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Variability in soil nematode populations due to tillage and crop rotation in semi-arid Mediterranean agrosystems

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Abstract

The soil nematode fauna was assessed as a potential ecological index for the progressive stages of degradation, as well as the possibilities of restoration of a Calcic Haploxeralf in a semi-arid environment in Spain. With this aim in mind, soil characteristics and nematode populations were compared in a virgin ecosystem (evergreen oak forest) and in a closely associated area subjected to intensive cereal cultivation. In addition, in the latter area, the effects of different tillage systems, local soil compaction and crop rotations were evaluated over a 3 year period. Nematode populations were compared in experimental plots subjected to three contrasted situations: (i) no-tillage versus conventional tillage, (ii) soil compacted by tractor traffic versus undisturbed by traffic, and (iii) barley monoculture versus barley–vetch or barley–sunflower rotations.

The soil with a virgin ecosystem had the greatest number and diversity of fungivorous (*Tylenchus*) and omnivorous predator (mononchids and dorilaimids) nematodes, whereas the values for endoparasites (*Heterodera avenae* and *Pratylenchus*) nematodes increased in tilled soil. The population of bacterial-feeding nematodes (rhabditids) was the same in virgin and cultivated areas. The greatest density and diversity in the no-tillage system occurred in the bacterial-feeding, fungivorous and omnivorous predator groups. A favorable effect of crop rotation was that the population of plant parasites (pathogenic) remained below crop damage concentrations. The effect of traffic on soil compaction was reflected conspicuously by the vertical distribution of soil nematodes within the soil profile. The population of plant parasites increased with depth, whereas the opposite occurred with the bacterial-feeding and omnivorous predator groups.

Keywords: Nematodes; Diversity; Tillage; Crop rotation; Semi-arid soils; Compaction

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1. Introduction

Unsuitable management practices are a major factor of soil degradation in semi-arid Mediterranean agrosystems. In general, extensive tillage leads to decreased crop yields through its effect on soil physical, chemical and biological processes (Edwards, 1989; Pimentel et al., 1989; Unger, 1990). The unfavorable effects of extensive tillage include compaction of the soil due to vehicle traffic, as well as progressive disruption of soil structure and decreased concentrations of soil organic matter. In consequence, alternative agricultural practices based on reduced tillage have been greatly encouraged in semi-arid ecosystems (White, 1990; Agenbag and Maree, 1991). Nevertheless, under such conditions, additional problems may arise from the unsuitable control of plant diseases (Rovira, 1986; Murray and Brown, 1987), increased bulk density, soil hardsetting (Hamblin and Tennant, 1979; López-Fando et al., 1993) and decreased crop growth rates (Cooke et al., 1980; Gates et al., 1981; Chan et al., 1987).

From a biological viewpoint, the evolution from virgin to cultivated soil frequently leads to a decreased variety and density of populations of soil invertebrates. In particular, tillage has been reported to cause a long-term depressive effect on soil biodiversity, its effect often being greater than that of the use of pesticides (Anderson, 1988).

Nematodes are one of the most representative groups of soil fauna, their density ranging from 2×10^5 individuals m^{-2} in arid soils to more than 3×10^7 individuals m^{-2} in humid ecosystems (Curry and Good, 1992). In spite of the large number of soil nematodes, their direct contribution to organic matter mineralization has been estimated to be small, probably less than 1% of the total soil respiration (Sohlenius, 1980; Petersen and Luxton, 1982). However, in virgin ecosystems, nematodes have been found to play an important role in the decomposition of soil organic matter and the release of nutrients through their interaction with the soil microflora (Coleman et al., 1984; Inghan et al., 1985). It has been pointed out that these circumstances may also be applicable to agroecosystems (Parmelee and Alston, 1986).

In addition to qualitative changes, Overhoff et al. (1991) observed that the vertical distribution pattern of nematode populations varied noticeably between different tillage systems. They found that the relative number of soil nematodes increased in the subsurface layers after tillage as a probable consequence of the translocation of nutrients in the topsoil, as well as changes in soil structure and physical properties. Further studies on nematode populations in soils subjected to different agricultural practices have shed additional light on the effects of tillage systems and environmental conditions, including temperature, moisture and soil compaction (Thomas, 1978; Stinner and Crossley, 1982; Baird and Bernard, 1984). In general, the total population and the number of species of nematodes tend to be less in conventional tillage than in no-tillage systems under semi-arid conditions (López-Fando et al., 1993). It has been reported that tillage practices, in addition to altering the availability of soil nutrients, have an important bearing on nematode populations, pointing to the synergistic activity of soil and biotic factors (Yeates and Hughes, 1990). However, in other situations the nematodes are not largely affected by tillage (Carter et al., 1988). A chief role of climatic characteristics can be postulated to explain the diverse results reported in the literature.

