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Preventing nematodes from spreading: A case study with *Radopholus similis* (Cobb) Thorne in a banana field

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ABSTRACT

During the last decade, new crop systems have been developed in the French West Indies to avoid repeated applications of nematicides in banana fields. These combine fallow or rotation crops and nematode-free *in vitro* plants. In many fields, however, after 2–4 years, the burrowing nematodes *Radopholus similis* progressively re-infest banana fields, leading growers to re-apply nematicides. Among different hypotheses for re-infestation, we studied the possibility that nematodes were disseminated by runoff water. The study was conducted in an experimental field on plots that were defined by ditches or marked with flags and weeded or not, prior to replanting with *in vitro* plants. Results showed that 50–80 cm deep ditches efficiently prevent *R. similis* dissemination and that dispersion by water runoff is the major route of contamination. In contrast, weed management during the fallow period had little influence.

1. Introduction

The burrowing nematode *Radopholus similis* is a major pest of banana worldwide (Gowen et al., 2005; Quénéhervé, 2008). In large commercial plantations of banana, nematode control is still based on the application of two to four nematicide treatments per year. An alternative cropping system has therefore been developed in Martinique (French West Indies), during the last 15 years that is based on the cleanup of lands contaminated by plant-parasitic nematodes prior to planting. This cleanup is done through either a fallow period or an appropriate crop rotation, and then nematode-free banana *in vitro* plants are planted. Consequently, growers may cultivate bananas for 2–3 years without nematicide application in banana fields free of the burrowing nematode (Chabrier et al., 2005b). After a 2–4-year period, some banana fields are re-infested with *R. similis*, leading to reduction in both yield and plantation longevity. Previous studies (Zem, 1983; Rivas and Roman, 1985; Quénéhervé et al., 2006) showed that several weeds may act as transitional hosts of *R. similis*. Another hypothesis, that nematodes are disseminated by runoff water, was selected for this study. Numerous authors have considered that water dissemination can be a major factor in their spread (Faulkner and Bolander, 1970a, b; Bur and Robinson, 2004; Robinson, 2004). Furthermore, DuCharme (1955) and Loos (1961) observed *R. similis* in drainage water.

In this study, we present the spatial monitoring of the recontamination of a banana field by *R. similis*. Experimental plots were set up to evaluate, plant by plant, the respective influence of (i) weeds as nematode reservoirs and (ii) runoff water circulation on the successive nematode infestations, and consequently on the following nematode-free period.

2. Materials and methods

This study was performed in a 1 ha field near the Northern Atlantic coast of Martinique (61°02′11″ West, 14°48′14″North). The field was on a steep slope (38%), but such slopes are often found in banana fields in the Windward Islands and French West Indies. The soil is a nitisol, developed on volcanic andesitic ashes; these soils are 71% clay and the major clay mineral is halloysite, which forms sand-size particles with organic compounds. In such peculiar soils, the percolation of water is similar to that in sandy soil. Khamsouk (2001) showed that at soil capacity, water conductivity varies between 50 and 60 mm h^{-1} and that this nitisol contains numerous pores of 30–300 μm, which are ideal for nematode movement (Wallace, 1958). On such bare soil at field capacity, 10–20 mm of water precipitation is needed to observe runoff with a rainfall intensity of 30–60 mm h^{-1}.

At the beginning of the study, up to 32,000 individuals of *R. similis* per 100 g of fresh banana roots were found after

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extraction by the centrifugation–flotation method (Coolen and d'Herde, 1972). This highly infested field was split into five parts; upstream, a band of 20 m width was preserved with *R. similis*-infested banana plants, while downstream, four plots designated 11, 12, 21 and 22 with surface areas between 685 and 1227 m^2 were marked out (Fig. 1).

All banana plants in these four plots were destroyed by two successive glyphosate injections (Chabrier and Quénéhervé, 2003). Plots 11 and 12 were surrounded by ditches, 50–80 cm deep, to isolate them from any water runoff or flooding from adjoining plots. Plots 21 and 22 were delimitated only by flags, so that runoff and leached water could pass freely from the nematode-infested upper band.

