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Passive transport of phytoparasitic nematodes by runoff water in the Sudano–Sahelian climatic area

Patrice Cadet[a,*], Jean Albergel[b,1]

[a]*Laboratory of Bio-Pedology, ORSTOM, BP 1386 Dakar, Senegal*
[b]*Laboratory of Hydrology, ORSTOM, BP 1386, Dakar, Senegal*

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Abstract

The aim of the work was to quantify the role of runoff in nematode transport, compared with soil particle transport, during the rainy season in the Sudano–Sahelian area. The measurements were made at the outlet of a 58 ha watershed located in the Nioro du Rip region, south of the Senegalese peanut-growing basin. Every time the rainfall was sufficiently strong to cause a runoff, water was collected to estimate the volume of runoff, the soil particles and the nematode contents. Soils in the different agronomic areas were also collected to determine the nematode infestation. Some 6000 m^3 of water run off during the rainy season, together with 18.6 t of soil and 279.5 million of nematodes, 127 million of which were major phytoparasitic species. The transport of the different species was not uniform. The first five runoff episodes supplied one-half the volume of runoff water and transported approximately half the phytoparasitic nematodes, but nearly three-quarters of the solid particles. Fifteen percent of the nematodes were transported during the intermediate stage of the rainy season, and approximately 30% during the final period, with equivalent water proportions but smaller quantities of soil. Of the 15 genera and species observed in the area, *Tylenchorhynchus gladiolatus*, *Scutellonema cavenessi*, *Helicotylenchus dihystera* and *Gracilacus parvula* represented 87% of the soil population, 61% being accounted for by the first two species. The average proportions of *T. gladiolatus* or *G. parvula* in the runoff water were greater than those in the soil, while the opposite was true for *S. cavenessi*, *P. pseudopratensis* and *T. mashhoodi*. *H. dihystera* was equally represented in both the soil and runoff water. The consequences of this "biological erosion" on the field infestation and on the cultural system based on fallowing are discussed.

Keywords: Sudano–Sahelian area; Senegal; Nematodes; Watershed; Runoff; Erosion

1. Introduction

The climate of the tropical countries of the Sudanese Sahel (600–700 mm annual rainfall) is characterized by a very long dry season extending from November to June, followed by a three-to four-month wet season. The number of rainfall episodes during this brief rainy season is small, but some are very violent and give rise to considerable runoff, causing intense erosion (Albergel, 1995). Whatever be the magnitude of the runoff, the finer, lighter-weight particles such as clays, silts and very fine-grained sands are carried off (Valentin et al., 1994). As a result of the spectacular nature of this phenomenon, as well as its impact on soils, it has been widely studied,

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* Corresponding author. Fax: (221) 832 16 75; e-mail: Patrice. Cadet@orstom.sn

[1] Present address: ORSTOM, P434, 1004 El Menzah. Tunisia. Fax: (2161) 75 02 54; e-mail: albergel@tunis-orstom.rio.org

