m above the rhizome; T2: injection of 2 ml of c.p. directly in the rhizome at the base of the pseudostem; T3: injection of 5 ml of a mixture of 1/3 of c.p. + 2/3 of water into the pseudostem 1 m above the rhizome; T4: injection of 5 ml of a mixture of 1/3 of c.p. + 2/3 of water directly in the rhizome at the base of pseudostem. The trial was arranged in a randomised complete block with four replications, each comprising up to 80 banana plants. The dynamics of *R. similis* in roots were monitored every 15 or 30 days for 120 days. At this time, soil populations of PPNs were also extracted from soil samples taken near the rhizomes in rows (R) or 1.5 m from any rhizome in inter-rows (IR) and counted.

Biotests to Assess the Efficiency of Soil Cleansing

Biotests to evaluate soil cleansing in commercial banana plots were developed to check the efficiency of fallow periods already improved by glyphosate injections. Soil samples were taken from the commercial plots at various times to be analysed. One micropropagated plant of 'Grande Naine' (AAA genome, Cavendish subgroup), a cultivar that is susceptible to *R. similis* and other banana PPNs, was planted in each of 25 pots filled with 2 L of the soil taken for analysis. The banana plants were to act as nematode traps, and any residual PPNs in the soil would be expected to multiply in their roots. Potted plants were kept in a greenhouse (23-30°C and 80-90% relative humidity) for 60 days. PPNs were then extracted from the roots and counted, to calculate percentages of infested plants (number of plants with nematodes as percentage of total of 25 analysed plants per sampled plot).

The efficiency of fallow periods in commercial banana plots was monitored further by measuring PPNs in the roots of the new banana crop planted at the end of the fallow period using nematode-free, micropropagated plants. Composite root samples were taken from at least 10 plants in the 3rd month after planting and in the following months.

Extraction of PPNs from Root or Soil Samples

In all experiments, PPNs were extracted from roots using a centrifugal-flotation technique (Coolen and d'Herde, 1972) and from soil with a Seinhorst elutriator (Seinhorst, 1962).

Inoculation Experiments in the Greenhouse

Three series of experiments were carried out under greenhouse conditions (23-30°C and 80-90% relative humidity) to select *R. similis* non-host rotational crops/and or resistant banana cultivars. In each of the experiments, 'Grande Naine' was used as susceptible reference banana cultivar.

For the first series of experiments, seeds or cuttings of different tropical legumes, pasture grasses and diverse other plants (Table 1) were obtained from manufacturers or collected locally in fields. All plants were grown in 2-L plastic pots filled with a halloysitic soil until there was sufficient vegetative development for experimentation. Ten fully developed plants of each plant species were then inoculated with a native pathogenic population of *R. similis* (initial population Pi = 100 adults + juveniles).

In the second series of experiments, the susceptibility of 8 to 15 selected Cavendish lines (mainly mass selections of 'Grande Naine') to *R. similis* or *Pratylenchus coffeae* (Tylenchida, Pratylenchidae) were compared by inoculating micropropagated plants provided by the company VITROPIC. For each line, 10 plants were inoculated with either *R. similis* or *P. coffeae* (Pi = 400).

In the third series of experiments, the susceptibility to *R. similis* of a series of banana hybrids already identified as being partially resistant to both black leaf streak and Sigatoka leaf spot was assessed. Hybrids identified as 'Flhorban 925', 'Flhorban 926', 'Flhorban 927', 'Flhorban 928' and 'Flhorban 929' were provided by the banana-breeding program of CIRAD. For each hybrid, 10 micropropagated plants were inoculated with a population of *R. similis* (Pi = 200).

In these three series of experiments, plants were arranged in a completely randomised design. Nine weeks after the inoculation, PPNs were extracted from roots and counted. The susceptibility of plants to the inoculated PPNs was assessed by the ability of the initial inoculated population to reproduce. The multiplication rate mR = Pf/Pi (Pi: initial population of PPNs; Pf: final population of PPNs) was calculated at the end of the experiments. Variances were equalised by log(mR+1) transformations. Analysis of variance (ANOVA) was performed for transformed data. Mean values were separated at $P < 0.05$ using the Newman-Keuls test. When the conditions for an ANOVA were not satisfied, data were treated with the Kruskall-Wallis test and means further separated with the Mann-Whitney test.