After 3 months, the four experimental plots were ploughed and natural vegetation was allowed to grow freely on plots 11 and 21 ("weedy fallow") whereas glyphosate was applied (1 080 g ha^{-1}) on plots 12 and 22 each time a weed reached the early flowering stage ("mulched fallow"). Every 4 weeks, a floristic inventory was taken.

Thirteen months later, nematode-free *in vitro* plants of the widely grown but nematode susceptible Cavendish banana cv. "Grande Naine" were planted. Nematode infestations were evaluated at the flowering period of the first cycle (25 weeks after planting) to the third cycle (96 weeks after planting) of production. At each flowering, five root samples (about 20 cm long) were collected from the base of each corm of each banana plant where *R. similis* densities are usually the highest (Quénéhervé, 1990; Araya and De Waele, 2005).

The presence or absence of *R. similis* was assessed on every banana plant from each plot using a qualitative method of nematode extraction with hydrogen peroxide on an aliquot of 5 g root per plant (Gowen and Edmunds, 1973). Following this assessment, positive samples were combined in groups of five to 10 to reduce the number of composite samples to be extracted for quantitative results in the mist chamber (Seinhorst, 1950). We analysed 710 samples by hydrogen peroxide maceration and 82 (1st cycle) to 89 (3rd cycle) samples by mist chamber incubation.

Yield parameters were measured individually at flowering or at the end of each cycle (dates of flowering and harvest, numbers of hands and fingers per bunch, bunch weight and proportion of harvested plants). These data were used to calculate an annual raw yield indicator, expressed in tonnes ha^{-1} $year^{-1}$ and calculated according to the following formula:

ARY = plant density × proportion of harvested plants × average bunch weight × (365 days $year^{-1}$/duration in days of production cycle).

Weather data were also collected at a station 250 m from the experimental field. On bare nitisol, rainfall of 60 mm h^{-1} intensity (strong shower) needs at least 12 min for runoff to begin on fresh bare soil (water potential of −10 kPa), and almost 20 min on dry soil (water potential of −100 kPa). For this reason, we may consider that water leaching may occur only when rainfall exceeds 10–20 mm, depending to the initial soil moisture.

3. Results

3.1. Evolution of the infested plants from first to third cycles

During the fallow period, all plots were covered by weeds after 5 weeks. Creeper weeds (*Mikamia micrantha* HBK and *Ipomea tilliacea* (Willd.) Choisy) dominated first, but there then developed many clumps of Poaceae (*Echinochloa colona* (L.) Link, *Eleusine indica* (L.) Gaertn, *Chloris radiata* (L.) Sw., *Paspalum fasciculatum* Willd., *Leptochloa filiformis* Beauv. and *Sorghum halepense* (L.) Pers.) and Cyperaceae (*Cyperus* spp.). Also present were some *Phenax soneratii* (Poir.) Wedd., *Euphorbia heterophylla* (L.) Kl. and Garcke, *Vernonia cinerea* (L.) Less, *Amaranthus dubius* Mart. and *Solanum torvum* Sw.

On plots 12 and 22, flora was destroyed three times by glyphosate application. On plots 11 and 21, Poaceae first replaced the creepers and were then replaced by *P. soneratii*, *E. heterophylla* and *S. torvum* after the second month. Throughout the fallow period, both plots were completely covered by weeds.

The rainfall data collected close to the study field are presented in Table 1. The study began during a rather dry year; rainfall of more than 20 mm that might have generated water runoff on bare soil occurred only 25 times in 459 days. But the second and third cycles occurred during wetter years, with more than 40 rainfalls exceeding 20 mm per year. On bare soil, rainfall that may generate leaching occurred approximately once every 8 days.

