Some observations on the influence of agricultural practices on the nematode faunae of some South Australian soils

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Summary – Three different soils from three localities were examined in September-November for numbers and diversity of nematodes. Numbers varied from 157 to 4027/50 g dw. Numbers of nematodes in modified shrub land were consistently less than those in pasture or wheat growing regimes. In the agricultural regimes plant parasitic forms, notably *Pratylenchus*, predominated; plant associated nematodes such as *Cephalenchus* occurred to a lesser extent. The most widespread nematode was the bacterial feeding *Acrobeloides nanus* which occurred at all sites. Fungal feeding nematodes also occurred at all sites but were particularly prominent at one site where a clavate-tailed aphelenchoid was the most common nematode. Predacious nematodes were least abundant in the agricultural plots but were more abundant in modified shrub land. Proportions of nematodes in six feeding groups were determined and fungal feeder/bacterial feeder ratios and trophic diversity calculated. Various indices were used to compare the occurrence of nematodes in different sites.

Résumé – Observations concernant l'influence des pratiques agricoles sur la faune nématologique dans quelques sols du sud de l'Australie – La densité et la diversité des nématodes présents dans trois types de sols provenant de trois localités ont été observées pendant les mois de septembre à novembre. Les nombres varient de 157 à 4027 pour 50 g de sol (poids sec). Les nombres de nématodes dans les sols sous paysage de buissons modifié sont nettement plus faibles que dans les pâturages ou les terrains cultivés en blé. Dans les terres cultivées, ce sont les formes phytoparasites qui dominent, en particulier le genre Pratylenchus; des nématodes associés aux plantes, tel Cephalenchus, sont, dans une moindre mesure, également présents. Le nématode le plus répandu est l'espèce bactériophage Acrobeles nanus, présente dans tous les sites examinés. Les nématodes fongivores sont également présents dans tous les prélèvements, et particulièrement abondants dans un site où un Aphelenchoïde à queue en massue constituait l'espèce la plus commune. Les nématodes prédateurs sont moins abondants dans les zones cultivées et plus abondants dans les sols sous paysage de buissons modifié. Les proportions des nématodes appartenant aux six groupes trophiques ont été déterminées et le rapport fongivores/bactériophages, ainsi que la diversité trophique, calculés. Différents indices ont été utilisés pour comparer les valeurs liées aux nématodes dans les différents sites.

Key-words: Nematodes, diversity, land use, soils, Australia.

Agricultural practices affect native soil biota through the introduction of new species of crop plants and organisms that are symbiotic (e.g. mutualistic or parasitic) with these plants, through cultivation and through application of agrochemicals. These collectively lead to changes in soil climate, structure and chemistry. Because nematodes are influenced by these man-made changes, assessment of the nematode faunae in soils under differing intensities of management may provide an index of the degree of disturbance and an indication of the longterm impact of various types of land use on soil properties and processes.

The nematode genera Anguina, Ditylenchus, Heterodera, Meloidogyne and Pratylenchus can significantly influence agricultural management in South Australia (Kimpinsky et al., 1976; McKay et al., 1976; Bird, 1978; Stanton et al., 1979; Georg et al., 1989); however, the native faunae are poorly known (Reay & Wallace, 1981; Nobbs, 1992).

Most soils in the semi-arid wheat belt of South Australia are derived from tertiary sediments which are strongly weathered and have low levels of organic carbon, plant-available phosphorus and nitrogen. The Mediterranean-type climate of South Australia has dominant winter rainfall and a high drought frequency. Cereal crops are typically grown for 1-2 years followed by a year of the grasses Lolium, Hordeum, Bromus and Vulpia and the legumes Medicago and Trifolium all of which are grazed by livestock. The dominant crop, wheat (Triticum aestivum), is sown in May-June and harvested in November-January.

Our work provides, from limited sampling, initial information on the abundance and diversity of the nematode fauna in the soil under native shrub land containing some introduced weeds and compares it with the nematode faunae of variously managed agricultural plots in the same localities.

Materials and methods

SOILS AND TREATMENTS

Three different types of soil, each from a different locality, were sampled for their nematode faunae. These soils were selected because considerable information about them has been collected and published in recent years (Table 1). The sites and management history of these soils and the times at which we sampled them are as follows:

Kapunda: a) conventionally cultivated wheat plots which had grown wheat every year since 1983 (CC); soil samples were taken by coring midway between rows and root samples by coring from directly above the plants after removal of the stems; b) direct drilled wheat in plots which had grown wheat every year since 1983 (DD); c) pasture at least six years old (Past); and d) residual native shrub land vegetation with modified under storey (Shrub). Sampled 22 September, 28 October and 25 November 1992.

Avon: a) conventionally cultivated wheat plots which had grown wheat without applied nitrogen every year since 1979 (except for a barley/vetch hay crop for control of herbicide-resistant ryegrass in 1991) (CC); b) direct drilled wheat plots as in a) (DD); c) wheat field subject to continuous traditional farming for a century (CF); d) medic-rich 2-year-old pasture (Past); e) improved pasture established as a trial in 1982 and fertilized only in that year (Trial); f) modified shrub land (Shrub). Sampled 7 October 1992.

Northfield: a) ungrazed pasture (Medicago littoralis dominant) on a trial site (Trial). Sampled 4 November 1992.

Table 1. Characteristics of the sites and soils sampled; soil characteristics are for 0-10 cm depth under pasture (soil data from Amato & Ladd, 1992).

	Kapunda	Avon	Northfield
Latitude (S), longitude (E) Average annual rainfall	34°19′, 138°55′	34°14′, 138°19′	34°52′, 138°38′
(mm)	496	353	516
Average air temperature (°C)	15.7	14.6	16.8
Soil classification (U.S.)	Alfisol	Entisol	Vertisol
Soil group (Australia)	Red Brown Earth	Solonised Brown Earth	Black Earth
% clay	13	12	43
silt	31	2	8
sand	54	79	33
Texture	silty loam	sandy loam	heavy clay
pH (soil: water = 1:5)	6.4	8.6	8.3
Organic C (%)	1.6	1.5	1.7

SAMPLING AND PROCESSING

At each sampling, five separate cores of soil, each of which was 5 cm in diameter and 0-15 cm deep (except for Avon soil where there were four replicates, 0-10 cm deep), were collected from each treatment and transported to the laboratory at 5-10 °C in a cooled polystyrene container. After thorough mixing, a 40 or 50 g field-moist subsample from each core was extracted over 5 days in misting chambers using a 10 min cycle with 10 s of misting. The samples were placed on two layers of "Kleenex" tissue held in place over 2 mm plastic mesh and collected through a 7.5 cm diameter funnel connected by a tube to within 1 cm from the bottom of a 20 × 2.5 cm Pyrex test tube.