The present study describes quantitative and qualitative changes in the soil nematode population, which were studied in relation to different crop rotations and tillage systems, with special emphasis on the effect of the latter on soil compaction.

2. Materials and methods

The systems studied belong to the CSIC experimental farm 'La Higueruela' (Toledo, central Spain), which has a semi-arid continental climate (between 6°C in winter and 23°C in summer, with 400 mm of annual rainfall). The profiles compared correspond to closely associated areas (a virgin and a cultivated site) of a Calcic Haploxeralf (Soil Survey Staff, 1975) or Calcic Luvisol (Food and Agriculture Organization of the United Nations, 1988). The former site lies under a virgin evergreen oak (*Quercus ilex* L. ssp. *ballota*) (= *Q. rotundifolia* Lam.) forest (climactic formation for this area) whereas the latter is subject to agricultural management and is used for cereal production (López-Fando and Bello, 1987). This soil is representative of so-called 'non-calcic brown soils of the Madrid facies' (Guerra et al., 1968), which occupies large areas of central Spain. Characteristic physical parameters of the virgin and cultivated soil profiles are reported in Table 1.

The plots of the experimental farm, where the present study was carried out, had previously been used for a series of long-term agricultural experiments (López-Fando and Almendros, 1995). The crops grown were barley (*Hordeum vulgare* L. cv. 'Aramir'), vetch (*Vicia sativa* L.) and sunflower (*Helianthus annus* L.). The experiment was arranged in a split-plot design: two tillage treatments (conventional tillage (CT) and no-tillage (NT))

Table 1
Some physical properties of the soil profiles

	Depth (cm)					
	0–19 A_p	19–36 B_t	36–52 B_{tk}	52–93 BC_{k1}	93–141 BC_{k2}	> 141 $2C_k$
Virgin						
Sand (g per 100 g)	64.2	68.4	59.9	51.5	23.1	42.5
Silt (g per 100 g)	20.3	17.4	15.0	23.1	53.6	41.0
Clay (g per 100 g)	15.5	14.2	25.1	25.4	23.2	16.5
Field capacity −33 kPa (g per 100 g)	21.8	15.2	20.4	19.6	25.8	22.2
Wilting point −1500 kPa (g per 100 g)	16.8	9.6	13.3	12.2	15.8	12.4
Particle density (Mg m^{-3})	2.66	2.65	2.63	2.64	2.68	2.68
Bulk density (Mg m^{-3})	1.47	1.52	1.44	1.48	1.62	1.47
Cultivated						
Sand (g per 100 g)	54.1	56.2	49.5	47.7	62.5	67.5
Silt (g per 100 g)	19.1	11.3	10.4	25.8	16.3	15.4
Clay (g per 100 g)	26.8	32.5	40.1	26.5	21.2	17.1
Field capacity −33 kPa (g per 100 g)	22.1	24.3	29.2	21.6	15.7	14.4
Wilting point −1500 kPa (g per 100 g)	10.2	13.3	15.4	12.1	8.5	7.1
Particle density (Mg m^{-3})	2.64	2.61	2.65	2.71	2.69	2.67
Bulk density (Mg m^{-3})	1.56	1.37	1.42	1.52	1.55	1.68

were applied to 9 m×80 m main plots and three crop rotations: barley–vetch (B→V) barley–sunflower (B→S) and barley monoculture (B→B), were applied to 9 m×40 m sub-plots. There were three replicates, to give a total of 36 sub-plots. In this study, special attention was given to the effect of tractor traffic on mechanically compacted soil. A fixed string was placed along the center of the plot so that the tractor would always pass through that center, making a clear division between the compacted and non-compacted area.

At the beginning of the experiment (October 1987), the topsoil had a total organic matter content of 0.85±0.15 g per 100 g and pH 6.0±0.9. In the NT plots, weeds were sprayed in October with 0.54 kg ha^{-1} glyphosate (*N*-(phosphonomethyl)glycine) before barley and vetch were sown with a triple-disk seed drill. In the case of the sunflower, a second treatment was carried out just before sowing in March with 0.54 kg ha^{-1} glyphosate. The CT plots were moldboard plowed (to 25–30 cm depth) followed twice by harrowing (to 10 cm depth) in October (repeated in March in the sunflower plots). They were sown in early November for barley and vetch and at the end of April for sunflower. The crops were harvested in May and June for vetch and barley respectively and in September for sunflower.

