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Nematode dispersion by runoff water: Case study of *Radopholus similis* (Cobb) Thorne on nitisol under humid tropical conditions

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ABSTRACT

To minimize application of nematicides in banana fields, crop systems have been developed in the French West Indies that combine fallow or rotation crops and nematode-free *in vitro* plants. After two to four years, populations of the burrowing nematode *Radopholus similis* have developed enough to cause economic losses, leading banana growers to use nematicides. To understand how banana fields are recontaminated, we studied the dissemination of *R. similis* by water flow. At a 1-m scale, we analyzed the dispersion of *R. similis* under a rainfall simulator: we isolated a 1-m^2 study plot, placed a *R. similis* suspension on the upstream soil surface, and simulated a 60 mm/h rainfall for 72 min. We collected soil samples every 10 cm downstream after 12 min of rainfall, and subsequently at 20-min intervals, and extracted the nematodes using a Seinhorst elutriator and then a Baermann funnel. Our results showed that the nematode dissemination follows an inverse exponential law, and depends more on soil moisture at the beginning of rainfall than on the length of rainfall: in fresh soil, 69–80% of the *R. similis* recovered were found less than 10 cm downstream from the nematode inoculation line, whereas in wetted soil, 76–85% of the recovered individuals were collected in the outlet tub located downstream from the apparatus. This passive dissemination model partially explains the distance covered by individual nematodes but not the low percentage of motile nematodes recovered in the outlet tub (10% and 36% in fresh and wet soils) compared to the percentage of motile nematodes found in the soil (80% and 84% in fresh and wet soils). Indeed, water runoff is likely to disseminate *R. similis* over long distances only when soil moisture is close to field capacity.

1. Introduction

The burrowing nematode *Radopholus similis* is a major pest of banana worldwide (Gowen et al., 2005). In most commercial banana plantations, nematode control is currently based on two to four nematicide treatments per year; product used, mainly organophosphorous (e.g. cadusafos and terbufos) or carbamates (e.g. oxamyl), are at least harmful, and may even

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be toxic for field workers and for the environment (Tomlin, 2003). In Martinique (French West Indies), in the last 15 years an alternative cropping system has been developed that is based on the disinfestation of land contaminated by nematodes followed by replanting with nematode-free banana vitroplants. Disinfestation is achieved either through a fallow period or an appropriate crop rotation after obligatory destruction of the banana plants by injecting herbicides (Chabrier and Quénéhervé, 2003). Using this cropping system, growers can cultivate bananas for two to four years without applying a nematicide (Chabrier et al., 2005). However, after four years, banana fields are often reinfested by the burrowing nematode.

Many authors consider that nematodes are disseminated mainly by water (Faulkner and Bolander, 1970a,b; Croll and Mathews, 1977; Burr and Robinson, 2004). As far as the burrowing nematode is concerned, in Florida, DuCharme (1955) reported that *R. similis* was disseminated by water in citrus orchards, and in Jamaica, Loos (1961) reported that *R. similis* was disseminated by surface water flowing from infected banana plantations. Since the phenomenon had been observed only empirically, field experimental studies were designed by Cadet and Albergel (1999) to understand the detailed mechanisms involved in dissemination. A further study (Cadet et al., 2002) showed that nematode dissemination by surface water differed widely among the different nematode species. In our current study, the dissemination of *R. similis* by runoff water was measured at the 1-m scale using a rainfall simulator. Our aim was to determine the distance *R. similis* individuals can be transported by runoff water, and are thus likely to be disseminated by surface water when upstream fields are contaminated and the water runs down a slope into a downstream plantation.

2. Materials and methods

Experiments were in two adjacent fields in the Rivière Lézarde plantation in central Martinique. The soil is a nitisol derived from volcanic (andesitic basalt) ashes. This type of soil is characteristic of the lowlands in central Martinique. The clay portion is predominant, but the main clay mineral is halloysite, which forms sand-size particles with organic compounds (Table 1). The diffusion of water in this type of soil is similar to that in a sandy soil. Khamsouk (2001) showed that, at field capacity, water conductivity varies between 50 and 60 mm/h. At the experimental site, the median conductivity, measured with a membrane infiltrometer, was 52 mm/h at the surface of the bare soil. The slopes, which vary from 3% to 13%, are representative of the slopes generally found in commercial plantations in Martinique. In this study, we simulated rainfall of 60 mm/h, the quantity observed typically for two days a month during the rainy season (Meteo-France, unpublished data), but only one day every three months during the dry season. The study was conducted during the dry season (February–April 2006); we studied two initial soil moisture contents: (i) soil at natural soil potential, i.e. approximately −10 kPa (pF 2); (ii) wetted soil, with nematodes applied after a simulated rain of 105–120 mm; in this case, the soil surface was close to water saturation.

