Biol Fertil Soils (1997) 24:288–293
© Springer-Verlag 1997

ORIGINAL PAPER

C. Villenave · P. Cadet · E. Pate · N. N'Diaye

Microcosm experiments on the development of different plant parasitic nematode fauna in two soils from the Soudanese-Sahelian zone of West Africa

Received: 14 January 1996

Abstract To test the hypothesis that the structure of plant parasitic nematode communities is affected by soil characteristics, experiments were conducted in a greenhouse with two soils with different physical and chemical characteristics and land management histories (fallow and a cultivated field) from adjacent plots. The cultivated soil was more sandy and had lower organic matter and nutrient contents than the fallow soil. Four nematode assemblages of *Scutellonema cavenessi, Helicotylenchus dihystera* and *Tylenchorhynchus gladiolatus* were inoculated in the soils. The pot experiment was conducted on millet during 2 months. Multiplication rates of *H. dihystera* were not significantly different in the two soils. *T. gladiolatus* had a lower multiplication rate in the fine-textured soil. *S. cavenessi* seemed to reproduce better in the coarse-textured soil when inoculated in low density with *H. dihystera*. The presence of plant parasitic nematodes in the cultivated soil caused a significant decrease of millet biomass, whereas plants in the fallow soil were less sensitive to nematode damage and were only affected when the soil was inoculated with *T. gladiolatus* alone. This experiment did not explain the distribution of plant parasitic species observed in the field. However, parameters other than the presence of a favourable host plant and micro-climatic conditions were found to induce differences in the reproductive rates of several species of plant parasitic nematodes.

Key words Phytoparasitic nematodes · Senegal · Millet · Multiplication rates · Soil physicochemical characteristics · *Tylenchorhynchus gladiolatus* · *Scutellonema cavenessi* · *Helicotylenchus dihystera*

C. Villenave (✉) · P. Cadet · E. Pate · N.'D. N'Diaye
Laboratoire de Nématologie, Orstom, BP 1386, Dakar, Senegal
Tel.: (221) 32-18-46; Fax: (221) 32-16-75;
e-mail: villenav@belair.orstom.sn

Fonds Documentaire ORSTOM
010011053

Introduction

The host plant is the most important determinant of the structure of a nematode community but edaphic factors are also important (Norton 1989). Several studies (Noe and Barker 1985; Francl 1993) suggest relations between soil characteristics, vegetation and nematode assemblages. Norton and Hoffmann (1974) found that the distribution of plant parasitic nematodes was correlated mostly to soil pH while organic matter content and percentage of sand-silt-clay were secondary factors. In other studies, the dominant soil factor was texture (Noe and Barker 1985; de Goede and Bongers 1994). The occurrence of some nematode species can be related directly to soil morphological properties which allow, for example, locomotion (Hassink et al. 1993). In other instances, elements such as available nitrogen, magnesium, sodium or copper may be correlated with nematode community structure (Noe and Barker 1985; Delaville 1995). Even if such studies did not explain the causal relationships between abiotic factors and the presence of certain nematode species, they do imply that factors other than vegetation may be important in the regulation of nematode population density, including plant parasitic nematodes.

The aim of this study was to determine whether the soils are responsible for the development of different plant parasitic nematode assemblages when a test plant is grown. Two soils with different physical and chemical characteristics were inoculated with several nematode fauna and the changes in the nematode fauna were recorded after one millet cropping cycle.