Nematode Strains Used for Inoculation Experiments in the Greenhouse

The two pathogenic strains of *R. similis* and *P. coffeae* used in inoculation experiments were isolated from banana roots in Capesterre (Guadeloupe) and monoxenically reared on carrot discs (O'Bannon and Taylor, 1968; Pinochet et al., 1995). A nematode suspension containing 100, 200 or 400 individuals was poured onto the soil surface to inoculate plants.

RESULTS AND DISCUSSION

Residual Populations of *Radopholus similis* in Roots and Soil after Glyphosate Injection

Regardless of the treatment, *R. similis* populations in roots steadily declined following injection of glyphosate until they could not be measured after around 120 days (Fig. 1A). Similar results were obtained for other endoparasitic nematodes (data not shown). After 120 days, the roots were completely rotten due to the action of glyphosate, which is primarily an herbicide. In accordance with the biotrophic status of *R. similis* and other PPNs, it is not surprising that nematode populations decreased with increasing root decay.

In contrast, detectable populations of *R. similis* persisted in the soil in most of the treatments 120 days after plants were inoculated with glyphosate (Fig. 1B). At this time, residual populations of *R. similis* in soil were significantly higher in rows than those in inter-rows. These results suggest that rhizomes, which survive longer than roots, could be the main sources of *R. similis* inoculum in soil. These results also highlight the fact that fallow combined with an injection of glyphosate does not fully cleanse the soil of *R. similis* 4 months after injection of glyphosate. Replanting a new banana crop at this time and in following months thus still carries a risk. Since *R. similis* has no known survival form in soils, it is likely that a gradual decrease in its populations in soil may occur over time. In order to determine the appropriate length of time to cleanse the soil, biotests were developed to evaluate the quality of sanitation during fallow periods.

Biotests to Assess the Efficiency of Soil Cleansing

Biotests made at different times after the beginning of fallow periods allowed to monitor the progress of the soil cleansing of *R. similis* and to determine when sanitation is completed (no *R. similis* detected in soil samples) (Fig. 2A). Moreover, measurements of *R. similis* populations in the roots of a new banana crop planted when no more *R. similis* were detected by biotests showed that recontaminations only occurred at the end of the second growth cycle or the beginning of the third cycle (Fig. 2B). These results clearly illustrate the benefits gained from the sanitising procedure. Currently, in the framework of very restrictive laws on the use of pesticides, the implementation of fallow periods correctly monitored by such biotests and then replanted using only healthy micropropagated plants of 'Grande Naine' has resulted in a 60% reduction in the use of chemical nematocides in the FWI.

Selection of *Radopholus similis* Non-Host Rotational Crops

With a multiplication rate (mR) between 0 and 1, several plants did not allow *R. similis* to reproduce, thus behaving as non-hosts of this nematode (Table 1). In contrast, the highest build-up of *R. similis* populations occurred with the banana cultivar 'Grande Naine', which was used as a susceptible control.

We found that *Macroptilium atropurpureum*, *Crotalaria spectabilis, Digitaria decumbens*, *Panicum maximum,* and *Ananas comosus* were not susceptible to *R. similis* (Table 1), which is consistent with observations of other authors (Birchfield and Bistline, 1956; Colbran, 1963, 1964; Edwards and Wehunt, 1971; Rivas and Roman, 1985). With an mR close to 0, *Neonotonia wightii*, which is a wild perennial relative of *Glycine max*, was in our study also not susceptible to *R. similis*. This was unexpected as Huettel (1989) found fourteen cultivars of *Glycine max* to be a host of *R. similis*. The two cultivars of *Sorghum vulgare* screened were slightly susceptible to *R. similis* with an average mR of 1.5 to 2.75. The susceptibility of *S. vulgare* to *R. similis* is consistent with previous reports (Tarté et al., 1981; De Waele et al., 2006). In the literature, sugarcane is reported as either a host or non-host of *R. similis* (Edwards and Wehunt, 1971; Keetch, 1972; Rivas and Roman, 1985). In our study, two cultivars of sugarcane were found to be non-host plants for *R. similis* and one to be a host. It would be interesting to thoroughly investigate the host status of sugarcane by challenging different sugarcane cultivars with

various *R. similis* populations. Finally, this study may also be the first to report that *Brachiaria humidicola* and an *Impatiens* sp. are non-host plants to *R. similis*.