The highest numbers of *R. similis* are normally found close to the banana corm (Quénéhervé, 1990; Araya et al., 1999). In commercial plantations, the soil around the base of the mats is usually bare, which is why we simulated rain on bare soil throughout the study. Experiments were performed on a bare fallow field (four plots) and on the adjacent weeded citrus orchard (two plots). Before the experiments, we took eight soil samples to check no *R. similis* were present in either field. Nematodes were extracted from the soil using an elutriation method (Seinhorst, 1962) and separated from remaining particles using Baermann funnels (Hooper, 1986). We also checked there were no *R. similis* in citrus roots using a centrifugation-flotation method (Jenkins, 1964).

Rainfall was applied using a rainfall simulator consisting in four parts: a frame, a standpipe, a collecting tub and a pyramidal tent (Asseline and Valentin, 1978).

The frame: an experimental plot of 1 m^2 was isolated from the surrounding area by borders made of vertical iron sheets 18 cm high (8 cm hammered into the soil, 10 cm left protruding above the surface of the soil).

The standpipe: a 4-m high galvanized standpipe with a nozzle to disperse the water was set up in the plot. A wiper motor moved the nozzle so that the water was sent up the plot. The rotation angle and the water pressure (40 kPa) were adjusted to the desired rainfall intensity of 60 mm/h.

The collecting tub: downstream, a buried outlet tub collected runoff water including the particles in suspension.

The pyramidal tent: this covered the whole facility to avoid interaction with wind or natural rain.

Each rainfall simulation comprised a separate experiment. Before each experiment, a nematode suspension was extracted from banana roots from a commercial plantation

Table 1 – Granulometry of nitisol in Martinique obtained with (i) standard procedures after sonification and dispersion in sodium hexametaphosphate (standard granulometry) and by (ii) sieving without dispersion (apparent granulometry).

	Standard granulometry		Apparent granulometry	
	Particle size (μm)	Weight of soil fraction (g/100 g)	Particle size (μm)	Weight of soil fraction (g/100 g)
Sand	50–2000	11.3	500–2000	1.91
			312–500	6.71
			200–312	26.96
			100–200	29.65
			50–100	29.43
Loam	2–50	14.6	0–50	5.34
Clay	0–2	73.4		

Table 2 – Numbers of nematodes applied during rainfall simulations.

Soil	Replicates – field	Volume suspension (cm^3)	Number of applied *R. similis*		
			Motile	Immotile	Total
Fresh	1 – fallow	400	26 560	19 840	46 400
Fresh	2 – fallow	500	29 800	35 800	65 600
Fresh	3 – orchard[a]	300	45 300	30 900	76 200
Mean ± 5% confidence interval		400	33 887 ± 11 334	28 847 ± 9 252	62 733 ± 17 093
Wetted	1 – fallow	230	14 145	13 800	27 945
Wetted	2 – fallow	300	39 000	17 400	56 400
Wetted	3 – orchard[a]	300	20 700	5850	26 550
Mean ± 5% confidence interval		277	24 615 ± 14 577	12 350 ± 6688	36 965 ± 19 062
Fisher's test with $P = 5\%$			ns	ns	ns

[a] As no *R. similis* were present either in Citrus roots or in soil, and as the soil surface of the inter-row of the orchard was similar to that of fallow, no differences were taken into account between the fallow and the orchard for statistical calculations.

to prepare an inoculum. Banana roots were placed in a mist chamber for one week to obtain a nematode suspension according to the method of Seinhorst (1950). Details of the different nematode suspensions are listed in Table 2.

The day before each experiment, a 1-m^2 study plot was isolated with iron sheets (as described above) and its surface was smoothed with a knife and checked with a bubble level. A downpipe 2 mm deep and 1 m long was laid out 40 cm downstream from the upper part of the study area. The nematode suspension was placed carefully on the surface of the soil along the whole length of the downpipe (Fig. 1).

