Nematode community profiling as a soil biology monitoring tool in support of sustainable tomato production: a case study from South Africa

Stephanus Malherbe[a,*], Diana Marais[a]

[a] Department of Plant Production and Soil Science, Faculty of Natural and Agricultural Sciences, University of Pretoria, Pretoria 0002, South Africa.

[*] Corresponding author. Tel. (+27) 76 575 3454.

Email address: stephanusmalherbe@gmail.com (S. Malherbe)

Abstract

Management of the biological component of agricultural soils is a vital aspect of sustainable food production systems. There is a need for soil biology metrics that producers can use as a decision support tool when it comes to managing the soil biological component of agricultural soils. We evaluated the usefulness of nematode community profiling as a soil biology monitoring tool in support of a sustainable commercial-scale tomato production system in South Africa. The objectives were to: 1) study the effects of land use change on nematode communities in the tomato production region, and 2) explore the correlation between tomato crop productivity and the nematode community metrics. The enrichment index was a sensitive indicator of land use change, but the structure index was not. Although the number and proportion of free-living and plant-parasitic nematodes increased and decreased respectively, the selective amplification of specific herbivorous genera was observed. *Helicotylenchus* spp. was sensitive to land use change and might serve as soil health indicator in this tomato production region. Regression analysis indicated a combination of variables associated with soil pH, free-living nematodes (notably the bacterivores) and specific plant-parasitic nematode genera (*Paratrichodorus* spp. and *Rotylenchus* spp.) predictedtomato yield ($R^2 = 0.846$). Despite the useful information gleaned from the nematode community metrics regarding soil food web functioning, the importance of ecologically and economically important nematode genera was re-emphasized. The results of this study highlight an important principle regarding development of soil health metrics for tomato agroecosystems: tomato crop health was not necessarily predicted solely by indicators of soil food web health and functioning.

Keywords: Diversity; Enrichment index; *Helicotylenchus* spp.; *Paratrichodorus* spp.; pH; Yield.

1. Introduction

Management of the biological component of agricultural soils is a vital aspect of sustainable food production systems. The soil's biological component can provide several ecosystem services to the crop producer; biological nutrient cycling and biological disease suppression attract the most attention from producers and scientists. Producers wish to manage the soil biological component in the same way as they manage fertilizer and pesticide applications based on appropriate laboratory tests or on-site observations (i.e., scouting for insect pests). Not surprisingly, a wide range of soil biology metrics has been described in the literature and several have been commercialized (Pulleman et al., 2012; Riches et al., 2013). Each metric has its theoretical, procedural, and practical shortcomings. The challenge for biologists is to devise a metric that satisfies the basic requirements of scientific excellence, procedural simplicity, and agronomic relevance (Doran and Zeis, 2000). Nematode Community Profiling (NCP) by means of functional guild analyses and related indices (De Goede and Bongers, 1994; Ferris et al., 2001;Yeates et al., 1993) is a promising soil biology metric that is being used increasingly to describe ecological and land use gradients.

Nematodes are ubiquitous to the soil environment. Vegetable crop producers are well-aware of the negative consequences plant-parasitic nematodes (PPNs) have on crop production. However, few producers are aware that nematode communities contain non-pathogenic nematodes which may provide positive outcomes to crop production. Apart from documenting the PPN community in soil, NCP can provide insights into soil food web stability and ecological functioning. For example, nematodes contribute directly and indirectly to nitrogen cycling in soils (Anderson et al., 1983; Buchan et al., 2013; Ferris et al., 1998) and this information may be used by producers for crop nutrient management. Producers may also use the metric to gauge the effect of specific soil or crop management practices on the quality of their soils. For example, nematode genera that are sensitive to disturbance can be used as indicators for assessing the severity of land use change or crop management practices (Zhao and Neher, 2013). To this end, NCP has been used to describe land use change in the vegetable production context by several authors (Bulluck et al., 2002; Li et al., 2014; Reeves et al., 2014; Ruan et al., 2013).

Although crop producers are under increasing pressure to improve the sustainability of their operations, economic considerations dominate the overall sustainability of modern-day crop production enterprises. For this reason, crop producers will always be interested in correlations between soil biology metrics and crop yield. Crop yield is influenced by the complex interactions among an array of biotic and abiotic variables. It remains a challenge to demonstrate consistent correlations between soil biology metrics and crop yield. Aspects of NCP have been correlated with the yield of various crops, including tomatoes (DuPont et al., 2009; Ferris et al., 2004; Wang et al., 2014).

Since 2003, the largest commercial tomato producer in South Africa implemented a 'nature-friendly'open field production system. This particular example of eco-agriculture has been described in literature, albeit superficially (Uphoff and Thies, 2011). Managing the soil microbiological content and diversity by means of compost, manures, compost tea, and Effective Microorganisms® formed an important part of this tomato production system. The objectives of this study were to investigate at a scientific level the following: i) the impact of land use change, i.e. the conversion of natural vegetation into tomato production units, on the soil nematode communities, and ii) whether there was a link between tomato crop productivity and NCP metrics.

2. Materials and methods

2.1 Site description

The study concentrated on commercial open-field tomato operations in the Lowveld biome centred on the town of Mooketsi (23°36’5.95”S; 30°5’37.02”E), Limpopo Province, South Africa. The area is dominated by a single vegetation type, the Tzaneen Sour Bushveld, and is located 631-832 m above sea-level (Mucina and Rutherford, 2006). The mean annual precipitation (781 mm), mean annual temperature (19.7°C), mean annual frost-free days (364 days) and mean annual potential evaporation (2097 mm) enables year-round tomato production.

2.2 Tomato production system

Fields intended for tomato cultivation were cleared, ploughed and ridged 12 weeks before planting date. Soil conditioners (such as compost or manures) were incorporated into ridges. Six-week old indeterminate tomato seedlings (cv. Nemo-Netta) were transplanted into the ridges and fertigated via drip irrigation as necessary. A stake-and-trellising production system was used. The mean planting density was 11500 plants ha^{-1}; plants were pruned so that the final planting density was 23000 fruit bearing stems ha^{-1}. Pest and disease control were performed in accordance with growers’ integrated pest management programs. First harvest started 10-12 weeks after planting and continued until week 25 after planting. Plant growth was terminated after 30 weeks and fields were abandoned to naturally recover for periods of one to seven years before the next cultivation event. No dedicated task-specific crop rotations were practiced, although cattle occasionally grazed the abandoned fields.

2.3 Sampling strategy

Soils in various stages of the tomato production cycle were surveyed from 2009 to 2013. Samples were taken once from the various tomato production sites within the same bioregion. Soil samples were taken from three-hectare open field tomato production units because the producers recorded tomato yield data at that scale. Twenty composite soil samples were taken at 15 cm depth from the production units. Soil samples reached the laboratory within 24 hours. Samples were taken when field clearing and ridging activities commenced (referred to as pre-plant soil) (56 samples, 45 %) and during the first ten weeks after planting (referred to as cultivated soil) (28 samples; 23%). Finally, samples were taken from undisturbed sites (referred to as natural soil) in the same bioregion (39 samples, 32 %), giving a total of 123 samples.The different groups of samples represented a soil management gradient which described a change in plant communities from natural grasslands, to bare soil and then to a homogenous population of a non-indigenous cultivated plant, the tomato (Table 1).