Materials and methods

Soils from a 17-year-old fallow field and from a nearby cultivated millet field (*Pennisetum typhoides*) were collected from 0- to 10-cm depth during the dry season (March 1995) at the experimental station of Thysse-Kaymor (Senegal, Nioro du Rip). The natural vegetation of the fallow was a shrub savanna dominated by *Combretum glutinosum* and *Guira senegalensis*. In this peanut cropping area of Senegal, the

Fonds Documentaire ORSTOM
Cote : B* 11053 Ex 1

Table 1 Physicochemical characteristics of the two soils (0–10 cm depth stratum)

Parameters		Fine-textured soil (fallow soil)	Coarse-textured soil (cultivated soil)
pH (H_2O)		5.7	6.0
pH (KCl)		5.5	5.7
Sand	%	37.5	69.5
Silt	%	42.7	22.4
Clay	%	17.7	5.6
C	‰	11.01	2.71
N	‰	0.84	0.31
C/N		13.1	8.7
P-Olsen (mg kg^{-1})		3.97	2.63
Exchangeable cations			
Ca (meq 100 g^{-1})		1.81	0.0
Mg (meq 100 g^{-1})		11.6	3.8
Na (meq 100 g^{-1})		0.01	0.0
K (meq 100 g^{-1})		0.11	0.30

cropping system is based on a peanut-millet rotation alternating with fallow periods (Diatta 1994).

Soils were sieved through 4-mm-mesh screen and autoclaved (140°C; 40 min). Physical and chemical analyses of the soils were done after sterilization. PVC plastic tubes (4.5 cm diameter, 17.5 cm high) were filled with 260 cm^3 of each soil, respectively, corresponding to 330 g of the fallow soil and 400 g of the cultivated soil.

Soils were both oxisols but with different positions in the toposequence, leading to different physicochemical characteristics. The texture was more sandy in the cultivated soil (sandy loam), with less than 6% clay, whereas the fallow soil contained 17.7% clay (loam) (Table 1). The carbon and nitrogen contents in the 0- to 10-cm soil, as well as the exchangeable cation contents, were higher in the fallow soil than in the cultivated soil. The soil of the fallow will be referred to as fine-textured soil and the soil of the cultivated field as coarse-textured soil.

Nematode inoculum

Ten treatments were set up with ten replicates each:

Fc–autoclaved fine-textured soil that remained non-inoculated (control)

FiF–autoclaved fine-textured soil inoculated with the whole nematode fauna from the fallow soil

FiC–autoclaved fine-textured soil inoculated with the whole nematode fauna from the cultivated soil

Fi(FC)/10–autoclaved fine-textured soil inoculated with 1/10 of total nematode fauna of the fallow plus 1/10 of total nematode fauna of the field

FiT–autoclaved fine-textured soil inoculated with *Tylenchorhynchus gladiolatus*

For the coarse-textured soil, the treatments will be named, respectively, Cc, CiC, CiF, Ci(FC)/10, CiT.

To prepare the inocula FiF, FiC, Fi(FC)/10, CiF, CiC and Fi(FC)/10, nematodes were extracted from the two soils using elutriation (Seinhorst 1962). Anhydrobiotic forms of the nematodes were reactivated during the extractions. Nematodes obtained were identified and counted in ten replicates. The obligatory plant parasitic nematodes were identified to species. The minor plant parasitic nematodes (plant feeders or fungi feeders) and free-living nematodes were counted but not identified. The phytoparasitic nematode density in the two soils was about 650–700 nematodes per 260 cm^3 of soil (Table 2). In the fallow, the plant parasitic nematode fauna was dominated by *H. dihystera* (90.2%). *S. cavenessi* was almost absent (0.3%), whereas the nematode assemblage of the adjacent millet field was dominated by *S. cavenessi* (96.4%); *H. dihystera* was not found. In FiC, FiF, CiC and CiF, nematodes were inoculated at the densities found in the natural sites.

S. cavenessi and *H. dihystera* were inoculated together (i(FC)/10) to look at the interactions between these two dominant species, whereas in the last treatment, special care was given to *T. gladiolatus*, another ubiquitous species in Senegal, which was not very abundant in the two soils 9.5% and 2.9% of the total number of phytoparasitic nematodes in the fallow and in the cultivated field, respectively (Table 2). Pure *T. gladiolatus* were obtained from laboratory cultures on millet.