For each experiment, rainfall was applied in four successive sequences. The first rainfall (12 min) corresponded to the time needed for the runoff water to reach the tub on the fresh soil (potential around −10 kPa). The three following rainfalls each lasted 20 min. At the end of each rainfall, we traced a grid downstream from the nematode set-down line. The grid consisted of quadrats measuring 10 × 10 cm^2. Each "column" in the grid, which was laid out along the slope of the stream, corresponded to a runoff trail with six quadrats, each of which corresponded to six distances from the initial lines, 0–10 to 50–60 cm (Fig. 1). At the end of each simulated rainfall, we collected the soil under every square along the two trails with a spatula. In this way we obtained two series of soil samples (10 cm × 10 cm wide × 1 cm deep). After sampling, we covered the lines that had just been sampled with glass plates (60 cm × 10 cm wide × 1 cm deep) to replace the soil that had been removed, and then applied the following simulated rainfall. After each rainfall, we also collected pairs of soil samples at the edge of the study area; these samples were collected at two depths (0–10 and 10–20 cm) and were used to measure water potential by ultrafiltration in a pneumatic pressure chamber (Teissier, 1984), and soil humidity.

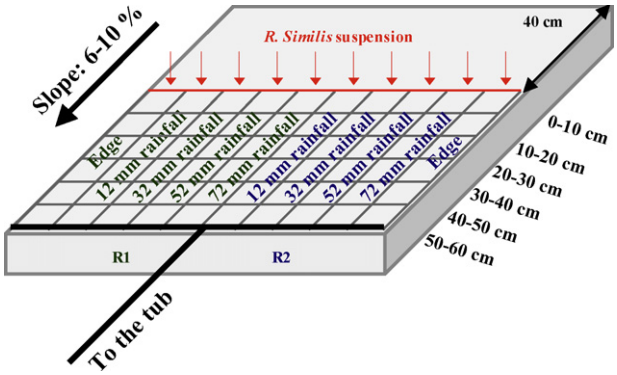

Fig. 1 – Diagram of a plot that received simulated rainfall.

Each experiment supplied two sets of 24 samples to evaluate nematode dispersion under four successive simulated rainfalls. Each experiment was repeated three times (Table 3). Nematodes were extracted from all the soil samples by elutriation (Seinhorst, 1962) and separated from any remaining particles using Baermann funnels (Hooper, 1986). Nematodes were then counted using an inverted light microscope and values were expressed as percentages of numbers inoculated. At the end of each experiment, we also collected the runoff water (including particles in suspension) in the outlet tub. Nematodes were extracted from runoff water by sieving (using a column of 80–25 μm sieves to collect nematode-size particles) followed by centrifugation-flotation (Jenkins, 1964).

Variance analyses were used to compare the results of the different rainfalls for each distance covered. Two variables were tested: the percentage of recovered nematodes and the percentage of motile individuals. When the Fisher test was significant for $P < 5\%$, mean values per treatment were classified using Duncan's multi-range test. To compare distribution among different layers, the percentages of recovered *R. similis* were transformed using the formula $\log(x + 10^{-5})$; linear regression was used to establish the relationship between depth and this variable, after checking that the residues were normally distributed using Shapiro–Wilk's test. If $\log(y) = ax + b$, then, $y = e^{ax} \times e^{b}$, results of linear regressions were expressed as $y = c \times e^{dx}$ (exponential regression).

3. Results

In fresh soils, the water potential measured in Teissier's chambers was close to −10 kPa at the beginning of the experiment. At this potential, capillaries with a diameter of more 30 μm are assumed to be filled with air (Wallace, 1958).

Table 3 – Conditions of rainfall simulations.

Soil	Field	Replicates	Rainfall before nematodes were set down	Water content when nematodes were set down (g/100 g)	Water potential (kPa)	Slope (%)
Fresh	Bare fallow	1a–1b	0	46.1	−10	10
Fresh	Bare fallow	2a–2b	0	47.2	−8	13
Fresh	Lime orchard	3a–3b	0	46.7	−8	5
Wetted	Bare fallow	1a–1b	1.45 h × 60 mm/h	63.0	More than −0.3	8
Wetted	Bare fallow	2a–2b	1.55 h × 60 mm/h	66.0	More than −0.3	8
Wetted	Lime orchard	3a–3b	2 h × 60 mm/h	64.6	More than −0.3	3

Water content in g of water per 100 g of dry soil. Water potential in kPa (kiloPascal), 1 kPa = 1000 Pa = 1000 kg $m^{-1}s^{-2}$. Slope in m/100 m.

