Eur. J. Soil Biol., 1996, 32 (2), 81-88

Influence of the soil on the transport of the spores of *Pasteuria penetrans*, parasite of nematodes of the genus *Meloidogyne*

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Received March 27, 1996; accepted May 22, 1996.

Abstract

Transport of spores of *Pasteuria penetrans* and of juveniles of *Meloidogyne javanica* was assayed under a water drip supply in four soils: a sandy soil, a clay soil and two sandy-clay soils. For the sandy soil, 67.7% of spores of *P. penetrans* and 78% of juveniles of *M. javanica* percolated with water in spite of high reproduction of *M. javanica* in that soil. For the clay soil, only 0.12% of juveniles and 10.6% of spores moved down. But 50% of spores still remained in that soil after extraction and so could not be available for attachment. Transport of juveniles of *M. javanica* and of spores of *P. penetrans* was easier in the sandy-clay soil which was originally free of *P. penetrans* and contained 6% less clay than the other which was naturally infested by *P. penetrans*. A survey conducted on vegetable crops in Senegal confirmed that juveniles of *Meloidogyne* spp. infected by *P. penetrans* were abundant in sandy soils with about 10% of clays. So, the availability of spores of *P. penetrans* to attach juveniles of *M. javanica* would depend on a balance of soil texture and porosity, and on the capacity of colloids to release spores adsorbed to the soil matrix.

Keywords: *Meloidogyne* spp., *Pasteuria penetrans*, percolation, phytoparasitic nematodes, soil, transport.

Influence du sol sur le transport des spores de Pasteuria penetrans, *parasite des nématodes du genre* Meloidogyne.

Résumé

Le transport de spores de *Pasteuria penetrans* et de juvéniles de *Meloidogyne javanica* a été étudié sous un flux d'eau dans un sol sableux, un sol argileux et deux sols sablo-argileux. Dans le sol sableux, 67,7 % des spores de *P. penetrans* et 78 % des juvéniles de *M. javanica* ont été recueillis dans l'eau de percolation malgré une forte multiplication de la population de *M. javanica* dans ce sol. Dans le sol argileux, 0,12 % seulement de juvéniles et 10,6 % de spores ont été recueillis dans le percolat. En outre, 50 % des spores n'ont pu être extraites de ce sol. Par conséquent, elles n'auraient pas été disponibles pour parasiter des juvéniles. Les juvéniles de *M. javanica* et les spores de *P. penetrans* ont plus facilement traversé le sol sablo-argileux qui, à l'origine, était indemne de *P. penetrans* et contenait 6 % d'argile de moins que l'autre sol sablo-argileux qui, lui, était naturellement infesté en *P. penetrans*. Une enquête conduite dans les zones de culture maraîchère au Sénégal confirma que les juvéniles de *Meloidogyne* spp. infectés par *P. penetrans* abondaient dans les sols sableux contenant environ 10 % d'argile. Par conséquent, la disponibilité des spores de *P. penetrans* au parasitisme dépendrait d'un équilibre texture/porosité du sol et de la capacité du sol à libérer les spores susceptibles d'être adsorbées par les colloides argileux.

Mots-clés : *Meloidogyne* spp., *Pasteuria penetrans*, percolation, nematodes phytoparasites, sol, transport.

INTRODUCTION

Except the very high specificity of the biochemical recognition of the cuticle of the nematode by the spores of *Pasteuria penetrans* (Davies & Danks, 1993), soil moisture and temperature have been the more important factors tested for their influence on the ability of the spores of *P. penetrans* to attach to juveniles of *Meloidogyne* spp. Stirling (1981) has shown that the optimal temperature for attachment (15 °to 20 °C) approximates the optimal temperature for nematode development. At high temperatures (about 100 °C), even though the attachment is decreased, the spores can still adhere to the cuticle

Eur. J. Soil Biol., 1164-5563/96/02/$ 4.00/© Gauthier-Villars

of the nematodes (Dutky & Sayre, 1978; Stirling *et al*, 1986), suggesting that the attachment is not only a heat-sensitive biochemical phenomena.