Table 1. Description of sample sites according to disturbance levels and soil quality variables in the lowveld tomato production region of the Limpopo Province of South Africa (mean ± standard error).

Site	**Description**	**N**	**pH**	**Stone (%)**	**Clay (%)**	**Silt (%)**	**Sand (%)**
Natural (N)	Undisturbed soils covered by natural vegetation	39	5.51 ± 0.1	10.7 ± 2.5	9.9 ± 1.8	5.9 ± 0.5	84.2 ± 2.1
Pre-plant (P)	Disturbed soils (freshly tilled, bare soil)	56	5.82 ± 0.08	10.5 ± 1.5	10.8 ± 0.8	6.0 ± 0.3	83.2 ± 1.0
Cultivated (C)	Disturbed soils (synthetic and organic fertilization, synthetic pesticides, monoculture of non-indigenous plant)	28	6.12 ± 0.16	12.2 ± 2.5	5.6 ± 1.2	4.8 ± 0.6	89.6 ± 1.7

2.4 Analyses

Soil physical properties were analysed according to standard methods (The Non-affiliated Soil Analyses Work Committee, 1990) by a commercial soil testing laboratory (Bemlab, Somerset-West, South Africa). Sand, silt, and clay content were determined with the hydrometer method on samples taken at 15 cm depth. Soil was air dried, sieved through a 2 mm sieve for determination of the stone fraction (weight/weight basis) and analysed for pH (1.0 M KCl).

Table 2. Summary of soil nematode community profiling variables used for characterizing land use change and variation in tomato crop productivity in the lowveld tomato production region of South Africa.

Variables	**Units**
Total population	Numbers 250 cm^{-3} Number of taxa 250 cm^{-3}
Trophic groups	Numbers 250 cm^{-3}
Herbivores; bacterivores (BF); fungivores (FF); omnivores; predators; free-living nematodes (FLN); plant-parasitic nematodes (PPN)	Number of taxa 250 cm^{-3} % of population (%)
Individual genera	Numbers 250 cm^{-3} % of population % of trophic group (% of tg)
Colonizer-persister (c-p) classification	% of population
c-p 1; c-p 2; c-p 3; c-p 4; c-p 5	
Indices or ratios	Index or ratio
Enrichment index (EI); structure index (SI); channel index (CI); basal index (BI); maturity index (MI): MI$_{1–5}$; MI$_{2–5}$; plant parasitic index (PPI); Shannon’s diversity index (Shannon’s H); FF/(FF + BF) ratio; (FF + BF)/PPN ratio	

Nematode community analyses were performed by a commercial nematode testing laboratory (Nemconsult, Upington, South Africa). Free-living nematodes (FLN) as well as PPNs were extracted according to the decanting sugar flotation procedure (Pofu and Mashela, 2012) and counted/identified by means of a compound microscope at 1000X magnification. Nematodes were identified to genus level only. Nematodes were assigned to trophic groups according to Yeates et al. (1993). Free-living nematodes included all the non-plant-parasitic nematode trophic groups, whereas PPNs included mostly the ectoparasites and the free-living stages of endoparasites (i.e., *Meloidogyne* spp.). The genus *Tylenchus* spp. is ubiquitous to the soil environment and was classified as a fungivore

(McSorley and Frederick, 1999). The nematode community composition data was used in subsequent NCP calculations according to the procedures reported in the literature (Bongers, 1999; Ferris et al. 2001; Table 2).

2.5 Data analysis

Univariate statistics were performed with PAST (PAleontological STatistics version 2.07b; Hammer et al., 2001). Outliers were identified by the interquartile range method and substituted by winsorisation. Data transformations were performed prior to data analysis: log10(x+1) (for nematode counts) and arcsin(√x) (for proportions). Statistical analyses were performed with transformed data, but actual data are used in tables. Levene's test determined that data transformation did not improve the homogeneity of variances during preliminary ANOVA testing. Consequently, statistical significance was established with Welch's F-test and *post hoc* means separation with pairwise Tukey's tests.

Regression analysis was used to explore the associations between the nematode community variables and tomato yield on the data for samples taken before and during the crop cultivation stage. Assessment of the FLN community in soil samples may not be available to crop producers as a routine analytical service because of additional costs or the local laboratory may not hold the required intellectual capital. For these reasons we followed the conventional approach to yield prediction by developing a regression model based on only the proportion of PPNs in the cultivated soils.

In all cases statistical significance was established with $\alpha = 0.05$. Error bars indicate the standard error of the mean in all graphs.

Table 3. Change in nematode community functionality and abundance along a land use change gradient (from undisturbed to disturbed to cultivated soils) in the lowveld tomato production region of South Africa.[a] Land use intensity levels are described in Table 1.

Variables[b]	**Units**	**Land use**			**Welch's *F*-test**		**Tukey's test**		
		Natural (N)	**Prepared (P)**	**Cultivated (C)**	***F*-value**	***P*-value**	**N vs P**	**N vs C**	**P vs C**
		Median					***P*-value**		
FLN	% of total population	52.0	61.9	69.6	4.845	0.011	ns[c]	0.001	ns
PPN		47.9	38.1	30.4	4.845	0.011	ns	0.001	ns
c-p 1		5.1	8.2	13.9	4.173	0.020	ns	0.004	ns
c-p 3		45.3	34.3	28.6	3.635	0.032	ns	0.006	ns
c-p 3–5		50.7	41.4	35.9	3.560	0.009	ns	0.009	ns
Fungivores		10.9	20.7	23.1	5.742	0.005	0.045	0.028	ns
PPI	Index	1.449	1.150	0.925	4.749	0.012	ns	0.002	ns
EI		36.1	47.1	52.5	4.556	0.014	ns	0.006	ns
Helicotylenchus spp.	% of total population	21.5	15.3	4.3	9.194	<0.001	ns	<0.001	0.018
Pratylenchus spp.		1.4	4.6	6.8	7.696	0.001	0.029	0.018	ns
Paratrichodorus spp.		0.1	0.5	1.5	4.484	0.015	ns	0.001	0.009
Mesorhabditis spp.		0.8	2.1	6.0	6.657	0.002	ns	<0.001	0.009
Cephalobus spp.		1.7	5.3	2.0	4.427	0.015	0.030	ns	ns
Helicotylenchus spp.	% of trophic group	38.0	35.7	8.4	12.650	<0.001	ns	0.001	0.002
Pratylenchus spp.		3.4	14.0	18.2	10.790	<0.001	0.010	0.005	ns
Paratrichodorus spp.		0.4	2.6	9.2	5.160	0.009	ns	0.001	0.007
Mesorhabditis		2.0	5.4	11.5	7.085	0.002	ns	<0.001	0.035

Variables[b]	Units	Land use			Welch's *F*-test		Tukey's test		
		Natural (N)	Prepared (P)	Cultivated (C)	*F*-value	*P*-value	N vs P	N vs C	P vs C
		Median					*P*-value		
spp.	Numbers 250 cm^{-3}								
Cephalobus spp.		4.7	14.9	5.6	4.715	0.012	0.028	ns	ns
Helicotylenchus spp.		169.7	118.0	7.7	20.320	<0.001	ns	<0.001	0.004
Pratylenchus spp.		13.1	26.4	67.5	3.960	0.024	ns	0.024	ns
Rotylenchus spp.		97.1	38.9	26.6	2.751	0.071	ns	0.046	ns
Paratrichodorus spp.		0.8	3.0	11.3	3.928	0.025	ns	0.002	0.015
Mesorhabditis spp.		4.1	10.2	34.3	4.274	0.017	ns	0.039	ns
Cephalobus spp.		29.9	1.6	1.4	5.217	0.008	0.001	0.001	ns

[a] Only significant and meaningful differences ($\alpha = 0.05$) are reported.