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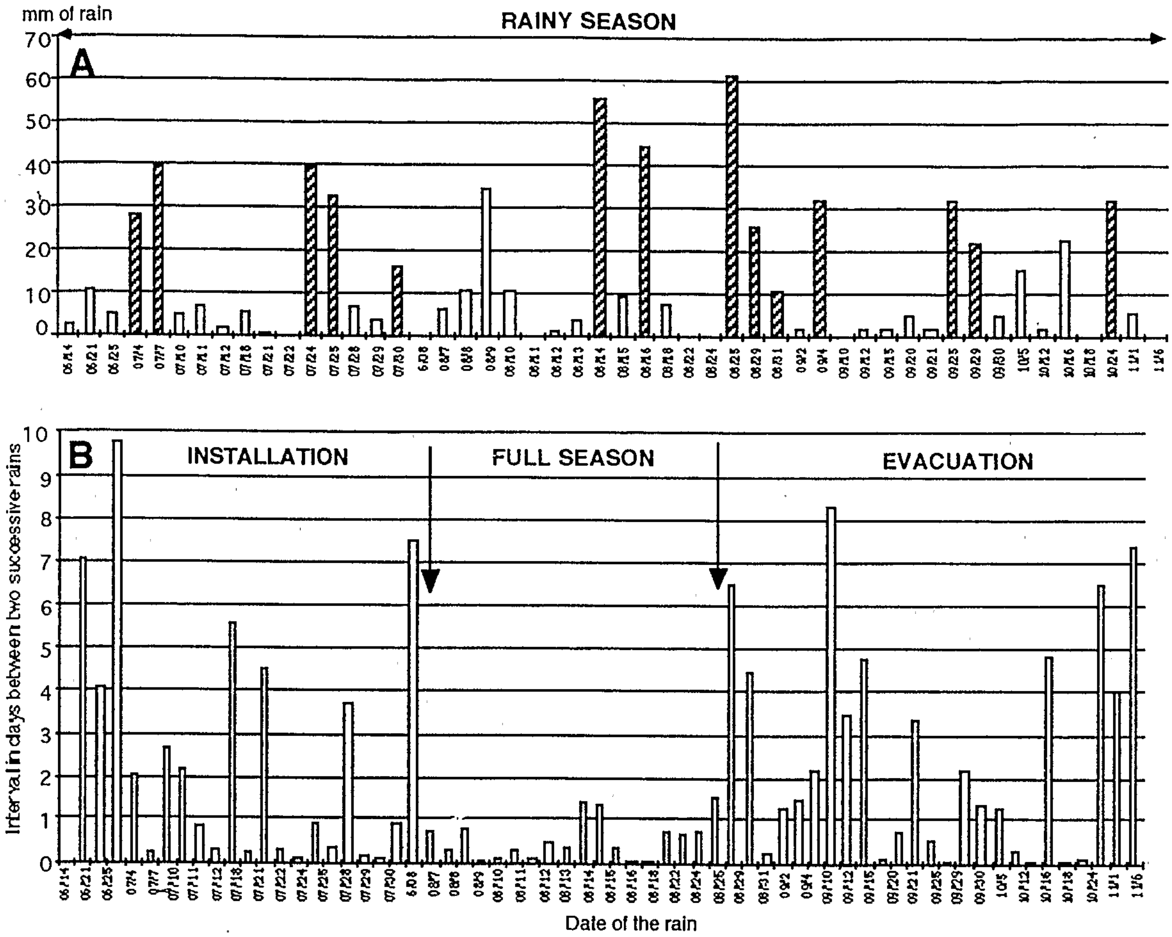

Fig. 1. Description of the rainy season: (A) Daily rainfall; the shaded bars represent rainfalls that gave rise to runoff. (B) Identification of the three stages in the rainy season from the interval (in days) between two rainfalls.

and numerous preventing techniques have been developed (Albergel et al., 1997).

However, in addition to carrying off solid particles, the runoff may transport organisms in the soil which are of similar size or mass to that of fine soil particles, for example, nematodes. The dissemination of nematodes by water is well known, and has been studied particularly in cases in which the parasites are carried by water intended for the irrigation of profitable industrial crops (Faulkner and Bolander, 1970; Waliullah, 1989; Shepherd and Barker, 1990). In the case of the rain-dependent cereal food crops of the Sudano–Sahelian region, the biological aspects of the erosion are not known.

Nonetheless, the pathogenic organisms transported by such water could infest the cultivated fields located along its path. A very large number of factors limit rainfall crops in this region, and climatic uncertainty lies at the top of the list. But with the emergence of the concept of low inputs sustainable agriculture, and possibly less control over pathogens, limiting factors such as nematodes (Germani and Gautreau, 1976; Germani et al., 1984) that were previously considered secondary for these types of crops, assume greater importance. Plants need a fully functional root system in order to draw the nutritive elements they require (Fortuner, 1997), as these are present or are supplied only in limited quantities. The aim of the present work is, thus, to quantify the role of runoff in nematode

Table 1
Physical and temporal characteristics of the three stages in the rainy season identified by the time elapsing between two consecutive rainfalls (panel A) and relative distribution of nematodes of different species of nematodes collected in the runoff water during the three stages of the rainy season (panel B)

	Rainy season Installation	Full season	Evacuation	Total
Panel A				
Precipitation	207.6 mm	176.8 mm	278.1 mm	662.5 mm
Length of rainy season stages	55 days	14 days	76 days	145 days
Average time between two rainfalls	3.1 days	1.1 days	3.6 days	
Average rainfalls height giving rise to runoff	27.8 mm	41.3 mm	25.7 mm	
Average rainfalls height not giving rise to runoff	4.5 mm	7.4 mm	4.8 mm	
Number of runoff episodes	5	2	7	14
Average duration of runoff	2 h 03	3 h 15	2 h 23	
Number of days without runoff	14	9	13	
Panel B				
Tylenchorhynchus sulcatus	100%	0%	0%	
Criconemella curvata	88%	0%	12%	
Pratylenchus pseudopratensis	75%	7%	18%	
Helicotylenchus dihystera	64%	7%	29%	
Gracilacus parvula	53%	24%	22%	
Tylenchorhynchus mashhoodi	50%	12%	38%	
Tylenchorthychus gladiolatus	50%	18%	32%	
Scutellonema cavenessi	40%	14%	46%	
Tylenchorhynchus ventralis	17%	12%	71%	
Paratylenchus sp.	2%	0%	98%	
Aphasmatylenchus variabilis	0%	0%	100%	

transport, compared with soil particle transport, during a rainy season.

