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RELATIONSHIP BETWEEN RAINDROP EROSION AND RUNOFF EROSION UNDER SIMULATED RAINFALL IN THE SUDANO-SAHEL: CONSEQUENCES FOR THE SPREAD OF NEMATODES BY RUNOFF

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ABSTRACT

This paper presents a rainfall simulation experiment carried out on three 50 m^2 plots in the Senegalese groundnut belt. One plot was not cultivated. Groundnut and millet had previously been grown in the other two.

The experiment consisted of three rain events applied over 5 days at the end of the dry season. Erosion was monitored inside the plots by the use of a relief meter and, at their outlets, by sampling the discharge. The number of indigenous nematodes, and an exotic species introduced before the first rain event, was monitored in the soil and in the discharge. This experiment allows, for the first time, a set of simple hypotheses to be proposed to explain the spread of nematodes by the runoff: raindrop impacts on the soil surface set them in suspension; then, their low bulk density and their relatively large size do not allow them to settle when the raindrops shake the water surface. Thus, nematodes follow the flow path where they are as far as its velocity remains significant. The biological aspects are decisive in the mobility of nematodes, which can vary by a factor of 100 depending on the trophic groups. A very high raindrop erosion occurred during the experiment, up to 60 tons per hectare for the first rain event after hoeing. This represents more than 40 per cent of the volume of soil previously moved by soil work. The geometric properties of the plough, and their hydraulic consequences, appear very ephemeral. And yet these large movements of soil inside the plots are little related to the sediment load at the outlet, which follows its own rules.

Analysis of the results indicates that the carrying capacity of the runoff at the scale of 10 m^2, on gentle slopes ploughed perpendicular to the slope, could not be directly calculable from the discharge. It could depend on the history of past discharges because the shape of the flow paths, which condition their carrying capacity, permanently interacts with the discharge. These interactions could explain the great difficulties encountered by the erosion models in the case of low discharges on non-cohesive soils. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: rainfall simulation; microrelief; splash erosion; runoff; nematodes

INTRODUCTION

Runoff and raindrops are both involved in the detachment of soil particles and their transport. Furthermore, they interact. In tilled soils, the parameters governing this interaction look simple: as the soil is bare and non-cohesive, the sediment load is always equal to the flow's transport capacity and the fulfilment of this equilibrium is the cause of erosion or deposition. However, this simple principle is proving to be poorly productive in erosion modelling: models at the watershed/event scale did not produce convincing results, mainly for small soil losses, which are usually over-predicted (Nearing, 1998). Bjorneberg *et al.* (1997) report soil loss predictions from the WEPP model (Water Erosion Prediction Project) of 200 kg m^{-1} when measured soil loss was less than 5 kg m^{-1}. Many other examples are reported by Jetten *et al.* (1999).

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In view of these difficulties, the conceptual questions about the hydraulics of inter-rill runoff remain open and widely studied (Abrahams *et al.*, 1986; Abrahams and Parsons, 1994; Gilley *et al.*, 1992; Prosser and Dietrich, 1995). Two problems hinder a better consideration of detachment and transport capacity of the runoff in tilled fields. The first is the quick evolution of tillage-induced microreliefs under the rain. The second is the permanent equilibrium between the channels' shape and their discharge. This equilibrium has been reported by Nearing *et al.* (1997) on the rills but remains poorly documented on the inter-rill runoff. Thus, the sediment movements caused by rainfall and runoff are well studied, but the biological contents of the runoff have rarely been considered. Nematodes are the most numerous multicellular organisms in the soil; 95 per cent of them live in the first 10 to 15 cm of soil depth (Murthy and Elias, 1970). Their mean size is 300 to 1500 μm in length and 10 to 15 μm in diameter. Their weight is comparable to a fine sand grain but their bulk density is lower and, furthermore, they are capable of making active movements. Cadet and Albergel (1998) carried out the first quantitative study of the capacity of runoff to spread nematodes. They showed that the runoff sampled at the outlet of a Sudano-Sahelian watershed was rich in nematodes. Under the Sudano-Sahelian climate, characterized by 6 to 8 months of drought, nematodes have the special feature of being able to become anhydrobiotic, that is resistant to drought (Demeure *et al.*, 1979). In this form, the nematodes are desiccated and become similar to a soil particle of very small size and mass. This behaviour suggests that the spread of nematodes by runoff should be under the control of biological processes and not just a mechanical process. This explains why the relative richness of the different species of nematodes is different in the soil and in the runoff (Cadet and Albergel, 1998). However, the processes which set the nematodes in suspension and the conditions of their transport remain unknown.

This article presents a simulated rainfall experiment carried out in the Senegalese groundnut belt, in cultivated fields tilled perpendicular to the slope. The results concerning raindrop erosion, soil losses and nematode transport are presented and discussed.

MATERIAL AND METHODS

The rainfall simulator

A new rainfall simulator was designed for this experiment (Esteves *et al.*, 2000). The basic unit of the simulator is a vertical galvanized standpipe of 6·58 m in height and 25 mm in diameter. An HQ106 Spraying System nozzle was screwed onto the top of the pipe, spraying upwards. A valve and an oil-immersed pressure gauge allowed fine control of pressure at the bottom of each pipe. Each basic unit watered a square area of 8 m by 8 m. A distance of 5·5 m between two single units gave the best uniformity of rainfall. Two lines of three units each were used to simulate rainfall in each experimental field plot of 5 m by 10 m.