Fig. 2 shows the location of infested plants at the first flowering period. On plot 11, surrounded by ditches and not

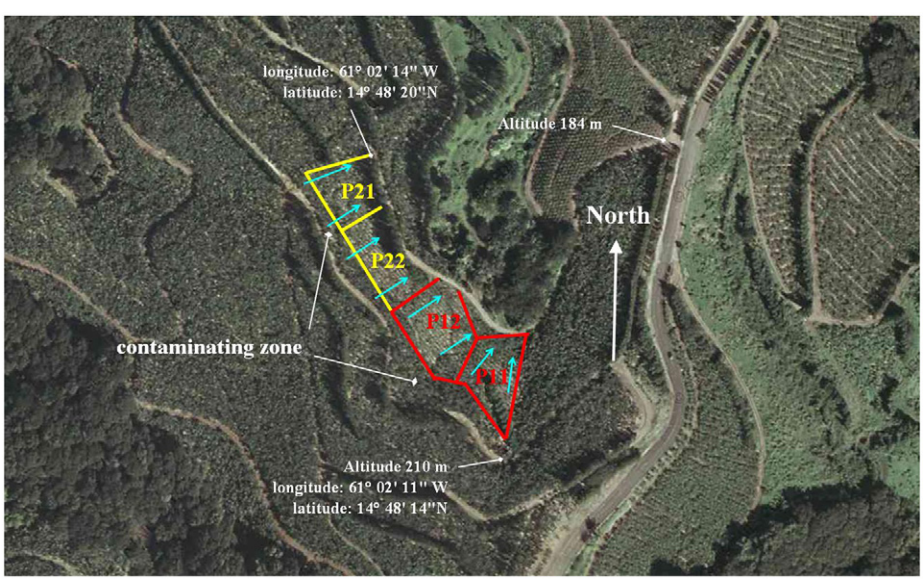

Fig. 1. Schematic map of the fields. P11 to P22: plot 11 to plot 22. Red line: plot border with ditches; yellow line: plot border without ditches. Blue arrows give the slope sense.

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weeded during the fallow period, five isolated mats were found infested, and five plants formed a group around plant 1150. At that place, the *in vitro* plant had died early and had been replaced by a ratoon sucker coming from an adjacent *R. similis*-infested field. This plant was destroyed at the end of the first cycle and replaced by an *in vitro* plant at the end of the second cycle. On plot 12, surrounded by ditches and weeded during the fallow period, six isolated plants were infested, most of them close to the northern ditch. On plot 22, with no ditches but weeded during the fallow period, 27 plants were infested; all were close to the upper border of the plot or to the northern ditch. On plot 21, also with no ditches but not weeded during the fallow period, 15 plants were infested; 12 of them were close to the upper border of the plot.

Fig. 3 shows the location of infested plants at the third flowering, slightly less than 2 years after planting. Only 10 plants were infested on plot 11 (only ditches). With the exception of the mats of the infested pocket downstream, former plant 1150, infested plants seemed to be randomly distributed. On plot 12 (ditches and weeded), nine plants were infested; five of them, highly infected, were close to the southern ditch, whereas the other four, much less infected, were randomly distributed. On plots 21 and 22 (no ditch), the upper border was totally contaminated and the distribution of infested plants seemed to follow lines from the top to downstream.

Fig. 4 summarizes the percentage of infected mats of each plot. On plots 11 and 12 surrounded by ditches, these percentages stayed very low (from 3.6% to 4.5%), whereas on plots 21 and 22, not surrounded by ditches, the percentages of infested plants were three times higher at first flowering and then increased dramatically (up to 45.5% and 41.8%).

In nematology, density and frequency provide different information about nematode infestations. In this study, the frequency was more important than density; in order to combine these data, we used a modified prominence value index (Beals, 1960; Quénéhervé and Ferris, 1990). This index, calculated as $P = \text{density} \times \text{frequency}^{1/2}$, used geometric means of *R. similis* concentrations in roots of infected plants. Geometric means were used because the *R. similis* distribution did not follow a normal law, and arithmetic means are not relevant. Depending on the plot, aggregative or even discrete distribution was observed (Figs. 2 and 3). In such cases, the modified prominence value index using geometric means is a better descriptor of the abundance of nematode communities. At the end of the first cycle, indexes were already 23 times lower on ditched plots and were equivalent on formerly weeded and mulched fallow (Table 2). After the third cycle, density increased even more dramatically than frequency in the plot not surrounded by a ditch and weeded during the fallow period.