2. Material and methods

The measurements were made at the outlet of a 58 ha watershed located in Keur Dianko (13°45 N and 15°40 W), in the Nioro duRip region, south of the Senegalese peanut-growing basin where one-half of the area is covered by crops. The other half is covered by fallow or natural vegetation, particularly in the highest part of the topographical sequence, where the soils are thinnest. The main crops of the region are millet and peanuts (Baujard, 1986). From June to October, every time the rainfall was sufficiently strong to cause runoff, 15-l pails were filled with water flowing from the settling basin of the hydrological measurement station. The pails were filled at the same intervals as those used by hydrologists taking the samples required to estimate the volume of runoff and erosion (Albergel and Perez, 1991). This interval might vary from 1 min during the time of heaviest runoff to more than 1 h at the end of the storm.

The 15-l pails were left to decant for several hours to bring the volume of water to 2 l by siphoning off the supernatant liquid. The nematodes were extracted from this sample in the laboratory, using Seinhorst' (1962) method. The species were divided into two groups: the species suspected to be dangerous for the crops of the region are considered as ''major'' and the other are grouped in the ''minor species''.

The number of individuals transported by the rainwater was calculated by the same method as that used to estimate the volume of runoff water and the quantity of solid particles transported, based on an estimation of the number of transported nematodes in the interval between two samplings (Toebes and Ourivaev, 1970).

Table 2
Physical or biological characteristics of the 14 runoff episodes observed during the rainy season

Date of runoff	Duration of runoff	Rainfall (mm)	Runoff volume (m^3	Transported matter (kg)	Major individuals (× 10^5)	Minor individuals (× 10^5)	Major nematodes/s	Minor nematodes/s
Jul-4	1 h 40 min	27.9	115	248	2.7	4.9	44	81
Jul-7	1 h 54 min	39.3	1593	8566	82.6	249.2	1208	3643
Jul-24	2 h 16 min	25.0	538	2226	78.4	148.5	961	1820
Jul-25	3 h 00 min	30.5	1016	2443	182.7	490.7	1692	4543
Jul-30	1 h 26 min	16.3	46	110	302.8	8.8	5868	170
Aug-14	3 h 00 min	55.6	716	1402	117.4	144.8	1087	1341
Aug-16	3 h 30 min	27.0	172	158	88.2	31.7	700	252
Aug-25	2 h 45 min	40.0	480	1066	42.2	59.9	426	605
Aug-25	2 h 58 min	21.4	255	463	112.0	99.1	1049	928
Aug-29	2 h 54 min	25.4	235	573	84.5	113.0	810	1083
Aug-31	2 h 10 min	10.6	40	42	16.6	14.4	213	184
Sep-4	3 h 00 min	31.8	667	1153	160.4	152.7	1485	1414
Sep-25	2 h 08 min	28.2	126	171	0.7	4.2	9	55
Sep-29	0 h 5 min	21.9	31	2	0.1	1.7	5	62
Total			6029	18623	1271.4	1523.6	1111	1156

Table 3
Nematode species and genera observed in the soil and in the runoff waters during the rainy season

Groups	Genus	Soil species	Water genus or species
Major species	*Tylenchorhynchus*	*T. gladiolatus*	+
		T. mashhoodi	+
		T. sulcatus[a]	+
		T. ventralis[a]	+
	Suctellonema	*S. cavenessi*	+
	Helicotylechus	*H. dihystera*	+
	Pratylenchus	*P. pseudopratensis*	+
	Criconemella	*C. curvata*[a]	+
	Gracilacus	*G. parvula*[a]	+
	Longidorus	*L. brevis*[a]	+
	Aphasmatylencus	*A. variabils*[a]	+
	Paratylenchus	*P. sp.*[a]	+
	Triversus	*T. annulatus*[a]	–
	Xiphinema	*X. parasetariae*[a]	–
	Aorolaimus	*A. macbethi*[a]	–
	Paratrichodorus	*P. minor*[a]	–
Minor species	*Trichotylenchus*	*T. falciformis*	*Trichotylenchus*
		T. rhopalocercus	
	Ditylenchus	*D. equalis*	*Ditylenchus*
		D. anchilispomosus	
	Aphelenchus	*Aphelenchus spp*	+
	Ecphyadophora[a]	*Ecphyadophora spp*[a]	+
	Filenchus	*Filenchus spp*	+
	Coslenchus	*Coslenchus spp*[a]	+

[a] Species or genera present in less than 15% of the soil samples.