Whatever the inoculum, the free-living nematodes dominated the nematode communities, representing from 72% to 89% of the total nematode numbers (Table 2). Facultative plant feeders were less abundant than obligatory phytoparasitic nematodes.

Greenhouse experiment

A 3-day-old millet seedling (*P. typhoides* cv. IKMW 8201) was transplanted in each tube. Soil was inoculated with nematodes 3–7 days after transplantation. The required inoculum was poured into a hole (5×100 mm) to one side of the seedling and covered with soil. The experiment was conducted in a greenhouse under natural climatic conditions (temperatures ranged from 20°C to 35°C; about 13 h light per 24 h). Tubes were watered daily.

The experiment was terminated 56 days after inoculation when data on shoot growth and final nematode populations were collected. Nematodes in each tube were extracted from soil and roots with Seinhorst's method. The oven-dried weight of root and shoot systems (1 week, 70°C) was measured. Multiplication rates were calculated: Pf/Pi=final number per tube/initial number per tube. Data were compared by the Mann-Whitney U-test (nematodes) and one-way analysis of variance: means were compared with LSD 5% (dry weight of millet plant).

Table 2 Source, number and composition of nematodes applied as inocula (number of nematodes per 260-ml tube, means, coefficients of variation (CV) and percentages (%) of the plant feeder nematode by species

	Fallow nematodes (iF)			Cultivated field nematodes (iC)			Mixture of cultivated field and fallow nematodes (i(FC)/10)			*T. gladiolatus* (iT)		
	Mean	CV	%	Mean	CV	%	Mean	CV	%	Mean	CV	%
Helicotylenchus dihystera	627	25	90.2	5	111	0.7	57	16	46.7	0	–	
Scutellonema cavenessi	2	67	0.3	641	14	96.4	58	11	47.4	0	–	
Tylenchorhynchus gladiolatus	66	12	9.5	19	49	2.9	7	35	5.7	89	16	100
Total obligatory plant feeders	695		100	665		100	122		100	89		100
Minor plant feeders	389	25		296	31		50	30		0	–	
Free living nematodes	3580	15		4083	18		1115	21		320	15	

Results

Final structure of the nematode fauna

Whereas the free-living nematodes were dominant in the original nematode fauna (more than 75% of the total nematode number), plant parasitic nematodes were more abundant than free-living nematodes in five of the eight treatments after 56 days (Table 3).

The final structure of the whole nematode fauna from the fallow did not differ in the two soils: the final total density of plant parasitic nematodes, minor plant feeder nematodes and free-living nematodes was similar in treatments FiF and CiF (Table 3). However, for the other three inocula, a greater abundance of the three ecological nematode categories was obtained in the coarse-textured soil when compared to the fine-textured soil.

Multiplication rates of the plant parasitic nematodes

H. dihystera failed to reproduce in any of the treatments: fewer *H. dihystera* were recovered than were inoculated (Table 3). The final numbers of *H. dihystera* were not significantly different in the two soils with the two different initial densities (iF and i(FC)/10). When introduced in low density (Fi(FC)/10 and Ci(FC)/10), the multiplication rate of *S. cavenessi* was significantly higher in the coarse-textured soil. No difference in the multiplication rates of *S. cavenessi* was measured with the cultivated field inoculum in the two soils (FiC and CiC). The multiplication rates of *T. gladiolatus* extracted from the cultivated soil and greenhouse culture were significantly (five fold) higher in the coarse-textured soil than in the fine-textured soil.

Final structure of the plant parasitic nematode fauna

The proportions of the main plant parasitic species had changed substantially by 56 days after inoculation (Table 3). *T. gladiolatus* became dominant (representing more than 80% of the total plant feeder nematodes) in all the treatments, except in the fine-textured soil inoculated with the nematode fauna from the cultivated soil.