Table 1
Weather data collected during the study at Bellevue's Meteorological station, 250 m from the experimental field

	Number of days	Cumulated rainfall (mm)	Number of days with rainfall	
			>10 mm	>20 mm
Year				
2002	365	1974	53	24
2003	365	2112	56	29
2004	366	3167	80	41
2005	365	3178	133	42
Period				
Fallow	459	2168	57	25
From planting to 1st flowering (nematode sampling)	178	1003	28	15
From 1st flowering to 3rd flowering (nematode sampling)	494	4463	111	62

3.2. Incidence of nematode dispersal on horticultural results

During this 3-year experiment (Table 3), only a few differences in yield parameters appeared among the treatments. Plots 12 and 21 produced bigger bunches with more fruits and a higher proportions of bunches were harvested (90.1% and 89.1%) on plot 12 at the end of the second and third cycles of production. As a result, yields were higher on plot 12. Conversely, plot 22 produced lower yields.

As few plants were infected at the end of the first and second cycles of production, and as *R. similis* damage usually tends to

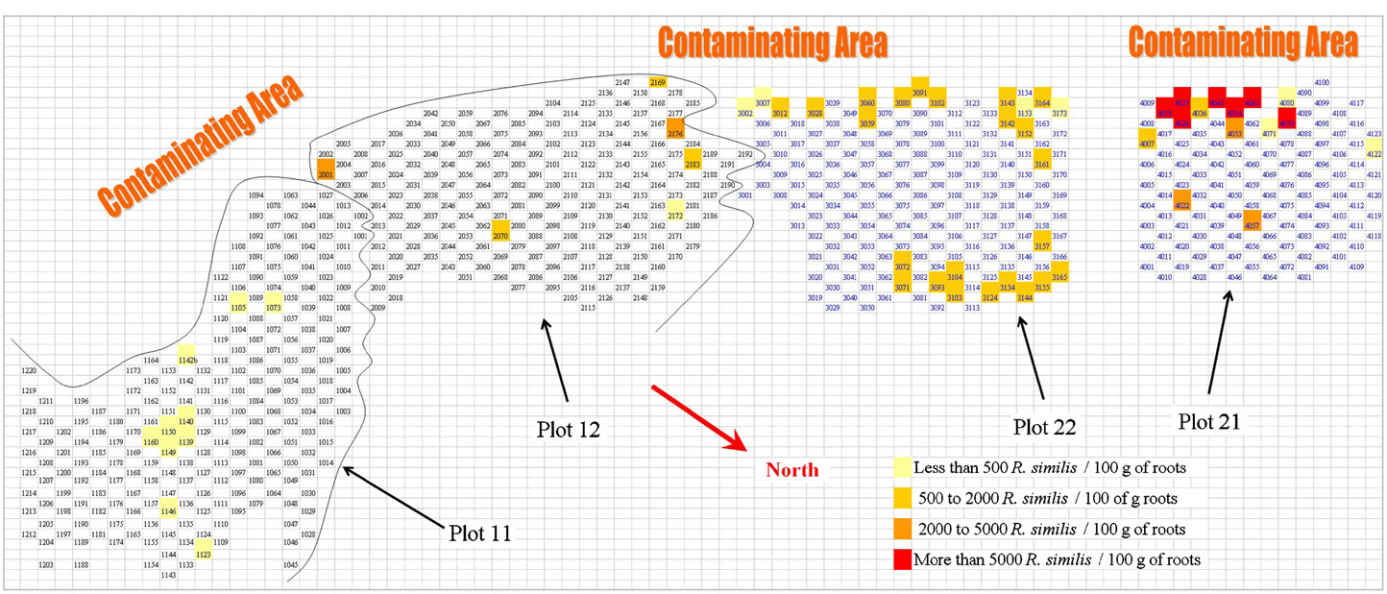

Fig. 2. Location of the infested (coloured) and uninfested plants at first flowering, 5.5–6 months after planting. Each number corresponds to a mat. Continuous lines represent ditches in the field.