To assess extraction efficiency soil from Kapunda was collected from 5-10 cm soil depth. It was mixed and then passed through 2 mm and 810 µm sieves before being weighed. Four 40 g samples were weighed out and extracted under the mister for 5 days with samples being collected and counted each day (only sample nº 2 yielded any nematodes on day 5). In two cases the overflow from the test tubes was collected in buckets and nematodes counted; in each case only ten nematodes were found and an average of ten was assumed. All soil in each of the samples after misting was extracted by the two Erlenmeyer technique followed by sieving and decanting through 125, 75, 53 and 38 µm sieves at the conclusion. The results (Table 2) showed that this method gave a 90 % extraction efficiency; we have not adjusted our results for this.

In the case of root samples the roots were gently washed free of soil and then extracted in the misting chambers for the same period of time as the soil. Soil moisture content was calculated for each soil after drying at 60 °C.

The contents of the tubes from the misting chambers were allowed to settle for 1 h and the supernatant was removed by suction to within 2.5 cm of the bottom of the tube (this supernatant was found to be free of nematodes). The contents were made up to a known volume with water and, after thorough shaking, a 5 ml aliquot was poured into a counting dish; this aliquot usually represented 25 % of the total sample. After counting all the nematodes in the aliquot under a dissecting microscope, the whole sample of living nematodes was allowed to settle for 1 h, the supernatant was removed by suction, the tube was shaken and an equal volume of boiling fixative (100 ml 40 % formaldehyde: 10 ml glacial acetic acid: 390 ml distilled water) was added and the tube was shaken again. After storage for at least 24 h, an average of 75 randomly selected nematodes per sample was identified, usually to the level of genus, using an Olympus Vanox AHBT research microscope fitted with differential interference contrast optics.

ANALYSIS

Because of the variability of soil moisture and bulk density between soils and samples, the total counts/50 g moist soil have been converted to number/50 g dry soil and number/m² (in 0-10 or 0-15 cm soil depth). Analysis of variance was carried out on data for four indicative populations.

Nematode taxa were assigned to feeding groups and the proportion of the nematodes in each of the feeding groups determined. From this the fungal feeder/bacterial feeder ratio (F/B) and trophic diversity (T = $1/\Sigma p_i^2$) where p_i is the proportion of individuals in the ith trophic group) were calculated (Freckman & Ettema, 1993).

Using the data for each taxon we calculated:

richness $SR = (s-1)/log_e N$ diversity $H' = \sum_{i=1}^s p_i log_e p_i$ evenness $\mathcal{J}' = H'/H' \max$ dominance $\lambda = \sum p_i^2$ diversity $H_2 = -log_e \lambda$

where

p is the proportion of individuals in the *i*th taxon s is the number of taxa

N is the number of individuals identified H' max is $\log_e s$

The Shannon-Weaver index (H') is commonly used to assess diversity but as it may be dominated by the abundant taxa or the overall number of taxa, both evenness and richness have been calculated (Pielou, 1975; Yeates, 1984). The Simpson Index (λ) has been used to assess dominance and its \log_e transformation offers an alternative measure of diversity (H_2) (Pielou, 1975).

The nematode Maturity Index (MI) proposed by Bongers (1990) for non-plant parasitic nematodes (i.e. for feeding groups 1-3, 5-6) is:

 $MI = \sum_{i=1}^{n} v_i \cdot p_i$ where v_i is the c-p value of the ith taxon pi is the proportion of the ith taxon

c-p values of 1-5 are given by Bongers (1990) to reflect the perceived r-k strategy gradient among nematodes.

The more restricted PPI (Plant Parasitic Index) (Bongers, 1990), which includes only plant pathogenic nematodes (feeding group 4) and $\Sigma MI = \sum_{i=1}^{n} v_i \cdot p_i$ (Yeates, in press) which includes all feeding groups, have also been calculated.

As the values of the derived indices and ratios may not be normally distributed it is not generally valid to apply routine statistical procedures to them.

Results

TOTAL NUMBERS OF NEMATODES

We estimated the total numbers of nematodes in the soils to range from 157 to 4027 per 50 g dry wt of soil or from 555 000 to 10 635 000 nematodes per m² of soil (Table 3). The Kapunda site was sampled three times at monthly intervals and no overall pattern was apparent although the numbers were greater in October than in September and November. Further, numbers under modified shrub land were always lower than numbers under pasture. Analysis of variance showed highly significant treatment, time and interaction effects (Table 4).

The data for Avon on a single sampling show a range almost as great as those for the three Kapunda samplings but it does appear that the number of nematodes under continuous farming is similar to that at the old trial site which was less than those under modified shrub land and conventional cultivation. The nematode numbers were greatest under pasture and direct drilled regimes (Table 3). At both Kapunda and Avon modified shrub land had relatively small populations of nematodes.

Overall differences between total numbers in the agricultural regimes at each location may reflect both seasonal and soil texture factors. The large population (4027/50 g dry soil) recovered from the Northfield trial (Table 3) where the soil had a higher clay content than the other soils (Table 1) may be related to soil texture through the impact of texture on microbial populations as described below.

Table 2. Assessment of efficiency of mister extractor based on extraction of 40 g (field moist) soil samples for 5 days.

Replicate	Water flow rate in tubes (ml/3 h)	Nematodes recovered from mister	Nematodes lost by overflow	Nematodes recovered by sieving after misting	Total nematodes /40 g soil	% recovered by mister
1	24	1331	10	108	1449	92
2	10	1185	10	241	1436	82.5
3	11	1197	10	127	1334	90
4	5	1148	10	101	1259	91

Table 3. Total nematode population estimates for each soil management regime and sampling date. Populations are expressed |50 g| dry soil $(\pm \text{ standard error})$, |50 g| field moist soil and $|m^2|$; sampling depths are indicated.