The native fallow community was dominated by *H. dihystera* (90%). The final structure of the plant-parasitic fauna derived from this inoculum did not differ between the fine-textured soil (FiF) and the coarse-textured soil (CiF): the resulting assemblage was dominated by *T. gladiolatus*, which represented more than 90% of the individuals.

On the contrary, the plant parasitic nematode fauna obtained from the cultivated soil was significantly different when inoculated in the two soils. Originally the community was dominated by *S. cavenessi* (96%). When the whole nematode fauna was applied (FiC and CiC), the proportion of *S. cavenessi* was higher in the fine-textured soil than in the coarse-textured soil, representing 89% and 15% of the plant feeding nematodes, respectively. The

Table 3 Final nematode assemblages 2 months after inoculation (numbers of nematodes per 260-ml tube)

Nematode inoculum soil type		Fallow nematodes			Cultivated field nematodes			Mixture of fallow and cultivated inoculum			Pot culture of *T. gladiolatus*		
		Fine textured	Coarse textured		Fine textured	Coarse textured		Fine textured	Coarse textured		Fine textured	Coarse textured	
Abbreviated name of treatment		FiF	CiF		FiC	CiC		Fi(Fc)/10	Ci(FC)/10		FiT	CiT	
Helicotylenchus dihystera	Final numbers	235	160	NS	2	3	NS	28	22	NS	0	0	
	Multiplication rate	0.37	0.26	NS	–	–		0.49	0.37	NS			
	% of plant feeders	4.39	3.02		0.16	0.05		3.76	0.64		0.00	0.00	
Scutellonema cavenessi	Final numbers	2	8	NS	1115	975	NS	45	75	*	0	0	
	Multiplication rate	–	–		1.74	1.52	NS	0.78	1.33	*			
	% of plant feeders	0.04	0.14		88.84	15.00		6.04	2.20		0.00	0.00	
Tylenchorhynchus gladiolatus	Final numbers	5115	5120	NS	140	5520	**	670	3320	*	3185	17965	**
	Multiplication rate	77	78	NS	7	290	**	96	474	*	36	202	
	% of plant feeders	95.6	96.8		11.2	84.9		89.9	97.2		100.0	100.0	
Total obligatory plant feeders	Final numbers	5350	5290	NS	1255	6500	**	745	3415	*	3185	17965	**
Minor plant feeders	Final numbers	490	380	NS	790	815	NS	165	405	*	0	0	
Free-living nematodes	Final numbers	3590	3060	NS	4200	5800	*	1580	4790	**	2180	5650	**

Average number of nematodes per tubes: * significantly different ($P<0.05$), ** significantly different ($P<0.001$), NS not significant

number of *S. cavenessi* was not different in the two soils, but the number of *T. gladiolatus* was about 40 times higher in the coarse-textured soil.

When *S. cavenessi* and *H. dihystera* were inoculated together in low density with *T. gladiolatus* (treatments Fi(FC)/10 and Ci(FC)/10), the final number of *H. dihystera* did not differ in the two soils, whereas the number of *T. gladiolatus* and *S. cavenessi* were higher in the coarse-textured soil than in the fine-textured soil (Table 3).

Influence of the different nematodes assemblages on millet production

In the control without nematodes the mean dry weight of millet shoots in the cultivated soil was 48% of that in the fallow soil (Table 4). In the fallow soil, the only nematode fauna that resulted in a decrease in total millet dry weight when compared to the control was the pure *T. gladiolatus* population. All nematode communities (except the nematode fauna from the fallow soil) caused reduced millet dry weight in the coarse-textured soil. The reduction of total plant weight in the coarse-textured soil was mainly due to the decrease in root weight. *T. gladiolatus*, inoculated alone, induced nearly identical yield loss in the fallow and cultivated soil relative to the control (Table 4), while the final density of this species was significantly lower in the fine-textured soil, one-fifth of the density in the coarse-textured soil.

