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Soil Free-Living Nematode Community in the *Triticum aestivum* Rhizosphere: Associations with Phenological Stages in a Rainfed Agriculture Area

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Abstract

Areas designated for cultivating wheat [*Triticum aestivum*] are the most extensive of all terrestrial crops. Due to its importance *T. aestivum*, has been the subject of numerous studies. In the present study, we investigated the effects of phenological stages of the wheat plant rhizosphere on the composition of soil free-living nematode communities. During the growth period [November 2020-August 2021], soil samples were collected at various intervals, corresponding to distinct phenological stages. Soil samples were obtained from the top layer [0 - 10 cm] for both biotic and abiotic analysis. The soil free-living nematode community was assessed using high-throughput sequencing of the 18S rRNA and its ITS gene regions. Our findings reveal that soil water content was significantly [$p < 0.05$] influenced by both the rainy season and the variations in plant cover. Soil organic matter content and salinity levels [EC] were also significantly [$p < 0.05$] affected by the sampling area [control versus plant cover]. Notably, plant cover was positively associated with specific dominant nematode taxa, including Dorylaimida and Ditylenchus. These populations exhibit increased relative abundance and dominance within the soil as phenological stages progressed and root system biomass expanded. The strongest significant association, specifically seen in the wheat field [WF], showed a negative correlation between Rhabditis and nematode diversity [H'], with a significance level of $p < 0.0001$. Throughout the study period, bacterivores remained the most common trophic group in both the wheat field and control area, making up 54.5% of all identified nematodes. These results strongly indicate that nematode populations were significantly affected by the factors examined in this study.

Keywords

Wheat Rhizosphere, Nematode Community, Biodiversity, Rainfed Management

1. Introduction

Healthy soils are fundamental for sustainable agricultural development, reflecting the capacity of soil to function within ecological boundaries to sustain productivity, maintain environmental quality, and promote plant and animal health [1]. Biological indicators, particularly soil nematodes—are commonly used in soil health assessments. These metazoans are among the most abundant multicellular organisms in soil and are considered sensitive bioindicators due to their presence across multiple trophic levels in the soil food web [2]. Their diverse feeding habits, rapid response to disturbances, and role in energy flow and ecosystem functioning make them powerful biological tools for monitoring soil ecosystem health and environmental changes [3], closely reflecting underlying soil conditions.

Land management practices such as tillage intensity, crop rotation, and nutrient management markedly influence nematode communities in the rhizosphere, the soil region directly influenced by root activity. Root exudates, a variety of chemical compounds released by plant roots [4], play a key role in shaping the soil food web, including rhizosphere nematodes. For example, continuous monocropping can reduce nematode diversity and disrupt decomposition pathways, ultimately impairing soil function. In contrast, crop rotations tend to enhance the abundance and metabolic footprint of beneficial bacterivorous and fungivorous nematodes. Conservation tillage methods [no-till, ridge-till] generally support higher nematode diversity and abundance compared to conventional plowing. Additionally, organic manure applications can stimulate nematode metabolic activity and suppress plant-parasitic groups, thereby promoting healthier plant growth [5]. Although few studies directly link rhizosphere nematode dynamics to plant phenology, management-induced changes in nematode communities can indirectly affect plant development. Healthy nematode assemblages, supported by sustainable practices, enhance nutrient availability and increase resilience to pests and diseases, potentially advancing key phenological stages [6] [7]. In contrast, practices that reduce nematode diversity may weaken plant vigor and disrupt developmental timing. Overall, nematodes are integral to soil ecosystem functioning—facilitating nutrient cycling and supporting plant health—while simultaneously serving as indicators of how plant phenology and agricultural practices shape soil biodiversity.

Since the dawn of human history, wheat [*Triticum aestivum*] has been one of the most important staple grains for human consumption. The "Green Revolution" has changed the face of global agriculture, significantly increasing the production of major food crops, particularly wheat and rice [8] [9]. Today, areas designated for growing wheat are the largest among all terrestrial crops, amounting to approximately 240 million dunams worldwide [10]-[12]. Since the 19th century, wheat has predominantly been grown worldwide using the "rainfed farming" method, which relies on natural precipitation without control over the amount, distribution, and intensity of the water supply. Sowing typically begins in early autumn with the onset of the first rain [13]. Considering wheat as a primary food for humans, many studies have investigated the aboveground part of the wheat plant. Studies on the belowground part have primarily addressed root responses to various parasites and plant diseases to improve yields and protect the aboveground part of the wheat plant [14]-[18]. In recent years, increasing attention has been directed toward soil health, recognizing that it is the basis for successful crop production [19]-[21].

The soil is one of the most diverse habitats on earth, combining physical, chemical, and biological processes whose composition is not constant [22]. The biotic component that inhabits the soil rhizosphere depends on many abiotic factors that affect the populations' size, composition, and activity [23] [24]. The trophic structure and the dynamics dictated by the different food varieties are essential factors in the nutrient-recycling cycles of terrestrial soil systems [25]. In the upper horizon [0 - 10 cm], a high organic matter content, considering the presence of crop roots, the biomass of the soil biota affects the soil's physicochemical properties and biological parameters [26]-[28]. The composition of the biotic communities of the rhizosphere varies concerning function, taxon, and genetics between developmental stages of a given plant [29]. Functional diversity indicates the ability of the soil biota population to utilize different carbon sources. Therefore, physicochemical measurements of the soil are effective tools for evaluating the activity of the soil's biotic composition, the functional diversity, and the interrelationships between different populations, such as bacteria, fungi, and nematodes.

As the plant reaches different phenological stages, the release of organic matter through the roots increases, leading to changes in both the abiotic and biotic components of the rhizosphere system [30]-[32]. In addition, when the water content in the soil decreases, the ratio between the population of fungi and the population of bacteria increases due to fungi's greater resistance to osmotic stress [33]. Soil free-living nematodes are among the most diverse in the Metazoan subkingdom [34], constituting a significant part of the food web in nature, classified as bacterivores [BF], fungivores [FF], plant parasites [PP], and omnivores-predators [OP]. The nematodes live in the water layer that surrounds the soil particles, in areas where the concentration of organic matter is high, and their movement is carried out through the soil pores [2] [35] [36]. Due to the multi-trophic level of fungus-feeding capability, they regulate the rate of organic compound decomposition [37] [38]. Hence, understanding the relationship between the changing phenological stages of wheat and its effect on the diversity and dynamics of the soil free-living nematode populations, density, diversity, and functionality in the rhizosphere area of the soil milieu is critical.

This study investigated the response of the soil free-living nematode community density, trophic diversity, and taxonomic composition to wheat plant phenological stages. Specifically, we aimed to characterize changes in the soil free-living nematode population trophic groups, diversity, and composition within the rhizosphere as the wheat plant progressed through its phenological stages, particularly during maturation and ripening. These changes were examined in relation to shifts in key soil abiotic parameters throughout the growing season. The above studies offer several insights into how nematodes interact directly with plant "direct universal link" development, little attention has been given to how these interactions might indirectly influence plant phenology. We hypothesized that the percentage of organic matter in the soil would increase with the phenological stages of the wheat, and [2] the nematode population composition and density in the soil rhizosphere would increase in diversity and trophic composition along the phenological stages of the wheat plant in response to the increase in belowground plant biomass and associated with changes in the soil abiotic components along the phenological stages during plant development.

2. Materials and Methods

2.1. Study Site

This study was conducted at Kibbutz Be'erot Itzhak, Israel [32˚02'05.1"N 34˚54'48.2"E], a wheat field 52 m above sea level with a multi-annual mean rainfall of 489 mm. It features a Mediterranean climate with an average minimum temperature of 2.8˚C and an average maximum temperature of 36.5˚C.

The soil composition is 77% sand, 6% clay, and 17% silt in the wheat field [WF], and 58% sand, 12%, and 29% silt in the control [CO] site. Both study areas primarily exhibit a sandy texture with relatively low clay content. The wheat agriculture in this region spans an area of approximately 80 dunams.

Soil Sampling

Soil samples were collected randomly from each area [WF and CO] at a 0 - 10 cm depth along each phenological stage of the wheat plant. A total of 8 sampling periods were conducted (**Figure 1**), covering the entire timeline from pre-sowing [t1] to post-plowing time [t294]. At each stage, soil samples were collected from the plant rhizosphere [WF] and open space [CO]. Each sampling event consisted of four replicates [individual samples], comprising five pooled randomly distributed samples as one replicate. The soil sampling process began in November 2020 before wheat sowing and continued through August 2021, after the harvest.