Approximately 180 soil samples (300 g) were collected in June, July, September, October and November, at depths of between 5 and 15 cm, in fallow of different ages and cultivated fields located in the drainage area, to determine the composition of soil phytoparasitic nematodes communities according to the proportions of fallows and fields on the watershed (50% each). The calculation was made with the densities of nematodes per dm^3 of soil. The same Seinhorst‘ (1962) method was used to extract the nematodes from the soil.

3. Results

3.1. Description of the rainy season

As soil humidity is important for the life of organisms and because soil humidity depends upon the frequency of rains, the rainy season was arbitrarily divided into three phases according to this parameter. Between 14 June and 6 November there were 50 days of rainfall (Fig. 1(A)) and 65 rainy sequences. The time elapsing between two rainfalls varied from a few hours to more than 9 days. Between the 8th and the 25th of August, there were 27 rainfalls with a maximum frequency of 48 h, suggesting that the soil is always humid during this period, which was therefore considered as the full season. At the beginning of the rainy season, the interval between rainfalls tended to decrease gradually, while the opposite occurred at the end of the season (Fig. 1(B)). The rainy season moved on over a period of 55 days, and disappeared over a period of 76 days. Total annual rainfall was 662.5 mm (Table 1 (panel A)).

The average amount of precipitation of the daily rains that caused runoff, such as that of rains that did not, was greater during the full-blown rainy season than at the beginning or the end (Table 1 (panel A)). The 14 runoff episodes occurred throughout the rainy season, at intervals varying from 1 to 25 days (average 8.6 days). There was a correlation between the

Table 4
Average relative proportions of the different major genera or species of nematodes in the runoff waters or in the soil and in the fallow and cultivated areas. (– not found)

	Water	Soil		
		Fields	Fallows	Watershed estimations
Dominant genera or species (in %)				
T.gladiolatus	45	41	14	26
S. cavenessi	21	47	25	34
G. parvula	16	0	11	7
H. dithystera	16	2	33	20
P. pseudopratensis	1	3	10	7
T. mashhoodi	1	6	5	5
Rare genera of species (in ‰)				
C. curvata	4.3	< 0.1	1.4	0.8
T.sulcatus	2.8	< 0.1	< 0.1	< 0.1
T. ventralis	1.0	0	1.2	0.7
A. variabilis	0.3	2.4	0.9	1.5
Paratylenchus	< 0.1	0.1	< 0.1	< 0.1
X. parasetariae	–	< 0.1	2.6	1.5
L. brevis	< 0.1	< 0.1	0.1	0.1
T. annulatus	–	< 0.1	0.5	0.3
A. macbethi	–	< 0.1	< 0.1	< 0.1
P. minor	–	< 0.1	< 0.1	< 0.1

quantity of soil particles transported and the volume of runoff water ($r = 0.978$), and they developed proportionally (a highly significant regression; $p < 0.001$). The greatest runoff or amount of soil particles transported occurred at the beginning of the rainy season. Runoff then tended to decrease in intensity, with the exception of the runoff on 4 September (Table 2). In all, there was a runoff of some 6000 m^3 of water during the rainy season, which took with it 18.6 t of soil. The maximum flow of major nematodes was 665.4 worms/l or 5868 worms/s, and occurred during the runoff on 30 July.

3.2. Comparison of nematode populations in the soil and in the runoff water

3.2.1. Survey of nematode species and genera present in soil and runoff water

In the plants rhizosphere, 24 species or genera were observed during the rainy season (Table 3). Only five major nematode species were present in over 15% of the soil samples taken: *Tylenchorhynchus gladiolatus*, *Tylenchorhynchus mashhoodi*, *Scutellonema cavenessi*, *Helicotylenchus dihystera* and *Pratylenchus pseudopratensis*.

Not all the genera and species observed in the soil were found in the runoff waters. The major species not found there, *Triversus annulatus*, *Xiphinema parasetariae*, *Aorolaimus macbethi* and *Paratrichodorus minor*, were not highly represented in the soil (fewer than 15% of the samples).

3.2.2. Relative proportions (%) of major phytoparasitic nematodes in soil and water

3.2.2.1. Average relative proportions Of the 16 genera and species of major nematodes observed in the region, *T. gladiolatus*, *S. cavenessi*, *H. dihystera* and *G. parvula* represented 87% of the soil population, 61% being accounted for by the first two species (Table 4). In the runoff water, these proportions rise to 98% and 66% respectively. The average proportions of *T. gladiolatus* or *G. parvula* in the runoff water were greater than those in the soil, while the opposite was true for *S. cavenessi*, *P. pseudopratensis* and *T. mashhoodi*. *H. dihystera* was equally represented in both soil and runoff water.