The spores can survive for a long time in dry soils (Stirling et Wachtel, 1980), but moisture to pF 4.2 reduces the development of *P. penetrans* in the nematode females (Davies *et al.*, 1991). In contrast, the increase of soil moisture (Brown & Smart, 1984), and series of desiccation and humectation favour the attachment of the spores (Oostendorp *et al.*, 1990). But the specificity of the attachment and the soil climatic conditions are not sufficient to explain the variable efficacity of the parasitoide. Spaull (1984) observed that the proportion of infected juveniles of *Meloidogyne* is higher in sandy soils than in clay soils. But soils characterized by a coarse texture without clay particules would favour the spores to percolate (Oostendorp *et al.*, 1990) and decrease spore attachment (Singh & Dhawan, 1992). A recent survey in vegetable crops in Senegal has shown that the type of soils does not influence the development of the populations of *Meloidogyne* spp. but affects their distribution between the soil and the roots: for the same root infestation, the population in a sandy soil is lower than the population in a sand-silt soil (Mateille *et al.*, 1995a). Besides that, a correspondence analysis showed that populations of *Meloidogyne* spp. infected by *P. penetrans* are more abundant in sandy soils than in heavy soils but that the presence of clays in the sandy soils was positive (Mateille *et al.*, 1995b). The aim of this work was to study the influence of physical characteristics of soils on the transport of juveniles of *M. javanica* and of spores of *P. penetrans* under a flow of water and to discuss the consequences on the availability of the two organisms for further attachment.

MATERIALS AND METHODS

Transport of juveniles of *Meloidogyne javanica* and of spores of *Pasteuria penetrans* in different soils

Characteristics of the soils

Four soils were compared. A sandy soil was sampled from a bare fallow at the experimental station of the Centre de Développement Horticole (Cambérène, Sénégal). A clay soil was sampled from a bare fallow at west valley of the Senegal river. Both soils were free of nematodes of the genus *Meloidogyne* and of *Pasteuria penetrans*. The two others were sandy-clay soils from the experimental station of the École Nationale Supérieure d'Agriculture (ENSA Thiés, Senegal). They were both highly infested with *M. javanica* (20 000 juveniles per dm^3). Although the two fields which these soils came from were very close to each other, one of them (soil+Pp), cultivated with African egg-plants (*Solanum aethiopicum* cv. Soxna), was highly infested with *P. penetrans* (80% of infected juveniles) and the other one, cultivated with tomatoes (*Lycopersicon esculentum* cv. Heinz) was free of *P. penetrans* (soil−Pp). The four soils were autoclaved (24 h at 120 °C) before they were used. Their physical characteristics are listed in *table* 1.

Table 1. – Physico-chemical characteristics of the soils used for studying the transport of the juveniles of *Meloidogyne javanica* and the spores of *Pasteuria penetrans*.

Particles (%)	Sandy soil	Sandy-clay soils		Clay soil
		Soil −Pp	Soil +Pp	
Clay (0-2 μm)	1.1	6.3	10.3	57.1
Fine silts (2-20 μm)	0.8	1.5	1.7	12.4
Coarse silts (20-50 μm)	0.9	2.4	2.4	10.0
Fine sands (50-200 μm)	53.4	46.3	44.0	21.7
Coarse sands (200-2000 μm)	43.3	42.5	40.7	0.2

Water properties of the soils

Soil water capacity: PVC tubes (10 cm high and 1.5 cm diameter), closed at the bottom by a sieve (50 μm mesh), were filled up to 9 cm-high with the soils sieved at 1 mm. The soils were saturated by immersion in distilled water for 6 hours. The tubes were kept out of the water to drain. When drainage was finished, the tubes full of soil were weighted before and after drying (36 hours at 60-70 °C). The soil water capacity was expressed as the percentage of the dry weight.

Water percolation: PVC tubes with soils were prepared following the techniques as described above until drainage. Then, they were placed on the top of 500 ml bottles under a drip water supply (*fig.* 1). The optimal flows of water were set just below choking up at 8 $\mu ml.mn^{-1}$ for the clay soil and at 10 $\mu l.m^{-1}$ for the other soils. The volumes of the percolates were measured every 30 mn during 5 hours.

Transport of juveniles of Meloidogyne javanica *in a bare soil*

The PVC tubes with soils were prepared following the techniques as described above and placed on the top of 500 ml bottles under the drip water supply. Second stage juveniles of *M. javanica* were inoculated into the top soil layer (0-1 cm). Inocula were 450±25 nematodes in the sandy soil, 650±10 in the sandy-clay soil−Pp, 750±10 in the sandy-clay soil+Pp and 450±20 in the clay soil. The juveniles were counted every 24 hours in the percolates. When no more juvenile was detected in the percolates, the columns of soil were gently pulled out of the tubes by air pressure and cut into three 3 cm-layers which were mixed in 250 ml of water each. The juveniles