The soil sampling process took place in the early morning. Each replicate from each sampling site was carefully placed into an individual plastic bag. The bags were then transported to the laboratory in an insulated container to prevent any temperature-related effects.

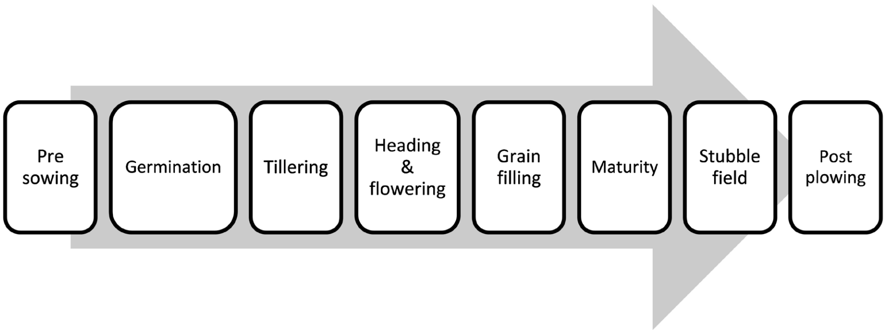

Figure 1. Soil sampling period according to wheat plant phenology: pre-sowing, germination, tillering, heading and flowering, grain filling, maturity, stubble field, and post-plowing.

Upon reaching the laboratory, each soil sample underwent sieving with a 2 mm mesh size to eliminate root particles and other organic matter. The sieved soil samples were subsequently stored at 4˚C until both abiotic and biotic analyses were conducted.

2.2. Soil Analysis

Soil moisture [SM] was determined gravimetrically [39], organic matter [OM] content and pH were determined according to Applebaum *et al.* [2023 [40], and soil conductivity [EC] was determined according to Corwin and Rhoades 1982 [41]].

2.3. Soil Free-Living Nematodes

Soil free-living nematode extraction: 200 g of a soil sample obtained from the field was used in the Baermann Funnel extraction method [42] [43] for 48 h, after which the nematodes were collected and counted under binoculars. All soil free-living nematodes [Tnem] data are expressed as the total number per 100 g of dry soil:

$$\text{Tnem}/100\text{ g dry soil} = \#\text{nem}/[100 - \%SM] \times 100$$

DNA extraction: After the nematodes were quantified, they were transferred to ephedrops for DNA extraction using the PureLink™ Genomic DNA Mini Kit from Invitrogen.

Gene amplification: 18S rRNA

Forward primer:

NF1: TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGGGTGGTGCATGGCCGTTCTTTAGTT

Reverse primer:

18sr2b: GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGTACAAAGGGCAGGGACGTAAT

The amplification results were sent for sequencing using the Illumina sequencing method [19] [44], and a taxonomic analysis was obtained. According to the family and genus level, the nematodes were classified into trophic groups using the Nemaplex website [40].

Indexes determination

Nematode-based indices serve as essential indicators of the structure and function of soil ecosystems, reflecting the life history traits of nematode communities. These organisms, present in various soil types, signify soil health and biological activity, playing a vital role in nutrient cycling and overall ecosystem dynamics.

a) **Shannon Weaver Index** [H']—an index used to measure species diversity in the sample according to the number of individuals observed of each species and their level of uniformity in the sample according to the formula [45]:

$$H = -\sum_{j=1}^{S} p_i \ln p_i$$

H'= -where p_i = the relative share of each species in the society in relation to all individuals in the sample n_i/N.

A higher index value indicates greater diversity, showcasing a wider range of species and a more balanced distribution of individuals among them. This diversity is crucial for ecosystem stability and resilience, enabling communities to adapt to environmental changes.

b) **Fungal and bacterial-feeding nematodes [FF/BF]**—are vital regulators of soil food webs and nutrient cycling. As a key trophic group in the soil ecosystem, they significantly influence the abundance and composition of microbial communities, directly affecting plant growth and enhancing soil health through nutrient release. It is well-established that different soil management practices, such as tillage and fertilization, can markedly alter nematode community structures, thereby shaping their essential roles within the soil food web [46].

c) **Maturity Index [MI]** is based on the c-p index and is proposed as a measure of the state of the ecosystem in the soil. Organized and undisturbed soils consistently exhibit higher MI values, while disturbed or enriched conditions result in significantly lower values [47].

d) **Nematodes Chanel Ratio [NCR]**—nematode channel ratio [NCR = BF/[BF + FF]], is the relative abundance of bacterial-feeding [BF] nematodes and fungal-feeding [FF] nematodes in the total number of nematodes, respectively. The value of NCR is between 0 and 1. When the value is 0, it means that it is completely controlled by fungi, and when the value is 1, it means that it is completely controlled by bacteria, with higher values in organic systems.

e) **Pp/[BF + FF]** describes the differences between detritus and grazing food webs, yielding the matter and energy transfer rates from autotrophs to heterotrophs. High values "indicate the consumption of living plant tissue by herbivores and the dominance of the grazing food web", and low values "indicate the predominance of the detritus food web associated with the decomposition of dead tissue by bacteria and fungi " [48].

2.4. Data Analysis

The sequencing data were demultiplexed using the Illumina BaseSpace Cloud to generate two FASTQ files per sample. The FASTQ files were imported into the CLC bio–Genomics Workbench and analyzed with the Data QC, OTU clustering, and

Taxonomic Profiling workflows [Qiagen, CLC Bio, Aarthas, Denmark]. After removing all reads of taxa that did not belong to nematodes, each replicate was normalized to 100%. Taxa registered as nematodes but not identified to the level of phyla or genera were included as part of the total reads but not analyzed statistically as genera. Repeated measure ANOVAs were used to test phenological effects on soil abiotic and soil free-living nematode community composition at the different levels. Significant differences were evaluated at the $p < 0.05$ level. Duncan's method was used to compare the phenological stages. Data were analyzed using XLSTAT [Addinsoft, New York, USA] statistical software for Excel. An ANOVA was used to determine whether significant differences existed between the phenological stages and the biotic parameters observed in the wheat field and control soils. The significance level for the variables and their interactions was set at 0.05.

3. Results

During the study period, soil moisture levels exhibited significant changes along the phenological stages (**Table 1**) between November 2020 and August 2021. A total of 594.2 millimeters of rainfall was recorded over the above period. Based on the rainfall dispersal, 38% of the rainfall was obtained before the pre-sowing stage. The most significant rainfall occurred at the grain-filling stage, with 558.5 mm. No rainfall occurred following this stage until the end of the growing season.

The OM (organic matter) content in the soil exhibited a significant difference ($p < 0.05$) during the wheat growing period compared to the control sampling site (**Table 1**). OM levels at the pre-sowing stage (t0) were similar to those measured at the end of the harvesting stage, indicating a net balance in organic matter for the growing cycle. However, a significant decrease in OM was observed during the growing season, likely related to the accelerated organic matter decomposition, plant nutrient uptake, and nutrient vertical loss.

The pH levels within the two sampling sites ranged from a minimum of 7.6 to a maximum of 8.1, with the wheat growing area (WF) consistently displaying slightly higher pH values than the control area (CO) over the entire study duration. However, no statistically significant differences were observed between the two sampling sites ($p > 0.05$) over the entire study period (**Figure 2**).

The total nematode population (**Table 1**) displays a significant difference in the presence of free-soil nematodes between the wheat field and the soil collected from the control area. In the wheat field, the total nematode population was found to be over 5-fold higher in comparison to the control sites, significantly greater ($p < 0.05$). Looking at the different phenological stages, t65 in the wheat field is the time point when the nematode population is the largest and stands at 765.2, whereas t294 is the lowest and stands at 31.6 (the numbers express the number of nematodes in 100 g of dry soil). At these two time points in the control field, the nematode population was the highest and lowest, as found in the wheat field. At each phenological stage tested throughout the study period (t0-t294), the nematode population in the wheat field was significantly greater than in the control area ($p < 0.05$).