During the two first simulated rainfalls, water potential increased (from almost −10 kPa to respectively −1.8 and −1.0), meaning that the capillaries were filled up progressively with water. After the second simulated rainfall, the water potential remained greater than −1 kPa at the surface of the soil and close to this value at a depth of −5 to −10 cm (Fig. 2). At these water potentials, capillaries with a diameter of less than 300 μm are full of water.

Table 4 – Dissemination of *R. similis* after 4 simulated rainfalls of different lengths at 60 mm/h on fresh soil (water potential from −8 to −10 kPa) and on wetted soil (close to water saturation): population recovered in the different quadrats and percentage of motile *R. similis*.

Distance covered (cm)	Rainfall (mm)	Fresh soil				Wetted soil			
		% Recovered		% Motile		% Recovered		% Motile	
0–10	12	71.68		78.9		13.75		79.3	
	32	71.82		81.8		13.10		88.5	
	52	68.96		87.5		11.85		85.7	
	72	79.50		86.4		6.77		87.6	
Mean		72.99	ns	83.7	ns	11.37	ns	85.3	ns
10–20	12	10.88		79.1		4.60		89.2	
	32	18.02		88.6		4.21		87.7	
	52	10.80		69.5		4.18		78.8	
	72	5.46		79.0		2.91		71.7	
Mean		11.29	ns	79.0	ns	3.98	ns	81.8	ns
20–30	12	5.92	ab	77.6		2.62		83.4	
	32	2.68	ab	82.0		0.78		95.5	
	52	7.02	a	86.2		2.62		73.6	
	72	2.07	b	83.3		2.09		77.6	
Mean		4.42	S	82.3	ns	2.03	ns	82.5	ns
30–40	12	6.50		90.4	a	1.49		94.5	
	32	3.45		65.7	b	1.31		78.6	
	52	4.32		79.9	ab	1.24		72.2	
	72	2.65		75.6	ab	1.71		62.8	
Mean		4.23	ns	77.9	S	1.44	ns	77.0	ns
40–60	12	4.59		54.6		1.79		90.0	
	32	2.53		68.4		1.42		93.8	
	52	6.84		87.9		1.60		90.4	
	72	2.24		81.3		1.05		89.5	
Mean		4.05	ns	73.0	ns	1.47	ns	90.9	ns
Bucket	12	0.42		3.6		75.75		38.4	
	32	1.50		10.0		79.17		31.6	
	52	2.07		7.8		78.50		25.2	
	72	8.08		14.3		85.47		23.2	
Mean		3.02	ns	8.9	ns	79.72	ns	29.6	ns

ns: not significant, S: significant ($P = 0.05$), HS: highly significant ($P = 0.01$). Variances of percentages of *R. similis* recovered were analyzed after log(x) transformation. Means in a row followed by the same letter are not different ($P = 0.05$) according to Duncan's multi-range test.

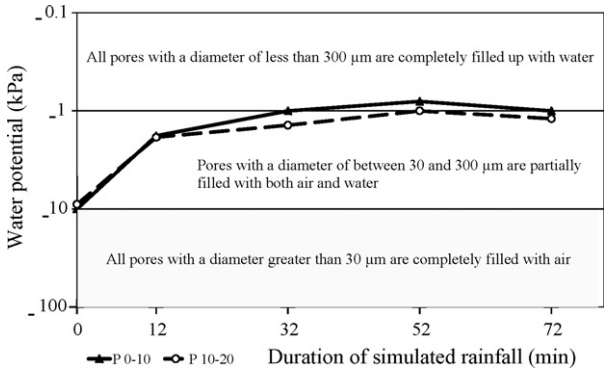

Fig. 2 – Variations in water potential during successive rainfall simulations. P 0–10 and 10–20: water potential at a depth of 0–10 cm and of 10–20 cm (in kPa). Means of 2 measurements × 3 experiments on dry soils.