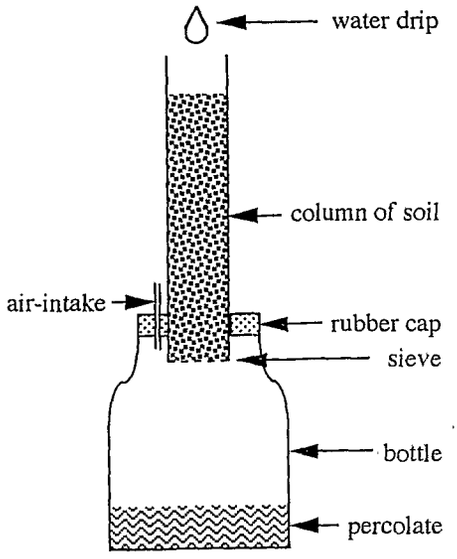

Figure 1. – Apparatus used for studying water percolation and transport of juveniles of *Meloidogyne javanica* and spores of *Pasteuria penetrans* in the soil.

were extracted according to the sieving technique (Seinhorst, 1956) and numbered.

Transport of juveniles of Meloidogyne javanica *in a cultivated soil*

Two-week-old tomato (*L. esculentum* cv. Roma) plants were transplanted in PVC tubes (20 cm high and 5 cm diameter), closed at the bottom by a sieve (50 μm mesh), and filled with soils. One week after transplantation, each plant was inoculated with 250 second stage juveniles of *M. javanica*. An intensive irrigation was applied to the plants corresponding to 85 ml in the sandy soil, 80 ml in the two sandy-clay soils, and 20 ml in the clay soil daily. The percolated water was collected and the juveniles were numbered daily in the suspension. For the clay soil, the counting of the juveniles was stopped 18 days after inoculation because of the saturation of the soil. The plants were uprooted about 34 days after inoculation, when the first symptoms of decay appeared. Nematodes were extracted from soil and roots (Seinhorst, 1950; 1962) and counted per plant.

Transport of spores of Pasteuria penetrans *in bare soil*

The PVC tubes with soils were prepared following the techniques as described above and placed on the top of 500 ml bottles under the drip water supply. Spores of *P. penetrans* were inoculated in the 0-1 cm-top of the soil column. Inocula were 415.10^5 spores in the sandy soil, 80.10^5 in the sandy-clay soil –Pp, 63.10^5 in the sandy-clay soil +Pp and 346.10^5 in the clay soil. Every 24 h the spores were extracted from the percolates by sieving at 0.3 μm and counted with a Malassez counting chamber. When no more spore was detected in the percolates, the columns of soil were gently pulled out of the tubes by air pressure and cut into 4 layers which were mixed in 10 ml of water each. After a 5mn decantation, the suspensions were sieved using a bank of sieves which the finest one was 0.45 μm. Then, the spores were counted as described above.

Statistical analysis

For all experiments, ten replicates were used for each soil. Data were analysed according to the Man Whitney U test. Proportions were transformed by Arcsin(sqrt) before analysis.

Relation between the abundance of *Pasteuria penetrans* and the soil texture

A survey was conducted in the main vegetable producing areas in Senegal. Soil was sampled at 150 different field locations. In each field, subsamples were taken along a transect (3 each 10 m) gathered in one collective sample. Nematodes were extracted by elutriation (Seinhorst, 1962). In the 50 samples where *P. penetrans* was present, the abundance of the actinomycete was estimated by counting the juveniles of *Meloidogyne* spp. infected by it and this was expressed in percent of the total juveniles.

The physical characteristics of the soil samples were analysed.

RESULTS

Movement of water

The clay soil retained two times more water than the sandy soil (*fig.* 2). The water capacities of the two sandy-clay soils were not different. But the water capacity of the sandy-clay soil +Pp was significantly different from those of the sandy and clay soils.

The total volumes of water which have percolated after 300 min were compared in the four soils (*fig.* 3A). The highest volume was obtained in the sandy soil (49.9 ml) where the rate of percolation was constant. The lowest volume was obtained in the clay soil (16.5 ml) where the rate of percolation was constant during the first two hours and decreased. The volumes obtained in the sandy-clay soils –Pp (43.3 ml) and +PP (41.3 ml) were not different but were significantly less than in the sandy soil and more than in the clay soil.

In the second experiment, percolation was followed in the two sandy-clay soils during 20 hours (*fig.* 3B). Rate of percolation was constant in the soil –Pp even though it significantly decreased in the soil +Pp at the end of the experiment.