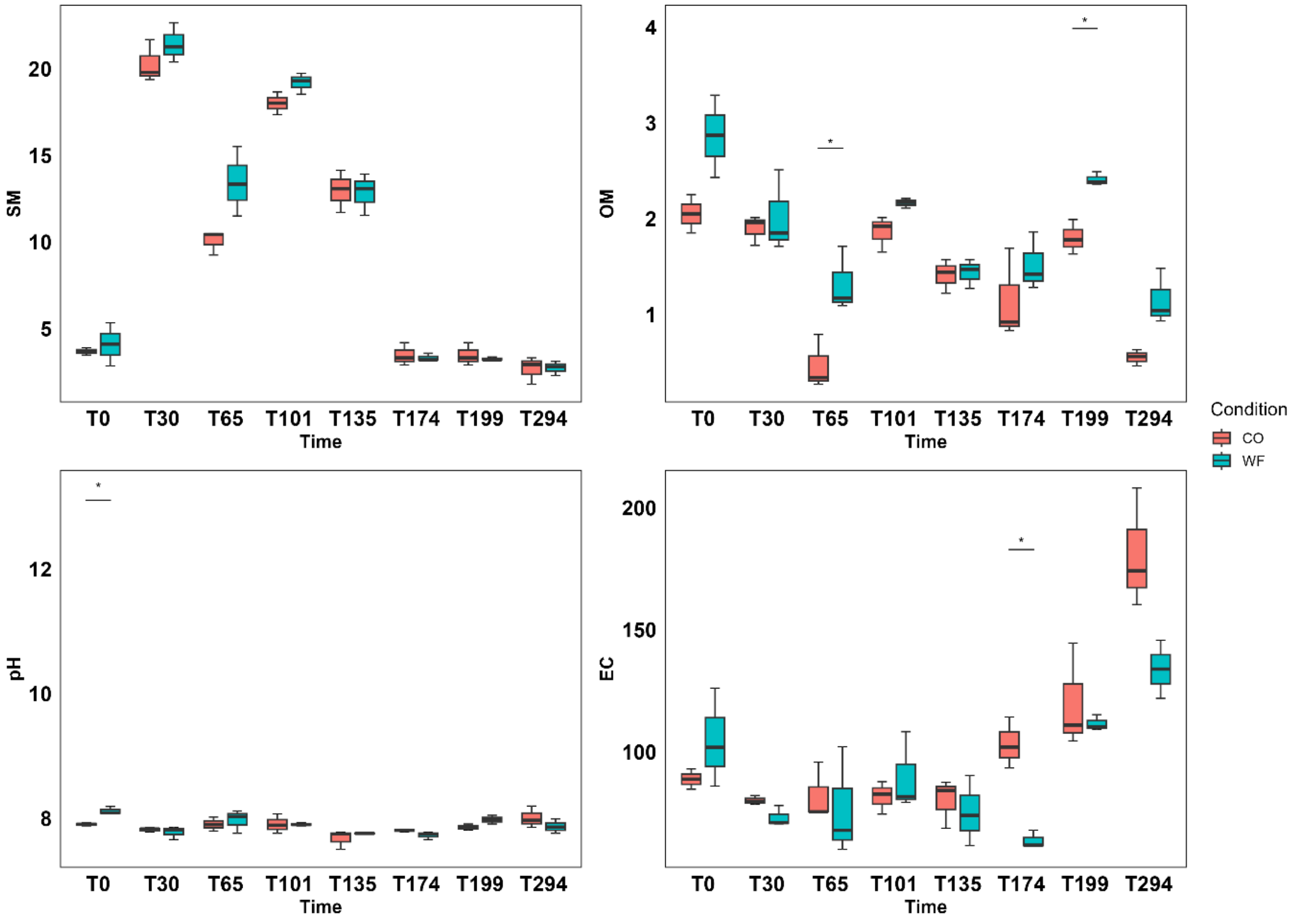

Figure 2. Changes in mean values of soil moisture (SM%), organic matter (OM%), pH, electric conductivity (ECµS cm^{-1}) along the phenological stages of wheat plants in the wheat field (WF) and control (CO) study sites. The small letters following the mean values represent significance ($p < 0.05$).

Table 1. The average number of free-living nematodes per 100 g of dry soil in the two sampling areas: WF (wheat field) and CO (control) soil, throughout the wheat growing period.

	WF	CO
t0	262.1 a	6.2 d
t30	448.4 b	187.5 c
t65	765.2 a	53.7 d
t101	508.3 b	29.8 d
t135	336.2 c	34.5 d
t174	461.4 b	27.3 d
t199	570.6 b	3.1 d
t294	31.6 d	2.7 d

A regression analysis was conducted to evaluate whether differences in soil biotic parameters between time paired WF and CO samples correspond to variability in abiotic parameters. The results (Figure 3) indicate that total nematode abundance was strongly associated with relatively small differences in soil moisture (SM) between WF and CO (slope = 0.0041 ± 0.0015, $R^2 = 0.61$, $p = 0.039$). The FF/BF ratio varied significantly with pH (slope = 0.58 ± 0.16, $R^2 = 0.73$, $p = 0.015$), while c–p values were inversely related to electrical conductivity (EC) [slope = −11.56 ± 0.16, $R^2 = 0.56$, $p = 0.023$] (Figure 3).

Notably, only the FF/BF ratio time series showed a strong correlation between WF and CO ($R^2 = 0.93$), whereas the time series for the other two indicators were not correlated ($R^2 < 0.01$).

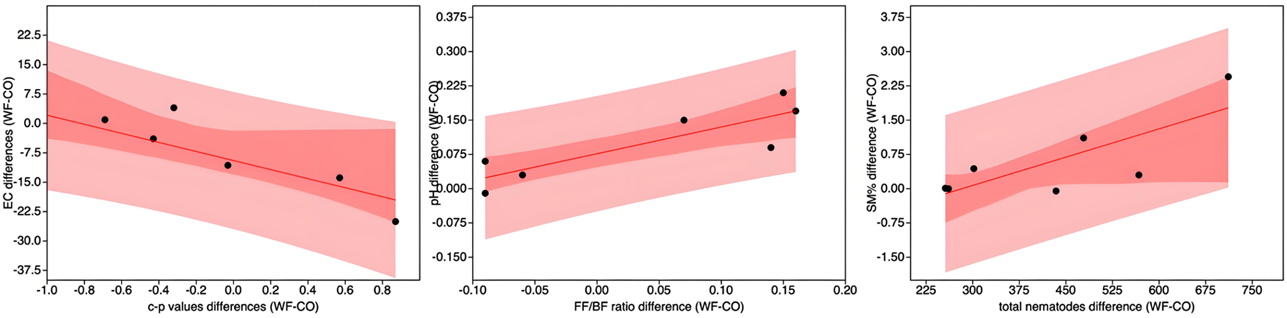

Figure 3. Effect of treatment-associated changes (*i.e.*, WF-CO) in abiotic parameters on changes in the nematode indicators.

2A total of 13 nematode phyla were identified along the phenological axis of wheat, where only the family *Triplonchida* was present in a relative abundance of less than 1% throughout the study period. Nematodes from the *Rhabditis* family were the most common (Table 2, Table 3), showing a significant difference ($p < 0.0001$) between the minimum point of 4.5% at time t0 in the control area versus the maximum point of 88.1% at time t174 in the wheat field. The next most common family in this study was Dorylaimida, which presented a presence in the range of 0% (t135) to 48.8% (t30), with both results obtained in the control area, also with a significant difference ($p < 0.01$). The Pearson test showed that the strongest significant relationship exists in the wheat field [a negative correlation], and it exists between Rhabditis and the variety of nematodes described by the Shannon Weaver Index [H'], where the significance level is $p < 0.0001$. The pH level has a significant negative effect on the variety of nematodes ($p < 0.01$). Soil conductivity (EC) was found to have a negative effect on the number of nematodes found in 100 g of dry soil, meaning that when soil conductivity increases, fewer nematodes are found. In the soil in the wheat field, the Dorylaimida family was found in a negative correlation with the abiotic factors, organic matter, pH and EC, and also in a negative correlation with the Rhabditis family, so that when their number increases, the number of free nematodes from the family Dorylaimida decreases. Considering the differences in soil moisture (%SM)in the wheat field and the control field, the %SM in the control field is influenced by various factors, such as EC, 'H, and the number of free-living nematodes (r = −0.61, 0.6, 0.57, respectively). By contrast, only a negative effect of soil moisture on soil conductivity was found in the wheat field, with a weaker correlation compared to the control field (Table 3).

Table 2. Pearson correlation of abiotic factors and relative abundance of the most common nematode families in the soil: Rhabditis, Dorylaimida, Panagrolaimus, Ditylenchus from the two sampling areas: Wheat Field and Control.

