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The effect of *Cercidium praecox* and *Prosopis laevigata* on vertical distribution of soil free-living nematode communities in the Tehuacán Desert, Mexico

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Abstract Vegetation cover is known to act as an abiotic mediator influencing the structure of soil fauna communities in arid and semi-arid ecosystems. The aim of the current research was to determine the spatial dispersion of the soil free-living nematode community under the canopy of *Cercidium praecox* and *Prosopis laevigata* during the rainy season. These shrubs are the dominant plant associations in the western part of the Tehuacán-Cuicatlán Valley in Mexico. Soil samples were taken from each 10-cm depth between 0 and 50 cm in August 2004. Our results demonstrated that the abundance and structure of the soil free-living nematode communities in the study area were strongly dependent on plant effects, specified by limited factors such as soil moisture and organic matter availability. The greatest degree of abundance of soil-free-living nematodes (88%) was found in the upper (0–10 cm) soil layer. Plant parasites were the most abundant trophic group under the two plants (58 and 36% under *Parkinsonia* (*Cercidium*) *praecox* and *Prosopis laevigata*, respectively), whereas omnivore-predators were the most dominant (96%) in inter-plant spaces. The fungivore/bacterivore (F/B) ratio was found to be the most useful tool of the ecological indices tested in the present study, reflecting the vertical distribution of the free-living nematode communities beneath different plant species in the different soil layers. The soil free-living nematode communities and their vertical distribution were found to be affected by plant ecophysiological

adaptation, soil moisture, and the interaction between them.

Keywords Desert · Distribution · Ecology · Nematode

Introduction

Trees and perennial shrubs play a key role in the functional activity of arid and semi-arid ecosystems, allowing the associated plant communities to grow beneath them (Wallwork 1976; Whitford 2002). Consequently, they strongly influence the aboveground as well as underground distribution and abundance of animal species (Ernst et al. 1989; Rohner and Ward 1999; Pen-Mouratov et al. 2004). The trees and shrubs in desert areas promote the landscape mosaic by the accumulation of soil organic matter, water, nutrients, and other resources (Noy-Meir 1985; Milton and Dean 1995; Montana et al. 1995; Zaady et al. 1996). Moreover, the low number of shrub patches in desertified shrublands leads to water, soil, and nutrient leakage from the ecosystem (Shachak et al. 1998).

Prosopis laevigata and *Parkinsonia* (*Cercidium*) *praecox* play this role in the terraces of the Tehuacán-Cuicatlán Valley. Both plants flower and fructify during the dry season, reaching their optimum flower and fruit productivity at the highest maximum temperature. This reproductive pattern can be attributed to the capacity of these two species to utilize water stored at great depths in the soil (Pavon and Briones 2001). However, Pavón and Briones (2001) observed an inverse pattern in the case of maximum air humidity. They emphasized that the main difference between the two plants in the western part of the Tehuacán Desert Valley was in their leafing pattern. *P. laevigata* exhibited a marked period of leaf production 2 months before the rainy season (March–April) and maintained its leaves throughout the year. On the other hand, *P. praecox* completely shed its

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leaves during the driest months and reached its peak leaf production during the wet season. Growth of new twigs was not observed in *P. praecox*, and leaf production occurred at old nodes.

According to Pavón and Briones (2001), these phenological patterns were mainly related to soil moisture and maximum temperature and, to a less significant degree, to relative humidity and photoperiod. *P. laevigata* and *P. praecox* are phreatophytic species whose roots can penetrate a depth of about 15 m (Crosswhite and Crosswhite 1984). Both species even share the same environmental requirements for germination, differing only in their littering patterns (Flores and Briones 2001).

There are numerous pieces of evidence (House 1989; Yeates et al. 1997; Liang and Steinberger 2001; Freckman and Virginia 1989; Parker et al. 1984; Wall and Virginia 1999) indicating that the belowground subsystem diversity strongly depends on the plant species diversity. Soil free-living nematodes are among the most important groups of soil biota that play a leading role as regulators of energy flow in soil systems (Chew 1974). Besides being one of the most numerous multicellular animals (Bongers and Ferris 1999) actively involved in fundamental ecological processes in soil, such as decomposition and nutrient cycling (Freckman 1988), free-living nematodes are widely used as indicators of the soil condition (Bongers and Bongers 1998). According to Yeates (2003), Papatheodorou et al. (2004), Lazarova et al. (2004), Shukurov et al. (2005), and Steinberger et al. (1989), the structure of the soil nematode community is very sensitive to substrate texture, climate, biogeography, and changes in soil properties. Furthermore, the dispersion and density of the soil free-living nematode community have been found to be closely dependent on plant distribution (Duponnois et al. 1999). Notwithstanding numerous publications dedicated to the study of the plant-nematode interaction, we asked how closely the nematode communities are dependent on the ecophysiological individ-