Discussion

Soil characteristics and plant-feeding nematodes final densities

In this experiment, we tested the influence of two soils on the transformation of different nematode fauna during a cropping cycle with a test plant. The differences in the soil characteristics resulted from management effects but above all from the position of the two plots in the toposequence; consequently the effects of the soils on the nematodes fauna are to be related to physical and chemical characteristics more than to anterior management practices. However, the original nematode communities used were linked to the natural vegetation present.

A critical difference between the two soils was the soil texture. The clay content was threefold higher in the fallow soil than in the cultivated soil. Carbon and nutrient contents were also higher in the fallow soil. Soil organic matter and nutrient content are usually correlated with clay content because organic matter is associated with clays, forming a stable organomineral complex (Feller et al. 1991).

Soil texture can influence nematode populations by facilitating or restricting the movement of nematodes toward roots or, in the case of amphimictic species, toward a mate (Norton 1989; Hassink et al. 1993). Differences in textural and nutrient properties of soil may consequently affect the quality of roots for nematode feeding. Differences in root quality may include different penetration rates (affecting the availability of feeding sites) and different nutritive contents (affecting the quality of feeding sites). Such differences may modify the quantity and quality of resources nematodes allocate to reproduction.

Table 4 Effect of the different nematode fauna on millet production (g dry weight plant^{-1}) in the two soils

	Soil type	Inoculum source				
		Control	Fallow nematodes	Cultivated field nematodes	Mixture of fallow and field nematodes	Inoculum of *T. gladiolatus*
Roots	Fine-textured soil (fallow)	0.64 ab	0.79 a	0.80 a	0.72 ab	0.49 b
	Coarse-textured soil (cultivated)	0.89 a	0.52 b	0.59 b	0.48 b	0.60 b
Shoots	Fine textured soil (fallow)	2.31 ab	2.21 ab	2.48 a	2.38 a	1.77 b
	Coarse-textured soil (cultivated)	1.11 a	1.15 a	0.80 b	1.02 ab	0.92 ab
Total	Fine-textured soil (fallow)	2.95 ab	3.00 a	3.28 a	3.10 a	2.26 b
	Coarse-textured soil (cultivated)	2.01 a	1.67 ab	1.40 b	1.50 b	1.53 b
Total* (% of control)	Fine-textured soil (fallow)	100 a	101.8 a	113.2 a	105.3 a	76.8 b
	Coarse-textured soil (cultivated)	100 a	83.1 ab	69.7 b	74.8 b	76.1 b

Numbers followed by different letters in the same line are significantly different ($P<0.05$)
* Numbers followed by different letters in these two lines are significantly different

Our results that we obtained with three species, *S. cavenessi* (amphimictic, migratory endoparasite), *T. gladiolatus* (amphimictic, migratory ectoparasite) and *H. dihystera* (parthenogenetic, ectoparasite), suggest that differences in reproductive ability may be due to the soil physical characteristics. *S. cavenessi* reproduced better in the sandy soil when it was inoculated in low density (0.23 cm^{-3}), whereas no differences between the sandy-cultivated soil and the clayey-fallow soil were measured when the inoculum was high (2.5 cm^{-3}). For this large species, 30 µm in diameter and 0.6–0.9 mm in length (Germani et al. 1985), movement and mating of the nematode should be facilitated by the more sandy soil, where pores greater than 20 µm in diameter might have been more abundant. On the other hand, when nematodes were inoculated in high density, meetings were not a constraint because of the high nematode concentration in space. Moreover, in our greenhouse cultures, resource accessibility did not limit reproduction by the nematodes. Millet roots rapidly colonized the entire pot volume. The different rates of reproduction in the two soils, and with the two initial densities, indicated that the size distribution of the soil pores was of major importance in explaining the reproductive rate of *S. cavenessi*. These results are consistent with the observations of several authors working on different species (Townshend 1972; Robbins and Hirschmann 1974): sandy texture allows the potential establishment of higher nematode populations. The same phenomenon might explain the higher muliplication rate of *T. gladiolatus* (20–25 µm diameter and 0.4–0.5 mm length; Fortuner and Amougou 1973) in the coarse-textured soil (in almost all the treatments) although it can move in smaller pores. The low initial density used for *T. gladiolatus* in all the treatments may have limited the possibility of mating without significant movement. *H. dihystera* is a parthenogenetic species and we did not find differences in the reproductive rate. This supported our notion that the soil texture would have affected reproductive rates particularly for amphimictic species. This effect of the soil texture is greatly linked with the soil water content. For a determined water input, the large pores are full of water in the sandy loam soil, whereas only pores of smaller diameter are full of water in the loam soil.