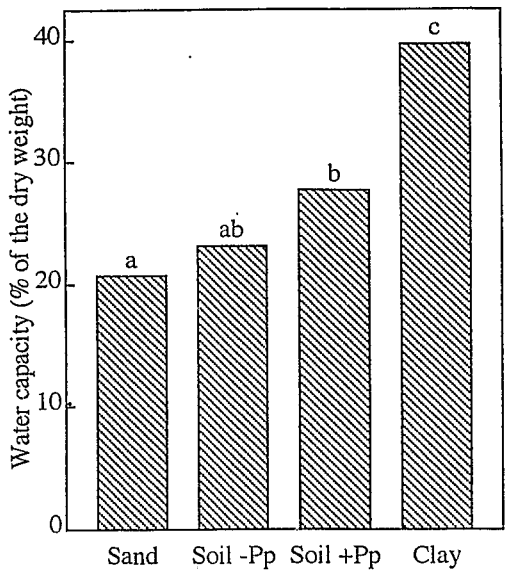

Figure 2. – Water capacity of the four soils studied (columns with the same letter are not significantly different, $p > 0.05$).

Transport of juveniles of Meloidogyne javanica

In the soils without plant, 60.5% of the juveniles of *M. javanica* percolated through the columns of sandy soils within 24 hours after inoculation (*fig.* 4). Then, the proportion of juveniles increased in the percolate during the next 100 hours and 78% had moved at the end of the experiment. During the first 24 hours, 22% of the juveniles percolated through the sandy-clay soil – Pp. The proportion increased in the percolate during the next 24 hours (26.5%). In the sandy-clay soil + Pp, only 3.3% of juveniles were numbered 90 hours after inoculation. After that, 1% more juveniles were detected in the percolate. In the clay soil, the juveniles appeared very sporadically: only 0.12% of the juveniles have moved down. At the end of the experiment, 12.6% of the juveniles were extracted in the sandy soil and 9.5% were not extracted (*fig.* 5). The proportions of non-extracted juveniles were very high in the sandy-clay soils (87% in the soil + Pp and 67.8% in the soil – Pp), and quite all the juveniles died in the clay soil (97.3%). The distribution of the juveniles which remained in the soils was heterogenous. More than 80% of the juveniles were recovered in the upper layer in the sandy soil. In the sandy-clay soils, they were concentrated in the median (soil – Pp) and in the lower layer (soil + Pp). In the clay soil, the few live juveniles remained in the two upper layers.

The percolation conducted in cultivated soils with tomato plants was stopped when a total supply of water of 340 ml in the clay soil, 2525 and 2565 ml in the sandy-clay soil – Pp and + Pp, and 2880 ml in the sandy soil were added (*fig.* 6). During the first month, the juveniles were rare in water percolating from the sandy and the sandy-clay soils, and quite absent in water percolating from the clay soil. During

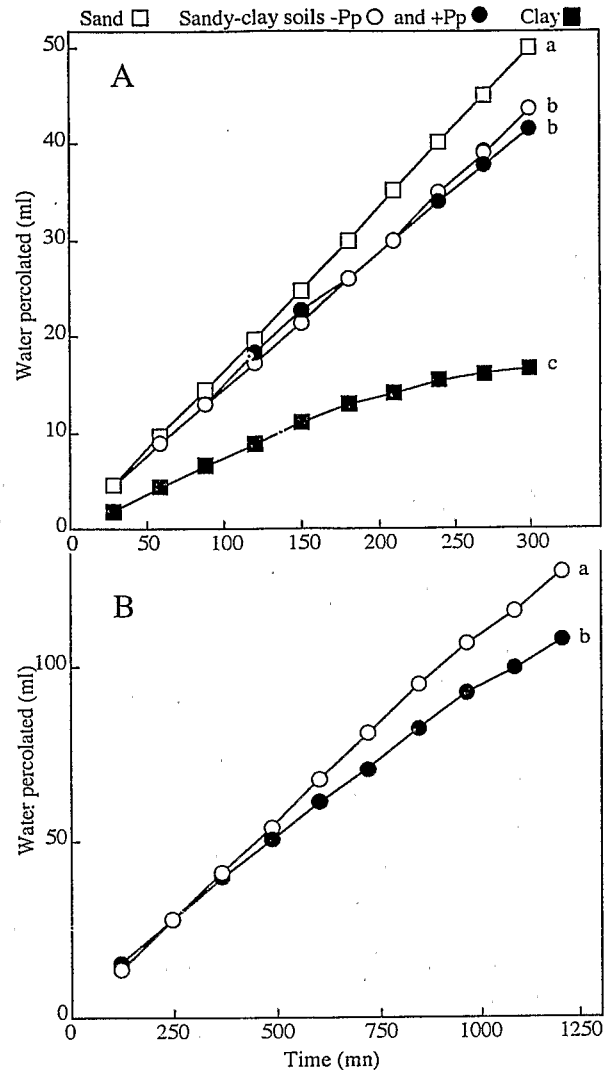

Figure 3. – Water percolation in the four soils during 5 hours (A) and in the sandy-clay soils during 20 hours (B) (last data with the same letter are not significantly different, $p > 0.05$).