Table 2
Physical parameters of the soil profile in the barley sub-plot, under conventional tillage (CT) and no-tillage (NT) at three dates

Soil depth (cm)	September (20.6°C)									December (4.7°C)								
	Bulk density (Mg m^{-3})			Moisture content (g per 100 g)			Cone resistance (MPa)			Bulk density (Mg m^{-3})			Moisture content (g per 100 g)			Cone resistance (MPa)		
	CT	NT	LSD	CT	NT	LSD	CT	NT	LSD	CT	NT	LSD	CT	NT	LSD	CT	NT	LSD
0–7.5	1.58	1.67	0.04	5.61	6.18	0.8	1.04	1.02	0.20	1.45	1.50	0.07	15.3	13.7	0.9	0.30	1.07	0.53
7.5–15	1.58	1.66	0.08	5.31	5.45	0.9	2.11	1.78	0.43	1.47	1.56	0.09	11.1	11.4	1.6	0.59	2.16	0.65
15–22.5	1.64	1.56	0.07	3.41	6.64	2.1	2.41	2.19	0.20	1.48	1.59	0.06	8.2	13.6	2.4	1.93	2.10	0.42
22.5–30	1.71	1.60	0.06	4.73	6.61	2.0	2.72	2.47	0.52	1.55	1.58	0.09	11.2	14.4	1.0	2.81	2.60	0.43
30–37.5	1.64	1.67	0.08	5.80	6.93	1.3	3.25	2.61	0.50	1.52	1.43	0.08	13.2	16.3	1.7	3.05	2.85	0.39
37.5–45	1.66	1.58	0.04	5.24	7.27	1.6	3.25	3.22	0.09	1.50	1.45	0.08	12.9	17.9	1.7	3.08	2.90	0.41

Soil depth (cm)	April (12.2°C)								
	Bulk density (Mg m^{-3})			Moisture content (g per 100 g)			Cone resistance (MPa)		
	CT	NT	LSD	CT	NT	LSD	CT	NT	LSD
0–7.5	1.54	1.54	0.07	11.1	8.8	2.2	0.28	1.10	0.37
7.5–15	1.63	1.59	0.10	12.2	9.4	1.4	1.85	2.03	1.20
15–22.5	1.63	1.68	0.09	8.0	13.1	1.7	3.25	2.70	0.32
22.5–30	1.68	1.63	0.09	9.0	13.0	2.6	3.25	2.79	0.27
30–37.5	1.67	1.57	0.06	10.2	11.6	1.5	3.25	2.85	0.24
37.5–45	1.65	1.54	0.06	11.1	15.2	2.3	3.25	2.95	0.17

LSD, least significant difference ($P<0.05$) of the preceding numbers in a row.

The number of nematodes in the soil was estimated in September 1988, in January, April, September and December 1989, and in January and May 1990. The phenological stages at which the soil samples were taken corresponded to: tillering, stem extension and ripening for barley, beginning of flowering and full ripening for vetch, and one to three pairs of leaves and ripening for sunflower. Soil samples ($1000\ cm^3$) were taken from the upper 10 cm, in three random positions in each plot. The samples were stored at 5°C until analyses. Samples from each plot were bulked and, after homogenizing and sieving (less than 2 mm), a subsample of $100\ cm^3$ was processed. Nematodes were extracted by the sugar centrifugation method (Nombela and Bello, 1983). The total nematodes in each subsample were identified and counted under a stereomicroscope.

The study of soil compaction was carried out in 1992 with samples taken in October, December and May. The samples were taken from a linear transect defined at a constant distance from the fixed string used as a guide for the tractor, corresponding to the zones compacted by the repeated passage of the major tractor wheels, and from undisturbed areas. Core samples ($100\ cm^3$) for nematological studied were taken from 0–45 cm depth at 7.5 cm depth intervals (three samples per zone).

2.1. Other analyses

Several soil physical properties were determined in 1989 on the NT and CT barley subplots. Soil resistance to penetration was measured to the 45 cm depth of the soil profile with a hand-held recording penetrometer (Rimik-cp10). Three measurements per sub-plot were made in September (prior to tillage), December (after sowing), and April (medium of the growing season). Soil cores (5 cm i.d. × 5 cm) were obtained from the 0–45 cm soil depth (three cores at each depth per replicate) to determine bulk density and soil moisture content (Table 2).

In the study of soil compaction by tractor traffic, penetration resistance was measured in at least 12 points per zone (with traffic and non-traffic) in B → S rotation and to a depth of 45 cm. Core samples ($100\ cm^3$) for determination of soil moisture content were taken from 0–45 cm depth at 7.5 cm intervals (three samples per zone).