Regarding the rare species, which represent less than 1% of the total soil nematode population, *C. curvata* and *T. sulcatus* were present to a greater

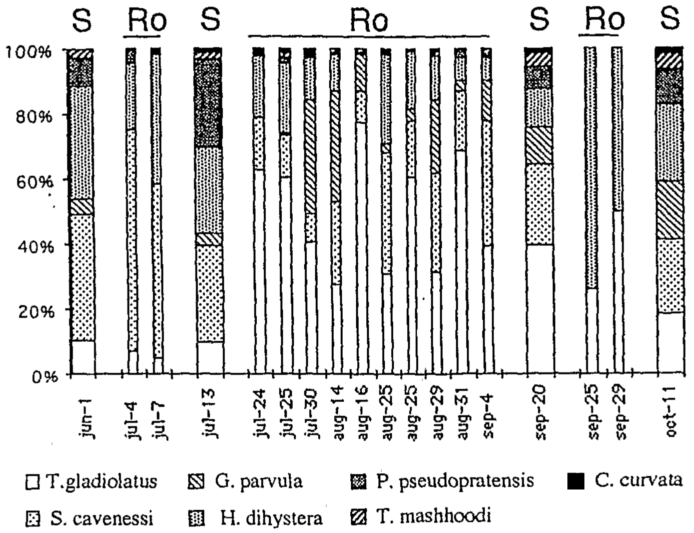

Fig. 2. Evolution of the structure of the major plant parastic nematode community in the soil (S) and in the runoff water (Ro).

extent in the water than in the soil, while the opposite was true for *A. variabilis* and *L. brevis*.

3.2.2.2. Evolution of the relative proportions during the rainy season Generally speaking, the structure of the earth-dwelling community varied little during the rainy season, unlike that of the water-borne community (Fig. 2). During the first two runoff episodes, there was a certain similarity between the proportions of the different species in the soil and in the surface waters. When the rainy season was well underway, the species composition of the water changed randomly, although there was a high proportion of *T. gladiolatus*. At the end of the rainy season, the structure of the nematode population in runoff waters was radically different from that in the soil. *S. cavenessi* was no longer present, and *T. gladiolatus* and *H. dihystera* predominated. However the number of nematodes was very low.

3.2.3. *Number of nematodes and species transported in the runoff water*

Over the rainy season as a whole, the number of individuals transported to the outlet of the drainage area was 279.5×10^6, 127×10^6 of which were major nematodes species (Table 2). The minor nematodes *Filenchus* and *Trichotylenchus* were the most numerous to be carried by the runoff waters, with 65.6 and 60.9×10^6 individuals respectively, followed by *T. gladiolatus* and *S. cavenessi*, with 56.7 and 27.0×10^6 specimens (Table 5). Aside from those which were not observed, the least numerous to be transported was *L. brevis*, with 80 individuals. The number of species observed during one runoff episode varied from 2 to 11. The number of species observed was roughly proportional to the number of nematodes transported.

3.3. *Nematode/runoff ratios*

The transport of these different species was not uniform over the rainy season. Overall, the first five runoff episodes occurring during the beginning of the rainy season supplied one-half the volume of runoff water and transported approximately half the phytoparasitic nematodes, but nearly three-quarters of the solid particles (Fig. 3). Fifteen percent of the nematodes were transported during the intermediate stage, when rainfall was most frequent, and approximately 30% during the final period, with equivalent water proportions but distinctly smaller quantities of soil. This is the pattern for four phytoparasitic species, including the most abundant: *T. gladiolatus* (Table 1 (panel (B)). In contrast, *S. cavenessi* was found in roughly equal quantities at the beginning and at the end of the rainy season, although it was totally absent from the last two runoffs. *P. pseudopratensis*, *C. curvata* and *T. sulcatus* appeared primarily during

Table 5

Numbers of individuals ($\times 10^5$) of the different major and minor nematode species or genera collected during each of the 14 runoff episodes. (0: no nematode observed; *: 160 *Paratylenchus*; 80 *Longidorus*)