Microrelief

The relief meter was designed and constructed at the IRD research centre in Dakar, Senegal (Planchon *et al.*, 1998). This device is made of a carriage which moves on a transverse beam and supports and controls a vertical rod, with a small sensor at the end. The rod moves vertically downwards until the sensor contacts the soil surface. The sensor weighs 1·5 g and does not disturb the soil surface when contacting it. The transverse beam moves on a transportable frame, 4·5 m wide and 1·2 m high, and was tied to four bases anchored to a depth of 50 cm in the ground. The stability of the bases was verified by the measurement of the elevation of each frame corner after each rainfall.

Measurements at the plot outlet

Discharge was measured with two 15 litre buckets alternately receiving the water at the outlet of each plot. This method allowed the collection of all the runoff, which was necessary for the nematode count. A pressure gauge in each of the buckets allowed a direct volumetric measurement of the discharge. In each bucket, a single 100 ml sample was taken for soil loss analyses.

Nematodes in the soil

Ten 250 cm^3 soil samples were collected from each plot before the first rain event. They were suspended in water and shaken for 10 min to reactivate the nematodes. The nematodes were then extracted by Seinhorst's method (Seinhorst, 1962) and counted under a stereoscopic microscope in two subsets: plant parasitic nematodes, distinguished by the presence of a stylet from freeliving nematodes (Luc *et al.*, 1990).

Meloidogyne nematodes

Uphill of each plot, before the first rain event, one litre of soil was removed and replaced with a mixture of soil and tomato roots infested with *Meloidogyne* juveniles. *Meloidogyne* juveniles are small nematodes (15 μm × 500 μm). They did not occur naturally in the experimental plots. They came from potted tomato seedlings, grown in the laboratory, which had been inoculated two months previously with 500 juveniles. The infestation density of the soil laid on the plots was estimated at 2400 juveniles per dm^3.

Nematodes in the runoff

All the runoff was collected in successive 15 litre buckets. The suspensions of sediments and nematodes were allowed to settle for at least 6 h. After this period, the top of the water was siphoned off in order to facilitate carriage of the samples, keeping only the bottom one litre which then contained all the nematodes.

The nematodes contained in the suspension were extracted in the laboratory by Seinhorst's (1962) method.

For practical reasons (distance from the laboratory), the nematodes were left in the water for several days before being counted. This allowed them long enough to recover their active form (1 to 3 days, according to Demeure (1978)). Thus the method used was non-selective and did not give the proportion of active and anhydrobiotic forms at the moment of sampling.

Three rains of 10 mm depth were applied to each plot during the 2 weeks preceding the experiment. This changed the soil to a moist condition which allowed ploughing. This also simulated the conditions that occur at the beginning of the rainy season and which lead the nematodes to recover their active form. The millet and groundnut plots were divided into two halves which received different surface treatments. The day before the first rain event, the groundnut plot had been hoed in the upper part and left bare and smooth in the downhill part. The millet plot had been hoed in the lower part and left bare and smooth uphill. Rain events 1 and 2 were applied in these conditions on days 1 and 3, respectively. Then, the unworked part of each plot was hoed and a third and last rain event applied on day 5. The fallow plot was left unworked and covered with loose residues of grass during the three rain events. Table I details the time schedule of the experiment. The rainfall intensity was 60 to 75 mm h^{-1} measured using collecting cans, each a square metre, inside the plots. Each rainfall event lasted 30 min.

RESULTS

Microrelief

Planchon *et al.* (2000) have modelled the microrelief erosion observed during this experiment on the basis of a simple raindrop erosion model. They concluded that raindrop erosion and compaction were the main processes controlling microrelief evolution. Nevertheless, despite a good prediction of roughness evolution, the decrease in surface storage capacity was underestimated by the model. This has been interpreted as the result of runoff which opened up the ridges as and when they overflowed. Figure 1 shows the microrelief of the lower part of the millet plot.

According to these results, we can estimate the volume of soil moved from the ridges to the troughs with the comparison of the initial and final soil surfaces. To do that, we must take into account the effect of compaction. This is done by Equation 1 where the initial and final elevations z_0 and z_1 are previously related to the mean values $\overline{z_0}$ and $\overline{z_1}$ of their respective DTM, before being compared. Only the positive values are summed. The same compaction coefficient applied on the ridges, where the ploughed layer is thick, and in the troughs, where the ploughed layer is thin, has the same consequences as raindrop erosion. This effect has been

Table I. Time schedule of the experiment. μRelief: microrelief measurement of a 4 m by 4 m area in the middle of a half plot (millet and groundnut) or in the middle of the whole plot (fallow). values in millimetres represent depth of the rain applied