3. Results and discussion

3.1. Soil nematode fauna as an indicator of soil degradation processes

Table 3 shows the different nematode groups categorized according to their trophic characteristics: plant parasites, omnivorous predators, bacterial-feeding, and fungivorous species. Such nematode groups are relevant in terms of crop production in the different situations. Whereas some groups (e.g. plant parasites) play the most direct role in plant survival and development, other groups (fungivorous, bacterial-feeding) play a role in the composition of soil microflora and, indirectly on the turnover of soil organic matter and availability of nutrients. In such a system, the omnivorous predators have a wide effect on the trophic system by controlling the composition of soil microfauna as well as the pool of readily available organic sources.

Table 3
Trophic groups of nematodes found in virgin and cultivated dryland ecosystems from central Spain

Plant parasite	Omnivorous-predator	Bacterial-feeding	Fungivorous
Pratylenchus	Dorilaimids	Rhabditids	*Tylenchus*
Paratylenchus	*Alaimus*		*Aphelenchus*
Xiphinema	*Plectus*		*Aphelenchoides*
Criconema	*Discolaimus*		
Tylenchorhynchus	Mononchids		
Heterodera avenae (larvae)			
Heterodera avenae (cysts)			
Helicotylenchus			
Trichodorus			
Longidorus			
Rotylenchus			

Table 4
Composition of the nematode population (expressed as the number of nematodes in 100 cm^3 of soil) of different horizons of the virgin soil (Calcic Haploceralf)

	Depth (cm)					
	0–19 A_p	19–36 B_t	36–52 B_{tk}	52–93 BC_{k1}	93–141 BC_{k2}	> 141 $2C_k$
Pratylenchus	–	2	–	–	–	–
Paratylenchus	–	10	5	–	–	–
Xiphinema	2	3	8	3	4	12
Criconema	8	13	–	–	–	–
Tylenchorhynchus	30	–	2	–	–	–
Heterodera avenae (larvae)	–	–	–	–	–	–
Heterodera avenae (cysts)	–	–	–	–	–	–
Tylenchus	144	24	32	5	–	–
Dorilaimids	110	2	30	5	2	2
Alaimus	14	1	3	–	–	–
Rhabditids	20	10	15	4	–	3
Discolaimus	10	2	–	–	–	–
Helicotylenchus	14	7	–	–	–	–
Aphelenchus	–	–	–	–	–	–
Longidorus	–	1	–	–	–	–
Mononchids	80	6	25	–	–	–
No. of individuals per 100 cm^3 soil	432	81	120	17	6	17
No. of genera	10	12	8	4	2	3

Table 4 shows the relative abundance of nematodes in the different horizons of the virgin soil in comparison with the values found in the soil subjected to cultivation (Table 5). The same occurred as regards diversity. The virgin soil had the greatest variety and a relative abundance of fungivorous (*Tylenchus*) and omnivorous predator (mononchids and dorilaimids) species. Plant parasite populations differed in the horizons in both soils (Fig. 1),

Table 5
Composition of the nematode populations (expressed as the numbers of nematodes in 100 cm^3 of soil) of different horizons of cultivated soil (Calcic Haploxeralf)

	Depth (cm)					
	0–19 A_p	19–36 B_t	36–52 B_{tk}	52–93 BC_{k1}	93–141 BC_{k2}	>141 $2C_k$
Pratylenchus	7	25	5	2	1	–
Paratylenchus	5	–	–	–	–	–
Xiphinema	–	3	4	–	–	–
Criconema	–	–	–	–	–	–
Tylenchorhynchus	2	10	5	–	1	–
Heterodera avenae (larvae)	1	–	–	–	–	–
Heterodera avenae (cysts)	–	–	1	–	–	–
Tylenchus	–	–	–	2	–	–
Dorilaimids	7	–	5	–	–	–
Alaimus	–	2	–	–	–	–
Rhabditids	22	–	2	–	–	–
Discolaimus	3	–	–	–	–	–
Helicotylenchus	–	–	–	–	–	–
Aphelenchus	–	5	–	–	–	–
Longidorus	–	15	5	–	–	–
Mononchids	–	–	–	–	–	–
No. of individuals per 100 cm^3 soil	47	60	27	4	2	0
No. of genera	7	6	7	2	2	0