Another parameter might explain the relatively low reproductive rates of *H. dihystera* and *T. gladiolatus* obtained with the fallow inoculum in the two soils. Indeed, prior to the experiment these nematodes fed on "fallow" plants whereas the plant parasitic nematodes from the other inocula fed on millet before the experiment. Nematodes may need adaptation period before feeding on new resources; changes of alimentary resources might be a handicap to reproduction (Baujard and Martiny 1995). When food quality limits reproduction, soil characteristics only play a secondary role.

Pathogenicity of the plant parasitic nematode assemblages

In the absence of nematodes, the biomass of millet produced was significantly different in the two soils: The fine-textured soil allowed higher total plant production than the coarse-textured soil. Higher available nutrient and organic matter contents explained these different potentialities.

In this experiment, the soil poorer in organic matter led to higher yield losses in the presence of nematodes. In agreement with other studies, fewer resources available for plant growth led to a higher sensitivity to nematode attack (Fortuner 1974). *T. gladiolatus* seemed to be more harmful in the fine-textured soil than in the coarse-textured soil. As a matter of fact, the nematode induced a comparable yield loss in the fallow soil and in the cultivated soil, in which the density was more than four fold higher (treatment FiT and CiT).

In the only treatment where the multiplication of *T. gladiolatus* was low (fine-textured soil inoculated with the whole cultivated field nematode fauna), the final density of *S. cavenessi* was high (4 cm^{-3}) but comparable to the density found in numerous field situations. In this treatment the activity of the phytoparasitic nematodes did not induce yield losses. In agreement with the study of Baujard and Martiny (1995), this result suggested that, in such experimental conditions, *S. cavenessi* is not very harmful to millet.

Structure of the plant parasitic nematode fauna in the field

The final plant parasitic nematode community was dominated by *T. gladiolatus* in nearly all treatments. *T. gladiolatus* appeared to be the best competitor under greenhouse conditions. In field situations, whatever the season (Pate, personal communication), this species seldom dominates the nematode community. The dominant species are *S. cavenessi* and *H. dihystera*; moreover the ratio of *S. cavenessi* to *H. dihystera* decreases from cultivated fields to ageing fallow (Cadet and Floret 1995). *T. gladiolatus* can have a very high multiplication rate (up to 500) when climatic conditions and favourable host plants are present. In contrast, the migratory endoparasite *S. cavenessi* always has lower multiplication rates (up to 16; Baujard and Martiny 1995). Other biological characteristics of the species may explain the difference in the structure of the communities in the fields and under experimental conditions. It is well known that *S. cavenessi* is very resistant to the dry periods by surviving under anhydrobiotic forms. It can also survive and remain active without nutritional resources for a relatively long period of time, from weeks to months (Duncan 1986). We may hypothesize that *H. dihystera* developed characteristics comparable to *S. cavenessi*. On the other hand *T. gladiolatus* might be more sensitive to a lack of resource at the restarting of its biological activity and it may be suited to feeding immediately on plant at the beginning of the wet season.