[b] FLN: free-living nematodes, PPN: plant-parasitic nematodes, c-p: colonizer-persister group, PPI: plant-parasitic index, EI: enrichment index.

[c] ns: not significant ($P > 0.05$).

3. Results

3.1 Soil management

Several of the community-scale functionality metrics changed significantly along the soil management gradient (Table 3). The proportion of free-living nematodes, c-p 1 nematodes, fungivores and the Enrichment Index (EI) were greater in the cultivated soils. In contrast, the proportion of plant parasitic nematodes, Colonizer-Persister (c-p) class 3, c-p 3-5 and the Plant-Parasitic Index (PPI) were greater in the natural soils but were significantly less in the cultivated soils. The Maturity Index (MI) and Structure Index (SI) were similar between land uses ($P > 0.05$) despite the contribution of the c-p 3-5 nematodes to the calculation of the SI. The Channel Index (CI), an indication of whether organic matter decomposition pathways are dominated by bacteria or fungi, did not differ significantly between land uses.

Specific nematode genera were sensitive to the land use change gradient in the studied agroecosystem. The prevalence of *Helicotylenchus* spp., regardless of how the counts were presented, was significantly reduced in the disturbed and cultivated soils than in the undisturbed soils (Table 3). The numbers and proportions of *Paratrichodorus* spp., *Pratylenchus* spp. and *Rotylenchus* spp. were greater in the cultivated soils than the undisturbed soils. The occurrence of *Mesorhabditis* spp. was greater in the cultivated than the undisturbed soils. The proportion of *Cephalobus* spp. in the pre-plant soils was greater than in the undisturbed or cultivated soils.

Information from the various indices can be represented visually as integrated graphs. The faunal profile confirmed the insignificant differences between land use changes, but visualized the change in the EI along the land use gradient (Figure 1). This change was very subtle based on the average of the data, but variation was substantial between each sample (Figure 1). The enrichment profile combines the percentage of bacterivores, fungivores, and herbivores on a ternary plot (Figure 2). This presentation of the data was able to distinguish between the land uses.

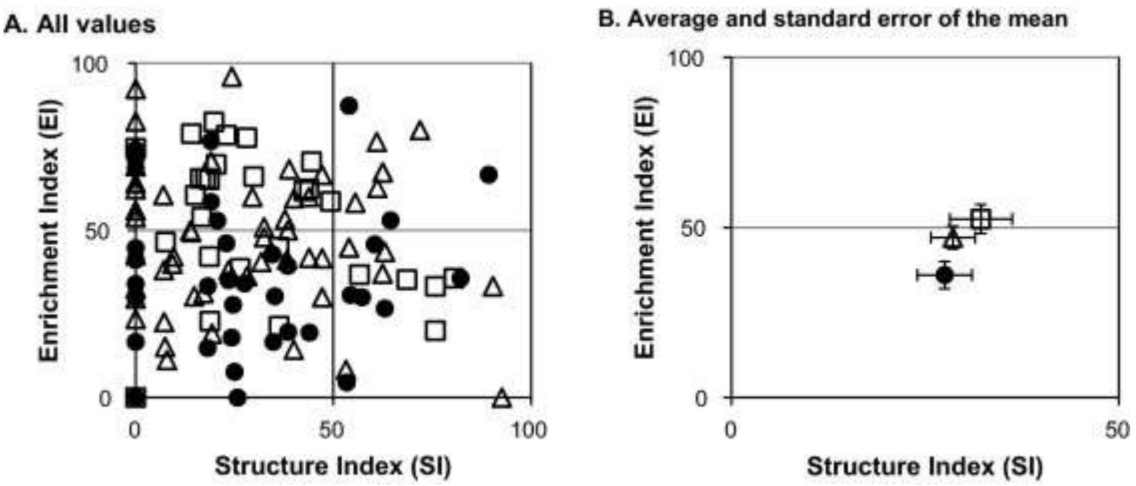

Fig. 1. The effect of different land uses on the faunal profile (enrichment index + structure index) of the nematode community in natural soils (●), physically disturbed soils (Δ), and soils containing actively growing tomato plants (□). Error bars in (B) indicate standard error of the means.

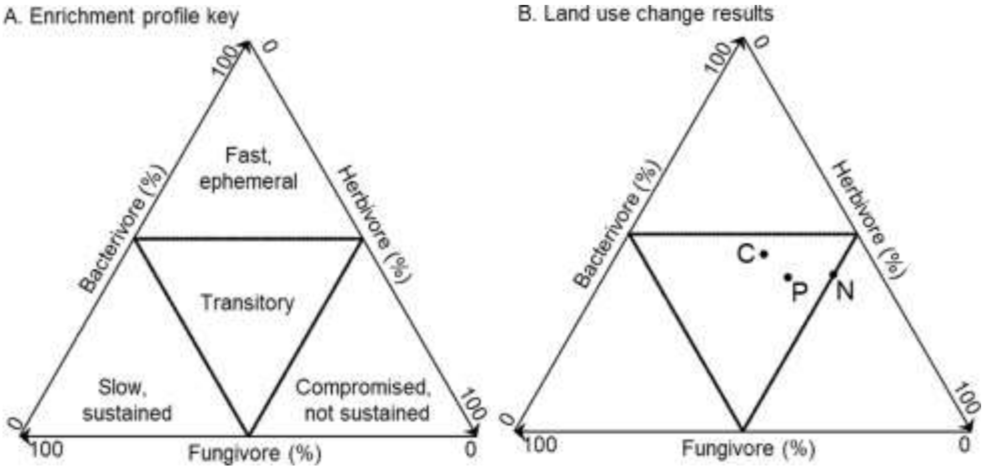

Fig. 2. Impact of different land uses on the enrichment profile (modified from Ferris and Bongers, 2006) of the nematode community in natural soils (N), physically disturbed soils (P), and soils containing actively growing tomato plants (C). Key: natural (N), prepared (P), and cultivated (C) soils.

3.2 Correlations with tomato yield

For the disturbed soil dataset, correlation analysis identified seven candidate variables for constructing a tomato yield prediction model: c-p 3-5 (%), bacterivores (%), *Cephalobus* spp. (% of the total population), *Diptherophora* spp. (% of total population and the trophic group), *Acrobeles* spp. (% of the trophic group) and *Granonchulus* spp. (% of the trophic group). However, the yield prediction regression model constructed using these variables was not satisfactory ($R^2 = 0.440$).