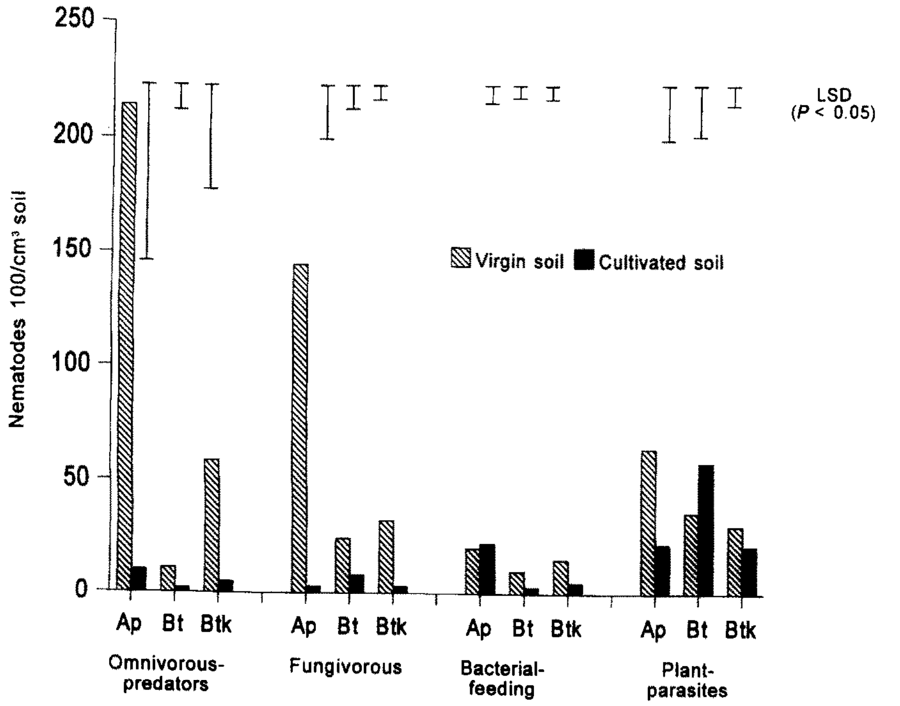

Fig. 1. Trophic groups of nematodes by horizon in two soil profiles (virgin ecosystem and cereal agrosystem). Bars indicate the least significant difference ($P < 0.05$).

Table 6
Comparison of nematode populations in plots under no-tillage (NT) or conventional tillage (CT), and subjected to three types of crop rotations

	Individuals per 100 cm^3 soil			
	NT		CT	
	Barley	Vetch	Barley	Vetch
Fungivorous	13.4a	11.3a	11.9a	13.0a
Bacterial-feeding	70.8b	82.0b	53.2a	53.7a
Omnivorous-predators	15.7a	14.3a	18.9a	17.7a
Plant parasites	33.9a	44.2b	36.0a	30.4a
Total	133.8ab	151.8b	120.0a	114.8a
	Barley	Sunflower	Barley	Sunflower
Fungivorous	8.2a	10.6a	7.7a	12.6a
Bacterial-feeding	65.5b	73.8b	40.2a	43.8a
Omnivorous-predators	10.5a	19.7b	9.8a	13.9a
Plant parasites	36.3b	28.7a	28.2a	25.0a
Total	120.6b	142.8b	85.9a	95.3a
	Barley		Barley	
Fungivorous	7.1a			6.6a
Bacterial-feeding	74.1b			47.9a
Omnivorous-predators	16.6a			23.8a
Plant parasites	54.1a			37.2a
Total	151.9b			115.5a

For each treatment (NT vs. CT), the numbers in a row (average of three replications) followed by the same letter are not significantly different at $P < 0.05$.

but plant pathogenic nematodes (*Pratylenchus* and *Heterodera avenae*) were dominant under the cereal systems (Tables 4 and 5).

3.2. The effect of tillage systems on soil nematode fauna

Table 6 shows the results of the nematological analyses grouped by trophic characteristics. For all treatments, the total numbers of nematodes tend to be significantly greater ($P < 0.05$) in NT than CT plots. Irrespective of crop rotations, the largest total number of bacterial-feeding nematodes was also found in the NT plots. The above results contrast with those reported by Wasilewska (1979) and Hendrix et al. (1986), who associated the largest population of bacterial-feeding nematodes in a CT treatment with the high intensity of biodegradation and mineralization, and the concomitant release of nutrients. In the present conditions, the highest values for soil nematode fauna (mainly bacterial-feeding) may be indirectly associated with the tillage system, through changes in soil properties, such as the greater concentration of soil organic matter, NO_3^- and moisture content in the NT plots (López-Fando and Almendros, 1995). Only the NT plots with vetch and barley (B → S

Table 7
Comparison of nematode populations (expressed as the numbers of nematodes in 100 cm^3 of soil) and some physical properties at different depths for the soil subjected to no-tillage and conventional tillage in areas subjected (wt) or not (nt) to traffic of agricultural vehicles