	4 Jul	7 Jul	24 Jul	25 Jul	30 Jul	14 Aug	16 Aug	25 Aug	25 Aug	29 Aug	31 Aug	31 Sep	25 Sep	29 Sep	Total
Major class															
T.gladilatus	0.19	3.99	47.60	110.57	122.40	32.59	68.12	12.91	67.51	26.58	11.46	62.90	0.18	0.06	567.05
Scutellonema	1.82	44.64	12.49	22.93	25.59	29.66	8.73	15.92	19.61	25.34	2.96	60.99	0	0	270.66
Gracilacus	0	0	0	2.12	106.13	40.03	9.63	1.21	4.38	19.67	0.59	19.86	0	0	203.61
Helicotylenchus	0.53	32.60	14.47	38.57	39.73	13.64	0.94	11.62	20.29	11.19	1.11	11.51	0.52	0.06	196.78
Pratylenchus	0.12	1.39	0.85	3.19	3.19	0.83	0	0	0.24	0.00	0.48	1.43	0	0	11.72
T. mashhoodi	0	0	0.03	2.60	2.78	0.66	0.63	0.19	0	1.43	0	2.45	0	0	10.76
Criconemella	0	0	0.57	2.12	2.12	0	0	0.37	0	0.26	0	0	0	0	5.44
T. sulcatus	0	0	2.39	0.61	0.61	0	0	0	0	0	0	0	0	0	3.61
T. ventralis	0	0	0	0	0.23	0	0.15	0	0	0	0	0.93	0	0	1.31
Aphasmatylenchus	0	0	0	0	0	0	0	0	0	0	0	0.34	0	0	0.34
Paratylenchus	0	0	0	0	0.0*	0	0	0	0	0.07	0	0	0	0	0.07
Longidorus	0	0	0	0	0.0*	0	0	0	0	0	0	0	0	0	8.00
Nb of species or genera	4	4	7	8	11	6	6	6	5	7	5	8	2	2	12
Minor class															
Filenchus	3.16	164.11	111.54	127.57	4.73	35.67	10.05	38.54	37.36	56.91	3.96	58.53	3.32	1.01	656.46
Trichotylenchus	0.28	4.34	7.19	323.15	0.72	103.5	19.09	11.41	50.52	28.00	5.36	55.26	0.15	0.39	609.36
Ditylenchus	1.08	32.69	20.61	6.08	1.28	1.83	0	4.68	4.35	8.76	1.39	10.91	0.62	0.24	94.51
Coslenchus	0	11.50	4.05	31.62	1.84	1.30	0.71	3.56	3.23	8.85	1.53	18.99	0	0	87.19
Aphelenchus	0.35	36.55	5.14	2.26	0.02	0.16	0.37	1.31	3.52	7.71	1.07	2.25	0.15	0.04	60.90
Ecphyadophora	0	0	0	0	0.19	2.38	1.52	0.37	0.16	2.81	1.04	6.74	0	0	15.21
Nb of genera	4	5	5	5	6	6	5	6	6	6	6	6	4	4	6

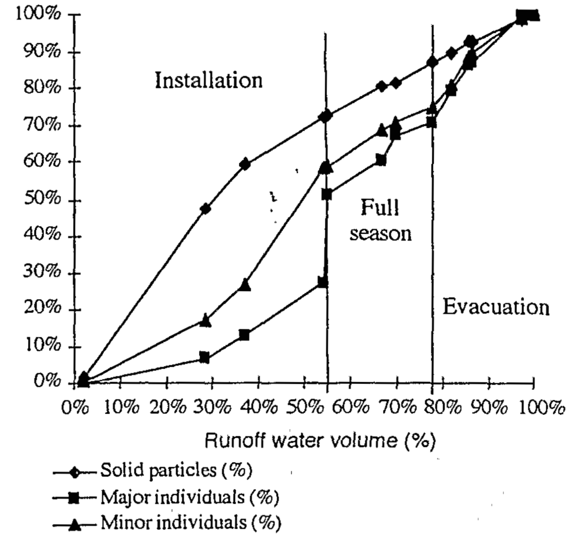

Fig. 3. Mass of solid matter, number of major and minor nematodes expressed in percentage of the final quantity plotted against the volume of runoff water (in % of the final quantity).

Table 6
Correlation coefficient of the total number of each nematode genus and species observed during each runoff, and the volume of runoff water or the total mass of solid particles transported. (The coefficients marked with a * are significant: $p < 0.05$)

	Runoff volume	Transported particles
Major	0 .207	0 .074
T. gladiolatus	0 .054	− 0 .119
Scutellonema	0 .658*	0 .514
Gracilacus	− 0 .182	− 0 .19
Helicotylenchus	0 .573*	0 .514
Pratylechus	0 .407	0 .289
T. mashhoodi	0 .126	− 0 .97
Criconemella	0 .103	− 0 .006
T. sulcatus	0 .099	011
T.ventralis	− 0 .063	− 0 .086
Aphasmatylechus	− 0 .151	− 0 .023
Longidorus	− 0 .246	− 0 .158
Minor	0 .786*	0 .569*
Filenchus	0 .902*	0 .857*
Trichotylechus	0 .431	0 .119
Ditylechus	0 .785*	0 .895*
Coslenchus	0 .630*	0 .392
Aphelenchus	0 .756*	0 .939*
Ecphyadophora	0 .760*	-0 .124

the first runoffs, while *T. ventralis* and *A. variabilis* were observed mainly at the end of the rainy season.