Table 4. Correlation of tomato yield with the soil nematode variables when the nematode community was analysed during the first 10 weeks of tomato cultivation. Variables were ranked according to the *P*-value. Only variables with a significant ($P < 0.05$) regression are shown.

Variable	*r*	R^2	*P*-value
pH	0.567	0.321	0.002
Shannon's H	−0.542	0.293	0.003
Zeldia spp. (% of tg [a])	−0.504	0.255	0.006
PPN (no. of taxa)	−0.479	0.229	0.010
Criconemella spp. (% of tg)	−0.474	0.224	0.011
*Rotylenchus*spp. (% of tg)	−0.474	0.224	0.011
Paratrichodorus spp. (% of tg)	−0.459	0.211	0.014
Paracrobeles spp. (% of tg)	0.438	0.192	0.020
Bacterivores (no. of taxa)	−0.433	0.188	0.021
Panagrolaimus spp. (% of tg)	−0.426	0.181	0.024
Total no. of taxa	0.421	0.181	0.024
Aphelenchus spp. (%) [b]	−0.395	0.178	0.025
FLN (no. of taxa)	0.390	0.156	0.038
Aphelenchus spp. (% of tg)	−0.383	0.152	0.040
Bacterivores (%)	−0.383	0.147	0.044

[a] % of tg: proportion of trophic group.

[b] %: proportion of total nematode count.

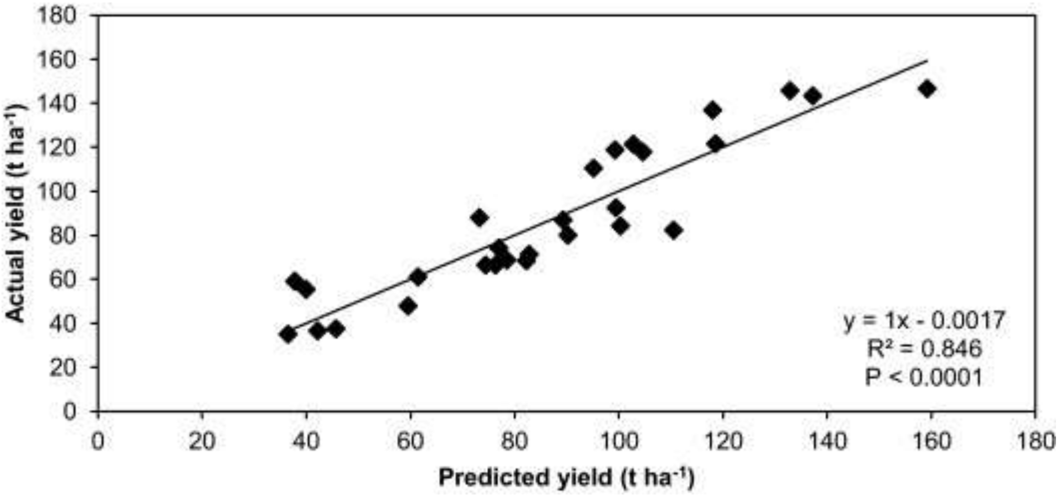

Fig. 3. Tomato yield prediction model based on the plant-parasitic and free-living nematode community profile of soils containing actively growing tomato plants. The variables and coefficients appear in Table 5.

Table 5. Descriptive statistics of the linear regression model for predicting tomato yield based on the nematode community profile of cultivated soils. This comprehensive model incorporates data from plant-parasitic and free-living nematode indices and associated variables. The combined R^2 of this linear model was 0.846.

Linear model components	**Coefficient**	**Standard error**	R^2
Constant	46.697	49.724	
pH	11.821	7.418	0.321
Shannon's H	−33.184	13.273	0.293
Zeldia spp. (% of tg) [a]	0.495	0.526	0.015
PPN (no. of taxa)	−4.430	12.665	0.229
Criconemella spp. (% of tg)	0.968	0.745	0.018
*Rotylenchus*spp. (% of tg)	−0.536	0.239	0.224
Paratrichodorus spp. (% of tg)	−0.827	0.343	0.211
Paracrobeles spp. (% of tg)	5.060	1.992	0.192
Bacterivores (no. of taxa)	−2.136	4.969	0.188
Panagrolaimus spp. (% of tg)	0.161	0.406	0.181
Total no. of taxa	−0.252	10.369	0.181
Aphelenchus spp. (%) [b]	0.000	0.405	0.178
FLN (no. of taxa)	3.576	11.926	0.156
Aphelenchus spp. (% of tg)	0.065	0.197	0.152
Bacterivores (%)	0.491	0.296	0.147

[a] % of tg: proportion of trophic group.

[b] %: proportion of total nematode count.

For the cultivated soil dataset, soil pH, *Paracrobeles* spp., the total number of taxa and the number of FLN taxa correlated positively with tomato yield (Table 4). Negative correlations with tomato yield were observed for three plant parasitic nematodes genera (*Criconemella* spp., *Rotylenchus* spp. and *Paratrichodorus* spp.), a bacterivorous genus (*Panagrolaimus* spp.) and a fungivorous genus (*Aphelenchus* spp.). Indices associated with bacterivorous nematodes (i.e., the number of taxa and its proportion of the total population) correlated negatively with tomato yield. Not only was the resultant model comprehensive (15 variables, see Table 5), but the predictive power of the linear regression was acceptable (R^2 = 0.846, see Figure 3). Regression analysis based on only the plant-parasitic nematode community resulted in a linear regression model that was not as comprehensive as the model outlined in Table 5 and Figure 3, but the R^2 of 0.77 was satisfactory (Table 6; Figure 4).

Table 6. Descriptive statistics of the linear regression model for predicting tomato yield based on the proportion of plant parasitic nematodes in the cultivated soils. Free-living nematodes were omitted from the regression analysis to test the usefulness of the conventional approach of yield prediction based only on the plant-parasitic nematode community. The combined R^2 of the linear model was 0.770 (Fig. 4).