Day	Rain event	Fallow	Millet		Groundnut	
			Upstream	Downstream	Upstream	Downstream
0	–	μRelief	μRelief	Hoeing μRelief	Hoeing μRelief	μRelief
1	1	33·4 mm	30·2 mm		38·2 mm	
2	–	–		μRelief	μRelief	
3	2	32·3 mm	32·4 mm		37·7 mm	
4	–	–	Hoeing μRelief			Hoeing μRelief
5	3	30·3 mm	34·5 mm		38·1 mm	
6 and 7	–	μRelief	μRelief	μRelief	μRelief	μRelief

evaluated by Planchon *et al.* (2000) and a correcting factor α has been proposed for each rain event. The value of α varies from 74 to 100 per cent.

$$E = \alpha \sum_{i \in grid} \max[(z_1^i - \overline{z_1}) - (z_0^i - \overline{z_0}), 0]s \qquad (1)$$

where E = volume of soil moved from the ridges to the troughs by raindrop erosion (litres); α = contribution of raindrop erosion to the difference of relative elevation (percentage); z_0^i, z_1^i = elevation of point i before and after the rain, respectively (mm); $\overline{z_0}$, $\overline{z_1}$ = mean elevation of the plot before and after the rain, respectively (mm); s = grid cell area (m).

We can also calculate the volume of soil moved by hoeing. To do that, we use Equation 1 with the microrelief after hoeing as $\overline{z_1}$, and before hoeing as $\overline{z_0}$. Table II shows the results.

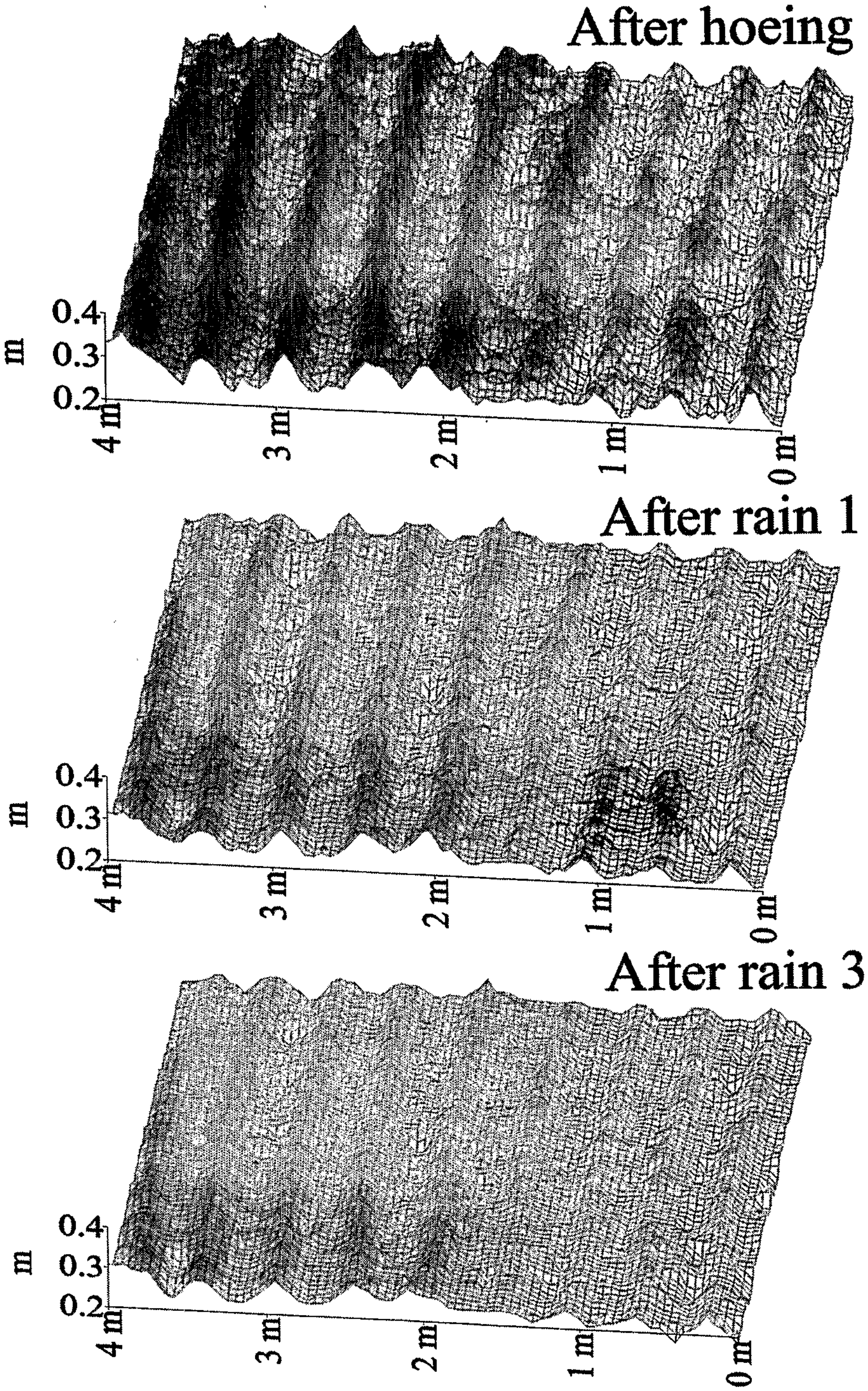
Raindrop erosion moved the soil from the ploughed ridges to the troughs. The volume involved during the first rain event represents 49 per cent (millet) and 57 per cent (groundnut) of the volume of soil previously moved to the ridges by ploughing. This represents about 60 tons per hectare if we take 1·6 as the bulk density, the mean value in the plots.