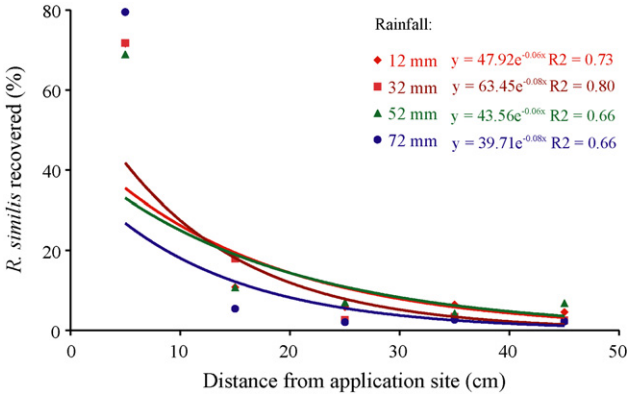

Fig. 3 – Dissemination of *R. similis* individuals after four simulated rainfalls of different lengths at 60 mm/h on fresh soil (water potential from −8 to −10 kPa). Abscissa: distance covered by individuals from the set-down line; Ordinate: percentage of nematodes recovered. Scale bar: confidence intervals for P = 5%; red curve corresponds to 12 mm rainfall, brown curve to 32 mm, green curve to 52 mm and blue curve to 72 mm.

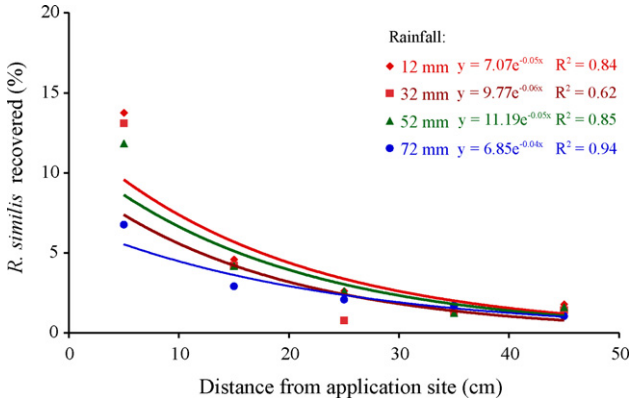

Fig. 4 – Dissemination of *R. similis* individuals after four simulated rainfalls of different lengths at 60 mm/h on wetted soil, close to water saturation. Abscissa: distance covered by individuals from the set-down line; Ordinate: percentage of nematodes recovered. Scale bar: confidence intervals for P = 5%; red curve corresponds to 12 mm rainfall, brown to 32 mm, green to 52 mm and blue to 72 mm.

In wetted soils, the water potential was always greater than −0.3 kPa meaning that all the pores with a diameter of less than 1000 µm were completely filled with water throughout the experiments (Wallace, 1958).

In both fields, preliminary soil and citrus root analyses failed to reveal the presence of any *R. similis* individuals. Only a few spiral nematodes *Helicotylenchus dihystera* (Cobb) Sher, and reniform nematodes *Rotylenchulus reniformis* Lindford and Oliveira, were detected. Given the absence of burrowing nematodes in the two fields, we aggregated the results from all the plots for interpretation and discussion.

The distances covered by *R. similis* individuals after each rainfall are illustrated in Fig. 3 for fresh soil, showing that the distance covered by the nematodes we added follows an inverse logarithmic law approximately. In fresh soil, all results were statistically analyzed (Anova) and revealed no significant differences (Table 4) in the percentage of *R. similis* individuals recovered among the four simulated rainfalls. From 69% to 80% of the recovered individuals were found in the 10 cm immediately downstream from the set-down line; only from

Table 5 – Volume of runoff water measured in the bucket after simulated rainfalls on fresh and wetted soils and calculation of the water flow during each rainfall.

Rainfall (mm)	Fresh soil		Wetted soil	
	Volume (dm^3)	Water flow (dm^3/min)	Volume (dm^3)	Water flow (dm^3/min)
12	0.02	0.002	7.11	0.59
32	0.10	0.005	11.75	0.59
52	0.55	0.027	11.69	0.58
72	2.43	0.121	10.91	0.55
Regression, R^2	$V = 0.009e^{0.077d}$, $R^2 = 0.999$ HS	$F = 0.0007e^{0.0696d}$, $R^2 = 0.987$ HS	ns	No significant differences between values

V: volume of the water collected in the bucket after d minutes (water collected after 12 min. for the first collection, and after 20 min. for the following collections); *d*: total duration of rainfall (from inoculation to collection); *F*: Water flow (*V*/12 for the first collection, *V*/20 for the following collections); HS: highly significant (*P* = 0.01); ns: not significant (*P* = 0.05).