the second month, the number of juveniles highly increased in water collected under the sandy soil. The numbers of juveniles remained very low in the water percolating from the two sandy-clay soils. At the end of the experiment, much more juveniles were extracted from the sandy soil than from the others (*table* 2). The total root infection was greater in the plants growing in the sandy and the sandy-clay – Pp soils than in the plants growing in the others. Consequently, the multiplication rate of *M. javanica* was lower in the sandy-clay soil + Pp and in the clay soil than in the sandy-clay soil – Pp. The best nematode development was obtained in the sandy soil.

Transport of the spores of Pasteuria penetrans

Irrespective of soil texture, the spores appeared in percolated water within the first 24 hours after

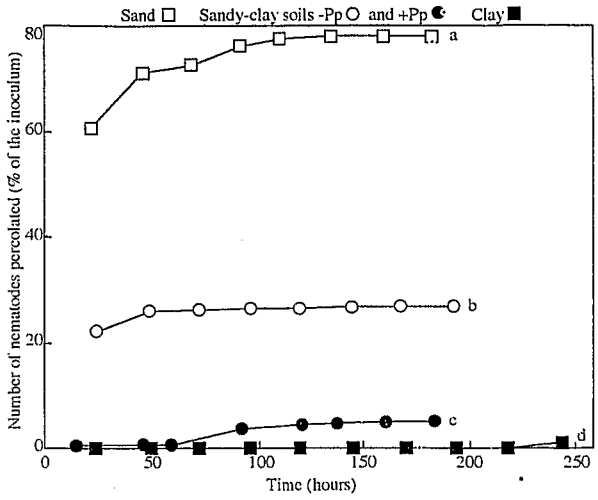

Figure 4. – Transport of juveniles of *Meloidogyne javanica* in the four soils (last data with the same letter are not significantly different, $p > 0.05$).

Table 2. – Soil and root infection with *Meloidogyne javanica* (number of juveniles per plant) and multiplication rates ([nematodes extracted + nematodes percolated]/inoculum) in the four soils.

Soil type	Nematodes extracted		Multiplication rate
	from the soil	from the roots	
Sand	3 152 a	25 440 a	121.9 a
Soil – Pp	206 b	22 452 a	90.8 b
Soil + Pp	275 b	16 829 b	69.0 c
Clay	397 b	14 651 b	60.2 c

inoculation (*fig.* 7). At the end of the experiment, 67.7% of the spores percolated through the sandy soil, 59.2% through the sandy-clay soil – Pp, 39.1% through the soil + Pp and only 10.6% through the clay soil.

After extraction from the soils, 39.4% of the spores were recovered from the clay soil. They were concentrated in the two upper layers. Most of the spores extracted from the sandy soil (22.4%) were recovered in the upper and the lower layers (*fig.* 8). In the two sandy-clay soils – Pp and + Pp, they were concentrated respectively in the second and the third layers. It resulted that the proportion of the spores which were not extracted was very low in the sandy soil (9.9%). One third of the spores were not recovered in the sandy-clay soils and the half of them were not extracted from the clay soil.

It appeared that the proportions of spores which percolated was in inverse ratio to the water capacities of the soils (*fig.* 9).

Abundance of Pasteuria penetrans *in natural conditions* (fig. 10)

According to the soil classes defined by Jamagne (1967), all the soil samples infected by *P. penetrans* in Senegal belong to the extreme sandy texture with

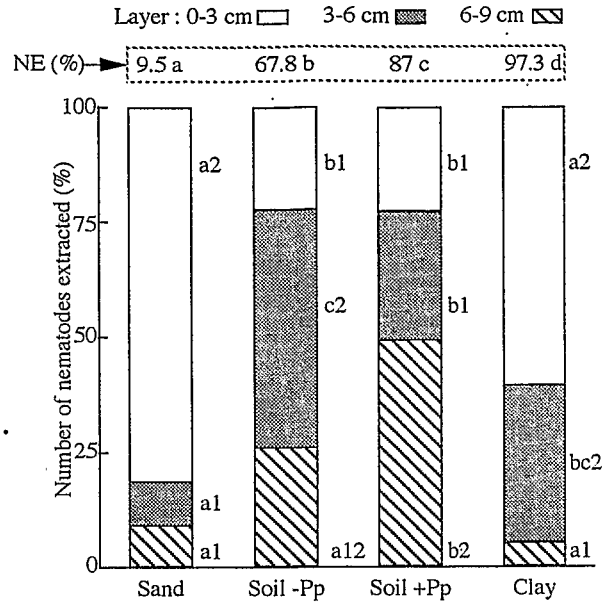

Figure 5. – Number of juveniles of *Meloidogyne javanica* extracted from the soils at the end of the experiment (NE = proportion of nematodes not extracted; data with the same letter and the same number, respectively for each layer and for each soil, are not significantly different, $p > 0.05$).