Selecting *R. similis* non-host plants that could be used as cover crops, not only to clear the soil of *R. similis* but also to replenish soil fertility, is a real alternative to fallow. Pineapple, sugarcane and the *Impatiens* sp. have already been introduced in banana cropping systems in the FWI. *Macroptilium atropurpureum*, *N. wightii*, *Brachiaria* and *Crotalaria* spp. are being considered as cover crops receiving increasing interest of growers. Given the fact that PPNs occur in multispecific communities, the susceptibility of these selected cover crops to PPNs other than *R. similis* will need to be considered.

Variation in Susceptibility of Selected Cavendish Lines to Nematodes

Although all tested Cavendish lines were susceptible to *R. similis*, they showed significant differences in their level of susceptibility (Fig. 3). 'Poyo' was the most susceptible of the tested lines (mR = 67), while the least susceptible lines were 'MA9827' (mR = 18), 'MB2' (mR = 32) and 'MA13' (mR = 34).

Multiplication rates were lower for *P. coffeae* than for *R. similis*, but variability of the susceptibility to the lesion nematode within the tested Cavendish lines was still detected (Fig. 4). 'Williams' (mR = 23.5) was found to be the most susceptible, while 'MB2' (mR = 9) showed the lowest susceptibility, along with 'Nord E1', 'L835', 'GB1' and 'Petite Naine'.

It is, of course, not surprising that Cavendish lines are susceptible to the PPNs tested in this study, since Cavendish cultivars have long been known to be suitable for reproduction of *R. similis* and *P. coffeae* (Gowen and Quénéhervé, 1990). Nevertheless, the differences in susceptibility measured in our experiments could be exploited commercially if producers of micropropagated Cavendish banana plants supplied growers with material less likely to increase pathogenic populations of nematodes.

Identification of Improved Banana Hybrids that are Resistant or Less Susceptible to *Radopholus similis*

All the banana hybrids tested had an mR value of less than 11 and displayed a level of susceptibility to *R. similis* that was significantly lower than that of the reference 'Grande Naine' (mR = 210) (Fig. 5). In particular, the hybrid 'Flhorban 924' had an mR of only 2.76, thus suggesting a status close to resistance. As all these hybrids have already been characterised as having partial resistance to both black leaf streak and Sigatoka leaf spot, they may have a promising future. However, more needs to be known about their agronomic qualities and commercial value before the potential contribution of these hybrids to a sustainable banana cropping system in the FWI is known.

Towards an Integrated Crop Protection Strategy against Plant-Parasitic Nematodes of Banana

A modular prophylaxis-based strategy against PPNs that integrates the results presented above is being developed in the FWI for banana cropping systems. It is based on three levels of interconnected modules.

The first level is composed of three modules devoted to soil and plant sanitation. It comprises i) the adoption of fallow periods, whose duration and quality of sanitation have proved satisfactory from biotests, ii) the rotation of banana crops with non-host plants to reduce *R. similis* populations in soils, and iii) the exclusive use of micropropagated banana planting material.

The second level includes two modules that are operational but not fully adjusted: i) the selection of PPN-resistant or tolerant cultivars among banana hybrids already characterised as partially resistant to both black leaf streak and Sigatoka leaf spot. This module is built on a technological platform designed to increase capacity for selecting banana hybrids and evaluating their agronomic performance and commercial value. It takes place in the framework of a workplan that has the objective to design more sustainable banana cropping systems, which reflects also the commencing ENDURE

network of excellence designed to reduce pesticide inputs in agriculture, promote alternative technologies and develop a unified knowledge of pest organisms in terms of ecology, epidemiology and genetics;

ii) the formulation of mathematical models to gain a better understanding of epidemic process, population growth of PPNs and crop losses. As an initial step, Tixier et al. (2006) have developed a predictive model that simulates the population dynamics of *R. similis* and *P. coffeae*. This model enables a reduction in the use of nematocides through a better knowledge of the population growth of PPNs.