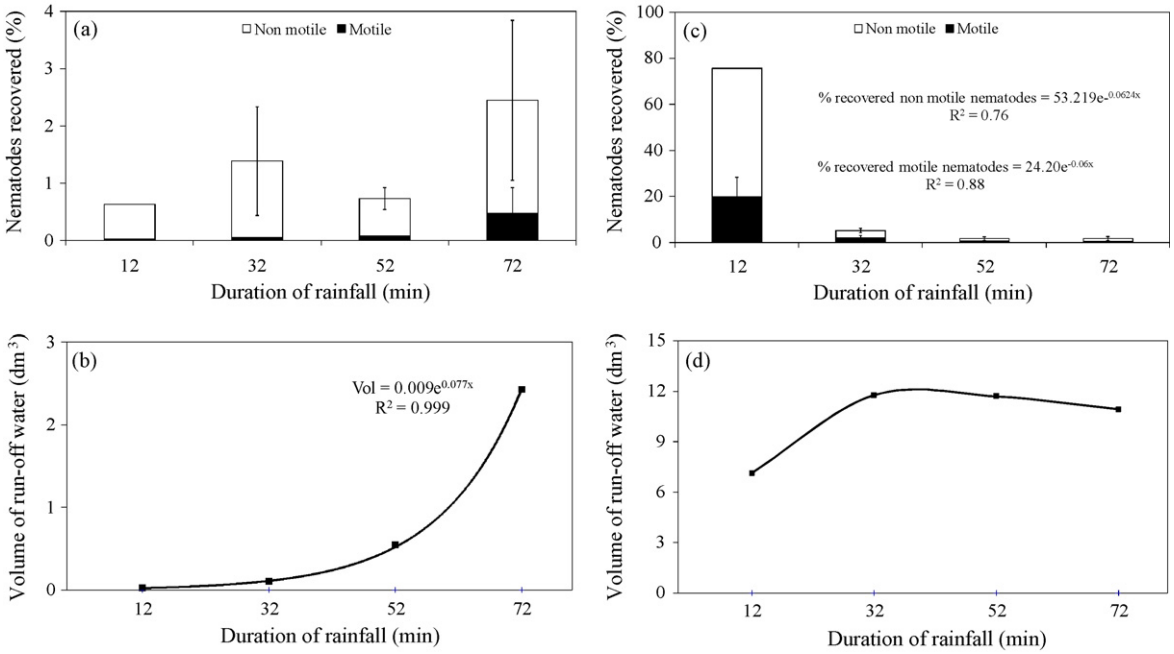

Fig. 5 – *R. similis* individuals collected from the outlet tub during experiments on fresh soil (water potential from −8 to −10 kPa, part a) and b) and wetted soil (close to water saturation, part c) and d). Scale bar: confidence intervals for *P* = 5%. Percentages of motile and non-motile nematodes are significantly different (Fisher's test with *P* = 5%) whatever the duration of the rainfall.

2.2% to 4.6% were recovered at a distance of between 40 and 60 cm. In fresh soil, *R. similis* specimens recovered from the outlet tub increased from the first to the last rainfall from 0.6% to 5.2%.

Fig. 4 shows that on wetted soil, the distance covered by the nematodes we added also followed an inverse logarithmic law approximately. All results were statistically analyzed (Anova) and revealed no significant difference (Table 4) among the four simulated rainfalls. From 76% to 85% of the recovered individuals were found in the outlet tub (Table 4). Only 7–14% of the recovered individuals were found in the 10 cm immediately downstream from the set-down line. Similarly, only 1.0–1.8% was recovered at a distance of more than 40 cm.

The amount of runoff water collected in the bucket increased exponentially during rainfall simulation on fresh soil (Table 5 and Fig. 5b). On wet soil, water flows were relatively constant (Table 5).

The populations of nematodes found in the bucket after each rainfall are presented in Fig. 5a (fresh soil) and 5c (wet soil); each scale bar corresponds to the proportion of *R. similis* recovered after 12 min (first bar) or 20 min (following bars). In Table 4, figures correspond to populations of *R. similis* found in the bucket after a 12–72 mm rainfall; to calculate them, we thus divided the cumulated number of nematodes recovered after the successive rainfalls by the total population recovered.

From a biological point of view, only a low proportion of motile nematodes reached the outlet tub (Table 6). This phenomenon was particularly apparent in fresh soil, where very limited numbers of nematodes were observed (cumulated total 247 individuals) compared to the number observed

Table 6 – Percentages of motile nematodes found downstream from the set-down line and in the outlet tub. Mean: mean percentages of 4 rainfalls × (3 × 2) replicates. Anova: analysis of variance within ranges of distance covered.