uality of different plants. Following this aim, we chose two plants with similar ecophysiological properties, except for a small difference. The goal of the present study was to determine the vertical dispersion of the soil free-living nematode community under the canopy of *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) (Mimosaceae) and *Parkinsonia* (*Cercidium*) *praecox* (Ruiz & Pavon) Harms (Caesalpinaceae), which have ecophysiological individuality, but are phenologically similar in appearance, and are the dominant plant association in the alluvial terraces in the western part of the Tehuacán-Cuicatlán Valley.

Materials and methods

Study site

The study zone is located on the alluvial terraces in the Zapotitlan Area (18°12'–18°25' North latitude and 97°24'–97°35' West longitude) in the western part of the Tehuacán-Cuicatlán Valley, about 240 km south of Mexico City (Fig. 1). The Zapotitlan area has an elevation range from 1,460 m above sea level (m.a.s.l.) at the alluvial terraces to 2,600 m.a.s.l. in the hills surrounding the valley (López-Galindo et al. 2003). The climate is dry-hot with summer rains, corresponding to the class Bsh according to the Köppen classification modified by García-Amaro (1973), with an average annual rainfall of 400 mm and an average annual temperature of 20°C (López-Galindo et al. 2003). The rainy season is divided into two periods by a well-defined dry period (canicula): light showers start in June, followed by a dry period in July, and storms from early August up to the middle of September, when most of the rainfall occurs. Soils are rocky and shallow, except in the alluvial terraces, where they are very deep. The terraces were formed by fluvial sediments deposited during the Pleistocene with a shallow A horizon and a

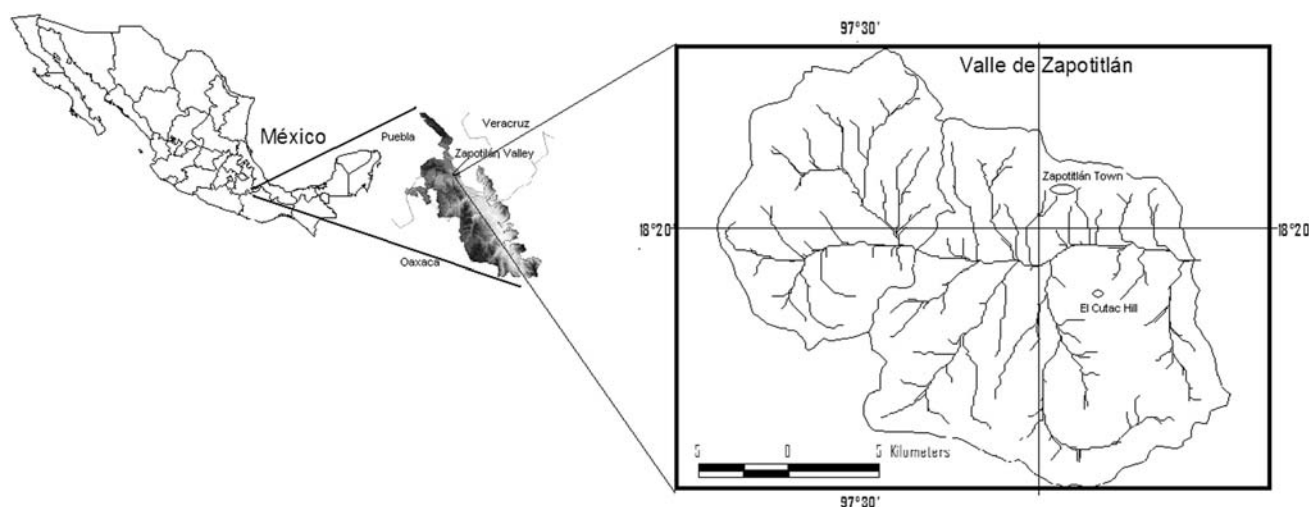


Fig. 1 Map of the study site location

sequence of C horizons of different thicknesses and textures (sandy loam and sandy silt loam), with a medium amount of organic matter (1.8%) and a large amount of carbonates. Soil classes are calcaric fluvisol and calcaric regosol with a loamy sand texture and pH from 7 to 7.6 (López-Galindo et al. 2003). The dominant plant association in the terraces is the mesquite, dominated by *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) (Mimosaceae) and other legumes, such as *Parkinsonia (Cercidium) praecox* (Ruiz & Pav. Ex Hook.) J. Hawkins and *Mimosa luisana* Brandegee (Mimosaceae), with a prevalence of columnar cacti (Davila 1997; Valiente-Banuet et al. 2001).