Soil and treatment			/50 g dry soil	/50 g moist soil	/m²
Kapunda (0-15 cm dep	th)			711	YEAR
September	Conventional cultivation Direct drilled Pasture Modified shrubland	(CC) (DD) (Past) (Shrub)	406 ± 86 513 ± 167 228 ± 57 157 ± 48	312 398 165 129	1,437,000 1,816,000 807,100 555,000
October	Conventional cultivation Direct drilled Pasture Modified shrubland	(CC) (DD) (Past) (Shrub)	2678 ± 312 2998 ± 612 1051 ± 252 800 ± 229	2464 2771 909 731	9,457,000 10,635,000 3,489,000 2,806,000
November	Conventional cultivation Direct drilled Pasture Modified shrubland	(CC) (DD) (Past) (Shrub)	556 ± 47 188 ± 48 756 ± 257 321 ± 160	451 150 588 284	1,856,000 629,000 2,692,000 1,000,000
Avon (0-10 cm depth)					
October	Conventional cultivation Direct drilled	(CC) (DD)	1553 ± 408 3125 ± 474	1360 2730	3,115,000 6,268,000
	Pasture Modified shrubland Continuous farming Old trial site	(Past) (Shrub) (CF) (Trial)	2812 ± 698 1586 ± 744 371 ± 212 614 ± 166	2489 1496 348 565	5,641,000 3,181,000 744,000 1,232,000
Northfield (0-15 cm	depth)				
November	Old trial site	(Trial)	4027 ± 467	3001	8,794,000

Table 4. Results of analysis of variance of the abundance /50 g dry soil of four nematode populations each assessed on three dates at Kapunda under four management regimes with five replicates. F ratios with $p \le 0001$ are denoted by ***

Source of variation	Degrees of freedom	F. ratio								
		Total	Pratylenchus	Acrobeloides	Mononchidae					
	2	49,39***	16.30***	22.24***	1.00					
treatment	3	8.00***	14.36***	10.47***	0.45					
time × treatment	6	7.08***	4.39***	7.96***	1.76					
error	48				21, 7-1					

Nematode taxa and feeding groups

Some 50 taxa (Kapunda 39, Avon 47, Northfield 23) were noted during the identification process but many were represented by only a few immature specimens. The only nematodes we have identified to species are *Acrobeloides nanus* (all sites), *Pratylenchus thornei* (Kapunda) and *P. neglectus* (Avon). Taxa which made significant contributions to the faunae are listed separately but others have been given as aggregates (Tables 5 and

6). At Kapunda the four taxa which made the greatest contributions to the fauna were Pratylenchus (21-57 % in agricultural areas), Acrobeloides nanus (4-28 % in all samples), Cephalenchus (5-24 % under conventional cultivation and pasture) and Tylenchidae (30-39 % in modified shrub land). At Avon Pratylenchus (25 and 36 % in CC and DD respectively), Cervidellus (23-31 % in CC, DD and shrub land), Tylenchorhynchidae (4-10 % under wheat and pasture) and Acrobeloides nanus (10-16 % in continuous farming and old trial) were significant contributors. The single sampling at Northfield yielded high proportions of Helicotylenchus (10 %), a clavate aphelenchoid (19%), Tylenchidae (19%) and Tylencholaimidae (22 %). Analysis of variance showed highly significant treatment, time and interaction effects in Pratylenchus and Acrobeloides nanus, but no effects were significant in the uncommon Mononchidae (Table 4).

Plant pathogenic nematodes were dominant (mean 56%) at the agricultural Kapunda sites in September with bacterial feeding and plant associated taxa contributing 76% of the fauna in modified shrub land (Table 7). In October the proportion of plant pathogenic forms in the agricultural plots was lower (mean 35%) but in these plots plant associated taxa had increased

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Table 5. Percentage composition of the nematode fauna under four management regimes (CC, conventional cultivation; DD, direct drilled; Past, pasture; Shrub, modified shrubland) at Kapunda, South Australia on three sampling occasions. Where taxa overlap specific populations are included only once; c-p values are from Bongers (1990, Tables 1 & 4); feeding groups are 1 bacterial feeding; 2 fungal feeding; 3 predactions; 4 plant pathogenic; 5 plant associated; 6 omnivorous. Values are from mean populations in 5 replicate samples.

Taxon	с-р	Feeding		Septe	ember			Oct	ober		November			
value	group	CC	DD	Past	Shrub	CC	DD	Past	Shrub	CC	DD	Past	Shrub	
Tylenchidae	2	5	0.8	0.3	0.7	38.9	9.0	12.4	8.7	30.4	13.4	4.7	21.5	36.0
Cephalenchus	2	5	5.2	1.4	10.9	2.8	22.0	9.9	24.1	0.9	6.6		11.3	4.8
Ditylenchus	2	2	2.0	2.5	4.6	5.0	0.5	0.7	4.3	26.7	724	1.4	4.7	10.2
Tylenchorhynchidae	3	4	2.4	1.1	7.3	0.4	1.7	7.7	5.1	0.5	2.4	1 -	2.1	45
Pratylenchus	3	4	55.0	44.5	57.7	0.4	37.3	21.6	29.5		53.2	47.5	34.1	1.6
Paratylenchus	2	4	-			0.4	-11	0.7		3.7	WHU.	80 41	-	1.2
Aphelenchina	2	2	5.1	21.5	4.8	10.1	9.0	11.1	4.5	4.5	3.9	8.3	6.3	5.6
Rhabditidae	1	1	7.2	3.5	0.7	3.7	2.3	6.2		5.8	5.9	4.6	1.2	0.4
Panagrolaimus	1	1	1.0	0.3	1.3	1.2	14	-	102	416	51,410		2.3	0.4
Acrobeloides nanus	2	1	12.3	22.6	4.3	6.7	18.0	28.2	5.1	5.0	8.6	14.3	10.0	8.1
Cervidellus	2	1	0.5	<u> 1940</u> 8		1		100	0.1	1.7	0.2	0.7	-	1.9
Cephalobidae	2	1	0.4	100	1.0	4.0	-			1.1	+	0.7	0.5	4.3
Plectidae	2	1	1.4	0.2	-	4.9	111	1		4.7	1.9	3.5	0.8	3.0
Wilsonema	2	1	-	40		13.3		4.00		0.4	7	9 -	0.2	4.0
Prismatolaimus	3	1	0.1	0.4		-	-	0.2	0.1	###B	0.8	5.5	0.5	0.8
Monhystera	1	1	3.7	0.2	0.5			1.2	0.5	4.7		-	-	1.8
Tripyla	3	3	-	0.7	- 3	1.0	-	104	0.3	3.8	4		-	2.4
Dorylaimidae	4	6	-	- 4	0.3	2.6	0.2	0.2	4.2	0.6	1.7	0.7	-	3.6
Tylencholaimus	4	2	-	-	0.5	0.4			8.7	0.6		2	3.8	1.2
Aporcelaimidae	5	6	2.0	0.8	3.1	1.7		3.4	2.9	1.1	0.6	2.2	0.7	0.5
Nygolaimidae	5	3	-		-	1.7	9.50	-		3.6	51540	-	-	1.0
Mononchidae	4	3	0.8	-11	2.1	0.4	848	-	1.9		0.8	5.9	-	6.0
Alaimus	4	1	-		1 L	0.6	-	1	1 3 TO			-	-	1.2

from 6.4 to 28.7 %; in pasture and modified shrub land the proportion of fungal feeders had almost doubled (12.7-24.7 %). In November the agricultural plots contained an average of 46 % plant pathogenic forms but the contribution of plant associated forms had decreased to 19.2 %.