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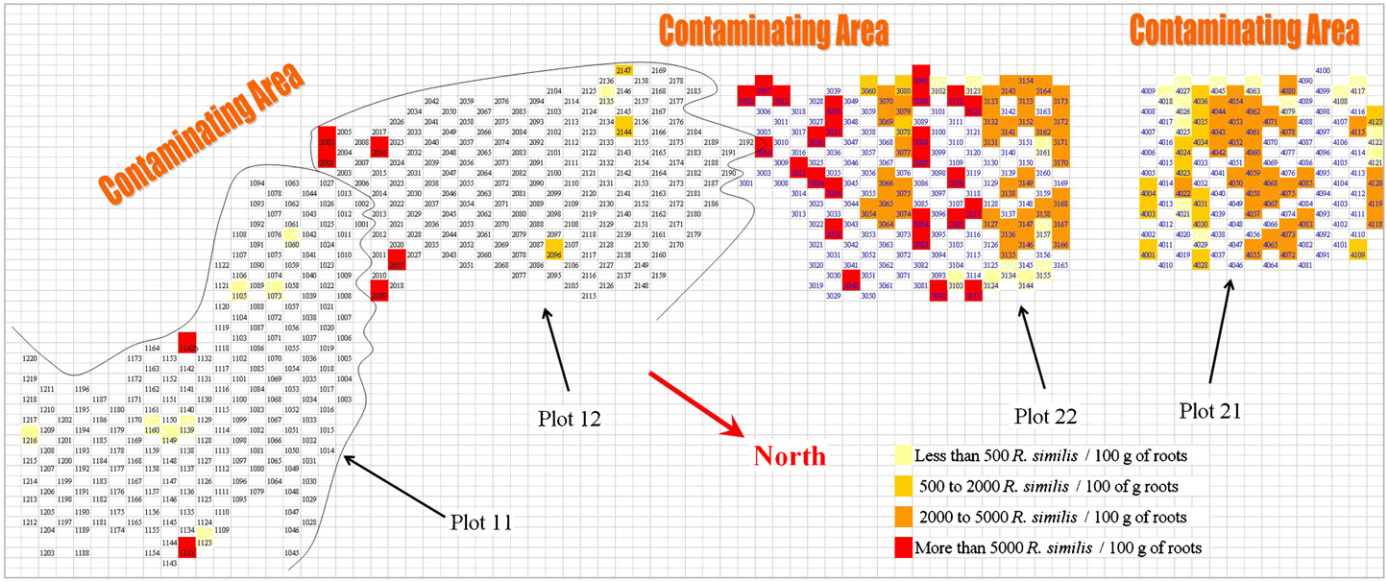

Fig. 3. Location of the infested (coloured) and uninfested plants at third flowering, 22–22.5 months after planting. Each number corresponds to a mat. Continuous lines represent ditches in the field.

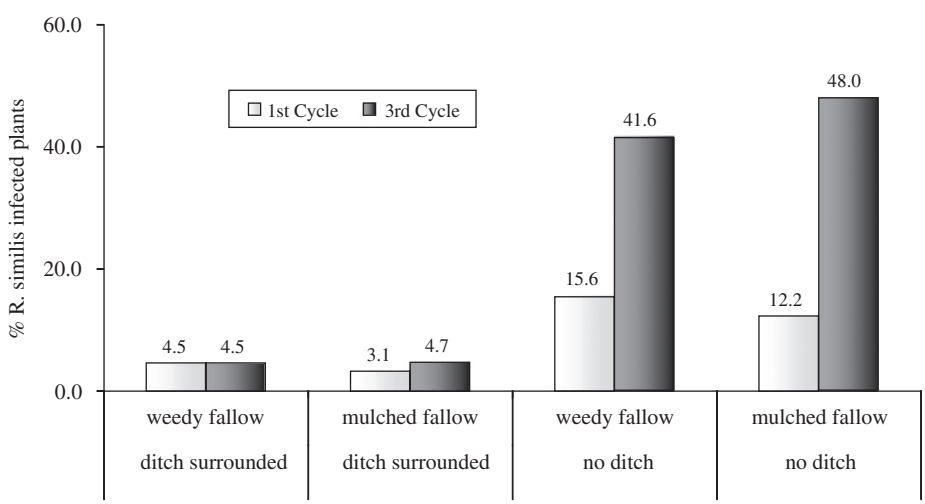

Fig. 4. Percentage of plants infected by *R. similis* after the first and third flowering.