The third level comprises three pre-modules that will evolve into new modules to further complete the backbone provided by modules of levels one and two. The first pre-module concerns the management of crop residues (mainly fragments of PPN-infected rhizomes) in banana fallows. The survival of PPNs in decaying banana crop residues and the influence of the localisation of such residues in the soil profile are being studied in relation to the overall infectious potential of soil. The second pre-module is the further identification and selection of nematotoxic plants that are suitable for crop rotations or integration into banana cropping systems. The allelopathic properties and biological effects of extracts from such plants on banana PPNs are being studied. The third pre-module is devoted to the development of a better understanding of links between soil biological diversity and overall soil functioning. This ongoing work, which is also being completed within the ENDURE network, is mainly aimed at studying whether soil biological diversity would favour the regulation of PPNs.

CONCLUSION

It is anticipated that the overall approach outlined in this paper will lead to an integrated crop protection strategy against PPNs in banana cropping systems.

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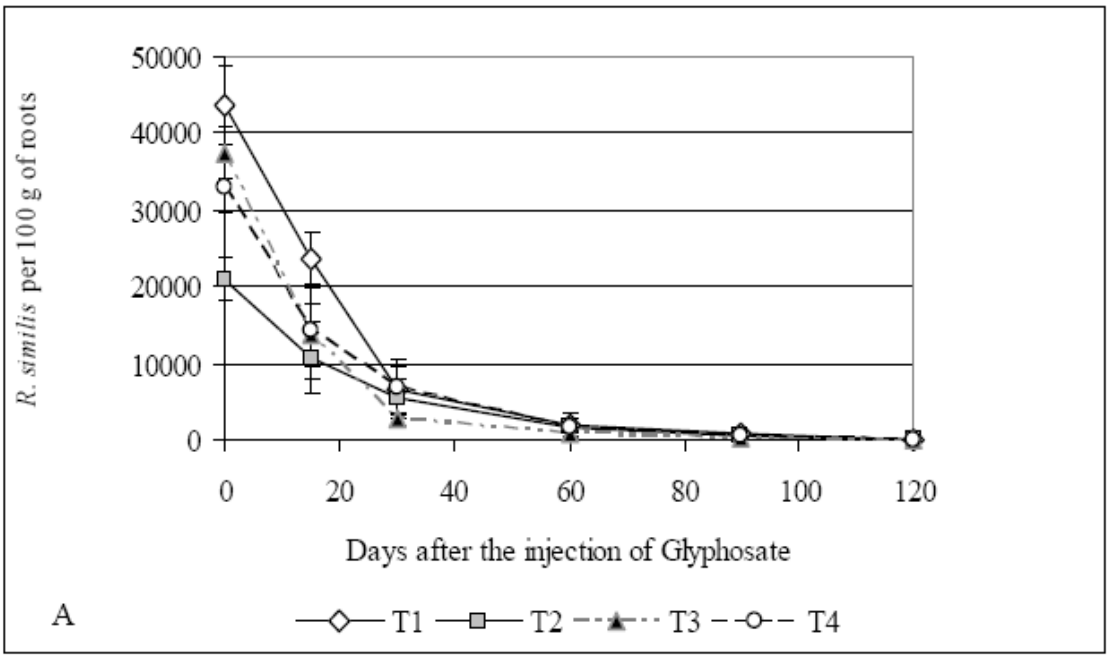
Tables

Table 1. Mean multiplication rates of *Radopholus similis* on different plant species and cultivars 9 weeks after inoculation with 100 nematodes per pot.

Common name	Botanical name	Multiplication rate mR=Pf/Pi
Siratro	*Macroptilium atropurpureum*	0.47 d
Perennial soybean 'Cooper'	*Neonotonia wightii*	0.02 d
Crotalaria	*Crotalaria spectabilis*	0.10 d
Sugarcane 'B 8008'	*Saccharum officinarum*	0.12 d
Sugarcane 'B69566'	*Saccharum officinarum*	0.10 d
Sugarcane 'R570'	*Saccharum officinarum*	6.88 b
Guinea grass	*Panicum maximum*	0.67 d
Pangola grass	*Digitaria decumbens*	0.00 d
Creeping signal grass	*Brachiaria humidicola*	0.10 d
Sorghum 'Supersile'	*Sorghum vulgare*	2.75 bc
Sorghum 'Sorgi'	*Sorghum vulgare*	1.50 c
Banana 'Grande Naine'	*Musa*, AAA, subgroup Cavendish	82.80 a
Pineapple 'Cayenne Lisse'	*Ananas comosus*	0.03 d
Impatiens	*Impatiens* sp.	0.10 d

Pf - final population; Pi - initial population; mR followed by the same letter are not significantly different at $P = 0.05$.