With the exception of *Trichotylenchus*, there was a significant correlation between the presence of the minor individuals and the volume of runoff water, and sometimes to the mass of solid particles as well (e.g., *Ditylenchus* and *Aphelenchus*). There was never a correlation between major individuals and solid transport. For only two species, *S. cavenessi* and *H. dihystera*, there was a correlation with the volume of runoff water (Table 6). This difference between the two nematode groups resulted essentially of the 30 July runoff, which, while relatively weak, bore a considerable number of major individuals, particularly *G. parvula* and *T. gladiolatus*, but no abnormally high number of minor individuals (Table 5). This runoff occurred at a time at which the abundance of soil phytoparasitic nematodes was increasing, whereas the abundance of minor parasitic nematode population remained stable (Fig. 4).

4. Discussion

Nematodes regarding certain characteristics, may be compared to soil particles. The fact that they are not very mobile prevents them from leaving their habitat as for example, an insect might do, when conditions become unfavorable. To compensate for this, the nematodes are endowed with extremely effective forms of resistance, foremost among which is anhydrobiosis (Demeure et al., 1979), an ability that helps them to withstand the 7–8 month dry season which characterizes the Sahelian–Sudanese climate (Rasmusson, 1987).

Their mass of between $15–100 \times 10^{-9}$ g corresponds to that of a "fine sand" grain in the classic soil grain size classification (sphere between 50 and 200 μm in diameter, $d = 2.67$). However, the size of nematodes, which range from 250 to 1500 μm in length and 12–30 μm in diameter, makes them generally much larger than the fine sand particles, and closer to the size of coarse sand. Mechanically speaking, this difference inevitably poses a hindrance to their being carried along by the runoff water. However, unlike solid particles, nematodes do make movements by which they may free themselves from the aggregates.

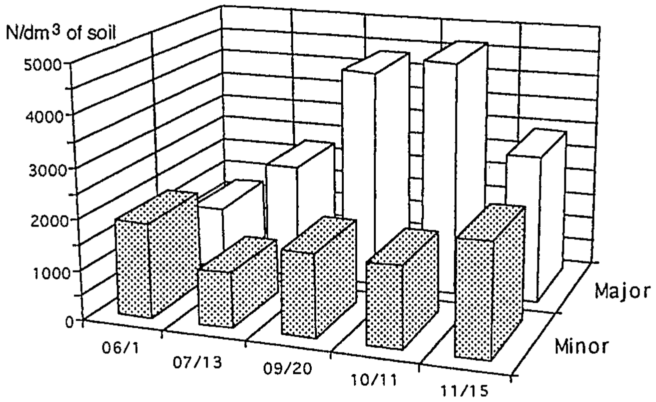

Fig. 4. Evolution of the average density of major and minor individuals per dm^3 of soil on the drainage area during the rainy season. (N: nematodes).

Considering the number of individuals per dm^3 as equivalent to that on a 100 cm^2 surface, the average level of soil infestation by phytoparasitic nematodes is 331,700/m^2, or approximately 200 billion over the entire 58 ha drainage area. Thus only 0.06% of these were transported by runoff. This may appear insignificant mathematically, but it is three times more than for the soil erosion: 18.6 t out of 80×10^3 t of soil in the 10 cm top layer ($d = 1.4$) and three times more than the number of nematodes estimated in the 18.6 t of transported soil particles. According to the high reproductive rate of nematodes, which can reach as much as 100–500 per month or bimonthly cycle (Baujard and Martiny, 1991; Siddiqi, 1972) and their ability to lay eggs immediately upon rehydration (Demeure et al., 1980), the theoretical reinfestation potential is high. Their pathogenic effect is enhanced by the fact these nematodes arrived with the first heavy rains, which also triggered off planting and germination, placing the parasites in the presence of relatively vulnerable plantlets.