Bacterial feeding nematodes averaged 20 % of the fauna in the agricultural sites at each of the three Kapunda samplings (Table 7). Predacious nematodes were the least abundant of the feeding groups in all samples from agricultural plots at Kapunda but in the modified shrub land they were usually more abundant than either plant pathogenic or omnivorous nematodes (Table 7).

In the Avon and Northfield samples predacious nematodes were the least abundant feeding group (Table 8). Plant pathogenic forms comprised the most abundant group in the conventional cultivation, direct drilled and pasture samples from Avon but the other three regimes were dominated by bacterial feeding nematodes. The greatest single contribution by any feeding group was from the 49 % of fungal feeding nematodes in the Northfield trial sample. These nematodes were predominantly the clavate aphelenchoid, other

Aphelenchina, Tylencholaimus and other Tylencholaimidae.

Calculation of the abundance of bacterial feeding and fungal feeding nematodes in the three soils shows some differences in the number of bacterial feeding forms but a markedly greater number of fungal feeding nematodes in the heavy clay at Northfield (At Avon pasture and trial sites there were on average more bacterial feeders than fungal feeders; 546 vs 165/50 g dry soil. At Kapunda under pasture there were similar numbers of bacterial feeders and fungal feeders; 65 vs 106/50 g dry soil. At Northfield there were far fewer bacterial feeders than fungal feeders; 475 vs 1989/50 g dry soil). The correlations with the clay content (Table 1) are + 0.3505 (n.s.) for bacterial feeding nematodes and + 0.9984 (p < 0.05) for fungal feeding nematodes.

The actual populations of each feeding group/50 g dry soil are shown in Figures 1, 2. The large populations of bacterial feeding, plant pathogenic and plant associated nematodes in both wheat regimes at Kapunda in October and the relative stability of numbers of other feeding groups are apparent (Fig. 1). At Avon, bacterial feeding nematodes were very abundant in the wheat,

Table 6. Percentage composition of the nematode fauna under six management regimes (CC, conventional cultivation; DD, direct drilled; Past, pasture; Shrub, modified shrubland; CF, conventional farming; Trial, former trial site) at Avon and one at Northfield, South Australia. See Table 4 for further explanation.

Taxon	<i>c-p</i> value	Feeding group			A	von			Northfield Trial
	value	group	СС	DD	Past	Shrub	CF	Trial	- I Hai
Tylenchidae	2	5	3.6	6.4	<u>-</u>	1.4	10.5	2.7	19.1
Cephalenchus	2	5	0.5	_		_	6.7		
Ditylenchus	2	2	3.0	1.4	1.8	3.7	3.8	1.1	1.6
Tylenchorhynchidae	3	4	5.8	4.1	10.7	1.4	6.9	0.1	
Pratylenchus	3	4	24.7	36.0	8.3	0.3	2.5	4.9	117
Helicotylenchus	3	4	_	-	_	-	_	-	9.9
Paratylenchus	2	4	18.7	5.6	27.8	1.1	1.2	16.5	2.2
Aphelenchoid clavate	2	2	-	_	_	0.4		_	18.9
Aphelenchina	2	2	4.2	3.4	4.5	7.9	7.4	4.9	6.6
Rhabditidae	1	1		0.5	0.3	4.4	0.2	1.1	-
Panagrolaimus	1	1	0.9	_	7.1	0.2	7.7	4.8	W .
Acrobeloides nanus	2	1	4.6	1.7	7.9	3.6	16.7	10.2	6.0
Cervidellus	2	1	30.2	31.2	11.3	23.8	4.6	18.7	0.7
Cephalobidae	2	1	0.2	3.1	0.8	12.0	5.0	1.2	3.8
Plectidae	2	1	1.7	0.3	0.2	6.4	5.3	9.1	0.2
Wilsonema	2	1	_	0.9	_	11.9	2.3	6.4	-
Prismatolaimus	3	1	_		_		1.5	_	_
Monhystera	2	1	_	-	_	1.3	_	-	1.0
Tripyla & Tobrilus	3	3		_	-	_	1.1	0.3	_
Dorylaimidae	4	6	1.8	5.5	8.1	3.2	14.1	6.0	6.6
Tylencholaimus	4	2	_	_	0.5	-	_	5.0	10.6
Tylencholaimidae	4	2	-	_	1.7	_	_	3.4	11.7
Actinolaimidae	5	6	-	_		14.7	_	_	_
Aporcelaimidae	5	6	_	_	1.4	1.8	0.9	1.1	0.6
Nygolaimidae	5	3	_	_	_	0.3	_	2.2	0.3
Mononchidae	4	3	_	_	_	_	0.5	_	_
Alaimus	4	1	_	_	_	_	1.1	-	_

Table 7. Indices of the nematode faunae under four management regimes on three sampling occasions at Kapunda; the equation for each index and details of the regimes are given under methods.