Figures



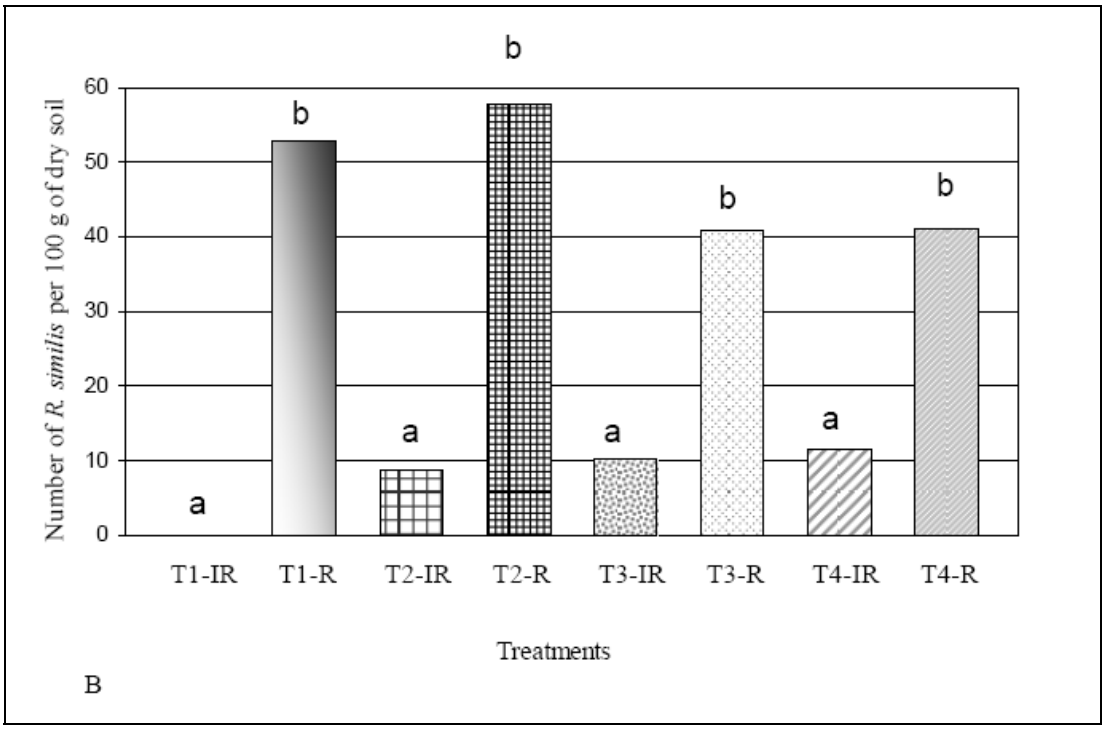
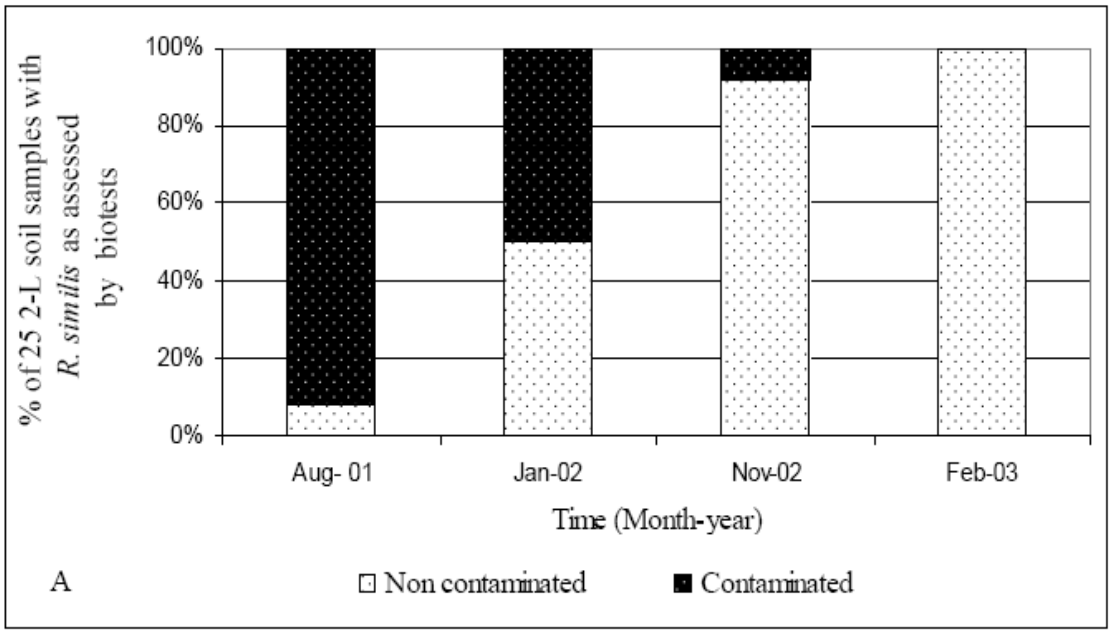