The greatest runoff occurred during the initial stage of the rainy season. Without vegetation to protect the soil, this was also the period of greatest erosion. While the quantity of soil transported was directly proportional to the volume of runoff water, this relation did not hold good for the major phytoparasitic nematodes, which tended to increase in number with each runoff episode at the beginning of the rainy season, more or less independently of runoff water volume. In other words, the presence of nematodes in runoff did not depend solely upon the mechanical laws that governed solid transport. A clear divergence appeared, for instance, on 30 July, between the large number of major nematodes transported and the low intensity of runoff, a contradiction that did not appear in the figures for soil particles or for minor nematodes. The carriage of major nematodes seems more to follow the pattern observed for a soluble soil chemical (Zhang et al., 1997).

This situation was probably the result of various factors:

A time factor: This runoff occurred precisely two months after the beginning of the rainy season. This period corresponded to one or two generations of nematodes, a fact which enables certain species – particularly those which, for lack of effective resistance, were represented by only a small number of individuals at the end of the dry season – to reconstitute a substantial population that could be detected in the runoff waters. This appeared to be the case with *T. mashhoodi*, *C. curvata*, *P. pseudopratensis* and, especially, *G. parvula*. The latter species, which was small (at least 10 times smaller than *S. cavenessi*) abruptly appeared in high proportions in the runoff, much higher than those in the soil. The fact that the greatest diversity of species in the nematode population was reached at this time supported this hypothesis.

A factor of localization: It was at approximately the same period (the end of the installation of the rainy season) that the herbaceous plants had colonized all available surfaces. They supported an intense nematode activity (Cadet and Floret, 1995) and kept the nematodes in the top soil horizon colonized by their roots, a layer which was in direct contact with the runoff.

Finally, even if only a small proportion of this community was carried away by runoff, that proportion represented, for the major phytophagous nematodes, a great number of individuals. For the minor nematodes, the overall soil-dwelling community varied little during the season. This difference between the two groups could be biological in origin. The minor nematodes multiplied at the expense of fungi in the soil, which, like all microorganisms, developed very rapidly once the soil was moist, whereas the major phytoparasitic nematodes were ''forced to await'' the renewed growth or the germination of the higher plants in order to reproduce.

Conversely, the very first runoff episodes at the beginning of the rainy season caused erosion which was intense but which bore off only a relatively small number of nematodes, a paradox which could be explained by the fact that the surface soil layer, at this period, contained only nematodes that had survived the dry season. Their number was necessarily limited, as the lack of host plants had kept them from multiplying yet. These species were the best equipped for entering into anhydrobiosis and were the most resistant to the dry season, as they were located in a horizon that was subjected to great temperature and moisture variations. They had the best chances of settling in newly cultivated fields, as they always arrived first, at the time of seed germination, and thus did not have to face inter-species competition. *S. cavenessi* seemed to be the most efficient species in this respect (Demeure, 1980), and indeed it did predominate on the region's crops despite its low reproduction rate (Germani et al., 1984; Germani, 1981). *H. dihystera*, in contrast, which was well represented during the first runoffs, did not take up residence on these crops, but was supplanted by *T. gladiolatus* in the fields (Pate et al., 1995). Thus it is probable that environmental factors regulated inter-species competition, in as much as millet, sorghum, and peanuts are host plants to all these species, including *H. dihystera* and *P. pseudopratensis*, which were transported in quantities practically equal to those of *T. gladiolatus*, but which disappeared in the fields.

In the middle and at the end of the rainy season, a good correspondence could be noted between the volume of runoff and the number of both major and minor nematodes transported. During this period, the size of the soil-borne population evolved little, but the soil was now well protected by vegetation. The impact of runoff decreased and physical and biological erosion were governed exclusively by mechanical laws. The stronger the runoff was, the greater was the likelihood that it would transport something.

This overall analysis concealed considerable disparities among different species. In particular, *S. cavenessi* was not detected in the waters of the last two runoffs although it was present in the soil at this period, as was shown by observations of samples taken in fallow and planted fields. Also the runoff of 25 September would potentially had been capable of transporting members of this species, as would that of 30 July, although it was much weaker. Only two ectoparasites, *T. gladiolatus* and *H. dihystera*, were present in these two runoffs.

5. Conclusion

The phenomenon of biological erosion that we have measured at the outlet of the watershed is reproduced naturally on all scales. One major consequence of this will be periodic reinfestation of the soil by nematodes, particularly at the time the fields are planted, which is precisely the same moment. If the cultivated fields are located upstream from the fallow land with regard to the passage of runoff waters, the advantage of nematode control exercised by the fact of lying fallow will be immediately destroyed with the first runoff and the first planting. The effect that lying fallow has had on the physical and chemical components of fertility will, of course, continue to favor the growth of the millet, but as the crop cycles progress it will disappear more rapidly when nematodes are present, in as much as these alter the efficiency of the root system. It is the dimension of ''sustainability'' that will be affected.

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