	September				October				November				
	CC	DĎ	Past	Shrub	CC	DD	Past	Shrub	CC	DD	Past	Shrub	
Taxa identified (s)	22	15	18	26	10	14	17	21	17	17	19	25	
Specimens identified (N)	319	264	220	208	415	435	394	320	456	251	419	330	
% bacterial feeding	26.6	27.2	7.8	34.4	20.3	35.8	5.8	23.4	17.4	29.3	15.5	25.9	
fungal feeding	7.1	24.0	9.9	15.5	9.5	11.8	17.5	31.8	3.9	9.7	14.8	17.0	
predacious	0.8	0.7	2.1	3.1	-	-	2.2	7.4	0.8	5.9	-	9.4	
plant pathogenic	57.4	45.6	65.0	1.2	39.0	30.0	34.6	4.2	55.6	47.5	36.2	2.8	
plant associated	6.0	1.7	11.6	41.7	31.0	22.3	32.8	31.3	20.0	4.7	32.8	40.8	
omnivorous	2.0	0.8	3.4	4.3	0.2	0.2	7.1	1.7	2.3	2.9	0.7	4.1	
F/B	0.27	0.88	1.27	0.45	0.47	0.33	3.02	1.36	0.22	0.33	0.95	0.66	
T	2.44	2.94	2.21	3.13	3.35	3.55	3.75	3.83	3.15	3.05	3.51	3.65	
SR	3.64	2.51	3.15	4.68	1.49	2.14	2.68	3.47	2.61	2.90	2.98	4.14	
H'	1.59	1.65	1.67	2.44	1.25	2.01	2.11	2.13	1.70	1.92	2.14	2.29	
J'	0.51	0.61	0.58	0.75	0.54	0.76	0.75	0.70	0.60	0.68	0.73	0.71	
λ	0.33	0.28	0.36	0.16	0.23	0.17	0.17	0.18	0.31	0.26	0.18	0.15	
H_2	1.11	1.29	1.03	1.81	1.46	1.78	1.76	1.71	1.16	1.34	1.74	1.92	
ΣΜΙ	2.53	2.45	2.77	2.16	2.37	2.23	2.99	2.10	2.57	2.65	2.43	2.31	
MI	1.90	1.99	2.35	2.15	1.67	1.91	2.58	2.10	2.04	2.39	2.11	2.30	
PPI	3.00	3.00	3.00	2.67	3.00	2.98	3.00	2.12	3.00	3.00	3.00	2.57	

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Table 8. Indices of the nematode faunae under various management regimes at Avon and Northfield; the equation for each index and details of the regimes are given under methods.

	Avon							
	CC	DD	Past	Shrub	CF	Trial	– Trial	
Taxa identified (s)	16	17	21	29	24	23	22	
Specimens identified (N)	337	290	322	265	208	318	481	
% bacterial feeding	37.6	37.7	27.6	63.6	44.4	51.3	11.8	
fungal feeding	7.2	4.8	8.5	12.0	11.2	14.7	49.4	
predacious		T	_	0.3	1.6	2.5	0.3	
plant pathogenic	49.2	45.7	46.8	2.8	10.6	21.5	12.1	
plant associated	4.1	6.4	7.7	1.4	17.2	2.7	19.1	
omnivorous	1.8	5.5	9.5	19.7	15.0	7.1	7.3	
F/B	0.19	0.13	0.31	0.19	0.25	0.29	4.19	
T	2.56	2.77	3.15	2.18	3.66	2.96	3.18	
SR	2.58	2.82	3.46	5.02	4.31	3.82	3.40	
H'	1.94	1.85	2.36	2.61	2.97	2.52	2.49	
Ī'	0.70	0.65	0.78	0.78	0.94	0.80	0.81	
	0.20	0.24	0.13	0.11	0.09	0.10	0.10	
H_2	1.63	1.42	2.03	2.21	2.46	2.35	2.26	
ΣMI	2.33	2.50	2.36	2.52	3.38	2.38	2.71	
MI	2.05	2.20	2.33	2.53	2.25	2.65	2.69	
PPI	2.62	2.88	2.41	2.61	2.89	2.23	2.82	

pasture and shrub sites whereas the Northfield trial had numerous plant pathogens, plant associated and, particularly, fungal feeding nematodes (Fig. 2).

Indices

The changes in the relative abundance of bacterial and fungal feeding groups at Kapunda are reflected in changes in the F/B ratio and trophic diversity (T) (Table 7). However, in each month, F/B was greatest under pasture and T greatest under shrub land. The actual values of these indices differed between the months.

Richness (SR) and diversity (H') were greatest under modified shrub land. Evenness (J') was consistently lowest under CC wheat. Dominance (λ) and H₂ diversity values show no consistent trends in the Kapunda data but generally λ was greatest in one of the wheat regimes and H₂ greatest under shrub land (Table 7). However, Σ MI was always least under modified shrub land. While MI was lowest under conventional cultivation, the PPI was essentially 3.0 under all agricultural regimes and lower in shrub land.

For comparable regimes (CC, DD, Past, Shrub) the Avon soil contained an average of 41.6 % bacterial feeding nematodes (Table 8) compared with 24 % for Kapunda in September (Table 7), and the additional two regimes (CF and Trial) also had a predominance of bacterial feeding nematodes. Again, F/B was greatest under pasture although values were generally lower than at Kapunda due to the abundance of bacterial feeding nematodes. In the comparable regimes (CC, DD, Past, Shrub) trophic diversity (T) was greatest under pasture

at Avon compared with shrub land at Kapunda although overall values in the two soils were similar. SR and H' were again greatest in soil beneath shrub land (Table 8). While λ and H₂ show no marked trends in the comparable regimes, the conventional farming (CF) and trial site are grouped at the extremes of each of these indices. The patterns of Σ MI, MI and PPI in the comparable regimes at Avon were similar to those at Kapunda. However, each index had its maximum in one of the additional regimes (CF or Trial).

The various indices for the nematode fauna of the Northfield trial site were generally similar to those for the Avon trial except for the effect of the presence of 49 % of fungal feeding nematodes.

Nematodes from roots

Our root samples always consisted of the roots within a 5 cm diameter core centred on plants which were physiologically two months older at the end of the sampling period. As the roots we sampled were mature and lacked root hairs we could not separate any distinct "rhizosphere soil" and extracted only gently washed roots. At all sampling times *Pratylenchus* comprised the greatest number of nematodes recovered, averaging 67% of the total (Table 9). The next most abundant form was *Acrobeloides nanus* (10%) and there was a variety of other bacterial feeding, fungal feeding and plant associated taxa. There are no obvious trends in the numbers or taxa of nematodes recovered from the roots; the amount of root in the samples was similar.