Fig. 1. *Radopholus similis* populations in banana roots and soil following the injection of banana plants with glyphosate. T1 to T4 are modalities and doses for glyphosate injection (see materials and methods). A: Numbers of *R. similis* in roots from 0 to 120 days after injection, B: Numbers of *R. similis* in soil in inter-rows (IR) and in rows (R) 120 days after injection.



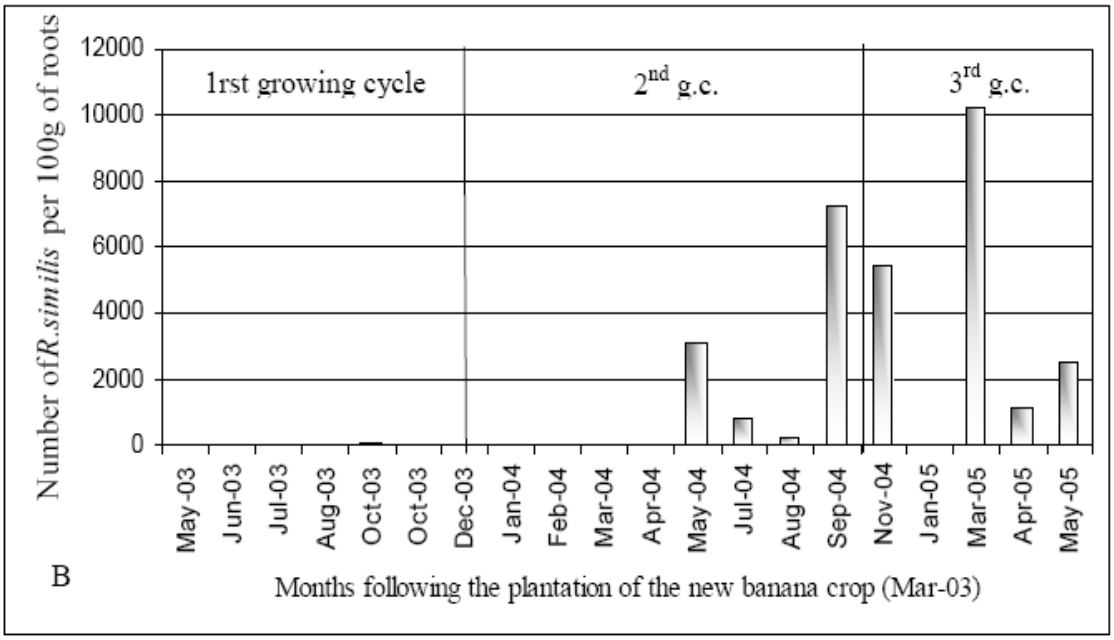


Fig. 2. Effect of a fallow period between banana crops on the population of plant-parasitic nematodes A: Levels of nematodes in plantation soil during the fallow period as assessed by biotests. B: Number of *R. similis* in roots sampled at intervals after the planting of a nematode-free banana crop after the fallow period.