Wheat Field										
Variables	SM (%)	OM (%)	pH	EC (μS*cm^{-1})	H’	Num of nematodes	Rha	Dor	Pan	Dit
SM (%)	1									
OM (%)	NS	1								
pH	NS	**0.46**	1							
EC	**−0.45**	NS	NS	1						
H’	NS	NS	**−0.58***	NS	1					
Num of nematodes	NS	NS	NS	**−0.51**	NS	1				
Rha	NS	NS	**0.48**	NS	**−0.72*****	NS	1			
Dor	NS	**−0.45**	**−0.5**	**−0.19**	NS	NS	**−0.41**	1		
Pan	NS	NS	NS	NS	NS	NS	NS	NS	1	
Dit	NS	NS	NS	NS	NS	NS	NS	NS	NS	1
Control										
Variables	SM (%)	OM (%)	pH	EC (Sμ*cm^{-1})	H’	Num of nematodes	Rha	Dor	Pan	Dit
SM [%]	1									
OM [%]	NS	1								
pH	NS	NS	1							
EC [Sμ*cm^{-1}]	**−0.61***	NS	**0.48**	1						
H’	**0.6***	NS	NS	**−0.43**	1					
Num of nematodes	**0.57***	NS	NS	NS	NS	1				
Rha	NS	NS	NS	NS	**−0.41**	NS	1			
Dor	NS	NS	NS	NS	NS	NS	NS	1		
Pan	NS	NS	**0.44**	NS	NS	NS	NS	NS	1	
Dit	NS	NS	NS	NS	NS	NS	NS	NS	NS	1

Values in bold are different from 0 with a significance level alpha = 0.05; NS- non-significant, * $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$; Rha—Rhabditis, Dor—Dorylaimida, Pan—Panagrolaimus, Dit—Ditylenchus.

The relationships (CCorA) (**Figure 2**) between the variables in the wheat field in the presence of aboveground plant material between t30 and t174 were as follows. The nematode family Dorylaimida positively correlated with aboveground and belowground plant biomass, where these variables showed a strong dependence. The Ditylenchus family was also positively related to the plant biomass, but not in the same order of magnitude, there species are known to occur in cooler as well as warmer regions of the world [49]. According to division into trophic levels, Dorylaimida and Ditylenchus are families characterized as parasites on plant roots and are known to cause annual yield losses of 7% in Egypt alone [50] and globally is estimated as 2.3%. Unlike these nematodes, the Rhabditis and Panagrolaimus families showed a negative relationship with the plant component of wheat, meaning that when wheat is established in the soil, their relative presence decreases. Furthermore, looking at the wheat growing period, the Panagrolaimus family exhibited a strong positive relationship with the abiotic factors and %SM, representing a bacterivore trophic group.

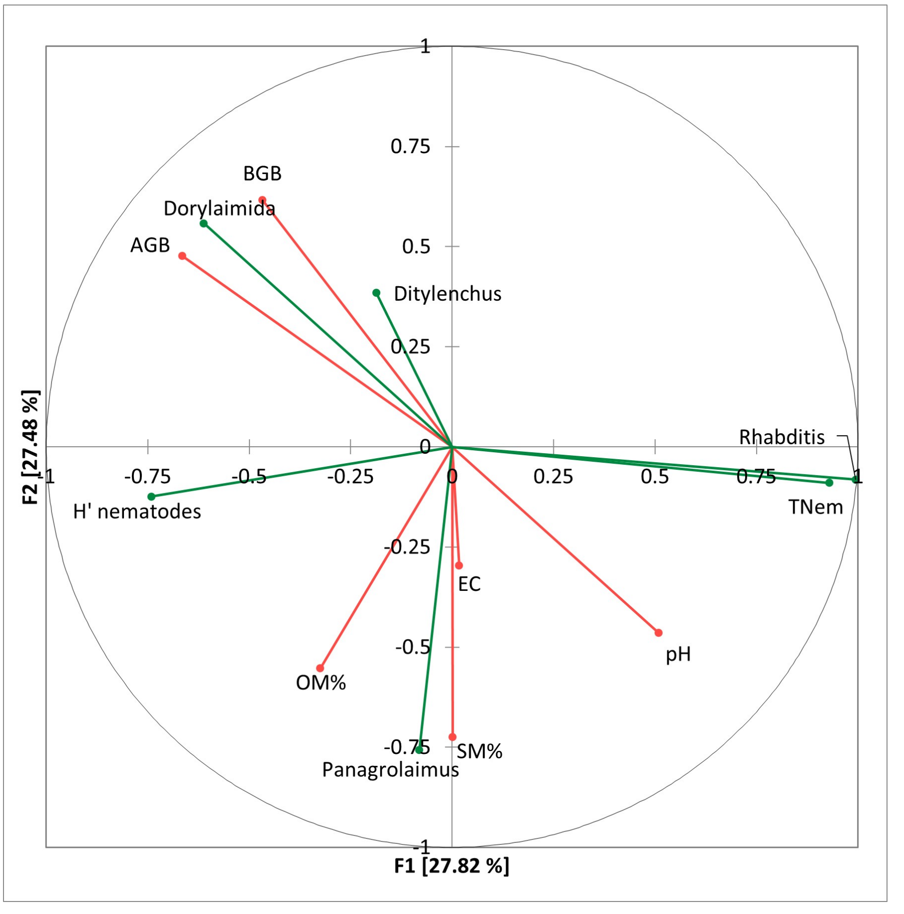

Figure 4. CCorA biplot testing the relationship between abiotic variables, plant biomass, root biomass per plant, and number and families of nematodes. The most frequent nematodes identified in the wheat field were Rhabditis, Dorylaimida, Panagrolaimus, and Ditylenchus at the sampling times t30-t174. TNem-number of nematodes per 100 g dry soil, AGB-aboveground biomass, BGB-belowground biomass (root biomass per plant).

The bacterivores (BF) are the dominant population throughout the research phases in the wheat field and the control area along the wheat phenological stages (Figure 4). The BF nematodes accounted for 54.5% of all nematodes identified throughout the study period. The bacterivore nematode population showed different trends in the two study sites, where a high presence of these fungi was observed in the wheat field in the early stages (t0-t135) along the phenological axis, and starting from t174 (full ripening stage), their relative abundance decreased. At the control study site, the relative abundance of BF was low in the first two stages, e.g., pre-sowing and germination (t0-t30), after which non-trendy fluctuations were observed in their relative presence in the area. The second largest tropical group was omnivores-predators (OP), which accounted for 18.8%. Their relative presence in the wheat field was small compared to the control area, where we saw an increase in presence along the studied phenological axis. The sampling point with the highest relative presence was identified at t30. In the control area, their level was maintained throughout the study period in relatively high numbers in the range of 15.2% - 48.9%, apart from the sampling point at t135, the beginning of seed ripening, where the detection level was 0%. Another population observed throughout the stages of the study is plant parasites, whose relative abundance was 15.2% in the general summary of all phenological stages in both study areas. The free-living nematodes feeding on plant material in the wheat field showed numerical stability in stages t0-t101 with a relative presence in the range of 2.7% - 14.8%. This trophic level also showed a change starting from stage t135 so that their relative presence increased to 7.2% - 23.9%. No trend was observed in the control field since their relative number varied from stage to stage in the range of 2.6% - 29.7% between minimum and maximum along the entire phenological axis. The smallest population in this study was the population of fungivore free-living nematodes, which comprised 11.5%. Overall, their relative presence was lowest compared to the different feeding routes throughout the different study phases in both sampling areas. In the wheat field, their relative number was constant, with a range of 7.9% - 11%, except for increases in t65 (16.6%) and t174 (22%), where the highest yield was also obtained throughout the study period. Their relative number at t0, the beginning of the study, was similar to the last sampling points along the phenological axis (t199-t294), where the average between them was 10.2% with a variation of 0.7%. In the control field, their number remained stable between t0-t65 (10.2% - 12.7%), after which a high peak was observed, where their relative abundance reached 28%. Finally, a decrease was observed from t174 to the last sampling stage t294 (0% - 3%) (Figure 5).