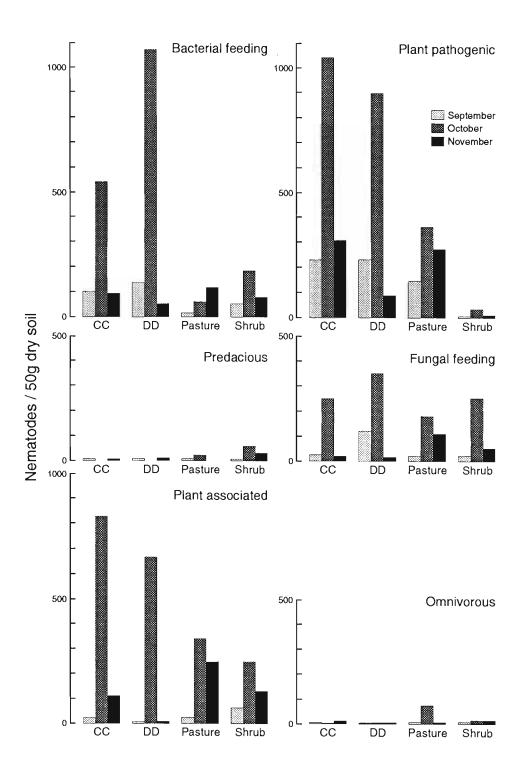


Fig. 1. Populations of nematode feeding groups at three sampling times under four management regimes at Kapunda, South Australia. (CC, conventional cultivation; DD, direct drilled; Past, pasture; Shrub, modified shrub land. Each value is the mean of 5 replicate samples).

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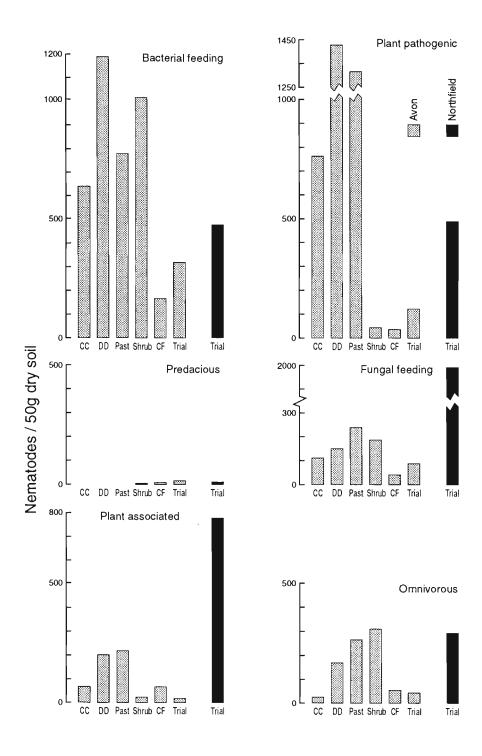


Fig. 2. Populations of nematode feeding groups under six management regimes at Avon and under one regime at Northfield, South Australia. [CC, conventional cultivation; DD, direct drilled; Past, pasture; Shrub, modified shrub land; CF, conventional farming; Trial, experimental trial site. Each value is the mean of 4 (Avon) or 5 (Northfield) replicate samples].

Table 9. Mean numbers (\pm standard errors) of nematodes by taxa extracted from washed roots recovered from 5 cm diameter 15 cm deep cores taken over wheat plants on three sampling occasions at Kapunda, South Australia; mean oven dry root weight is given; n = 5 in each case.

	September	October	November	Mean
Pratylenchus	1342 ± 324	957 ± 377	1017 ± 223	1105
Acrobeloides nanus	108 ± 24	284 ± 107	100 ± 23	164
Aphelenchina	78 ± 28	120 ± 33	122 ± 42	107
Tylenchidae	71 ± 14	76 ± 26	38 ± 3	62
Rhabditidae	115 ± 54	19 ± 11	29 ± 9	54
Cephalenchus	186 ± 129	1 ± 1	21 ± 18	69
Panagrolaimus	10 ± 6	45 ± 12	43 ± 19	33
others	47 ± 18	63 ± 15	34 ± 17	48
Total	1957 ± 318	1565 ± 503	1404 ± 245	1642
root weight (g)	0 .545 ± 0.940	0.628 ± 0.147	0.690 ± 0.090	0.621

Discussion

The total estimates of nematode populations (Table 3) reflect overall management impacts on the endemic fauna. Data of Reay and Wallace (1981) and Nobbs (1992) for native vegetation and pastoral shrub land in South Australia indicate populations of 50-300 and 200-300/50 ml soil from September to November and, given management effects, our results are compatible with these. As shown by Nobbs (1992) there are great changes in abundance of nematodes over a full year and although at our wheat sites we might have expected to recover Heterodera avenae, which has been recorded from agricultural sites (including Avon) in South Australia (Rovira et al., 1981), it has been shown that the soil inhabiting larval form of these nematodes is not found in the soil at the times that we sampled (Georg et al., 1989).

The taxa we identified show differences between management regimes and soils (Tables 5, 6). Yeates (1984) showed that under pasture the soil was more important than season or year in determining the composition of the nematode fauna and results from the present work indicate that, as sand content increases, so do the number of taxa. In the Kapunda samples *Paratylenchus*, *Wilsonema*, Nygolaimidae and *Alaimus* were

generally restricted to shrub land. The Avon soil vielded sizeable populations of *Paratylenchus* in all management regimes and Cervidellus was also abundant; in this soil Wilsonema, Nygolaimidae and Alaimus each had a distribution different from that at Kapunda. The most significant difference between the nematode fauna in the heavy clay at Northfield and the other soils was the presence of Helicotylenchus and the clavate aphelenchoid in the former. Studies of nematodes in ecological successions (e.g. Wasilewska, 1979) and under various management regimes (e.g. Bergeson & Ferris, 1986; Yeates & Hughes, 1990; Freckman & Ettema, 1993) can show that such regimes have significant effects on the abundance of particular taxa. It is important to note that such effects are soil specific and, as our results indicate, different effects may be found in different soils. The presence or absence of a particular species is determined by many factors and thus cannot be used as a general indicator for the effects of any particular soil type.

Freckman and Ettema (1993) introduced the concept of trophic diversity to nematode ecology and found that few treatments had a significant effect on trophic diversity across management regimes in fine loamy soils in Michigan (U.S.A.). At Kapunda, trophic diversity was consistently highest in shrub land but in the more sandy soil at Avon areas under continuous farming had the highest trophic diversity (Tables 7, 8). The ratio of fungal feeding nematodes to bacterial feeding nematodes has been used as an index of relative availability of food resources and decomposition pathways (Wasilewska, 1979; Hendrix et al., 1986). While differences in the ratio may be statistically significant (e.g. Freckman & Ettema, 1993; Yeates et al. 1993), the ratio is also very dependent on the proportion of "rhizosphere soil" in the samples (e. g. Hofman & s'Jacob, 1989). In the present work, although pastures consistently showed the highest ratio of the four agricultural regimes, there was considerable variation. The values for F/B under pasture were 0.31 at Avon and 1.27, 3.02 and 0.95 at Kapunda; in the heavy clay at Northfield, the ratio was 4.19 (Tables 7, 8). It appears that individual F/B ratios are too greatly influenced by soil type and season in these South Australian soils to be useful indicators of soil processes. That is not to say, however, that such ratios may not be useful discriminators under defined soil and climatic conditions.