Distance covered (cm)	Fresh soil			Wetted soil		
	Mean	Anova		Mean	Anova	
0–10	83.7	a	HS	85.3	a	HS
10–20	79.0	a		81.8	a	
20–30	82.3	a		82.5	a	
30–40	74.9	a		77.0	a	
40–60	73.6	a		90.9	a	
Outlet tub	8.9	b		29.6	b	

ns: not significant, S: significant (*P* = 0.05), HS: highly significant (*P* = 0.01). Means in a row followed by the same letter are not different (*P* = 0.05) according to Duncan's multi-range test.

Table 7 – Comparison of the percentages of motile *R. similis* in fresh and wet soil (mean percentages of 4 rainfalls). Anova: analysis of variance within ranges of distance covered.

Distance covered (cm)	Fresh soil	Wetted soil	Anova
0–10	83.7	85.3	ns
10–20	79.1	81.9	ns
20–30	82.3	82.5	ns
30–40	77.9	77.0	ns
40–60	73.1	90.9	S
Outlet tub	8.9	29.6	HS

Variances were analyzed after log(x) transformation. ns: not significant, S: significant ($P = 0.05$), HS: highly significant ($P = 0.01$). Means in a row followed by the same letter are not different ($P = 0.05$) according to Duncan's multi-range test.

in wetted soil (24 812 individuals). Proportion of motile *R. similis* differs significantly between fresh and wet soil only when samples were collected at more than 40 cm from inoculation line (Table 7).

4. Discussion

R. similis varies in size from 12 μm in width for the smallest juveniles to 27 μm in width for the largest females, and from 240 to 780 μm in length (Van Weerdt, 1958). The nematodes thus need capillaries with a diameter ranging from 20 to 300 μm to be able to enter and to move actively through soil (Wallace, 1958, 1960; Otobe et al., 2004). Pores with diameters ranging from 30 to 80 μm are common in the nitisol on which this study was performed, and the pores in our study were thus nearly 1.5–2 times larger than the size of *R. similis* according to Wallace (1958 and 1960). As can be seen in Fig. 2, in fresh soils, capillaries of 30–300 μm that enabled *R. similis* to move actively were progressively filled up. Such conditions are especially suitable for movements of nematodes that are of similar sizes to *R. similis* (Wallace, 1968). In fresh soil, at the beginning of rainfall simulation, the water potential was close to −10 kPa. At this potential, conditions were suitable for a nematode the size of *R. similis* to enter or to move about within the soil pores. Furthermore, it took between 11 and 12 min for runoff water to enter the tub; this period may be long enough for motile specimens to enter the soil and escape the soil surface water flow that appeared later. Subsequently, although fresh soils were moistened during successive rainfalls, they were able to leach during soil sampling (which took about 5 min). Their water potential was therefore close to −1 kPa from the 12th min of rainfall to the end of the experiment. This potential corresponds to water filling pores with a diameter of 300 mm. Thus, adults and fourth stage juveniles (J4) could still enter and move in "fresh soil" throughout the experiment.

Conversely, wetted soils were close to water saturation, with a water potential greater than −0.3 kPa. Thus, soil pores suitable for *R. similis* movement were filled with water. It is unlikely that nematodes the size of *R. similis* can easily enter wet soils (Wallace, 1959, 1960).

As can be seen in Fig. 4, the distribution of *R. similis* in the first centimetre of wetted soil follows an exponential law approximately, coherent with a passive transportation. Indeed, in the event of purely passive transport, the probability for a nematode of passing from one compartment to another is constant and the distribution of the nematodes as a function of distance thus should follow a geometrical series. This model appears to be less appropriate for fresh soils (Fig. 3): in this case, the model should take into account the active penetration of nematodes in the macro- and meso-porosity of the soil. As a result, nematodes may reach deeper layers of soil, exceeding the 1 cm depth we sampled, and consequently, escape the surface water flow.

Fig. 5a illustrates the erratic arrival of *R. similis* individuals at the outlet tubs in fresh soil. Indeed, no correlation was found between volumes of runoff water and the number of specimens found in the outlet tub (Fig. 5a *vs.* b). By contrast, in wetted soils, the arrival of *R. similis* individuals appeared to follow an inverse exponential law (Fig. 5c *vs.* d). A larger number of nematodes were caught by water flow during the first simulated rainfall, after which the number progressively decreased, maybe because of a decrease in the upstream nematode population. The percentages of motile *R. similis* extracted from outlet tubs were very low (Table 5). This is consistent with the hypothesis according to which active individuals were more prone to escape runoff water flows by actively entering the soil pores.