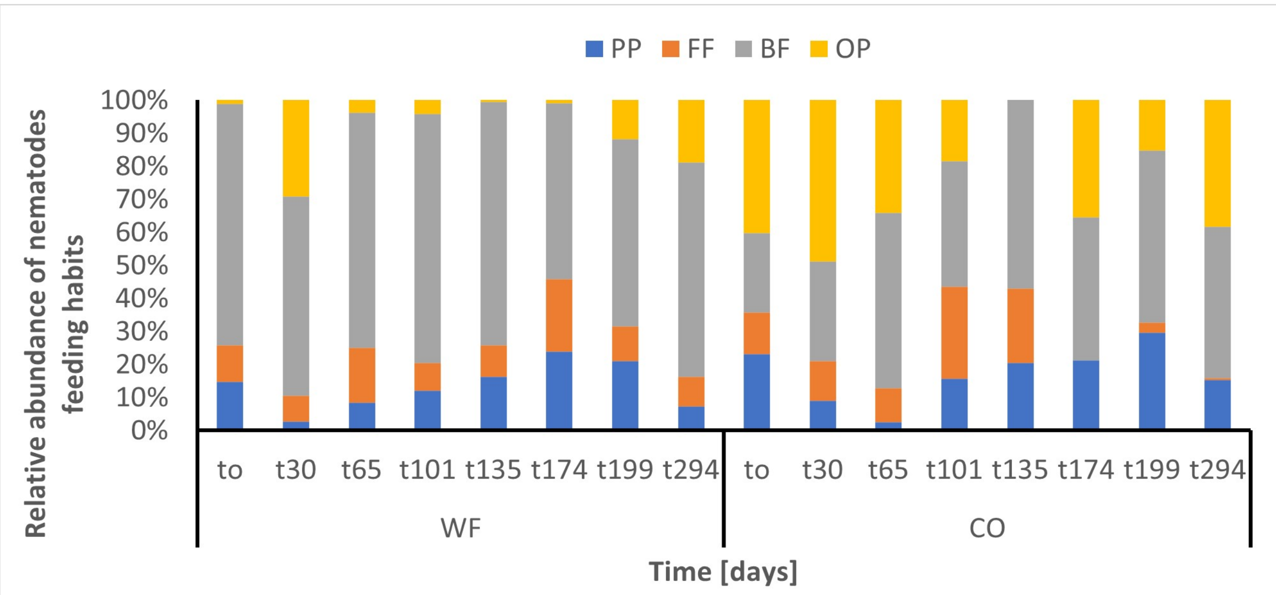

Figure 5. Changes in the relative abundance in the division into trophic levels of the nematode population according to plant parasites (PP), fungivores (FF), bacterivores (BF), omnivores-predators (OP) in the WF (wheat field) and CO (control) area along the phenological axis.

Table 3. The presence of 13 phyla at each one of the seven phenological stages in soil samples obtained at WF—wheat field and CO—control.

			Pre-sowing (to)-1		Germination (t30)-2		Tillering (t65)-3		Heading and flowering (t101)-4		Grain filling (t135)-5		Maturity (t174)-6		Stubble field (t199)-7	
Trophic group	c/p value	Phyla	WF	CO	WF	CO	WF	CO	WF	CO	WF	CO	WF	CO	WF	CO
Fungi feeders (FF)	4	Dorylaimida	XX		XX		XX		XX		XX					
	3	Araeolaimida							XX						XX	
	2	Ditylenchus	XX		XX		XX		XX		XX		XX			
	2	Par aphelenchus							XX		XX					
		Total FF	2	0	3	0	2	0	4	0	3	0	1	0	1	0
Bacteria feeders (BF)	2	Hetero ce phaio bus	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX		XX	
	2	Drilocephalobus			XX	XX	XX		XX	XX		XX		XX	XX	
	2	Monhysterida					XX			XX		XX				
	1	Rhabditis	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX
	3	Triplonchida					XX									
	1	Panagrolaimus	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX
		Total BF	3	3	4	6	4	3	4	5	3	5	3	3	4	2
Plant parazites (PP)	2	Tylenchida	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX
	2	Paratylenchus	XX		XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX	XX
		Total PP	2	1	2	2	2	2	2	2	2	2	2	2	2	2
OP	4	Doryllium				XX						XX		XX		
						1						1		1		
		Total present (13)	7	4	9	9	8	5	10	7	8	8	6	6	7	4

Fungal-feeding nematodes, including *Dorylaimida* and *Ditylenchus*, were consistently detected across all wheat phenological stages but were absent in the control treatment (Table 4). No fungal-feeding nematodes were observed at the control site at any stage. In contrast, the bacterial-feeding nematodes *Heterocephalobus*, *Rhabditis*, and *Paratylenchus* were present in both wheat field (FW) and control (CO) samples throughout all phenological stages. *Monhysterida* and *Triplonchida* were exclusive to the control soil samples and were not detected at any phenological stage in the wheat field. Additionally, the plant-parasitic nematode groups *Tylenchida* and *Paratylenchus* were consistently observed across all phenological stages in both control and wheat field sites (Table 4).

Indices values

FF/BF

Our analysis of the OTU number and the relative abundance calculation revealed that FF/BF values were less than 1 (BF values are greater than FF values) in both study areas and along the entire phenological axis under study (Table 4).

This index indicates that the dominant feeding pathway in the studied soil is the bacterial pathway of the free-living nematode population in the soil. The ratio helps to understand the importance of BF abundance and the changes in the main decomposition pathways.

Maturity index (C-P values)

The mean c-p values (Table 4) show that the total average c-p value of the control field (1.94) was higher compared to the wheat field (1.84). c-p value close to 1 indicates that the studied population is characterized as colonizers. In the control field, the highest c-p value was 2.63 at t294, while the lowest value (1.34) was recorded at t0. The highest value, approximately 3, was found at t135, indicating that the population is not characterized only as colonizers or persisters. The lowest value, 1.26, was obtained in the following sampling at t174.

PP/(BF + FF), the ratio of obligatory plant parasites to bacterivores and fungivorous in the present study (Table 4), shows differences in the soil nematode communities in WF and CO. These values in the WE are increasing significantly relative to CO, starting at germination to heading & flowering, following a decrease at the maturity stage. The breakdown of dead tissues by bacteria and fungi provides a slow release of unstable protein molecules once thought to be essential for biological processes.

Table 4. Changes in soil free-living nematode indices throughout the phenological development stages of wheat.

Wheat plant Phenological stage	FF/BF		Maturity index c-p values		Nematod chanel ratio(CNR）		Shanon index		PP/(B + F)	
	WF	CO	WF	CO	WF	CO	WF	CO	WF	CO
Pre-sowing	0.08	0.13	1.30	2.03	0.87	0.65	1.23	1.62	0.15	0.63
Germination	0.15	0.02	1.70	1.73	0.88	0.72	1.27	1.24	0.65	0.22
Tillering	0.06	0.15	1.80	1.27	0.81	0.84	1.64	1.82	0.37	0.04
Heading & flowering	0.08	0.01	1.30	1.62	0.90	0.58	1.40	0.53	0.82	0.24
Grain filling	0.25	0.18	1.90	2.99	0.88	0.72	1.22	1.63	0.16	0.26
Maturity	0.40	0.04	2.10	1.26	0.71	1.00	1.12	1.00	0.03	0.49
Stubble field	0.35	0.00	1.90	2.33	0.84	0.95	1.90	1.71	0.85	0.54
Post plowing	0.04	0.00	2.60	2.31	0.88	0.99	1.25	0.77	0.04	0.33

Nematode channel ratio (NCR)

The nematode channel ratio [NCR] is a crucial metric for evaluating soil health and the efficiency of decomposition concerning microbial carbon content in organic soils and overall soil quality. The NCR is significantly shaped by land use and cropping practices, ensuring optimal results. NCR values reach a maximum of 0.90 during the heading and flowering stages, while a minimum of 0.71 is observed at the maturity stage (Table 4). The high NCR values indicate that fungi feeders are the dominant regulators of the system.

Shannon index

In analyzing the number of taxa and population density, it is evident that the

Shannon index values for both WF and CO are significantly higher at the stubble field stage, with WF reaching a value of 1.90. This indicates a relatively low level of diversity, underscoring the limited number of species present.

4. Discussion

The findings indicate a non-significant negative correlation between aboveground and belowground plant biomass and the number of free-living nematodes in the soil. These results contrast with previous studies that reported a positive relationship between these factors [51] [52]. The observed discrepancy may be due to the limited sampling period, which focused on the time when wheat plants were present in the soil, specifically from t30 to t174. However, when considering the entire phenological timeline of the study, a non-significant positive correlation was observed. Similarly, Esnard *et al.* (1998) [53] reported a positive effect of wheat plant biomass on free-living nematode abundance in the soil. However, they noted that this effect declined after 12 weeks, attributing it, among other factors, to the accumulation of bacteria and fungi in the soil.