	No-tillage									Conventional tillage								
	0–7.5 cm		7.5–15 cm		15–22.5 cm		22.5–30 cm		LSD ($P<0.05$)	0–7.5 cm		7.5–15 cm		15–22.5 cm		22.5–30 cm		LSD ($P<0.05$)
	nt	wt	nt	wt	nt	wt	nt	wt		nt	wt	nt	wt	nt	wt	nt	wt	
Nematode																		
Pratylenchus	1.7	12.3	10.0	18.3	6.7	16.7	11.7	27.0	6.7	0.0	5.0	0.7	1.7	1.7	1.7	6.7	14.0	6.8
Paratylenchus	0.0	0.0	0.0	3.3	5.0	6.7	10.0	26.0	5.8	0.0	1.7	1.7	0.0	0.0	0.0	1.7	15.0	7.0
Xiphinema	1.3	1.0	8.3	3.3	27.3	32.3	25.7	32.7	9.8	1.0	4.0	0.7	0.0	2.0	3.0	10.7	7.7	5.0
Heterodera avenae (cysts)	3.7	1.0	1.0	3.0	1.0	0.0	0.7	0.0	1.0	0.0	0.3	1.3	1.3	0.3	0.0	0.0	0.0	0.6
Tylenchorhynchus	54.0	41.7	33.0	36.7	16.7	13.3	8.3	18.3	10.0	59.3	36.7	37.3	37.3	29.0	21.7	22.0	22.0	15.1
Dorilaimids	30.0	22.3	18.3	13.3	17.3	9.3	13.3	5.7	3.8	21.7	15.7	16.0	23.0	10.7	13.7	7.7	13.0	9.2
Alaimus	0.0	1.7	3.3	1.7	2.7	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.7	0.7	0.0	0.3	1.1
Rhabditids	39.7	27.7	17.0	17.7	16.7	18.0	15.0	15.0	7.5	28.7	16.7	26.3	21.0	10.7	20.3	6.7	16.3	4.0
Longidorus	0.0	2.3	0.7	2.3	1.7	11.7	11.3	19.7	5.7	0.0	0.0	1.7	0.0	0.7	1.7	3.7	9.0	3.8
Monochids	0.7	0.7	0.7	0.0	1.7	5.0	1.7	0.0	1.6	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0
Total no.	131.1	110.7	92.3	99.6	96.8	114.0	96.0	144.4	21.2	111.7	79.8	85.7	84.3	57.8	62.8	59.8	97.3	23.2
No. of genera	7	9	9	9	10	9	9	7	1.6	5	7	8	5	9	7	7	8	1.6
Cone resistance (MPa)																		
October	1.13	1.34	1.35	1.32	1.43	1.27	1.91	1.73	0.19	0.31	0.81	0.50	0.68	0.41	0.63	0.58	0.70	0.10
December	0.83	1.50	1.36	1.92	1.41	1.48	1.37	1.72	0.22	0.29	0.67	0.52	1.01	0.46	0.89	0.65	1.27	0.13
May	0.73	1.67	1.78	2.98	2.02	2.69	2.09	2.49	0.31	0.38	1.17	0.59	2.01	0.97	3.00	1.98	3.44	0.39
Moisture content (g per 100 g)																		
October	6.12	6.88	7.33	8.53	7.99	7.70	8.00	9.53	0.92	6.17	5.44	6.81	6.79	7.60	7.61	8.37	7.74	0.72
December	11.40	14.39	15.53	14.70	15.54	13.75	15.14	17.17	1.33	12.04	11.60	11.24	11.14	14.13	12.53	18.13	17.59	0.97
May	6.91	6.60	8.41	8.31	8.27	8.66	11.25	9.63	0.86	6.51	6.30	7.49	7.49	9.36	8.67	9.07	9.01	1.21

LSD, least significant difference ($P<0.05$) of the preceding numbers in a row.