A relatively small amount of water moves these considerable quantities of soil. During the first rain event, each litre of rain carried 210 g (groundnut) and 180 g (millet) from the ridges to the troughs. By comparison, the highest sediment load during the experiment was 3·5 g l^{-1}.

The volume of soil moved by the next two rainfalls was only 68 per cent (groundnut) and 42 per cent (millet) of the volume moved by the first rain event. For groundnut-up and millet-down, the volume moved by rainfalls 2 and 3 was split so that the volumes moved by the three rainfalls follow a geometric progression. This is in agreement with the idea that the cumulative volume moved by raindrop erosion should asymptotically tend to the volume initially moved by hoeing (Planchon *et al.*, 2000). It is also in agreement with the exponential decrease of roughness after successive rainfalls (Mwendera and Feyen, 1992; Magunda *et al.*, 1997). This led to a reduction of the volume by a factor of 2·02 (groundnut) and 2·54 (millet) from one rain event to the next. For the fallow plot, we only know the cumulative result of the three rainfalls, thus the same adjustment is not possible. For this plot, the volume is divided up with a geometric progression of one over 2·28, which is an intermediate value between those of the groundnut and millet plots. Table III shows the results.

Runoff

Figure 2 shows the discharge during the three rain events.


After hoeing

After rain 1

After rain 3

Figure 1. Microrelief of the downhill part of the millet plot

Table II. Volumes of soil moved by hoeing and by raindrop erosion. The gross volume is the volume of soil moved from the ridges to the troughs (raindrop erosion) or from the troughs to the ridges (hoeing). It was calculated from Equation 1. The contribution of splash has been calculated by Planchon *et al.* (2000). The volume transported is the product of the two former columns and the area of the plot. The specific splash erosion is the volume transported by splash over the volume of rain.

	Gross volume (l m^{-2})	Contribution of splash (%)	Volume transported by splash (l)	Specific splash erosion (g l^{-1})
Groundnut upstream				
Rain event 1	4·1	92	94·3	215
Rain events 2 + 3	2·8	100	70	66
Groundnut downstream				
Hoeing	8·9	-	-	-
Rain event 3	5·1	85	108·4	210
Millet upstream				
Hoeing	10·1	-	-	-
Rain event 3	4·9	87	106·6	176
Millet downstream				
Rain event 1	5·5	74	101·8	177
Rain events 2 + 3	2·3	97	55·8	49
Fallow				
Rain events 1 + 2 + 3	0·5	n.a.	26·6	9

Table III. Estimation of the volume of soil moved by raindrop erosion for each plot and each rain event. The volumes were calculated from the results of Table II by the mean of geometric interpolations

Plot	Millet	Millet	Groundnut	Groundnut	Fallow
Subplot	Upstream	Downstream	Upstream	Downstream	-
Area (m^2)	25	25	25	25	50
Rain event 1 (l)	-	101·8	94·3	-	16·3
Rain event 2 (l)	-	40·0	46·8	-	7·2
Rain event 3 (l)	106·6	15·8	23·2	108·4	3·1

Rain event 1. Figure 2a represents the hydrographs of the first rain event. In the groundnut plot, the upstream part, which was hoed, did not overflow during the first 25 min of rain. In the downstream part, which was bare and unworked, runoff started after 7 min of rain. The runoff coefficient was 90 per cent after 24 min of rain, which led to an average value of 45 per cent for the whole plot. In the fallow plot runoff started later (at 10 min) and was lower (60 per cent for the whole plot). In the millet plot, the downstream part, which was hoed, received the rain plus the runon from the unworked upstream part, and overflowed after 24 min of rain. One minute later, the upstream part of the groundnut plot also overflowed. At the end of the rain, the runoff coefficients were 81 per cent for the groundnut plot and 67 per cent for the millet plot.

Rain event 2. Figure 2b represents the hydrographs of the second rainfall. The fallow plot hydrograph was comparable to the first rain event. This indicates that initial moisture had little influence on the hydrograph for the smooth unworked areas. For the two other plots, the first part of the hydrograph was consistent with rain event 1. The hoed parts of each plot overflowed earlier: 15 min for the millet plot (hoed downstream) and 16 min for the groundnut plot (hoed upstream).

Rain event 3. Figure 2c represents rain event 3. The fallow plot hydrograph was comparable to rains 1 and 2. The millet plot had been hoed upstream before the rain and this part did not overflow. Runoff from the downstream part was similar to rain event 1 and started one minute earlier. The groundnut plot had been hoed downstream, so it received runoff from the upstream part and overflowed at 21 min.