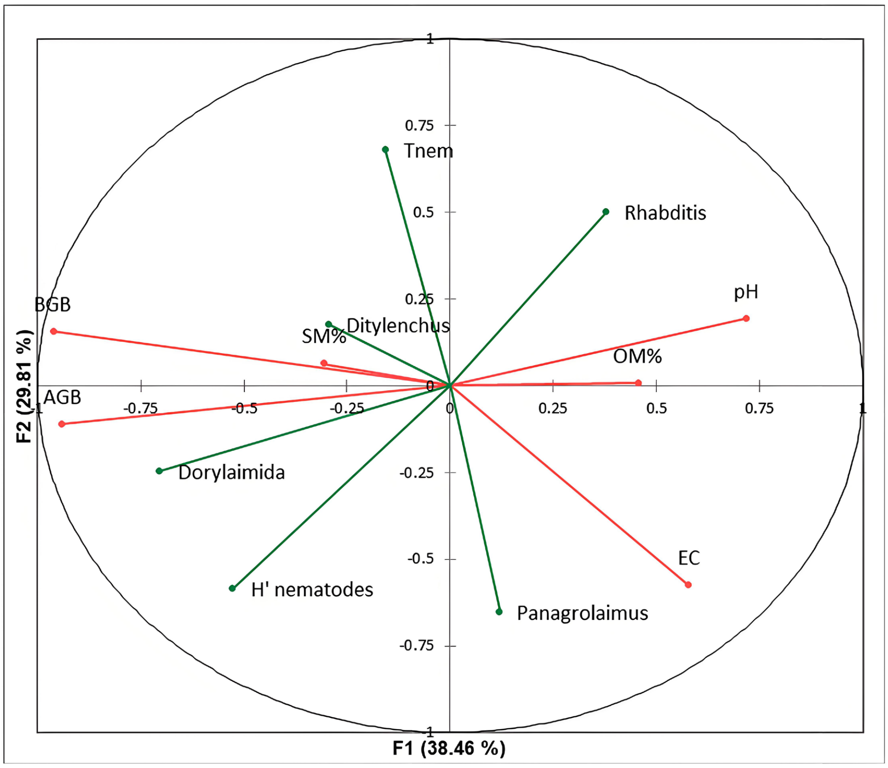

Figure 6. CCorA biplot testing the relationship between abiotic variables, plant biomass, root biomass per plant, and number and families of nematodes. The most common nematodes were Rhabditis, Dorylaimida, Panagrolaimus, and Ditylenchus, identified in the wheat field at the t30-t294 sampling times.

Dorylaimida, Panagrolaimus, Ditylenchus, and Rhabditis emerged as the four most prevalent families throughout the studied phenological axis. Rhabditis stood out as the most dominant across the entire phenological axis (**Figure 6**). This is in line with studies that substantiated the prevalence of this type, belonging to the bacterivore trophic group, in crops in general and in wheat cultivation in particular [54]-[57]. Dorylaimida, categorized as omnivore-predators, represents the second most significant dominant family. This observation gains support from a barley study where these two families emerged as the most extensive and prevalent, with Rhabditis consistently exhibiting dominance and control over nematodes belonging to Dorylaimida throughout the sampling duration [58].

Moreover, in dedicated wheat agricultural systems, Dorylaimida exhibited dominance compared to wheat crops grown in intercropping setups [59]. Our study established a non-significant positive correlation between Rhabditis and the soil organic matter content [%OM], whereas it revealed a correlation with pH, displaying a behavioral pattern that is more independent than initially anticipated. This does not agree with a study attributing the sudden surge in the Rhabditis nematode population in the soil to an increase in the presence of organic matter, leading to an increase in the bacterial population and subsequently to a rise in nematodes that feed on them [60].

The fluctuations in the relative abundance among trophic groups of free-living soil nematodes vary across distinct stages of agricultural growth [38] [61]. In our ongoing investigation, based on nematode DNA sequencing and OTU outcomes, we observed that the prevailing trophic group in both the wheat field and the control field inclined toward bacterivores. Additionally, the FF/BF ratios illustrate consistent nematode control at the trophic level that feeds on bacteria across all phenological stages, observed in both the study and control areas. This finding aligns with studies that identified this group as the largest and most dominant among the various trophic groups in cultivated agricultural soils [60]. The NCR in the present study had lower values than those found by van Eekeren *et al.* (2008) [62] in meadows and conifer forests, emphasizing the strong preference for fungal pathways in the soil food web [61] [63].

The functional guilds, described as the MI index, are divided into five c-p groups from 1 to 5. We found that the average c-p value in the wheat field throughout the phenological stages is cp-1.8, that is, approximately cp-2, which characterizes a population of colonizers, an r-strategy, similar to the results of [64]. This group is characterized by a high reproduction rate, a short life cycle, and tolerance to various disturbances in the soil [65]. In the group of colonizers, the dominant nematodes are those based on bacterial nutrition, which have high metabolic activity [47]. The nematode family Rhabditis, with an r-strategy and cp-1, as shown in another study [66] [67], and Dorylaimida, with a k-strategy and cp-4, are the two most dominant families in this study and exhibit different life cycles.

Ecological indices decisively reflect both the consequences of anthropogenic intervention—such as environmental effects and agricultural practices and, in the present case, the critical feature of the phenological developmental stages of the wheat plant. The indices proposed by Ferris *et al.* (2001) [61], Bongers (1990, 1999) [47] [66], Ingham *et al.* (1985) [52], Yeats *et al.*, (1993) [2] and Freckman and Coswell (1995) [51] are particularly informative due to their integration of qualitative characteristics (including trophic groups and c-p classes) and quantitative measures (such as abundance) of nematode communities providing a comprehensive and insightful overview of the soil ecosystem conditions, in tandem with plant developmental stages, and effectively enabling the reliable detection of ecosystem responses to external influences.

In conclusion, this study demonstrates significant variation across multiple taxonomic levels, functional groups, trophic-level compositions, and population diversities between the phenological and control axes. This study highlights the critical role of the wheat plant's phenological stages in shaping the dynamics of soil-biotic populations. Specifically, in Baal agriculture, winter wheat (*T. aestivum*) plays a pivotal role in shaping the composition and shifts in the soil's bacterial, fungal, and nematode communities through plant-soil interactions. Moreover, this study offers valuable insights for predicting the broader effects of abiotic environmental factors on soil biotic communities. Further research across additional sites is needed to corroborate and extend our findings.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

[1] Lu, Q., Liu, T., Wang, N., Dou, Z., Wang, K. and Zuo, Y. (2020) A Review of Soil Nematodes as Biological Indicators for the Assessment of Soil Health. *Frontiers of Agricultural Science and Engineering*, **7**, 275-281. https://doi.org/10.15302/j-fase-2020327

[2] Yeates, G.W., Bongers, T.D., De Goede, R.G.M., Freckman, D.W. and Georgieva, S.S. (1993) Feeding Habits in Soil Nematode Families and Genera—An Outline for Soil Ecologists. *Journal of Nematology*, **25**, 315-331.

[3] Zhang, Z., Zhang, X., Xu, M., Zhang, S., Huang, S. and Liang, W. (2016) Responses of Soil Micro-Food Web to Long-Term Fertilization in a Wheat-Maize Rotation System. *Applied Soil Ecology*, **98**, 56-64. https://doi.org/10.1016/j.apsoil.2015.09.008

[4] Salas, A. and Achinelly, M.F. (2020) Community Structure of Soil Nematodes Associated with the Rhizosphere of Solanum Lycopersicum in a Major Production Area in Argentina: A Case Study among Agroecosystem Types. *Journal of Soil Science and Plant Nutrition*, **20**, 43-54. https://doi.org/10.1007/s42729-019-00099-8

[5] Fernandez-Gnecco, G., Covacevich, F., Consolo, V.F., Behr, J.H., Sommermann, L., Moradtalab, N., *et al.* (2022) Effect of Long-Term Agricultural Management on the Soil Microbiota Influenced by the Time of Soil Sampling. *Frontiers in Soil Science*, **2**, Article ID: 837508. https://doi.org/10.3389/fsoil.2022.837508

[6] Steel, H. and Ferris, H. (2016) Soil Nematode Assemblages Indicate the Potential for

Biological Regulation of Pest Species. *Acta Oecologica*, **73**, 87-96. https://doi.org/10.1016/j.actao.2016.03.004

[7] Mashela, P.W., De Waele, D., Dube, Z., Khosa, M.C., Pofu, K.M., Tefu, G., *et al.* (2017) Alternative Nematode Management Strategies. In: Fourie, H., Spaull, V., Jones, R., Daneel, M. and De Waele, D., Eds., *Nematology in South Africa*: *A View from the* 21*st Century*, Springer International Publishing, 151-181. https://doi.org/10.1007/978-3-319-44210-5_7