This microcosm experiment did not explain the distribution of plant parasitic species observed in the field. However, parameters other than the presence of a favourable host plant and microclimatic conditions were found to induce differences in the reproductive rates of several spe-

cies of plant parasitic nematodes. Furthermore, these results apply only to the microcosm experiment where no microarthropodes, protozoans, fungi and bacteria had been inoculated.

Acknowledgements The authors thank R. Venette for helpful comments on the manuscript. This study was done in the Fallow-Biodiversity program (contract TS3–CT93-0220) co-ordinated by C. Floret.

References

Baujard P, Martiny B (1995) Ecology and pathogenicity of the Hoplolaimidae (Nemata) from the Sahelian zone of West Africa. 2. Laboratory studies on *Scutellonema cavenessi* Sher, 1964. Fundam Appl Nematol 18:335–345

Cadet P, Floret C (1995) An initial study of fallow periods on nematodes community in the Soudaniese-Sahelian zone of Senegal. Acta Oecologia 16:77–88

de Goede RGM, Bongers T (1994) Nematode community structure in relation to soil and vegetation characteristics. Appl Soil Ecol 1:29–44

Delaville L (1995) Etude des structures spatio-temporelles de la nématofaune phytoparasite associée à la canne à sucre. Relations avec les caractéristiques physiochimiques du sol. Thèse de doctorat. Université Pierre et Marie Curie, Paris VI. UFR 927 Sciences de la Vie

Diatta M (1994) Mise en defens et techniques agroforestières au Sine Saloum (Senegal) – Effets sur la conservation de l'eau, du sol et sur la production primaire. Thèse de Doctorat, University of Strasbourg I

Duncan LW (1986) Effect of bare fallow on plant parasitic nematodes in the Sahelian zone of Senegal. Rev Nématol 9:75–81

Feller C, François C, Villemin G, Portal JM, Toutain F, Morel JL (1991) Nature des matières organiques associées aux fractions argileuses d'un sol férralitique. C.R. Acad Sci Paris 312 serie II:1491–1497

Fortuner R (1974) Evaluation des dégats causés par *Hirschmaniella oryzae* (Van Breda de Hann, 1902) Luc&Goodey, 1963, nématode endoparasite des racines du riz irrigué. Agron Trop 29:708–714

Fortuner R, Amougou G (1973) *Tylenchorhynchus gladiolatus* n.sp. (Nematoda:Tylenchida), nématode associé aux cultures du Sénégal et de Gambie. Cah ORSTOM, Sér Biol 21:21–24

Francl LJ (1973) Multivariate analysis of selected edaphic factors and their relationship to *Heterodera glycines* population density. J Nematol 25:270–276

Germani G, Baldwin JG, Bell AH, Wu X-Y (1985) Revision of the genus *Scutellonema Andrassy*, 1958 (Nematoda: Tylenchida). Rev. Nématol 8:289–320

Hassink J, Bouwman L, Zwart K, Bloem J, Brussaard L (1993) Relationships between soil texture, physical protection of organic matter, soil biota, and C and N mineralization in grassland soils. Geoderma 57:105–128

Noe J, Barker KR (1985) Relation of within-field variation of plant parasitic nematode population densities and edaphic factors. Phytopatol 75:247–252

Norton DC (1989) Abiotic soil factors and plant-parasitic nematodes communities. J Nematol 21:299–307

Norton DC, Hoffmann, JK (1974) Distribution of selected plant parasitic nematodes relative to vegetation and edaphic factors. J Nematol 6:81–86

Robbins RT, Hirschmann H (1974) The effects of soil types, particle size, temperature and moisture on reproduction of *Belonalaimus longicaudus*. J Nematol 6:1–6

Seinhorst JW (1962) Modifications of the elutriation method for extracting nematodes from soil. Nematologica 8:117–128

Townshend JL (1972) Influence of edaphic factors on penetration of corn roots by *Pratylenchus penetrans* and *P. minyus* in three Ontario soils. Nematologica 18:201–212