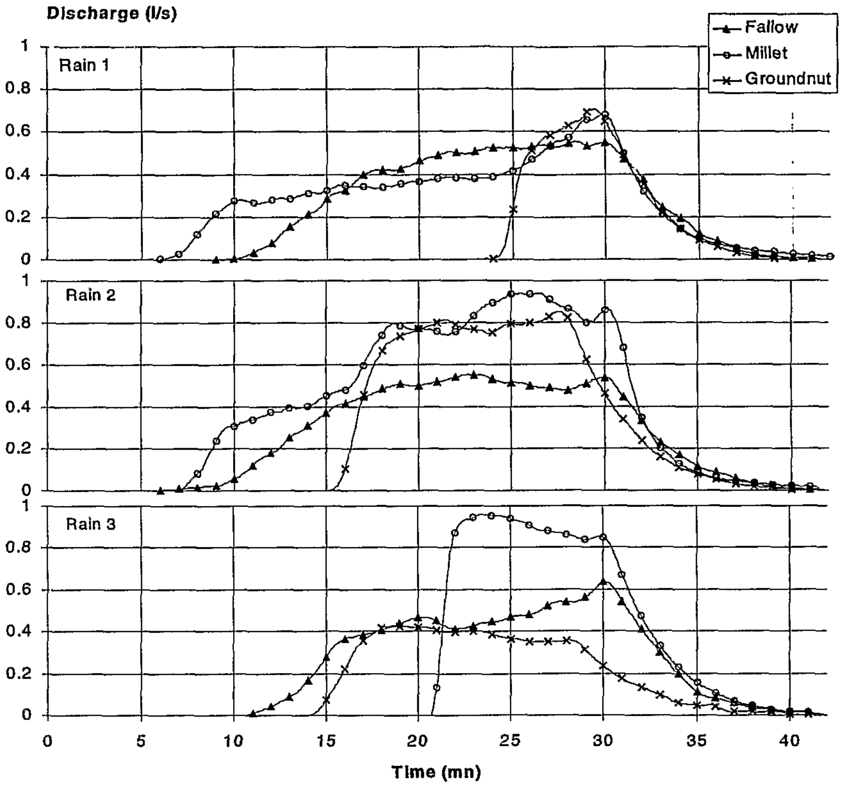


Figure 2. Hydrographs of the three simulated rainfall events in the three plots

Erosion at plot scale

Figure 3 shows the sediment loads. Table IV indicates the soil losses for each rain event.

Fallow plot. On the fallow plot, the discharges of the three rain events were similar. The sediment loads decreased with time. Sediment load was higher at the first rain event. The next two rain events were comparable.

Groundnut plot. During rain events 1 and 2, the groundnut plot was hoed in its upstream half and left smooth and bare downstream. Sediment loads rose in successive peaks followed by exponential decreases. During rain event 1, the first peak occurred at 7 min, when runoff started in the downstream part. A second peak occurred when the upstream hoed part overflowed. During rain event 2, the first peak occurred at only 25 min, when the maximum discharge of rain event 1 was exceeded. The peak was followed by an exponential decrease. During rain event 3, the plot's downstream half was hoed and the sediment load was the highest of the whole experiment. The total soil loss during this rain event was 1·2 kg which represents about 0·75 litres. This volume is compatible with that moved by the break caused by the overflow of a single ridge. In this case, the soil removed settled nearby, but here, a ridge was located next to the outlet and part of the soil moved when the ridge overflowed could have been carried away but was not representative of the whole plot.

Millet plot. The millet plot was hoed downstream. Like the fallow plot, but with higher sediment loads, we can see that sediment loads (a) decreased exponentially with time and (b) are comparable between rain events 2 and 3.

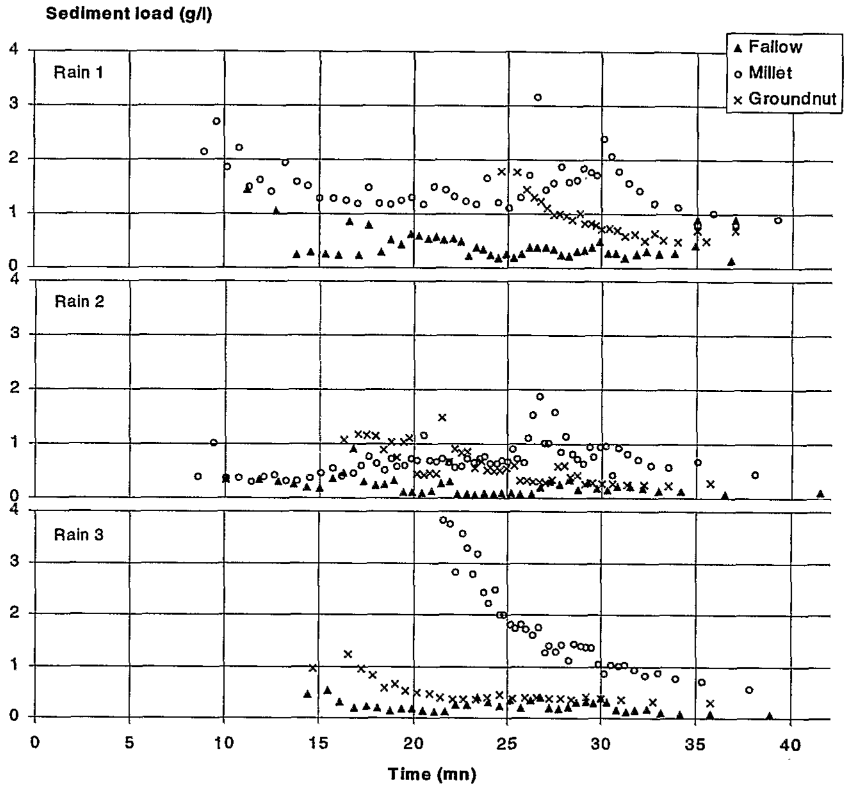


Figure 3. Sediment loads during the rain events. Each dot represents a sample point