Linear model components	**Coefficient**	**Standard error**	R^2
Constant	122.980	12.656	
Ditylenchus spp.	17.314	35.156	0.003
Criconemella spp.	51.146	40.457	0.018
Helicotylenchus spp.	-63.104	22.551	0.016
Meloidogyne spp.	23.359	25.308	0.129
Pratylenchus spp.	−36.609	18.494	0.000
Rotylenchulus spp.	−85.966	59.909	0.022
Rotylenchus spp.	−93.473	22.103	0.224
Tylenchorhynchus spp.	−19.164	18.364	0.060
Chitwoodius spp.	−322.590	312.63	0.083
Paratrichodorus spp.	−118.370	27.843	0.211
Longidorus spp.	352.580	227.850	0.0004
Xiphinema spp.	−491.990	401.560	0.005

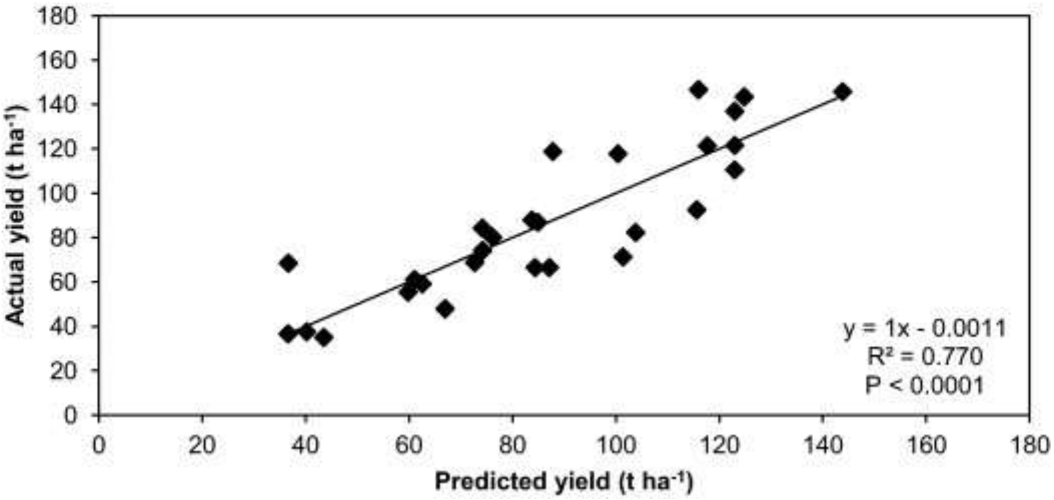

Fig. 4. Tomato yield prediction based on the plant-parasitic nematode community only of the soils containing actively growing tomato plants. Variables and coefficients appear in Table 6.

4. Discussion

Successful vegetable production relies on intensive tillage and heavy use of fertilizers and synthetic pesticides. Pressure is mounting on vegetable producers to improve the sustainability of their operations. Soil biology management will be an important component of sustainable agriculture of the future and it has two facets: 1) beneficial soil biology contributes to nutrient cycling and disease suppression, while 2) plant-parasites continue to threaten crop productivity. Hence, there is a need for soil biology metrics with relevance to commercial vegetable production. In scientific literature, several soil health/quality metrics have been applied to the tomato production context (Tu et al., 2006). In this study, we evaluated nematode community profiling as a means to study the effects of soil management on the soil food web as well as the association of NCP variables with tomato yield.

4.1 NCP and land use change

Changes in functional guilds in response to land use change were mirrored in several of the derived indices (EI, PPI, MI). The c-p 1 population - which was dominated by bacterivorous nematodes – was closely linked to the EI and increased 4.9-fold along the land use gradient. Bacterivores increase when organic matter in the form of compost is applied (Briar et al., 2011; Zhao and Neher, 2013) or during intensive irrigation (Ferris et al. 2004). In our study, the EI ranged from moderate to high, but the SI was always low – this was in agreement with several studies on tomato or vegetable production systems (Berkelmans et al., 2003; Briar et al., 2011; Bulluck et al., 2002; Ferris et al., 2004; Ugarte et al., 2013). The EI increases with soil disturbance (Liu et al., 2012) as soil microbes access organic matter exposed by tillage. Indeed, tillage reduced the SI and the particulate organic matter content of soils (Ugarte et al., 2013). The c-p 3 and c-p 3-5 populations - which was dominated by herbivores, omnivores, and predators – were closely linked to the SI calculation and declined along the land use gradient. The SI in our study was influenced by a decline in omnivores and predators and an increase in specific PPNs. The consistent use of tillage, synthetic fertilizers and pesticides probably contributed to the declining SI and increasing EI. Consequently, the SI was not a sensitive indicator of land use change in the studied tomato production context, but similar findings were reported previously (Figure 1; Briar et al., 2011; Bulluck et al., 2002). The faunal and enrichment profiles distinguished between land use changes and were sensitive to crop management effects associated with nutrient enrichment.

Specific nematode genera can be used as sentinels for describing the impact of soil management or land use change. Our results indicated that *Mesorhabditis* spp. was a consistent indicator of nutrient enrichment and this was in agreement with previous studies (Zhao and Neher, 2013). The resilience of *Cephalobus* spp. to tillage was confirmed in our study (Fiscus and Neher, 2002) and *Helicotylenchus* spp. was identified as a candidate soil health indicator in the specific agroecosystem studied (to be discussed in more detail in section 4.4). The cost and complexity of analyses can be reduced by monitoring the occurrence of these genera in the soils of this tomato production region in South Africa.

The tomato producers in South Africa have also been exposed to the school of thought among academics and agri-consultants that place emphasis on measuring and managing the soil fungal and bacterial biomass ratios before and during crop production by means of compost and compost tea. Although the theory of this assertion was based on earlier ecosystem studies (Dornbush et al., 2008; Griffiths et al., 1997; Ingham et al., 1986), its relevance to sustainable vegetable production has not been demonstrated to date. The fungal:bacterial ratio is often reported in ecological studies, but apart from the peculiar limitations associated with each measurement technique (i.e., microscope-based assays vs molecular methods vs biochemical/metabolic procedures), the theoretical basis remains uncertain. Others used NCP as proxy for studying the soil food web at microbiological level, but results were inconclusive: the NCP indicators of fungal and bacterial dynamics were more reliable than actual measurements of fungal and bacterial biomass (Neher et al., 1999; Neher and Campbell, 1994). From a functional index perspective, the CI aims to describe whether organic matter decomposition pathways were dominated by bacteria or fungi (Ferris et al., 2001). In our study, the CI did not differ between land uses. Thus, the scientific relevance of the fungal:bacterial ratio in the agricultural context, not the natural ecosystems context, still requires clarification.

4.2 NCP and tomato yield

Tomato production is an intensive operation and agronomic success depends on rigorous tillage and heavy use of fertilizers and synthetic pesticides. PPNs remain a persistent risk to tomato growers all over the world. Intensification leads to increased PPN numbers but decreased PPN diversity in various cropping systems including tomatoes (Hu et al., 2014; Li et al., 2014; Ruan et al., 2013; Ugarte et al., 2013; Yardim and Edwards, 1998). Intensification leads to breakdown of nematode-related disease suppressive mechanisms (Carrascosa et al., 2014; McSorley et al., 2008; Sanchez-Moreno and Ferris, 2007). Despite pursuing a ‘nature-friendly’ tomato production strategy, these South African producers consistently used high levels of synthetic pesticides, insecticides and herbicides in addition to the organic crop and soil management technologies. Furthermore, the use of *Meloidogyne* spp. resistant rootstocks might have favoured the selective amplification of PPNs not associated with crop failure in this tomato production region; similar observations were made by Johnson and Campbell (1980) and Greco and Di Vito (2011).