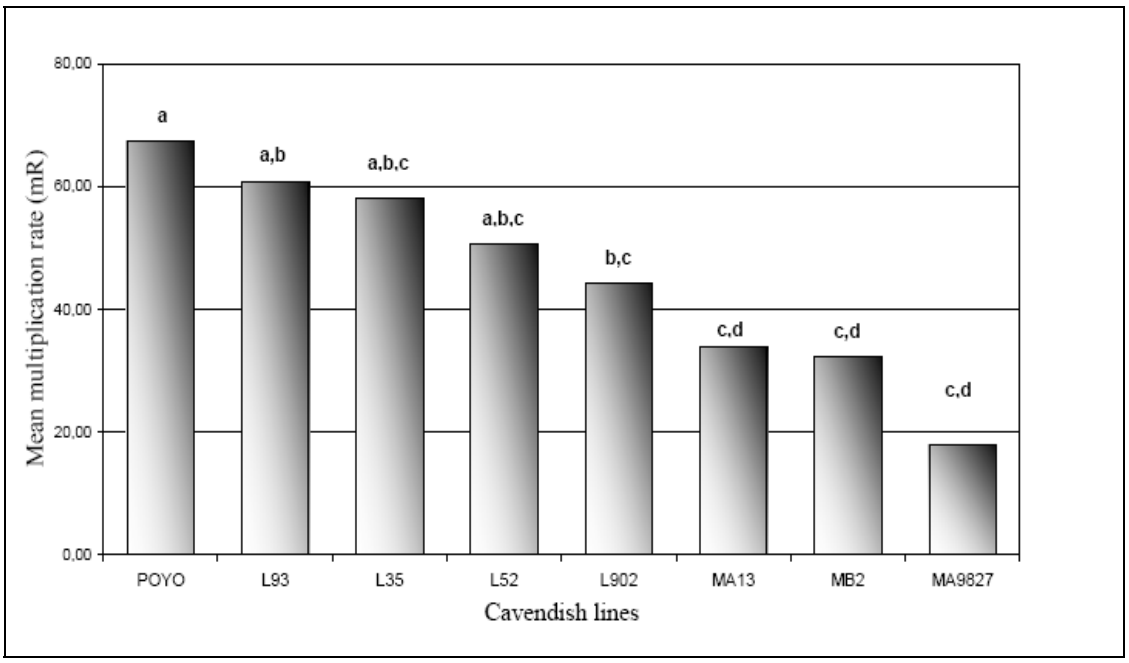


Fig. 3. Mean multiplication rates of *R. similis* on selected lines of Cavendish banana 9 weeks after inoculation with 400 nematodes per pot. Bars with the same letter are not significantly different at $P = 0.05$.