Table IV. Soil loss (in kg) at the plot outlets

	Fallow	Millet	Groundnut
Rain event 1	0·23	0·27	1·05
Rain event 2	0·14	0·42	0·73
Rain event 3	0·13	0·19	1·18
Total	0·5	0·88	2·96

Meloidogyne nematodes

Table V indicates the timing of the catching of the first *Meloidogyne* juvenile at the outlet of each plot. Results are contrasting. The first *Meloidogyne* was observed during the first, the second and the third rain event for the millet, groundnut and fallow plots, respectively, and the depth of runoff observed at these timings was noticeably variable: 1·9 mm in the millet plot and more than 31 mm in the other two. Little is known about how runoff or rain could set the nematodes in suspension and transport them. When *Meloidogyne* juveniles are in suspension in laboratory conditions, they settle with a vertical velocity of 3 cm min^{-1} (Seinhorst, 1962). This velocity is too slow to allow nematodes to settle in natural conditions, when the water surface is agitated by raindrop impacts, unless the water is deep enough. In this case, the deepest layer should be protected from raindrop agitation. The random movements of nematodes allow them to remain free even when they contact solid material. This behaviour is used in the concentration method of Seinhorst (1962). From this basic knowledge of nematode behaviour, we can formulate a few hypotheses which are able to explain our results: (a) nematodes are set in suspension by raindrop impacts, at the same time as the soil particles which contain them; (b) they remain in suspension even if the flow velocity is very low; (c) despite the agitation of the water surface by raindrops, they have a high probability of settling when in still water; (d) while being carried in the runoff, they have a high probability of encountering obstacles (soil or vegetation)

Table V. Characteristics of rainfall and runoff when the first *Meloidogyne* juvenile was captured at the outlet of each plot

	Surface treatment at rain 1	Rain	Cumulated rainfall (mm)	Cumulated runoff (mm)
Fallow	Unworked	Rain 3	86·8	31·2
Groundnut	Hoed upstream	Rain 2	54·8	31·5
Millet	Hoed downstream	Rain 1	35·5	1·9

but also of escaping when moving. These rules concern only the active forms. Anhydrobiotic forms behave like silt particles, which are approximately the same size. Therefore, the active forms tend to remain longer in suspension in the runoff.

According to these hypotheses of behaviour, our results can be explained as follows.

Groundnut plot. The upstream part of the groundnut plot, where the *Meloidogyne* juveniles were deposited, was bare and smooth. Once in suspension, the velocity of the flow lines was too high to allow the nematodes to settle out. Furthermore, the depth of the flow was small and the nematodes were kept in suspension by the added influence of raindrop impact. Downstream, the runoff coming from the upper part flowed through the successive ridges so that, when the flow reached the outlet, a continuous flow path of high velocity had been formed and nematodes could not stop in this part of the plot. The consequence was that *Meloidogyne* juveniles were present in the discharge in the first minutes of runoff. This situation was the same during rain event 2. At rain event 3 the upper half of the plot had been hoed and no more *Meloidogyne* juveniles were observed in the discharge. This can be understood if we consider that *Meloidogyne* juveniles had to cross a puddle along a trough before reaching a flow path which could carry them to the outlet. Crossing puddles is highly unlikely according to our hypothesis.

Millet plot. On the millet plot, hoed upstream, *Meloidogyne* juveniles did not appear during rain event 1. This situation was similar to the groundnut plot, rain event 3. The first *Meloidogyne* juvenile appeared at rain event 2. One can think that the continuity of flow paths was better and the flow velocity was higher at rain event 2, after the ridges had been eroded. In these conditions, the probability of a nematode crossing the ploughed area should be higher. Nevertheless, *Meloidogyne* juveniles arrived very late at the outlet (15 s before the end of the rain) and were not seen during rain event 3, when the downhill half of the plot was hoed. This result confirms the hypothesis that nematodes easily follow a flow path where the velocity is always significant but have little probability of crossing calm areas.

Fallow plot. In the fallow plot, *Meloidogyne* juveniles only appeared at rain event 3. This plot was covered by a loose dry grass and flow velocities were low everywhere excepted in a single central flow path. In these conditions, and according to our hypothesis, there were numerous instances when the movement of nematodes would have been obstructed before they reached the central flow path and were captured at the outlet.

Indigenous nematodes

Estimation of soil infestation. Table VI indicates the number of nematodes in each plot and each trophic group. The differences between the three plots are significant in each trophic group.

Control soil samples were taken before each rain event. They confirmed that the number of nematodes remained constant over the duration of the experiment, which was in accordance with physiological data: (a) the biological cycle of phytoparasitic nematodes is more than three weeks and requires the presence of a living plant's root; (b) at least 8 days are required between the reactivation of anhydrobiotic forms and the time that eggs are laid; and (c) freeliving nematodes have a shorter biological cycle but never shorter than 8 days (Demeure, 1980).