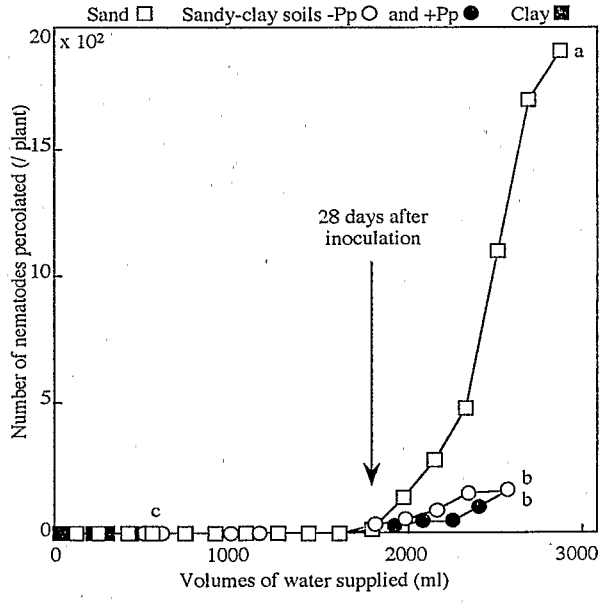

Figure 6. – Transport of juveniles of *Meloidogyne javanica* in the four soils under a tomato plant (last data with the same letter are not significantly different, $p > 0.05$).

more than 80% of sand and less than 20% of silt and 17% of clay. But most of the less infected populations of *Meloidogyne* spp. (< 5%) were found in the most sandy soils. The soils where 5 to 10% of the juveniles were infected were more silty. Finaly, the samples where more than 25% of the juveniles were infected were more clayey with a very low proportion of silt.

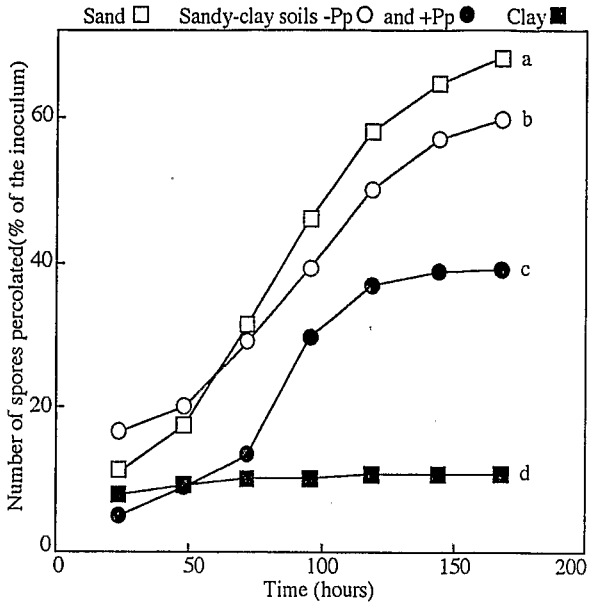

Figure 7. – Transport of spores of *Pasteuria penetrans* in the four soils (last data with the same letter are not significantly different, $p > 0.05$).

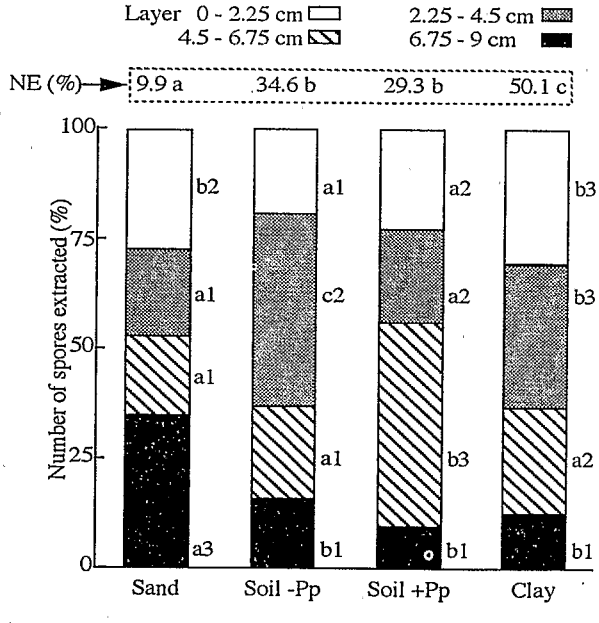

Figure 8. – Number of spores of *Pasteuria penetrans* extracted from the soils at the end of the experiment (NE = proportion of spores not extracted; data with the same letter and the same number, respectively for each layer and for each soil, are not significantly different, $p > 0.05$).