[8] Hedden, P. (2003) The Genes of the Green Revolution. *Trends in Genetics*, **19**, 5-9. https://doi.org/10.1016/s0168-9525(02)00009-4

[9] Khush, G.S. (2001) Green Revolution: The Way Forward. *Nature Reviews Genetics*, **2**, 815-822. https://doi.org/10.1038/35093585

[10] Shewry, P.R. (2009) Wheat. *Journal of Experimental Botany*, **60**, 1537-1553. https://doi.org/10.1093/jxb/erp058

[11] Halila, H., Jamal, M., El-Hanafi, S., Assefa, S., Oweis, T. and Baum, M. (2017) Role of Sustainable Wheat Production to Ensure Food Security in the CWANA Region. *Journal of Experimental Biology and Agricultural Sciences*, **5**, 15-32. http://www.fao.org/family-farming/detail/en/c/1060157/

[12] FAO (2026) Cereal Production Prospects Remain Positive, but Rising Input Costs Add Uncertainty ahead of Sowing. http://www.fao.org/worldfoodsituation/csdb/en/

[13] Luebs, R.E. (1970) Dryland Agriculture in California. Grain Cropping with Winter Rainfall. *California Agriculture*, **24**, 12-13.

[14] Badaruddin, M. and Meyer, D.W. (1994) Grain Legume Effects on Soil Nitrogen, Grain Yield, and Nitrogen Nutrition of Wheat. *Crop Science*, **34**, 1304-1309. https://doi.org/10.2135/cropsci1994.0011183x003400050030x

[15] Bakht, J., Shafi, M., Jan, M.T. and Shah, Z. (2009) Influence of Crop Residue Management, Cropping System and N Fertilizer on Soil N and C Dynamics and Sustainable Wheat (*Triticum aestivum* L.) Production. *Soil and Tillage Research*, **104**, 233-240. https://doi.org/10.1016/j.still.2009.02.006

[16] Cook, R.J. and Haglund, W.A. (1991) Wheat Yield Depression Associated with Conservation Tillage Caused by Root Pathogens in the Soil Not Phytotoxins from the Straw. *Soil Biology and Biochemistry*, **23**, 1125-1132. https://doi.org/10.1016/0038-0717(91)90024-e

[17] Orion, D. and Glazer, I. (1987) Nematicide Seed Dressing Forpratylenchus *MEDITERANEUS* Control in Wheat. *Phytoparasitica*, **15**, 225-228. https://doi.org/10.1007/bf02979584

[18] Orion, D. (2000) Nematodes of Agricultural Importance in Israel. *Nematology*, **2**, 735-736. https://doi.org/10.1163/156854100509583

[19] Eshel, G., Unc, A., Egozi, R., Shakartchy, E., Doniger, T. and Steinberger, Y. (2021) Orchard Floor Management Effect on Soil Free-Living Nematode Communities. *Soil Research*, **60**, 310-319. https://doi.org/10.1071/sr21196

[20] Wang, K.H. and Hooks, C.R. (2011) Managing Soil Health and Soil Health Bioindicators through the Use of Cover Crops and Other Sustainable Practices. Chapter, 4, 1-18. https://extension.umd.edu/sites/extension.umd.edu/files/2021-03/Chap4-Soil-Health-web-version.pdf

[21] Rinot, O., Levy, G.J., Steinberger, Y., Svoray, T. and Eshel, G. (2019) Soil Health Assessment: A Critical Review of Current Methodologies and a Proposed New Approach. *Science of The Total Environment*, **648**, 1484-1491.

https://doi.org/10.1016/j.scitotenv.2018.08.259

[22] Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.N. and Swift, M.J. (1997) Agricultural Intensification, Soil Biodiversity and Agroecosystem Function. *Applied Soil Ecology*, **6**, 3-16. https://doi.org/10.1016/s0929-1393(96)00149-7

[23] Brady, N.C (1974) The Nature and Properties of Soils. 8th Edition, MacMillan Publisher Co. Inc., 14-20, 111-128.

[24] Liao, H., Zhang, Y., Wang, K., Hao, X., Chen, W. and Huang, Q. (2020) Complexity of Bacterial and Fungal Network Increases with Soil Aggregate Size in an Agricultural Inceptisol. *Applied Soil Ecology*, **154**, Article 103640. https://doi.org/10.1016/j.apsoil.2020.103640

[25] Belmonte, S.A., Celi, L., Stahel, R.J., Bonifacio, E., Novello, V., Zanini, E., *et al.* (2018) Effect of Long-Term Soil Management on the Mutual Interaction among Soil Organic Matter, Microbial Activity and Aggregate Stability in a Vineyard. *Pedosphere*, **28**, 288-298. https://doi.org/10.1016/s1002-0160(18)60015-3

[26] Scharroba, A., Dibbern, D., Hünninghaus, M., Kramer, S., Moll, J., Butenschoen, O., *et al.* (2012) Effects of Resource Availability and Quality on the Structure of the Micro-Food Web of an Arable Soil across Depth. *Soil Biology and Biochemistry*, **50**, 1-11. https://doi.org/10.1016/j.soilbio.2012.03.002

[27] Mayzlish-Gati, E. and Steinberger, Y. (2006) Ameba Community Dynamics and Diversity in a Desert Ecosystem. *Biology and Fertility of Soils*, **43**, 357-366. https://doi.org/10.1007/s00374-006-0117-2

[28] Briones, M.J.I. (2014) Soil Fauna and Soil Functions: A Jigsaw Puzzle. *Frontiers in Environmental Science*, **2**, 7-29. https://doi.org/10.3389/fenvs.2014.00007

[29] Broeckling, C.D., Broz, A.K., Bergelson, J., Manter, D.K. and Vivanco, J.M. (2008) Root Exudates Regulate Soil Fungal Community Composition and Diversity. *Applied and Environmental Microbiology*, **74**, 738-744. https://doi.org/10.1128/aem.02188-07

[30] Weisskopf, L., Tomasi, N., Santelia, D., Martinoia, E., Langlade, N.B., Tabacchi, R., *et al.* (2006) Isoflavonoid Exudation from White Lupin Roots Is Influenced by Phosphate Supply, Root Type and Cluster-Root Stage. *New Phytologist*, **171**, 657-668. https://doi.org/10.1111/j.1469-8137.2006.01776.x

[31] Griffiths, B.S., Ritz, K., Ebblewhite, N. and Dobson, G. (1998) Soil Microbial Community Structure: Effects of Substrate Loading Rates. *Soil Biology and Biochemistry*, **31**, 145-153. https://doi.org/10.1016/s0038-0717(98)00117-5

[32] Landesman, W.J., Treonis, A.M. and Dighton, J. (2011) Effects of a One-Year Rainfall Manipulation on Soil Nematode Abundances and Community Composition. *Pedobiologia*, **54**, 87-91. https://doi.org/10.1016/j.pedobi.2010.10.002

[33] Bardgett, R.D., Leemans, D.K., Cook, R. and Hobbs, P.J. (1997) Seasonality of the Soil Biota of Grazed and Ungrazed Hill Grasslands. *Soil Biology and Biochemistry*, **29**, 1285-1294. https://doi.org/10.1016/s0038-0717(97)00019-9

[34] Bernard, E.C. (1992) Soil nematode Biodiversity. *Biology and Fertility of Soils*, **14**, 99-103. https://doi.org/10.1007/bf00336257

[35] Bongers, T. and Bongers, M. (1998) Functional Diversity of Nematodes. *Applied Soil Ecology*, **10**, 239-251. https://doi.org/10.1016/s0929-1393(98)00123-1

[36] Schlüter, S., Gil, E., Doniger, T., Applebaum, I. and Steinberger, Y. (2022) Abundance and Community Composition of Free-Living Nematodes as a Function of Soil Structure under Different Vineyard Managements. *Applied Soil Ecology*, **170**, Article 104291. https://doi.org/10.1016/j.apsoil.2021.104291

[37] Freckman, D.W. (1988) Bacterivorous Nematodes and Organic-Matter Decomposition. *Agriculture, Ecosystems & Environment*, **24**, 195-217. https://doi.org/10.1016/0167-8809(88)90066-7

[38] Neher, D.A. (2010) Ecology of Plant and Free-Living Nematodes in Natural and Agricultural Soil. *Annual Review of Phytopathology*, **48**, 371-394. https://doi.org/10.1146/annurev-phyto-073009-114439

[39] Black, C.A., Evans, D.D. and Dinauer, R.C. (1965) Methods of Soil Analysis, Madison. American Society of Agronomy, Vol. 9, 653-708.