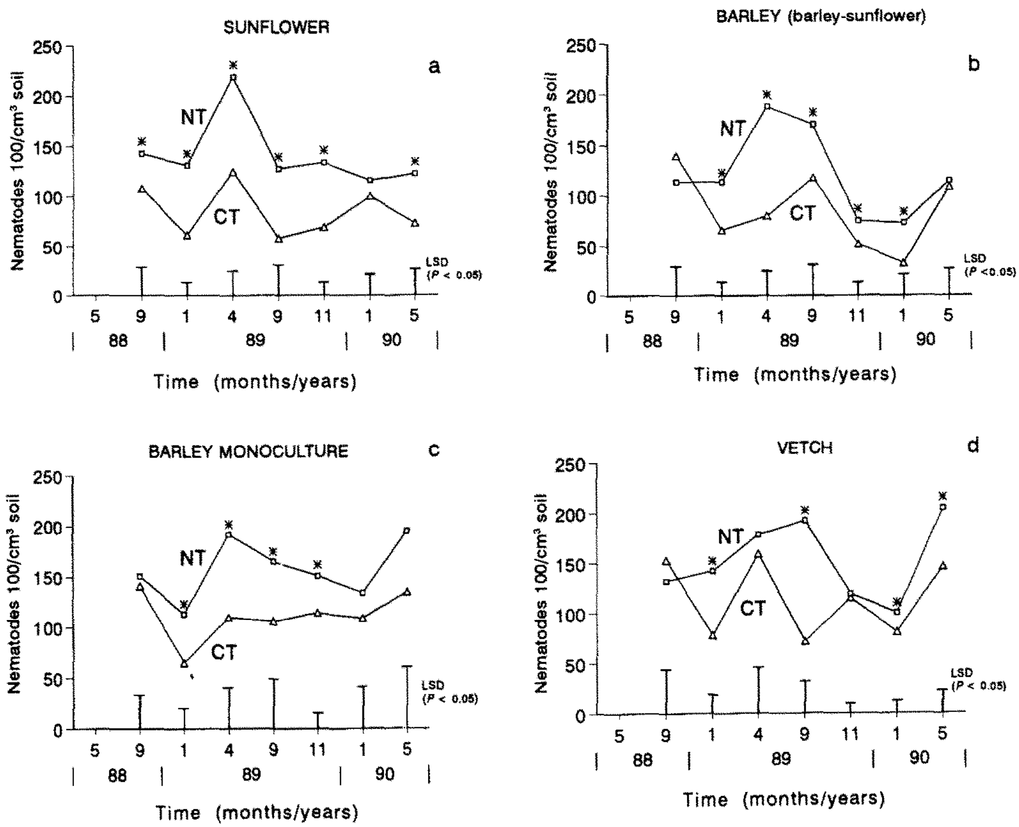

Fig. 2. Total number of nematodes in soil for different months and years, with different crops: (a) sunflower, in barley–sunflower rotation; (b) barley, in barley–sunflower rotation; (c) barley, in a barley monoculture; (d) vetch, in barley–vetch rotation. Bars indicate the least significant difference ($P<0.05$).

rotation) for plant parasites, and with sunflower for omnivorous predators, showed a larger number than the CT plots. The density of fungivorous species were similar for both tillage systems, regardless of the crop.

Fig. 2 shows the changes in the numbers of nematodes with time. In all crops, the greatest values ($P<0.05$) were found in NT plots. In the case of bacterial-feeding nematodes (data not included), the results were also significantly greater under NT than CT. The greatest population density observed in spring might have been due to optimal soil microenvironmental factors such as temperature, moisture content and bulk density (Table 2) as well as to the increased number of plant parasites. The latter is associated with the active growth of the host plants. These factors became sub-optimal in September, leading to decreased nematode populations between September and January, which increased thereafter.

3.3. *The effect of soil compaction on nematode fauna*

Table 7 compares the nematode populations of the NT and CT systems in areas compacted by tractor traffic and in the non-compacted areas of the corresponding plots. In the NT plots,