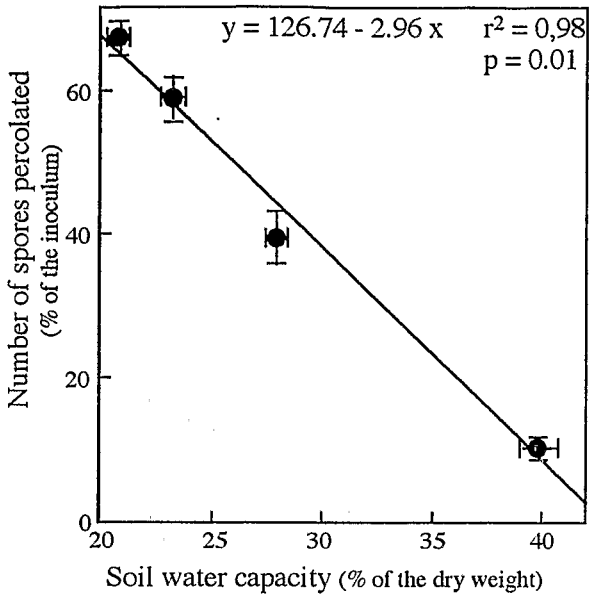

Figure 9. – Number of spores of *Pasteuria penetrans* percolated in the soils according to the soil water capacity (bars represent standard error, $p \leq 0.05$).

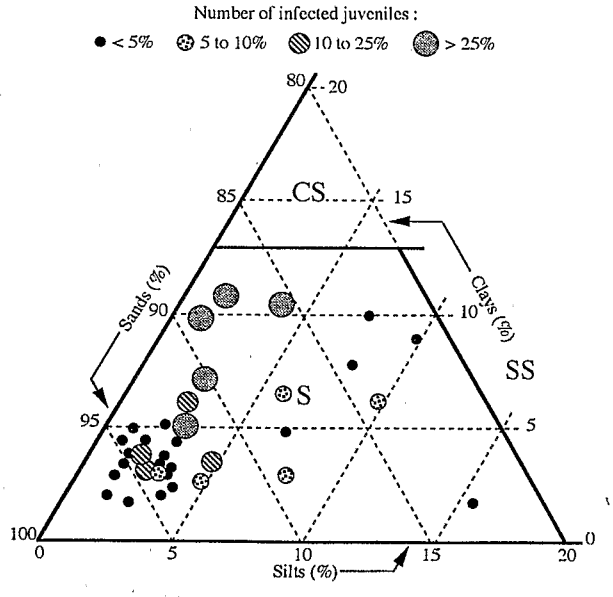

Figure 10. – Number of juveniles of *Meloidogyne* spp. infected by *Pasteuria penetrans* (% of the total population of nematodes) in the soil samples collected in vegetable fields according to the soil texture (S = sand; CS = clay sand; SS = silty sand).

DISCUSSION

The water capacity increases with the gradient of clays. The sandy soil did not retain water because of its light structure and its large porosity. The difference observed between the two sandy-clay soils, although it was not significative, could result from the fact that clay particules are more abundant in the soil +Pp than in the soil−Pp (10.3% vs. 6.3%). The same phenomena occurs in the clay soil which contains 57% of colloids and then retains the highest proportion of water. These physical characteristics were confirmed by water percolation. More the soil contains clay particles, more the pores are reduced which decreases percolation of water and permeability

(Duchaufour, 1991). The two sandy-clay soils have intermediate porosities compared with the sandy and the clay soils. However, because of its clay content, the sandy-clay soil+Pp is long-term less permeable than the soil−Pp after a reorganization, during water percolation, of the finest particles which fill the pores. These characteristics influence the transport of the juveniles of *M. javanica* and of the spores of *P. penetrans*.