Regression analysis results highlighted the negative association of PPNs with tomato yield, even when the entire nematode community and associated indices were considered (Table 4). The combination of species of *Criconemella*, *Helicotylenchus*, *Meloidogyne*, *Paratrichodorus*, *Pratylenchus*, and *Rotylenchus* observed in our dataset are common to South African soils (Barbercheck and Von Broembsen, 1986; Marais and Swart, 2002). These nematodes were also described frequently in tomato production systems elsewhere in the world (Anwar et al., 2013; Briar et al., 2011; Bulluck et al., 2002; Cadet and Thioulouse, 1998; Ferris et al., 2004; Johnson and Campbell, 1980; McSorley et al., 1999). Several of these genera are known to form galls or gall-like symptoms on tomato roots (i.e., ‘stubby root’), an aspect that easily confound inexpert disease identification by producers and may lead to selection of cultivars with inappropriate disease resistance packages.

Crop health is influenced by the composition of PPN populations and the interactions between genera/species. The composition of the PPN community, the effect of the biophysical environment, and the presence of a plant host dictates the interactions of individual PPN genera relative to each other (Norton, 1989). For example, root-knot and lesion nematodes are competitive and, thus, tend to be mutually exclusive in the same rhizosphere (Cadet et al., 2002; Chavez et al., 2014). *Helicotylenchus* spp. and *Pratylenchus* spp. competed with each other on two different plant species (Villenave and Cadet, 1998). On rice, *Tylenchorhynchus claytoni* suppressed *Helicotylenchus crenatus* (Prassad and Rao, 1977). Hence, there exists an opportunity to manage the PPN balance and provide a form of biological control.

An unexpected result of our study was the negative correlations for the total number of taxa, the number of FLN taxa, omnivorous taxa and diversity as measured by the Shannon's diversity index, which suggests that high tomato yield is not associated directly with high nematode diversity, abundance of FLNs, or species richness (Table 4). Although Ferris et al. (2004) observed long-term positive and negative correlations between tomato yield and the EI and CI respectively, DuPont et al. (2009) observed highest tomato yields in bare fallow soils – the other land uses (cover crop mix, grain, and legumes) had 10-fold higher PPN numbers (as well as the characteristic high EI but low SI). It simply means that tomato producers will continue to pursue production in near-sterile soils, hence the continued use of solarisation, fumigation, and bare fallow as means of managing PPNs (Chellemi et al., 1993, 1997), regardless of the negative long-term implications for soil quality and agroecosystem health.

4.3 NCP in perspective

The presence/absence of plants was the primary distinguishing factor between nematode community profiles of different land uses (Gebremikael et al., 2014). In our study, the land use gradient described a change in plant populations from natural grasslands, to bare soil and then to a non-indigenous cultivated plant, the tomato. Although this study highlighted the usefulness of community-level functionality metrics, its limitations were also observed. For example, biological nitrogen supply cannot be inferred from FLN numbers when a plant is present in the soil (Carrascosa et al., 2014; Gebremikael et al., 2014). Although there was evidence of enrichment, as visualized by the enrichment and the faunal profiles, the selective amplification of economically important PPNs was not detected by the community-level indices (also noted by Berkelmans et al., 2003). The decline in the PPI observed in our data (Table 3) would create the impression among tomato producers that their 'nature-friendly' production system was effective in reducing the PPN threat because herbivores numbers usually increase in tomato production systems over time (Bulluck et al., 2002; Gebremikael et al., 2014). However, the increase in *Paratrichodorus* spp. and the concomitant decline of *Helicotylenchus* spp. during land use change could have important implications for the South African tomato producers.

4.4 *Helicotylenchus* spp. as soil health indicator

Helicotylenchus spp. is commonly associated with the PPN community of tomato production systems and is endemic to soils in the traditional tomato producing regions in South Africa (Marais and Buckley, 1993; Marais and Swart, 2002). However, the economic impact of this nematode on tomato production is uncertain (Singh et al., 2013). Pure culture studies indicated that it caused tomato yield reduction at high densities, but had no effect at low densities (Tebenkova, 1987). In other cropping systems, such as sugarcane and millet, *Helicotylenchus* spp. was identified as a mitigating species (Cadet et al., 2002; Villenave and Cadet, 1998). In other words, when it was the dominating genus, *Helicotylenchus* spp. reduced the severity of infestations associated with *Meloidogyne* spp., *Pratylenchus* spp. and *Tylenchorhynchus* spp. Interactions of *Helicotylenchus* spp. and *Meloidogyne*spp. were observed for tomato production systems by other researchers (Tebenkova, 1987). In our study, *Helicotylenchus* spp. appears to be a sensitive indicator of land use change in the South African tomato production systems studied. Its positive influence on tomato yield could not be proven in this study. Other studies confirmed the sensitivity of *Helicotylenchus* spp. to tillage (Masse et al., 2002) and various forms of biotic, abiotic and xenobiotic stress (Liu et al., 2012). For this reason *Helicotylenchus* spp. can be regarded as an indicator of soil health in this context, because its dominance is associated with undisturbed or 'healthy' soils.

4.5 *Paratrichodorus* spp.: a 'new' threat to tomato producers?

Tomato producers are well-aware of the destructive capabilities of the more commonly studied PPNs such as *Meloidogyne* spp. and *Pratylenchus* spp. and their role in tomato disease complexes. Although the economic or agronomic impact of *Paratrichodorus* spp. infestations on tomatoes have been noted, it is not well described in literature or given only local importance (Anwar, 1994; Greco and Di Vito, 2011; Singh et al., 2013). It is often a component of PPN communities associated with tomatoes. The results of this study suggest that *Paratrichodorus* spp. was selectively amplified during land use change (Table 3) and was associated with yield decline (Tables 4 and 5, Figures 3 and 4). *Paratrichodorus* spp. is an ectoparasite that feeds on epidermal cells in the elongation and meristematic zone of the root (Schilt and Cohn, 1975). It is a known vector of plant viruses (reviewed by Brown et al., 1989). Populations are higher in sandy and sandy loam soils in the presence of a suitable host (Schilt and Cohn, 1975). Their numbers decrease in absence of a suitable host (Schneider and Ferris, 1987), thus explaining the effectiveness of bare fallow and soil solarisation as control measure (Chellemi et al., 1997; Chellemi et al., 1993; Johnson and Campbell, 1980; McSorley et al., 1999). However, control of *Paratrichodorus* spp. through solarisation and bare fallow was lost when duration was reduced or producers persisted with long-term monocropping of tomatoes (Johnson and Campbell, 1980). Fumigation tends to increase their numbers (McSorley and McGovern, 1996). Compost usage during a dry season increased *Paratrichodorus* spp. numbers (McSorley et al., 1999).

Additional treatment options include tactical flooding (McSorley et al., 1999) and rotations that include soybean (Chavez et al., 2014). Although the use of cover-crops may be deemed more 'nature-friendly' than more aggressive and interventionist approaches (i.e., the use of conventional or biological control measures), it may take a long time with uncertain outcomes (DuPont et al., 2009; Lavelle et al., 2004; Masse et al., 2002; Summers et al., 2014).