Table 2
Evolution of prominence value index of plots and percentage of plants infected by *R. similis* from the first to the third flowering

Plot	Cycle	11	12	21	22
		Ditch surrounded, weedy fallow	Ditch surrounded, mulched fallow	No ditch, weedy fallow	No ditch, mulched fallow
Infected plants (%)	1st	4.5	3.1	15.6	12.2
	3rd	4.5	4.7	41.6	48.0
Prominence value index	1st	239	348	5748	7658
	3rd	320	4208	44 135	13 501

This index was calculated following the formula: PV = (number of infested plant/number of plants)$^{1/2}$ × (geometric mean of *R. similis* population in infested plants).

cumulate with time (Quénéhervé, 1993), results in Table 4 are limited to those obtained during the third cycle of production. For the most part, few differences were observed (Table 4). The gross yield reduction caused by *R. similis* reached only about 4% of the average yield for this last production cycle.

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Table 3
Effect of fallow management and ditch protection on the yield of a banana field over three successive production cycles

Plot	11	12	21	22
Number of plants	221	192	123	173
First cycle of production				
Interval planting–flowering (days)	185.1 ± 0.3	184.3 ± 0.3	183.8 ± 0.5	188.9 ± 0.4
Number of hands/bunch	7.5 ± 0.1	7.8 ± 0.1	8.1 ± 0.2	8.1 ± 0.1
Number of fingers/bunch	145.1 ± 3.4	155.9 ± 3.6	161.1 ± 3.9	162.4 ± 3.3
Duration of the cycle (days)	272.8 ± 2.3	280.2 ± 1.7	275.9 ± 2.8	283.0 ± 1.8
Bunch weight (kg)	28.2 ± 0.6	31.3 ± 0.7	29.4 ± 0.8	29.7 ± 0.8
% Harvested plants	85.0	80.2	84.6	77.5
Gross yield (t ha^{-1} $year^{-1}$)	57.7	58.9	59.3	53.3
Second cycle of production				
Interval previous harvest–flowering (days)	164.4 ± 2.8	161.2 ± 2.1	160.7 ± 3.6	168.2 ± 2.3
Number of hands/bunch	8.7 ± 0.2	9.1 ± 0.2	9.7 ± 0.3	8.9 ± 0.2
Number of fingers/bunch	184.8 ± 6.1	193.0 ± 5.1	211.4 ± 8.4	186.1 ± 6.4
Duration of the cycle (days)	244.5 ± 2.8	241.3 ± 2.4	242.6 ± 3.3	249.1 ± 2.8
Bunch weight (kg)	42.5 ± 1.3	44.0 ± 1.0	44.1 ± 1.7	41.7 ± 1.4
% Harvested plants	86.8	90.1	82.9	78.0
Gross yield (t ha^{-1} $year^{-1}$)	99.1	108.0	99.0	85.8
Third cycle of production				
Interval previous harvest–flowering (days)	161.6 ± 4.0	161.4 ± 2.4	157.1 ± 4.7	169.2 ± 4.9
Number of hands/bunch	8.2 ± 0.2	8.3 ± 0.2	9.1 ± 0.2	8.4 ± 0.2
Number of fingers/bunch	171.3 ± 5.5	174.5 ± 5.3	193.8 ± 7.6	175.5 ± 5.2
Duration of the cycle (days)	249.4 ± 2.5	250.6 ± 1.8	247.5 ± 2.9	253.0 ± 2.7
Bunch weight (kg)	42.5 ± 1.2	41.9 ± 1.1	46.5 ± 1.9	41.2 ± 1.4
% Harvested plants	74.1	89.1	70.7	68.8
Gross yield (t ha^{-1} $year^{-1}$)	82.9	97.9	87.3	73.5

11: ditch surrounded, weedy fallow; 12: ditch surrounded, mulched fallow; 22: no ditch, mulched fallow; 21: no ditch, weedy fallow. Confidence intervals were calculated with a 5% error.