Predacious nematodes, since they represent the top trophic level in the soil microfauna, have been suggested to be useful indicators of soil biological conditions (e.g. Arpin et al., 1984; Wardle & Yeates, 1993) but their low abundance in agricultural or mineral soils may limit their usefulness, as has been found by Freckman and Ettema (1993). We have also found that these nematodes occur in very low numbers. At Kapunda they occurred in greatest numbers in shrub land (Table 7) whereas in the sandy loam at Avon they were recovered at low

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frequency in three of the treatments (including conventional farming); they were also present at Northfield (Table 8). It is also worth noting that at Avon, tardigrades (known to be predators of soil microbiota, Hallas & Yeates, 1972) were present at an average of 15/50 g dry soil (ca 30 000/m²) and they probably utilize a similar resource to the predacious nematodes. As is the case with the F/B ratio, underlying soil factors may mean that predacious nematodes do not provide a generally applicable index of biodiversity.

Species richness is a basic measure of biological diversity. By applying the same calculation to similarly identified nematodes under grazed pastures Yeates (1984) found values of 2.60-4.69. Converting the results of Freckman and Ettema (1993) to SR (rather than the number of taxa identified) gives values of 5.47-6.61 for identification to species level. As was the case in the Freckman and Ettema (1993) data, our highest values were under the least disturbed regime (shrub land). The highest value was in sandy loam at Avon and values in this soil were consistently higher than in the silty loam. This agrees with the results of Yeates (1984) who showed SR to be greatest in the most coarse textured of the sites he sampled. Soil texture apparently plays a significant role in influencing nematode diversity.

The various indices of diversity, evenness and dominance all depend on assumptions about the relative contribution of each taxon to the particular fauna and until different assumptions are proposed and accepted (Wolda, 1981) most workers will continue to use those that we have chosen. Diversity (H') and species richness are correlated and, in our study, greatest under shrub land (except for the anomalous conventional farming). Evenness (J') and H' were lowest under conventional cultivation at Kapunda (i.e. the regime with the greatest degree of disturbance) but at Avon values for direct drilled were slightly lower (Tables 7, 8). Dominance, as measured by Simpson's λ, was highest under the regimes with greater disturbance and lowest under shrub land. H, diversity, computed from λ , showed the opposite, consistent effect.

Bongers (1990) proposed the maturity index as a "measure of environmental disturbance" but for our data from Kapunda, the pasture samples rather than those from modified shrub lands have the greatest MI values (2.35-2.58). While at Avon the shrub land MI (2.53) is greater than that for pasture, an even higher value (2.65) has been found for the trial site (= once fertilized pasture). Our MI are compatible with those of Bongers (1990) and are slightly greater than those of Freckman and Ettema (1993). Values for New Zealand pastures calculated from the data of Yeates (1984) are 2.11-3.54 (Yeates, in press) which are generally greater than Bonger's values. However, in a range of disturbed situations, MI was lowered (Yeates, in press) in keeping with the proposal of Bongers (1990). At Kapunda if all and soil nematodes are plant included

the Σ MI as proposed by Yeates (in press) pasture has the highest Σ MI and MI values in September and October while direct drilled ranks third, but in November the ranking of these regimes is reversed (Table 7). At Avon when the four regimes used at Kapunda are considered shrubland has the highest Σ MI and MI values and conventional cultivation the lowest (Table 8); however, continuous farming and the old trial site do not show consistent relations to the other regimes. Certainly among the regimes common to Kapunda and Avon sites neither Σ MI nor MI values can, with a single sampling, consistently indicate the degree of disturbance.

The plant parasitic index (PPI) for agricultural sites at Kapunda is dominated by taxa with c-p=3 and the PPI has a value of approximately 3 (Table 7). Where other taxa are involved in shrub land, the PPI is lower. At Avon and Northfield there is a more heterogeneous range of plant parasites and the PPI is more variable but shows no general trend. While Freckman and Ettema (1993) found statistically significant changes in the PPI with different degrees of human intervention, as in the present work, there was no obvious trend.

Indices of biological populations can potentially condense complex population information and thus indicate relative levels of biodiversity, agronomic productivity, pollution/disturbance and ecosystem sustainability. Not only are these aspects themselves interrelated but also soil effects may be greater than management effects (Yeates, 1984) and sediment texture may have a greater effect on nematode diversity than heavy metal pollution (Tietjen, 1980). There may be significant direct or indirect interactions between populations of different classes of soil organisms (e.g. nematodes with enchytraeids, tardigrades, earthworms) (Yeates, 1968; Hallas & Yeates, 1972; Yeates, 1981; Ingham et al., 1985). At a given site, seasonal, depth and management factors inter alia may significantly affect indices (e.g. Yeates, 1984; Yeates et al., 1993). Investigating nematodes in a single soil in Michigan, Freckman and Ettema (1993) found disturbance could be reliably detected by multivariate analysis and MI, with added information coming from diversity indices and functional groups (= feeding groups). Our analysis of nematodes of some South Australian soils has found several indices confounded by textural effects but various measures of diversity (SR, H', J', λ) warrant further investigation. If we regard shrub land as the least disturbed regime, the nematode maturity index does not appear satisfactory.

The three soils which we studied were included in the series examined by Amato and Ladd (1992) who found a close correlation between native soil microbial biomass and soil clay content and the proportion of total soil pore space attributable to fines pores (less than 6 μ m diam.). We have found a significant positive correlation between the numbers of fungal feeding nematodes and the clay content of the soils. Differences in protection of microbes from nematode-grazing in soils of differing tex-

tures is important in nutrient cycling (e.g. Ingham et al., 1985) and may be an important factor in the survival of released biocontrol agents (Bird & Rider, 1993; Ryder & Rovira, 1993). Indeed, such "native" soil effects are probably significant in the natural distribution of soil biota, including nematodes and further work is required better to characterise the South Australian nematode fauna. The composition of the soil biota has important consequences for plant nutrient cycling as shown by Ingham et al. (1985) and in differing migration abilities such as those of amoebae and nematodes reported by Griffiths and Caul (1993).