[40] Applebaum, I., Doniger, T. and Steinberger, Y. (2023) Temporal Dynamics of Soil Nematode Population in an Acacia Saligna Invaded Mediterranean Sand Dune Ecosystem. *Nematology*, **25**, 979-991. https://doi.org/10.1163/15685411-bja10270

[41] Corwin, D.L. and Rhoades, J.D. (1982) An Improved Technique for Determining Soil Electrical Conductivity-Depth Relations from Above-ground Electromagnetic Measurements. *Soil Science Society of America Journal*, **46**, 517-520. https://doi.org/10.2136/sssaj1982.03615995004600030014x

[42] Cairns, E.J. (1960) Methods in Nematology: A Review. *Nematology*, **1**, 33-84.

[43] Wiesel, L., Daniell, T.J., King, D. and Neilson, R. (2015) Determination of the Optimal Soil Sample Size to Accurately Characterise Nematode Communities in Soil. *Soil Biology and Biochemistry*, **80**, 89-91. https://doi.org/10.1016/j.soilbio.2014.09.026

[44] Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., *et al.* (2010) QIIME Allows Analysis of High-Throughput Community Sequencing Data. *Nature Methods*, **7**, 335-336. https://doi.org/10.1038/nmeth.f.303

[45] Shannon, C.E. (1948) A Mathematical Theory of Communication. *Bell System Technical Journal*, **27**, 379-423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

[46] Twinn, D.C. (1974) Nematodes. In: Dickinson, C.H. and Pugh, G.J.F., Eds., *Biology of Plant Litter Decomposition*, Elsevier, 421-465. https://doi.org/10.1016/b978-0-12-215002-9.50011-3

[47] Bongers, T. (1990) The Maturity Index: An Ecological Measure of Environmental Disturbance Based on Nematode Species Composition. *Oecologia*, **83**, 14-19. https://doi.org/10.1007/bf00324627

[48] Matveeva, E.M. and Sushchuk, A.A. (2016) Features of Soil Nematode Communities in Various Types of Natural Biocenoses: Effectiveness of Assessment Parameters. *Biology Bulletin*, **43**, 474-482. https://doi.org/10.1134/s1062359016040099

[49] Luc, M., Bridge, J. and Sikora, R.A. (2005) Reflections on Nematology in Subtropical and Tropical Agriculture. In: Luc, M., Sikora, R.A. and Bridge, J., Eds., *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture*, CABI Publishing, 1-10. https://doi.org/10.1079/9780851997278.0001

[50] Abd-Elgawad, M.M.M. (2021) Biological Control of Nematodes Infecting Eggplant in Egypt. *Bulletin of the National Research Centre*, **45**, Article No. 6. https://doi.org/10.1186/s42269-020-00463-0

[51] Freckman, D.W. and Caswell, E.P. (1985) The Ecology of Nematodes in Agroecosystems. *Annual Review of Phytopathology*, **23**, 275-296. https://doi.org/10.1146/annurev.py.23.090185.001423

[52] Ingham, R.E., Trofymow, J.A., Ingham, E.R. and Coleman, D.C. (1985) Interactions of Bacteria, Fungi, and Their Nematode Grazers: Effects on Nutrient Cycling and Plant Growth. *Ecological Monographs*, **55**, 119-140. https://doi.org/10.2307/1942528

[53] Esnard, J., Marban-Mendoza, N. and Zuckerman, B.M. (1998) Effects of Three Microbial Broth Cultures and an Organic Amendment on Growth and Populations of

Free Living and Plant-Parasitic Nematodes on Banana. *European Journal of Plant Pathology*, **104**, 457-463. https://doi.org/10.1023/a:1008638419552

[54] Kamra, A. and Vinay, B.K. (2016) Multitropic Interaction with Nematodes and Climate. In: Chattopadhyay, C. and Prasad, D., Eds., *Dynamics of Crop Protection and Climate Change*, Studera Press, 169-185.

[55] Liang, W.J., Lavian, I., Pen Mouratov, S. and Steinberger, Y. (2005) Diversity and Dynamics of Soil Free-Living Nematode Populations in a Mediterranean Agroecosystem. *Pedosphere*, **15**, 204-215.

[56] Khanum, T.A., Mehmood, N. and Khatoon, N. (2021) Nematodes as Biological Indicators of Soil Quality in the Agroecosystems. In: Bellé, C. and Kaspary, T.E., Eds., *Nematodes-Recent Advances*, *Management and New Perspectives*, IntechOpen, 1-12.

[57] Li, X., Lewis, E.E., Liu, Q., Li, H., Bai, C. and Wang, Y. (2016) Effects of Long-Term Continuous Cropping on Soil Nematode Community and Soil Condition Associated with Replant Problem in Strawberry Habitat. *Scientific Reports*, **6**, Article No. 30466. https://doi.org/10.1038/srep30466

[58] Rahman, L., Chan, K.Y. and Heenan, D.P. (2007) Impact of Tillage, Stubble Management and Crop Rotation on Nematode Populations in a Long-Term Field Experiment. *Soil and Tillage Research*, **95**, 110-119. https://doi.org/10.1016/j.still.2006.11.008

[59] Bai, P., Liu, Q., Li, X., Liu, Y. and Zhang, L. (2018) Response of the Wheat Rhizosphere Soil Nematode Community in Wheat/walnut Intercropping System in Xinjiang, Northwest China. *Applied Entomology and Zoology*, **53**, 297-306. https://doi.org/10.1007/s13355-018-0557-9

[60] Liu, Y., Li, X. and Liu, Q. (2016) Soil Nematode Communities in Jujube (Ziziphus Jujuba Mill.) Rhizosphere Soil under Monoculture and Jujube/Wheat (*Triticum aestivum* Linn.) Intercropping Systems, a Case Study in Xinjiang Arid Region, Northwest of China. *European Journal of Soil Biology*, **74**, 52-59. https://doi.org/10.1016/j.ejsobi.2016.02.001

[61] Ferris, H., Bongers, T. and de Goede, R.G.M. (2001) A Framework for Soil Food Web Diagnostics: Extension of the Nematode Faunal Analysis Concept. *Applied Soil Ecology*, **18**, 13-29. https://doi.org/10.1016/s0929-1393(01)00152-4

[62] van Eekeren, N., Bommelé, L., Bloem, J., Schouten, T., Rutgers, M., de Goede, R., *et al.* (2008) Soil Biological Quality after 36 Years of Ley-Arable Cropping, Permanent Grassland and Permanent Arable Cropping. *Applied Soil Ecology*, **40**, 432-446. https://doi.org/10.1016/j.apsoil.2008.06.010

[63] Villenave, C., Saj, S., Pablo, A., Sall, S., Djigal, D., Chotte, J., *et al.* (2010) Influence of Long-Term Organic and Mineral Fertilization on Soil Nematofauna When Growing Sorghum Bicolor in Burkina Faso. *Biology and Fertility of Soils*, **46**, 659-670. https://doi.org/10.1007/s00374-010-0471-y

[64] Laasli, S., Mokrini, F., Lahlali, R., Wuletaw, T., Paulitz, T. and Dababat, A.A. (2022) Biodiversity of Nematode Communities Associated with Wheat (*Triticum aestivum* L.) in Southern Morocco and Their Contribution as Soil Health Bioindicators. *Diversity*, **14**, Article 194. https://doi.org/10.3390/d14030194

[65] Quist, C.W., Gort, G., Mooijman, P., Brus, D.J., van den Elsen, S., Kostenko, O., *et al.* (2019) Spatial Distribution of Soil Nematodes Relates to Soil Organic Matter and Life Strategy. *Soil Biology and Biochemistry*, **136**, Article 107542. https://doi.org/10.1016/j.soilbio.2019.107542

[66] Bongers, T. (1999) The Maturity Index, the Evolution of Nematode Life History

Traits, Adaptive Radiation and Cp-Scaling. *Plant and Soil*, **212**, 13-22.
https://doi.org/10.1023/a:1004571900425

[67] Bongers, T., Alkemade, R. and Yeates, G. (1991) Interpretation of Disturbance-Induced Maturity Decrease in Marine Nematode Assemblages by Means of the Maturity Index. *Marine Ecology Progress Series*, **76**, 135-142.
https://doi.org/10.3354/meps076135