Table 4
Effect of *R. similis* infestation on banana plants: average yield parameters collected on infected and uninfected mats

Plot	11	12	21	22	Average loss (%)
Number of plants					
Infected	10	9	56	72	
Uninfected	211	183	67	101	
Interval previous harvest– flowering (days)					
Infected	158.8 ± 20.8	151.0 ± 11.2	161.4+8.2	165.2+7.9	−1.7 ± 1.2
Uninfected	161.8 ± 4.1	161.8 ± 2.5	158.8 ± 5.7	171.7+6.2	
Plant height					
Infected	3.16 ± 0.18	3.14 ± 0.19	3.26 ± 0.08	3.20+0.08	
Uninfected	3.2 ± 0.04	3.13 ± 0.04	3.19 ± 0.06	3.26+0.06	
Plant circumference					
Infected	77.1 ± 6.8	78.4 ± 3.5	79.1 ± 2.0	74.0+1.9	
Uninfected	75.3 ± 0.9	75.2 ± 1.1	77.5 ± 1.7	74.9+1.4	
Number of hands/bunch					
Infected	7.4 ± 2.2	7.7 ± 2.0	8.1 ± 0.9	6.3+0.9	−13.1 ± 8.0
Uninfected	8.2 ± 0.2	8.2 ± 0.2	9.0 ± 0.3	8.4+0.2	
Number of fingers/bunch					
Infected	179.0 ± 23.1	185.5 ± 22.2	195.8 ± 12.6	174.2+8.7	2.9 ± 3.3
Uninfected	170.9 ± 5.5	174.0 ± 5.4	192.3 ± 9.5	176.2+6.5	
Duration of the third cycle (days)					
Infected	249.5 ± 11.6	243.3 ± 9.8	244.6 ± 5.0	250.3+4.9	−1.7 ± 1.2
Uninfected	249.4 ± 2.5	250.9 ± 1.9	249.7 ± 3.2	254.8+3.0	
Bunch weight (kg)					
Infected	38.6 ± 5.4	42.9 ± 4.8	45.7 ± 2.9	41.0+2.5	−2.7 ± 4.8
Uninfected	42.6 ± 1.2	41.9 ± 1.1	47.1 ± 2.6	41.3+1.6	
% Harvested plants					
Infected	88.9	77.8	67.9	66.7	−2.7 ± 13
Uninfected	75.4	89.6	72.9	71.7	
Gross yield (t ha^{-1} $year^{-1}$)					
Infected	90.4	90.1	83.5	71.7	−3.97 ± 7.1
Uninfected	84.5	98.3	90.2	76.4	

11: ditch surrounded, weedy fallow; 12: ditch surrounded, mulched fallow; 22: no ditch, mulched fallow; 21: no ditch, weedy fallow. Average loss = (1–R) *100, with R: ratio between measures on infected and uninfected plants.

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4. Discussion

During the fallow period, several host plants of *R. similis* were observed: among them, *E. colona*, *P. fasciculatum*, *E. indica*, *P. soneratii* and *S. torvum* are reported as good hosts of *R. similis* (Quénéhervé et al., 2006). It was rather surprising that only a few differences appeared between weedy and mulched fallow. This is probably the result of a very efficient previous fallow period that destroyed almost all *R. similis* of the previous banana plants.

In contrast, the presence of ditches had a very important effect on nematode dissemination. Plants at the upper part of plots without ditches 21 and 22 immediately downstream from the infested area were highly likely to be contaminated. On plot 22, it also seems that a spot of *R. similis* had remained at the lowest extremity of the plot. In contrast, on plots 11 and 12, if we discount downstream plant 1150, the few contaminated plants seemed to be randomly distributed.