Conclusion

A restricted sampling of South Australian soils showed a diverse nematode fauna (more than 50 species). Management regimes greatly affected nematode diversity and, as in previous work, the effect of soil texture was significant. Indices such as species richness and Shannon index were the best of the indices tested in revealing trends in the composition of the nematode fauna but even these have major limitations. Soil and climate affect nematode faunae so strongly that the use of any faunal index will probably be limited to districts with uniform soil and climate.

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References

- AMATO, M. & LADD, J. N. (1992). Decomposition of ¹⁴C-labelled glucose and legume material in soils: properties influencing the accumulation of organic residue C and microbial biomass C. *Soil Biol. Biochem.*, 24: 455-464.
- Arpin, P., Ponge, J.-F., Dabin, B. & Mori, A. (1984). Utilisation des nématodes et des Collemboles pour caractériser des phénomènes pédobiologiques. *Revue Écol. Biol. Sol*, 21: 243-268.
- Bergeson, G. B. & Ferris, J. M. (1986). Influence of tillage methods on *Pratylenchus* spp. in two soil types. *Pl. Dis.*, 70: 326-328.
- BIRD, A. F. (1978). Root-knot nematodes in Australia. CSIRO Div. hortic. Res. techn. Paper, 2: 1-26.
- BIRD, A. F. & RYDER, M. H. (1993). Feeding of the nematode *Acrobeloides nanus* on bacteria. J. Nematol., 25: 493-499.
- Bongers, T. (1990). The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia*, 83: 14-19.
- FRECKMAN, D. W. & ETTEMA, C. H. (1993). Assessing nematode communities in agroecosystems of varying human intervention. *Agriculture, ecosyst. Envir.*, 45: 239-261.

- GEORG, D. G., FISHER, J. M., DUBE, A. J. & WAYTE, S. E. (1989). The relation between time of sowing and cereal cyst nematode (*Heterodera avenae* Woll). *Austr. J. exp. Agric.*, 29: 647-653.
- GRIFFITHS, B. S. & CAUL, S. (1993). Migration of bacterial-feeding nematodes, but non protozoa, to decomposing grass residues. *Biol. Fertility Soils*, 15: 201-207.
- HALLAS, T. E. & YEATES, G. W. (1972). Tardigrada of the soil and litter of a Danish beech forest. *Pedobiologia*, 12: 287-304.
- HOFMAN, T. W. & s'JACOB, J. J. (1989). Distribution and dynamics of mycophagous and microbivorous nematodes in potato fields and their relationship to some food sources. *Ann. appl. Biol.*, 115: 291-298.
- Hendrix, P. F., Parmelee, R. W., Crossley, D. A., Coleman, D. C., Odum, E. P. & Groffman, P. M. (1986). Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience*, 36: 374-380.
- INGHAM, R. E., TROFYMOW, J. A., INGHAM, E. R. & COLE-MAN, D. C. (1985). Interactions of bacteria, fungi and their nematode grazers: effects on nutrient cycling and plant growth. *Ecol. Monogr.*, 55: 119-140.
- KIMPINSKI, J., WALLACE, H. R. & CUNNINGHAM, R. B. (1976). Influence of some environmental factors on populations of *Pratylenchus minyus* in wheat. *J. Nematol.*, 8: 310-314.
- McKay, A. C., Fisher, J. M., Wilkinson, G. N. & Eckert, S. R. (1986). The effect of initial gall and plant density on gall production by *Anguina funesta*, the vector of annual ryegrass toxicity. *Nematologica*, 32: 322-338.
- Nobbs, J. M. (1992). The response of soil nematodes to environmental stimuli in arid South Australia. *Trans. Roy. Soc. S. Austr.*, 116: 77-78.
- Pielou, E. C. (1975). Ecological diversity. New York, John Wiley, 165 p.
- REAY, F. & WALLACE, H. R. (1981). Plant nematodes associated with native vegetation in South Australia. *Nematologica*, 27: 319-329.
- ROVIRA, A. D., BRISBANE, P. G., SIMON, A., WHITEHEAD, D. G. & CORRELL, R. L. (1981). Influence of the cereal cyst nematode (*Heterodera avenae*) on wheat yields in South Australia. *Austr. J. exp. Agric. anim. Husb.*, 21: 516-523.
- RYDER, M. H. & ROVIRA, A. D. (1993). Biological control of takeall of glasshouse-grown wheat using strains of *Pseudomonas corrugata* isolated from wheat field soil. *Soil Biol. Biochem.*, 25: 311-320.
- STANTON, J. M., FISHER, J. M. & BRITTON, R. (1979). Resistance of cultivars of *Avena sativa* to, and host range of, an oat attacking race of *Ditylenchus dipsaci* in South Australia. *Austr. J. exp. Agric. anim. Husb.*, 24: 267-271.
- TIETJEN, J. H. (1980). Population structure and species composition of the free-living nematodes inhabiting sands of the New York Bight apex. *Estuarine & coastal marine Sci.*, 10: 61-73.

Fundam. appl. Nematol.

- WARDLE, D. A., YEATES, G. W. (1993). The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: evidence from decomposer foodwebs. *Oecologia*, 93: 303-306.
- WASILEWSKA, L. (1979). The structure and function of soil nematode communities in natural ecosystems and agrocenoses. *Polish ecological Stud.*, 5: 97-145.
- WOLDA, H. (1981). Similarity indices, sample size and diversity. *Oecologia*, 50: 296-302.
- YEATES, G. W. (1968). An analysis of the annual variation of the nematode fauna in dune sand, at Himatangi Beach, New Zealand. *Pedobiologia*, 8: 173-207.
- YEATES, G. W. (1981). Soil nematode populations depressed in the presence of earthworms. *Pedobiologia*, 22: 191-195.

- YEATES, G. W. (1984). Variation in soil nematode diversity under pasture with soil and year. *Soil Biol. Biochem.*, 16: 95-102.
- YEATES, G. W. (in press). Modification and quantification of the nematode maturity index. *Pedobiologia*, 38.
- YEATES, G. W. & HUGHES, K. A. (1990). Effect of three tillage regimes on plant and soil nematodes in an oats/maize rotation. *Pedobiologia*, 34: 379-387.
- YEATES, G. W., WARDLE, D. A. & WATSON, R. N. (in press). Relationships between nematodes, soil microbial biomass and weed management strategies in maize and asparagus cropping systems. Soil Biol. Biochem, 25: 857-868.