5. Conclusion

In this study, we explored the utility of nematode community profiling (NCP) as soil biology management decision tool in a commercial open field tomato production system in South Africa. NCP was useful for describing land use change in the South African tomato production region studied and the results were in agreement with other agricultural land use studies using the same metric. The numbers of individuals per genus, as well as their proportions of the total population and the trophic group were useful for exploring the correlation with tomato yield. However, it was unexpected to find negative correlations for the total number of taxa, the number of FLN taxa, omnivorous taxa, and diversity as measured by the Shannon diversity index, which means high tomato yield was not associated directly with high nematode diversity, abundance of FLNs, or species richness. Despite the useful information gleaned from these coarse-focus metrics, the importance of ecologically and economically important nematode genera was re-emphasized. Soil health does not guarantee crop health when viewed from a soil food web functionality perspective only. Future research should focus on elucidating the interactions within the PPN community of this (and other) tomato production region. Only then can plant-based control measures (i.e., rotations) be adjusted, in a scientific manner, in relation to the producers' specific soil biology management objective.

6. Acknowledgements

The financial support of the tomato producers of Bertie van Zyl (Pty) Ltd made this study possible. We acknowledge the technical assistance of Albert Ramolotja and Bart Schonken.

7. References

Anderson, R.V., Gould, W.D., Woods, L.E., Cambardella, C., Ingham, R.E., Coleman, D.C., 1983. Organic and inorganic nitrogenous losses by microbivorous nematodes in soil. Oikos 40: 75-80.

Anwar, S.A., 1994. Effect of *Meloidogyne incognita* and *Paratrichodorus minor* on the growth of tomato. Afro-Asian J. Nematol. 4, 155-160.

Anwar, S.A., Mahdi, M.M., McKenry, M.V., Qadir, A., 2013. Survey of plant-parasitic nematodes associated with four vegetable crops cultivated within tunnels. Pakistan J. Zool. 45, 595-603.

Barbercheck, M.E., Von Broembsen, S.L., 1986.Effects of soil solarization on plant-parasitic nematodes and *Phytophthora cinnamomi* in South Africa. Plant Dis. 70, 945-950.

Berkelmans, R., Ferris, H., Tenuta, M., van Bruggen, A.H.C., 2003. Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management. Appl. Soil Ecol. 23, 223–235.

Bongers, T., 1999. The Maturity Index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. Plant Soil 212, 13–22.

Briar, S.S., Miller, S.A., Stinner, D., Kleinhenz, M.D., Grewal, P.S., 2011. Effects of organic transition strategies for peri-urban vegetable production on soil properties, nematode community, and tomato yield. Appl. Soil Ecol. 47, 84–91.

Brown, D.J.F., Ploeg, A.T., Robinson, D.J., 1989. A review of reported associations between *Trichodorus* and *Paratrichodorus* species (Nematoda: Trichodoridae) and tobraviruses with a description of laboratory methods for examining virus transmission by trichodorids. Revue Nematol. 12, 235-241.

Buchan, D., Gebremikael, M.T., Ameloot, N., Sleutel, S., De Neve, S., 2013. The effect of free-living nematodes on nitrogen mineralisation in undisturbed and disturbed soil cores. Soil Biol. Biochem. 60, 142-155.

Bulluck, L.R., Barker, K.R., Ristaino, J.B., 2002. Influences of organic and synthetic soil fertility amendments on nematode trophic groups and community dynamics under tomatoes. Appl. Soil Ecol. 21, 233–250.

Cadet, P., Spaull, V.W., McArthur, D.G., 2002. Role of plant parasitic nematodes and abiotic soil factors in growth heterogeneity of sugarcane on a sandy soil in South Africa. Plant Soil 246, 259-271.

Cadet, P., Thioulouse, J., 1998. Identification of soil factors that relate to plant parasitic nematode communities on tomato and yam in the French West Indies. Appl. Soil Ecol. 8, 35–49.

Carrascosa, M., Sánchez-Moreno, S., Alonso-Prados, J.L., 2014.Relationships between nematode diversity, plant biomass, nutrient cycling and soil suppressiveness in fumigated soils. Eur. J. Soil Biol. 62, 49-59.

Chavez, H., Taylor, C.R., Rodríguez-Kábana, R., 2014. Population dynamics and interactions between plant parasitic and non-parasitic nematodes: an empirical analysis. Appl. Soil Ecol. 78, 11–17.

Chellemi, D.O., Olson, S.M., Mitchell, D.J., Secker, I., McSorley, R., 1997. Adaptation of soil solarization to the integrated management of soilborne pests of tomato under humid conditions. Phytopathology 87, 250-258.

Chellemi, D.O., Olson, S.M., Scott, J.W., Mithcell, D.J., Mcsorley, R., 1993. Reduction of phytoparasitic nematodes on tomato by soil solarization and genotype. J. Nematol. 25, 800-805.

De Goede, R.G., Bongers, T., 1994. Nematode community structure in relation to soil and vegetation characteristics. Appl. Soil Ecol. 1, 29-44.

Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Appl. Soil Ecol. 15, 3-11.

Dornbush, M., Cambardella, C., Ingham, E., Raich, J., 2008. A comparison of soil food webs beneath C3- and C4-dominated grasslands. Biol. Fertil. Soils 45, 73–81.

DuPont, S.T., Ferris, H., Van Horn, M., 2009. Effects of cover crop quality and quantity on nematode-based soil food webs and nutrient cycling. Appl. Soil Ecol. 41, 157-167.

Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. J. Nematol. 38, 3-12.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.

Ferris, H., Venette, R.C., Scow, K.M., 2004. Soil management to enhance bacterivore and fungivore nematode populations and their nitrogen mineralisation function. Appl. Soil Ecol. 25, 19–35.

Ferris, H., Venette, R.C., van der Meulen, H.R., Lau, S.S., 1998. Nitrogen mineralization by bacterial-feeding nematodes: verification and measurement. Plant Soil 203, 159–171.

Fiscus, D. A., Neher, D. A., 2002. Distinguishing sensitivity of free-living soil nematode genera to physical and chemical disturbances. Ecol. Appl. 12, 565-575.

Gebremikael, M.T., Buchan, D., De Neve, S., 2014. Quantifying the influences of free-living nematodes on soil nitrogen and microbial biomass dynamics in bare and planted microcosms. Soil Biol. Biochem. 70, 131-141.

Greco, N., Di Vito, M., 2011. Main nematode problems of tomato. Acta Hort. 914, 243-250.

Griffiths, R.P., Entry, J.A., Ingham, E.R., Emmingham, W.H., 1997. Chemistry and microbial activity of forest and pasture riparian-zone soils along three Pacific Northwest streams. Plant Soil 190, 169-178.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1-9.

Hu, C., Wang, X.H., Qi, Y.C., 2014. Characteristics of soil nematode communities under two different land use systems. Biol. Agric. Hortic. 30, 119-130.

Ingham, E.R., Trofymow, J.A., Ames, R.N., Hunt, H.W., Morley, C.R., Moore, J.C., Coleman, D.C., 1986. Trophic interaction and nitrogen cycling in a semi-arid grassland soil. I. Seasonal dynamics of the natural populations, their interactions and effects on nitrogen cycling. J. Appl. Ecol. 23, 597-614.

Johnson, A.W., Campbell, G.M., 1980. Managing nematode population densities on tomato transplants using crop rotation and a nematicide. J. Nematol. 12, 6-19.