Fourteen months later, little had occurred on plot 11: we found *R. similis* in only three new plants (among 210 previously uninfested). In plot 21, contamination spots developed upstream to downstream, following lines of planting, which, in that plot, were disposed parallel to the main slope. In plot 22, spots developed not only in the slope direction, but also along diagonal lines (see for example the line formed by plant 3015–3024–3034), which, in the field, corresponded to a major water runoff pathway. It also seems that some contamination spots grew in all directions, perhaps because *R. similis* was disseminated by root contact. O'Bannon and Tomerlin (1969) showed that *R. similis* can rapidly move on roots of *Solanum nigrum* and thereby migrate 21 cm per month. At such a speed, it may theoretically spread from one banana plant to another in 11 months, as the average distance between banana plants was 2.3 m. However, in our study, *R. similis* spread a lot faster than previously described. In plots without ditches, *R. similis* migrated up to 14 m in 17 months, corresponding to five or six distances between two plants.

On the whole, these results suggest that although several spreading phenomena may occur simultaneously, spread by runoff was probably the major way of dissemination. Numerous authors consider that nematodes, including *R. similis*, can be disseminated by runoff water (Bur and Robinson, 2004). Duncan et al. (1990), however, observed that in a Florida citrus orchard, *R. similis* was unable to disseminate through root-free soils. In Florida, bare soil acts as barriers that are wide enough to avoid water runoff and thus nematode dispersion. Conversely, in our experiment, runoff water crossed plots without ditches up to 25 times per cycle of production.

Paradoxically, we found in small-scale studies, that dissemination by runoff water affected only a marginal portion of the *R. similis* population (Chabrier, unpublished data). This phenomenon apparently requires many conditions: soil has to be close to water saturation, nematode population has to be close to the soil surface and rain intensity has to be high enough. But, as banana plants concentrate up to 30 times the water flows that run along their stem (Bassette and Bussière, 2004), and as *R. similis* populations are concentrated near the corm (Quénéhervé, 1990; Araya and De Waele, 2005) and thus the plant base, these conditions occur more often than we would expect. Moreover, although nematode numbers from a single square metre may be very low, in the field, water flow may collect nematodes from areas of several hundreds of square metres, thereby disseminating populations large enough to infest banana plants downstream. When ditches are present, they can prevent contamination from an entire plot upstream and also large runoff inside the plot, so that little, if any, water dissemination occurs. This is probably why we observed hardly any dissemination inside plots 11 and 12.

However, at flowering of the third cycle, although the *R. similis* distribution in the northern half of plot 12 looked like those observed overall in plot 12, four mats were extensively attacked near the border of the eastern ditch. It is possible that these plants had some roots in contact with the ditch wall and thus were likely to be contaminated by some nematodes transported and decanted in the ditch.

Despite these differences in nematode infestation, there was little impact on yield indicators. In the French West Indies, the main damage caused by *R. similis* is by plants toppling over (Blake, 1972; Chabrier et al., 2005a) and thus nematode damage is also linked to other phenomena, especially wind during fruit fill. As no high winds (more than 60 km h^{-1}) occurred between flowering and harvest of the second and third cycles, few bunches were lost.

5. Conclusion

Ditches efficiently isolated field sectors and thus protected banana plants from *R. similis* infestation. However, other studies (Faulkner and Bolander, 1970a, b; Waliullah, 1989; Tapia et al., 2007) showed that irrigation canals and ditches may also drain nematodes and disseminate them. In the eastern border of plot 12, this dissemination occurred but was limited to four plants. Depending on their depth and orientation, ditches may thereby favour or prevent dissemination.

What is more, in this study, the main *R. similis* dissemination process clearly involved leaching. Even though *R. similis* leaching appears as a secondary phenomenon at the 0.1 m scale (Chabrier, unpublished data), runoff water is an efficient dissemination process on a field scale. As a result, although ditches are efficient in preventing *R. similis* dissemination, they are likely to be even more efficient with nematodes such as *Scutellonema cavenessi*, whose behaviour favours their leaching (Cadet et al., 2002).

In this study, prevention was efficient enough to delay field infestation by more than 3 years. By combining efficient fallows with appropriate set-up and management, *in vitro* plant planting and ditches to prevent recontamination, it is now possible to manage an intensive banana field without any nematicide.

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