Table VI. Nematodes in the soil and in the runoff for each plot and each trophic group. Calculation of their rates of capture

	Rain event	Phytoparasitic nematodes			Freeliving nematodes		
		Millet	Fallow	Groundnut	Millet	Fallow	Groundnut
Density of nematodes in the soil thousands per dm^3		15·4	11·3	5·1	10	27·1	8·1
Volume of soil moved (dm^3, see Table III)	1	102	16	94	102	16	94
	2	40	7	47	40	7	47
	3	122	3	132	122	3	132
Number of nematodes set in suspension (× 1000)	1	1569	184	484	1018	442	760
	2	617	81	240	400	194	377
	3	1886	35	676	1224	85	1060
Number of nematodes captured at the outlets (× 1000)	1	0·35	0·09	0·20	28	5	39
	2	0·79	0·36	0·26	7	11	96
	3	0·22	0·03	0·41	96	19	57
	Total	1·36	0·48	0·87	172	34	192
Rate of capture (the number captured over the number set in suspension, %)	1	0·02	0·05	0·04	3	1	5
	2	0·13	0·45	0·11	12	5	26
	3	0·01	0·07	0·06	8	22	5
	Mean	0·05	0·19	0·07	7	10	12
Duration of runoff (min)	1	6·0	21·2	26·8	6·0	21·2	26·8
	2	12·8	24·4	22·7	12·8	24·4	22·7
	3	14·5	21·3	9·3	14·5	21·3	9·3
Specific rate of capture (the rate of capture by the duration of rain over the duration of runoff, %)	1	0·11	0·07	0·05	14	2	6
	2	0·30	0·55	0·14	28	7	34
	3	0·02	0·10	0·19	16	31	17
	Mean	0·15	0·24	0·13	19	13	19

Freeliving nematodes were significantly more numerous in the fallow plot than in the previously cultivated plots (Table VI). Fallow lands naturally have a higher organic matter content than cultivated fields (Masse *et al.*, 1998). This could explain the differences in the nematode populations because freeliving nematodes live at the expense of soil bacteria and organic matter (Pate, 1997).

Phytoparasitic nematodes were the most numerous in the millet plot (15 000 per dm^3) and the fallow plot (11 000 per dm^3). Millet is a very suitable plant for nematodes. Similarly, plots recently left fallow supported large numbers of nematodes (Masse *et al.*, 1998) Groundnut, which is less susceptible to nematodes (Baujard and Martiny, 1995), had fewer nematodes (5000 per dm^3).

The number of mobilized nematodes was calculated, according to our working hypotheses, as the number of nematodes in the soil in the plots multiplied by the volume of soil moved by raindrop erosion during the rain (Table VI). The volume of soil moved on the unworked half plots was ignored. This number of mobilized nematodes was used to calculate a capture rate which is the number of captured nematodes divided by the number of mobilized ones. This rate was subsequently corrected to take into account the runoff duration. According to our hypotheses (outlined in the section dealing with the *Meloidogyne* results), nematodes mobilized before the state of the runoff have a very low probability of moving a significant distance. Thus, the corrected capture rate is the number of nematodes captured per minute of runoff divided by the number of nematodes mobilized per minute of rain. These results are reported in Table VI. Figure IV shows the corrected capture rates for each rain event.

The main results in Table VI are the following.

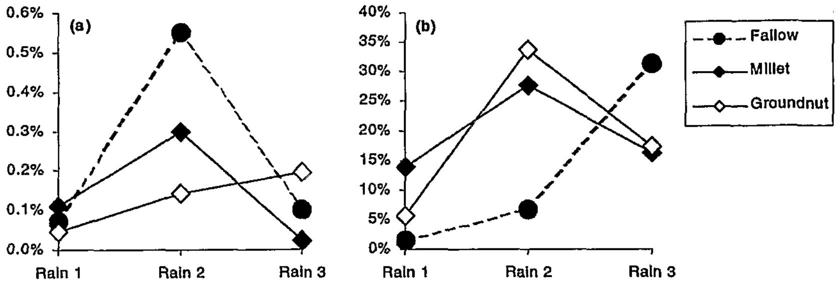


Figure 4. Specific rates of capture of phytoparasitic nematodes (a) and freeliving nematodes (b) for each rain event in the three plots

The average capture rates were very different for the two trophic groups: 0·13 to 0·24 per cent for the phytoparasitic nematodes and 13 to 19 per cent for the freeliving nematodes. This contrast was equally high for all plots. It was therefore independent of soil surface feature, soil tillage or previous crop. There are two explanation for these differences. The first is that the behaviour of nematodes in the runoff is different for each species (Cadet and Albergel, 1998). The second is the proportion of active forms and anhydrobiotic forms at the time of the rains. This proportion is unknown but was certainly very different for freeliving nematodes and phytoparasitic ones. Since freeliving nematodes have a shorter biological cycle than plant parasitic ones, their reactivation is certainly faster.

Nematodes captured in the fallow plot were 5·3 (freeliving) and 2·3 (phytoparasitic) times fewer than in the other plots. These differences are related to differences in the volume of soil moved by raindrop impact and the corrected rates are closer from one plot to the other than the raw number of captures. Thus, the corrected rate of capture in the fallow plot was only 1·4 lower than in the other plots for the freeliving nematodes, and was actually greater for the phytoparasitic nematodes.