Lavelle, P., Blouin, M., Boyer, J., Cadet, P., Laffray, D., Pham-Thi, A.T., Reversat, G., Settle, W., Zuily, Y., 2004. Plant parasite control and soil fauna diversity. CR Biol. 327, 629–638.

Li, Y., Cao, Z., Hu, C., Li, J., Yang, H., 2014. Response of nematodes to agricultural input levels in various reclaimed and unreclaimed habitats. Eur. J. Soil Biol. 60, 120-129.

Liu, M., Chen, X., Griffiths, B.S., Huang, Q., Li, H., Hu, F., 2012. Dynamics of nematode assemblages and soil function in adjacent restored and degraded soils following disturbance. Eur. J. Soil Biol. 49, 37-46.

Marais, M., Swart, A., 2002. Plant nematodes in South Africa. 4. Modimolle area, Limpopo Province. Afr. Plant Prot. 8, 25–32.

Masse, D., Pate, E., Ndiaye-Faye, N., Cadet, P., 2002. Effect of fallow improvement on the nematode community in the Sudanian region of Senegal. Eur. J. Soil Biol. 38, 205-211.

McSorley, R., Frederick, J. J. 1999. Nematode population fluctuations during decomposition of specific organic amendments. J. Nematol. 31, 37-44.

McSorley, R., McGovern, R.J., 1996. Efficacy of 1,3-dichloropropene formulations for control of plant-parasitic nematodes on tomato. Proc. Flo. State Hort. Soc. 109, 184-187.

McSorley, R., Ozores-Hampton, M., Stansly, P.A., Conner,J.M., 1999. Nematode management, soil fertility, and yield in organic vegetable production. Nematropica 29, 205-213.

McSorley, R., Wang, K.H., Church, G., 2008. Suppression of root-knot nematodes in natural and agricultural soils. Appl. Soil Ecol. 39, 291-298.

Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland, South African National Biodiversity Institute, Pretoria, South Africa.

Neher, D.A., Campbell, C.L., 1994. Nematode communities and microbial biomass in soils with annual and perennial crops. Appl. Soil Ecol. 1, 17-28.

Neher, D.A., Weicht, T.R., Savin, M., Görres, J.H., Amador, J.A., 1999. Grazing in a porous environment. 2. Nematode community structure. Plant Soil 212, 85–99.

Norton, D.C., 1989. Abiotic soil factors and plant-parasitic nematode communities. J. Nematol. 21, 299-307.

Pofu, K. M., Mashela, P. W., 2013. Using relative penetration and maleness indices in *Meloidogyne incognita* to establish resistance type in *Cucumis myriocarpus*. Afr. J. Biotechnol. 10, 390-393.

Prasad, K.S.K., Rao, Y.S., 1977. Interaction between *Tylenchorhynchus claytoni* and *Helicotylenchus crenatus* in rice. Indian J. Nematol. 7, 170-172.

Pulleman, M., Creamer, R., Hamer, U., Helder, J., Pelosi, C., Peres, G., Rutgers, M., 2012. Soil biodiversity, biological indicators and soil ecosystem services – an overview of European approaches. Curr. Opin. Env. Sust. 4, 529-538.

Reeves, J., Cheng, Z., Kovach, J., Kleinhenz, M.D., Grewal, P.S., 2014. Quantifying soil health and tomato crop productivity in urban community and market gardens. Urban Ecosyst. 17, 221-238.

Riches, D., Porter, I. J., Oliver, D. P., Bramley, R. G. V., Rawnsley, B., Edwards, J., White, R. E., 2013. Review: soil biological properties as indicators of soil quality in Australian viticulture. Aust. J. Grape Wine Res. 19, 311-323.

Ruan, W.B., Ren, T., Chen, Q., Zhu, X., Wang, J.G., 2013. Effects of conventional and reduced N inputs on nematode communities and plant yield under intensive vegetable production. Appl. Soil Ecol. 66, 48-55.

Sánchez-Moreno, S., Ferris, H., 2007. Suppressive service of the soil food web: effects of environmental management. Agr. Ecosyst. Environ. 119, 75–87.

Schilt, H.G., Cohn, E., 1975. Pathogenicity and population increase of *Paratrichodorus minor* as influenced by some environmental factors. Nematologica 21, 71-80.

Schneider, S.M., Ferris, H., 1987. Stage-specific population development and fecundity of *Paratrichodorus minor*. J. Nematol. 19, 395-403.

Singh, S.K., Hodda, M., Ash, G.J., 2013. Plant-parasitic nematodes of potential phytosanitary importance, their main hosts and reported yield losses. EPPO Bull. 43, 334–374.

Summers, C.F., Park, S., Dunn, A.R., Rong, X., Everts, K.L., Meyer, S.L.F., Rupprecht, S.M., Kleinhenz, M.D., Gardener, B.M., Smart, C.D., 2014. Single season effects of mixed-species cover crops on tomato health (cultivar Celebrity) in multi-state field trials. Appl. Soil Ecol. 77, 51–58.

Tebenkova,T.M., 1987. Competitive relationships between the nematodes *Helicotylenchus digitiformis* and *Meloidogyne* spp. on tomatoes in Tadzhikistan. In, Paraziticheskienematodyrasteniĭ Tadzhikistana.Izd-vo “Donish’, Dushanbe, pp. 34-41.

The Non-Affiliated Soil Analyses Work Committee, 1990. Handbook of standard soil testing methods for advisory purposes.Soil Science Society of South Africa, Pretoria, South Africa.

Tu, C., Ristaino, J.B., Hu, S., 2006. Soil microbial biomass and activity in organic tomato farming systems: effects of organic inputs and straw mulching. Soil Biol. Biochem. 38, 247-256.

Ugarte, C.M., Zaborski, E.R., Wander, M.M., 2013. Nematode indicators as integrative measures of soil condition in organic cropping systems. Soil Biol. Biochem. 64, 103-113.

Uphoff, N., Thies, J.E., 2011. Eco-Agriculture, in: Lal, R. (Ed.), Encyclopedia of Soil Science, second ed. Taylor and Francis, New York, pp. 1-5.

Villenave, C., Cadet, P., 1998. Interactions of *Helicotylenchus dihystera*, *Pratylenchus pseudopratensis*, and *Tylenchorhynchus gladiolatus* on two plants from the Soudano-Sahelian zone of West Africa. Nematropica 28, 31-39.

Wang, K. H., Radovich, T., Pant, A., Cheng, Z., 2014. Integration of cover crops and vermicompost tea for soil and plant health management in a short-term vegetable cropping system. Appl. Soil Ecol.82, 26-37.

Yardim, E.N., Edwards, C.A., 1998. The effects of chemical pest, disease and weed management practices on the trophic structure of nematode populations in tomato agroecosystems. Appl. Soil Ecol. 7, 137-147.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993.Feeding habits in soil nematode families and genera - an outline for soil ecologists. J. Nematol. 25, 315-331.

Zhao, J., Neher, D. A., 2013. Soil nematode genera that predict specific types of disturbance. Appl. Soil Ecol. 64, 135-141.