The highest percentage of percolated juveniles was obtained in the sandy soil and the lowest in the clay soil. In the clay soil, most of the live nematodes stay in the upper layer where they were inoculated. Same behaviours of nematode between light and heavy soils were previously observed (Prot, 1978; Wout, 1979). At the end of the experiment, the juveniles which were not extracted from the soils correspond to juveniles which died by inanition (Loos, 1961) or by asphyxia (Van Gundy *et al.*, 1962) when they stayed for a long time in soils saturated with water and without any host plant. In the sandy soil, many juveniles remained in the upper layer where they were inoculated. That could be due to a reorganisation of the soil particules at the surface under the water supply which has carried the coarse particles down. Then, the finest particles concentrated in the upper layer prevent the juveniles to move down. Once again, the percolation of juveniles was less important in the soil+Pp than in the soil−Pp, and much more nematodes died in the first soil than in the other. The soil +Pp, which contains more fine particles, prevents the juveniles to move much more than in the soil−Pp (Van Gundy, 1985).

When the transport of the juveniles is tested in pots with host-plants, the differences observed on the percolation are strenghened: the multiplication rate is higher when the clay content is low (Van Gundy, 1985). Then, nematodes muliplicate more in a sandy soil than in a clay soil, but the loss of nematodes by percolation is more important in sand. That agrees with previous observations: in vegetable producing areas in Senegal, for the same root infestation, sandy soils are less infested by *Meloidogyne* spp. than clay soils (Mateille *et al.*, 1995a). Even thought the sandy soils allowed populations of *Meloidogyne* spp. to move and to reproduce very well, they favour the flow of the hatched juveniles down in the lower strata of the soil and prevent the juveniles to be parasitized by spores of *P. penetrans* or the infected juveniles to infest the roots. According to the texture, the best equilibrium for nematode moving, reproduction and availability for root infestation would be found in the sandy-clay soil +Pp.

The transport of the spores of *P. penetrans* is more influenced by the soil texture than those of the juveniles of *M. javanica* because of their immobility and their thinner size (Sayre & Wergin, 1977). Almost all the spores have flown down in the sand soil whereas quite all of them are kept in the clay soil. The sandy-clay soils show intermediate situations but the lower percolation observed in the soil +Pp could be certainly due to its higher content of clay particles. In fact, the balance of the soil particles according to their size determine the porosity which influences directly the percolation of the spores. The smallest pores which allowed the spores of *P. penetrans* to flow have to be more than the diameter of the spores ($d \approx 4$ μm according to Sayre & Wergin (1977)). Considering the soil particles as spheres, each pore is defined by three spheres whose diameter have to be more than $D = d\sqrt{3}/(2-\sqrt{3}) \approx 26$ μm, corresponding to fine particles. But, because of their size (about 10 μm diameter), the moving of juveniles of *Meloidogyne* spp. requires soil particles larger than 65 μm (coarse particles). Consequently, the soils which are fitted for moving and development of the populations of *Meloidogyne* (corresponding to sandy soils) are not necessary fitted to keep of the spores of *P. penetrans* for attachment. But that loss of the spores can be reduced by other phenomena. We noticed that more abundant are the clay particles more the spores are difficult to be extracted from the soil by the flotation-sieving technique. That could be due to electrochemical adsorption of the spores on the colloides. Considering the negative charge of the surface of the spores (Afolabi *et al*, 1995), they could be kept on clay particles by cation bridges as Ca^{2+} or Mg^{2+}. So, the availability of the spores for attachment would depend on the ionic charge of the soil solution and on cation saturation of the soil matrix. That may explain why, in natural conditions, the populations of infected juveniles of *Meloidogyne* species were found in sandy soils containing the highest proportions of clays and confirms the positive correspondance between the abundance of *P. penetrans* and the abundance of clays (Mateille *et al.*, 1995b).

So, we can conclude that, from a physical point of view, the proportion of the soil fractions, their spatial distribution and the flows of water (rain and irrigation) determine the transport and the mouvement of the juveniles of *Meloidogyne* spp. and the spores of *P. penetrans*, and consequently the probability of attachment. But the optimal balance of soil fractions for nematodes are not appropriated for spores of *P. penetrans*. In that conditions, the pool of spores can be maintained in the soil by adsorption on soil particles and their availability for attachement could depend on competitive electrochemical interactions between nematodes and spores on one hand, and between spores and soil particles on the other hand, the whole being controlled by the soil solution and water supplies.

Acknowledgements

The survey was supported by a grant from the EC Project STD 3 n° TS3 * CT92-0098: Biocontrol of damaging root-knot nematode (*Meloidogyne* spp.) pests of staple food and cash crops by including suppressive soils with the bacterial parasite *Pasteuria penetrans*. The authors thank Dr J.-L. Chotte (Laboratoire de Bio-pédologie, ORSTOM, Dakar, Sénégal) for interpretation advice.

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EUROPEAN JOURNAL OF SOIL BIOLOGY

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VOLUME 32 / N° 2 ISSN 1164-5563 1996