The average capture of freeliving nematodes tended to increase with time. This was true for both the raw number of captures and for the corrected rates. This result must be interpreted cautiously because the experimental conditions differed from one rain event to the next. However, we can compare, rain after rain, the ratio of the raw number of freeliving nematodes over the raw number of phytoparasitic nematodes captured. This ratio was, respectively for the three rains, 113, 109 and 263 freeliving nematodes for one phytoparasitic one. This means that, at rain event 3, the freeliving nematodes dramatically increased their capturability. This may correspond to the transformation of anhydrobiotic forms into active forms 3 days after rain event 1.

We also compared the capture rates of phytoparasitic and freeliving nematodes on a plot basis. For each plot, we have calculated the ratio of the capture rate of freeliving nematodes divided by the capture rate of phytoparasitic nematodes. This ratio was always greater than one because more freeliving nematodes were captured than phytoparasitic ones. It was equal to 30, 141 and 195 for fallow, groundnut and millet plots, respectively. This result shows that the freeliving nematodes were less mobile in the fallow plot even though they were the most numerous there. This demonstrates that soil tillage and previous crops influence the mobility of nematodes. Tillage probably enhanced the soil surface humidification and the reactivation of the freeliving nematodes which are present mainly in the top soil layer. The lack of measurement of the proportion of active forms (which are supposed to be more mobile) did not allow a more detailed interpretation of these ratios.

DISCUSSION AND CONCLUSION

Cadet and Albergel (1998), on the basis of measurements under natural rainfall in a 3 ha watershed, showed that nematodes can be transported by runoff regardless of the eroded soil. This result is confirmed.

Our experiment led to a better understanding of the mechanisms involved in the suspension process and the transport of nematodes by runoff. The hypothesis derived from the results concerning *Meloidogyne* nematodes allowed us to explain all the next results.

We have shown that raindrop erosion sets in suspension a large number of nematodes which can then spread over a long distance. Raindrop erosion of soil is fundamentally a small-scale process but its consequences, as regards spreading nematode infestations, is considerable. This spread of nematodes certainly plays a major role in nematode population dynamics in this area although it remained unknown until now. Nevertheless, a number of questions remain unresolved. The large difference in the rates of capture of the two trophic groups is not fully explained. More generally, the complete demonstration of the hypothesis made in this paper would require: (a) the specific counting of the active forms of the nematodes instead of the non-selective Seinhorst method; (b) the distinction of each nematode species; and (c) a better understanding of biological aspects.

The use of exotic nematodes such as *Meloidogyne* has demonstrated that the migration of nematodes is generally fast but requires a flow path with a continuous and significant flow velocity from the source of the nematodes to the outlet. This condition is generally not satisfied when the source of nematodes is a localized small area in a ploughed field. In this situation, active flow paths are very few and most of the surface water is almost immobile in puddles. There, the impact of raindrops agitates the water surface and shakes the suspension of nematodes leading to a high probability that the nematodes will contact soil or vegetation.

These results can be usefully compared to soil erosion results. During a single rainfall, up to 19 per cent of the nematodes set in suspension by raindrop impact reached the plot outlet. On the other hand, about 60 tons of sediment per hectare can be moved, from the ridges to the troughs. At the same time, only 0·25 tons per hectare came out of the plot which represents only 0·4 per cent of the sediment moved at a decimetre scale by raindrop impact.

The dynamics of raindrop erosion and sediment load are different. Raindrop erosion is a continuous process while sediment load at the outlet is linked to the increases of the discharge. A peak of turbidity was observed when the discharge increased. At this point, turbidity decreased exponentially. This dynamic is very different from that of raindrop erosion and there was no evidence that the sediments collected at the plot outlet had been previously detached by raindrop impact. In a field ploughed perpendicularly to the slope, flow paths are few. They are fed with the flood of the puddles in the troughs.

Despite the large amount of sediment moved by raindrop erosion, flow paths are fed with water flowing at very low velocity and consequently with a negligible carrying capacity. Erosion of ploughed soils at plot scale appears to be loosely connected with raindrop erosion. It could have its own dynamic, as described by Govers (1992) and Nearing *et al.* (1997) on rill erosion. These authors highlighted the interaction between the shape of the rill and the properties of the flow in it, mainly in non-cohesive materials. This equilibrium between the shape of the flow paths and the flow carrying capacity has been mainly studied for rills but there is no evidence that the same physical principles are not relevant to inter-rill runoff. The peaks of sediment load observed when the discharge increased could therefore be attributed to the flow path reaching a new equilibrium between its shape and the new discharge. The main consequence of this new equilibrium is the decrease of the carrying capacity causing a decrease in sediment load.

Nearing (1998) gave a statistical interpretation of the difficulties encountered by erosion models in the case of low discharge in ploughed, non-cohesive soils, which correspond to our experimental conditions. The comparison between raindrop erosion and runoff erosion, and some indications given by the study of nematode transport by runoff, suggest that these difficulties could have a deeper cause. Since the discharge of a flow path interacts with its shape, the carrying capacity of the flow might depend more on the history of the successive discharges than on the discharge in itself. Thus in the case of small discharges in ploughed fields, it might be impossible to assign a carrying capacity to a given discharge at the scale of ten square metres.

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