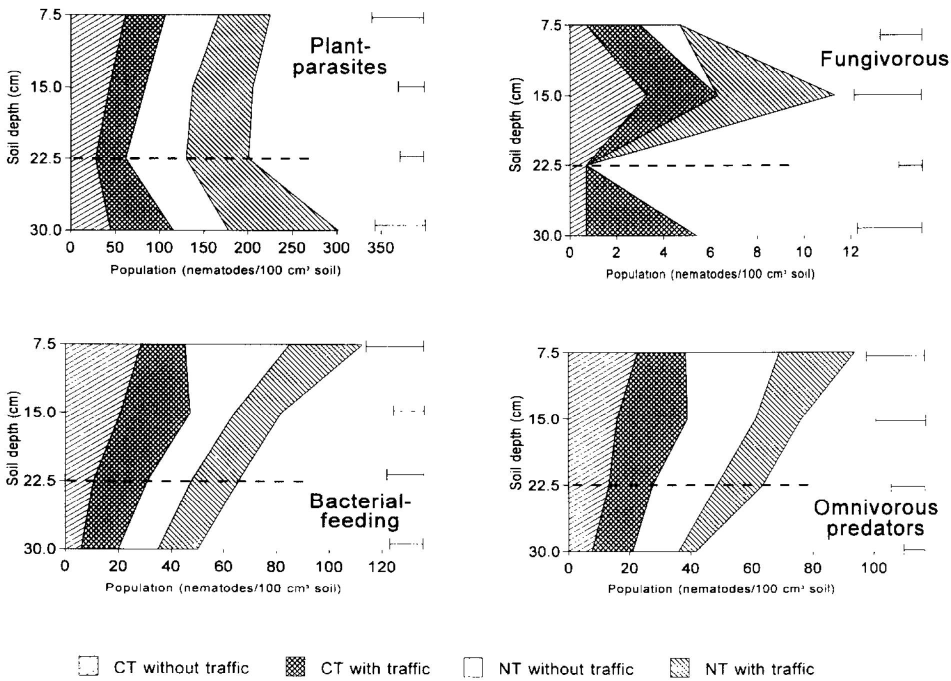

Fig. 3. Vertical distribution of trophic groups of soil nematodes, corresponding to conventional tillage (CT) and no-tillage (NT) and subjected (wt) or not (nt) to the effect of mechanical compaction due to traffic. The dotted line indicates the depth of the plow layer. Bars indicate the least significant difference ($P<0.05$).

the greatest numbers of nematodes (*Pratylenchus* spp., *Paratylenchus minor*, *Xiphinema* spp. and *Longidorus* spp.) were observed in the compacted areas, where the numbers tended to increase with depth.

The same trends in nematode population occurred in the CT plots, although the size of the population was lower and the differences were significant ($P<0.05$) only for *Pratylenchus*, *Paratylenchus* and *Longidorus* at a depth of between 22.5 and 30 cm in the compacted areas. The numbers of *Xiphinema* were exceptionally high in the deep layer of the soils unaltered by traffic. It may be concluded that mechanical compaction led to a relative increase in endoparasite nematodes in soil. The size of the populations of dorilaimids, rhabditids, and stunt nematodes (*Tylenchorhynchus* or *Merlinius* spp.) decreased with soil depth both in NT and CT plots.

The small number of *Heterodera avenae* points to the beneficial effect of crop rotations in terms of their control. In addition, the low number in both NT and CT (Table 7) of mononchids species also suggests a remarkable effect of agricultural practices on nematode diversity when compared with the virgin site (Table 4). The greatest numbers of *Tylenchorhynchus* spp. or *Merlinius* spp. in the upper rather than the deep layers are typical of the distribution of nematode fauna in dry environments (Nombela et al., 1994).

Fig. 3 shows the distribution of soil nematode fauna among the different trophic groups. There were no significant differences in total nematode populations between the traffic and non-traffic areas for fungivorous and bacterial-feeding groups. The populations of plant parasites at 15–22.5 cm depth in NT plots (with and without traffic) were significantly greater than in CT plots (with and without traffic). At 22.5–30 cm depth, the NT plots with traffic were significantly different from the other treatments. However, the study of the vertical distribution of soil nematode fauna revealed, mainly in the case of fungivorous nematodes, that at 22.5 cm depth, which coincided with the depth of the plow layer, there was an abrupt decline in population size. The increase with depth in the size of the population of plant parasites (mainly endoparasites), contrasting with the decrease in the number of omnivorous predators and bacterial-feeding species (Fig. 3), may possibly be explained by changes in the levels of soil porosity that are appropriate to the size of these soil nematodes.

4. Conclusions

A considerable decrease in the total number and diversity of soil nematodes was observed in cereal agrosystems subjected to intensive tillage. As opposed to the corresponding virgin ecosystem, the most characteristic genera were plant parasites (pathogenic), mainly represented by *Pratylenchus* spp.

In semi-arid conditions, compared with the CT system the NT system led to increased nematode populations, especially of bacterial-feeding nematodes. This is probably associated with the increased concentration of soil organic matter (López-Fando and Almendros, 1995) and moisture content.

The changes in the composition of the nematode population in the course of the year depended very much on the crop and the management system. The dense populations recorded in spring were related to the active growth of the host plants. Under these conditions, populations of plant parasites (pathogenic) can be controlled successfully through crop rotations, at least below the values that are associated with plant damage. In CT plots, as a result of plowing, mechanical inversion of upper soil layers led to further increases in the numbers of nematodes.

No generalized effect of soil compaction produced by tractor tracks was observed on the total populations of the four trophic groups of soil nematode fauna. Nevertheless, important changes occurred in the vertical distribution of nematodes, the different trophic groups showing characteristic patterns: the number of plant parasites tended to increase with depth, whereas the opposite occurred with omnivorous predators and bacterial-feeding species.

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