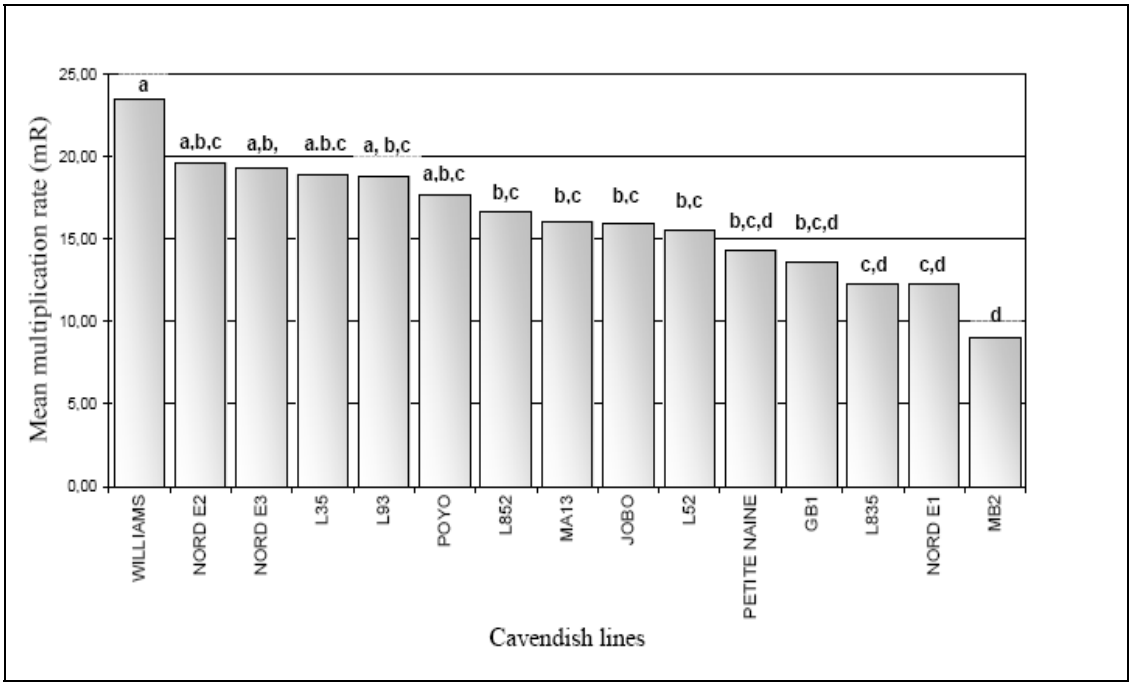


Fig. 4. Mean multiplication rates of *P. coffeae* on selected lines of Cavendish banana 9 weeks after inoculation with 400 nematodes per pot. Bars with the same letter are not significantly different at $P = 0.05$.

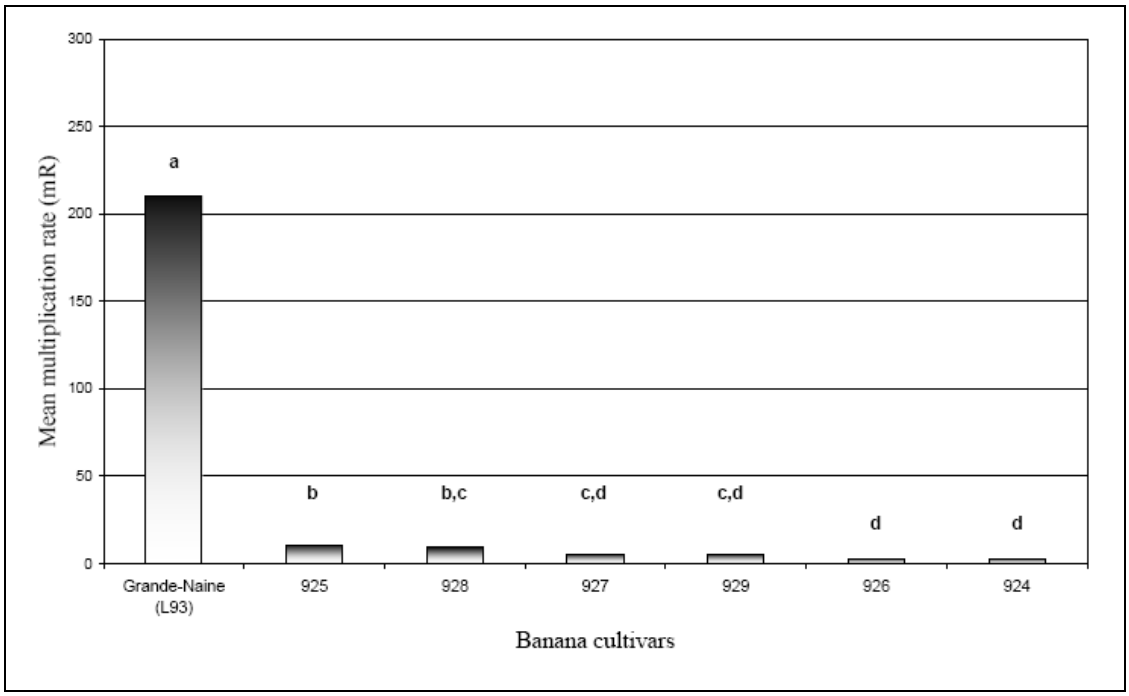


Fig. 5. Mean multiplication rate of *R. similis* on banana hybrids partially resistant to black leaf streak and Sigatoka leaf spot 9 weeks after inoculation with 200 nematodes per pot. Bars with the same letter are not significantly different at $P = 0.05$.