In the literature, several authors reported the dispersion of phytoparasitic nematodes by water (reviewed by Burr and Robinson, 2004), particularly in rivers and in irrigation and drainage canals (Waliullah, 1986; Faulkner and Bolander, 1970a,b; Tapia et al., 2007) but very few experimental studies, most conducted in Senegal, dealt with nematode dispersion by runoff water at a scale ranging from the 1 to 100 m^2 plots. Thus, we observed the opposite phenomenon to that observed by Planchon et al. (2000), Cadet et al. (2002) and Villenave et al. (2003) who performed comparable studies but in radically different ecological environments (sandy soils under Sahelian conditions *vs.* nitisol in the humid tropics). These authors observed that in Senegal, the behaviour of *Scutellonema cavenessi* Sher facilitated its dispersion by runoff water, and that dispersion increased with time. In their studies, nematode behaviour for example during the anhydrobiotic state (Demeure and Freckman, 1985), may have greatly influenced their dissemination by runoff water: according to Villenave et al. (2003), the soil depth where the nematodes live probably explains the likelihood of being leached by runoff water. In our tropical humid conditions, the dispersion strategy of *R. similis* is based mainly on its dissemination within perennial plant materials such as the banana corm (Quénéhervé and Cadet, 1985; Marin et al., 1998) and, up to now, no anhydrobiotic state strategy has been observed in this species. In contrast, in Sahelien conditions, the dissemination strategy of *S. cavenessi* appears to be mainly based on wind dispersal (Baujard and Martiny, 1994) of anhydrobiotic forms but may also be facilitated by leaching caused by runoff (Cadet et al., 2002). The strategy of *S. cavenessi* appears to be particularly suited to parasitism of annual plants, which are only present for a few months each year.

In contrast, *R. similis* is mainly known as a major parasite of perennial plants, such as coconut (Griffith et al., 2005), pepper (Koshy et al., 2005), tea (Gnanapragrasam and Mohotti, 2005) and especially citrus (Duncan, 2005) and banana (Gowen et al.,

2005). It can also parasite many annual plants such as *Solanum nigrum* or *Phenax soneratii* or *Arachis* spp. (Zem, 1983, Quénéhervé et al., 2006). But even if *R. similis* can infest economically important annual crops such as maize and groundnut (Milne and Keetch, 1976), this species is not considered as a major pest of these crops. The poor dispersion capacity of *R. similis*, combined with its poor survival ability in soil (Feldmesser et al., 1960, Tarjan, 1961), means this parasite is only likely to cause economic losses in perennial crops.

In the present study, the proportion of motile *R. similis* decreased significantly among nematode disseminated over 60 cm. These results are consistent with those we observed while studying nematode leaching in soil column (Chabrier et al., 2008). In this previous paper, we observed that non-motile nematodes are much more likely to be leached and that active *R. similis* may flee leaching. After the present study, we can also hypothesis that active *R. similis* were partially trapped by the soil porosity but also actively enter soil when pores of 30–300 μm were partially filled-up with water. This hypothesis should explain why the proportion of motile nematode is significantly higher in buckets downstream wetted soil than downstream fresh soil (Table 7). It should also explain why, on fresh soils, quite no significant differences appeared between distributions of recovered nematodes after successive rainfalls (Table 4). This last observation does not fit with a completely passive model. On wetted soil, absence of significant difference between successive rainfalls may be explained by the fact that a too large proportion of *R. similis* have been taken to the bucket by the water flow after the first minutes; thus distributions may be better explained by a passive model.

5. Conclusions

Our results show that the dissemination of *R. similis* by runoff water in banana fields is far from significant in fresh soils. To be significant, the soil has to be close to water saturation, nematode individuals have to be present on the surface of the soil, and rain intensity has to be sufficient.

However, the main damage caused by nematodes is when banana plants topple over (Blake, 1972; Chabrier and Quénéhervé, 2003). This occurs mainly during tropical showers, which are usually short but of high intensity and accompanied by wind squalls. Plants are much more likely to topple over when the soil is very wet. In fact, suitable conditions for dissemination of *R. similis* by runoff water can occur several times a month during the rainy season, when *R. similis* individuals leave the unearthed roots of fallen plants. It is thus possible that water runoff disseminates *R. similis* when soil moisture is between field capacity and water saturation. What is more, the proportion of nematodes recovered in the outlet tub on wetted soils suggests that runoff water can disseminate nematodes over long distances within a few minutes.

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