The study was conducted in an area-terrace of about 1,400 ha, half of which has already transformed into badlands, and about 400 ha of this area is in different stages of deterioration. Vegetation is patchily distributed and is composed mainly of 12 families (Godínez, com pers.unpublished data): Agavaceae (*Agave marmorata* and *Agave karwinskii*), Apocynaceae (*Vallesia glabra* and *Plumeria rubra*), Cactaceae (*Coryphantha pallida*, *Echinocactus platyacanthus f. grandis*, *Ferocactus robustus*, *Mammillaria carnea*, *Mammillaria sphacelata*, *Myrtillocactus geometrizans*, *Neobuxbaumia tetetzo*, *Nopalea cochenillifera*, *Opuntia pilifera*, *Opuntia pubescens*, *Opuntia pumila*, *Pachycereus hollianus*, *Pachycereus marginatus*, *Peniocereus viperinus* and *Stenocereus stellatus*), Celastraceae (*Maytenus phyllantoides*), Caesalpiniaceae (*Parekinsonia praecox*), Crassulaceae (*Thompsonella minutiflora*), Euphorbiaceae (*Euphorbia antisiphilitica*, *Manihotoides pauciflora* and *Jatropha dioica*) Olaceae (*Ximeniia Americana*), Simaroubaceae (*Castela tortuosa*), Ulmaceae (*Celtis pallida*), Vervena-ceae (*Lantana achyranthifolia*) and Zygophyllaceae (*Morkillia mexicana*).

Sampling

Soil samples were collected randomly from under four individual *P. laevigata* and *P. praecox* plants in August 2004, during the rainy season. The plants were between 4 and 10 m apart. Samples were also taken from the same layers of the exposed inter-space areas between the shrubs in the open, bare areas—and served as control. These areas were devoid of microbial soil crusts or accumulations of organic matter.

Soil samples were taken at 10-cm intervals from the upper 50-cm depth (at 0–10-, 10–20-, 20–30-, 30–40-, and 40–50-cm depths). Each individual sample was stored in an individual Ziploc plastic bag and placed in a cool chest until arrival at the Microbiology Laboratory at FES Iztacala, UNAM, Mexico. All soil samples were sieved (mesh size 2 mm) to remove root particles and other organic debris. The soil samples were stored at 4°C until chemical and biological analyses were performed. Sets of subsamples from each replicate were used to determine soil moisture, total organic matter, and the soil free-living nematode community.

Laboratory analysis

Soil moisture was measured gravimetrically by drying subsamples from each sample in an oven at 60°C for a minimum of 72 h.

Total organic carbon was determined by using a modified method of Rowell (1994), which is based on organic matter oxidation by chromic and sulfuric acids. Five milliliters K-dichromate 1-N solution and 10 ml concentrate H₂SO₄ were added to 0.5 g dry soil in a 250-ml Erlenmeyer flask. A gentle 1-min shake of the Erlenmeyer flask was followed by 30-min settling after which 100 ml distilled water was added. Five milliliters of concentrated phosphoric acid and three drops of N-phenylanthranilic acid (98%) indicator (0.1 g N-phenylanthranilic acid and 0.1 g NaCO₃ dissolved to a final 100 ml distilled water) were also added.

A titration solution made from 0.5 N Fe(NH₄)₂(SO₄)₂·6H₂O was used to determine the percentage of organic matter (OM). The titration solution was prepared by weighting 139 g Fe(NH₄)₂(SO₄)₂·6H₂O and dissolving it in 500 ml distilled water to which 50 ml H₂SO₄ concentrate was added. Distilled water was added to this solution to a final volume of 1 l. A solution without soil was used as a blank in order to determine the titration factor (correction factor–FC).

The equation used in order to calculate the percentage of organic matter was: $OM(\%) = [(5 - (\text{mlFeSO}_4 \times N\text{FeSO}_4 \times FC))] / (\text{g dry soil}) \times 0.69$ where 5 ml K-dichromate 1 N solution, N normality of FeSO₄, FC correction factor, 0.69 constant, FC = 10 ml FeSO₄ were used to titrate the blank. Soil free-living nematode communities were extracted from 100 g soil samples using the Baermann funnel procedure (Steinberger and Loboda 1991). The recovered organisms were counted, preserved in formalin (Steinberger and Sarig 1993), and identified according to order, family, and genus (if possible), using a compound microscope.

Ecological indices and statistical analysis

The characteristics of the nematode communities were described using the following indices: (1) absolute abundance of individuals 100 g⁻¹ dry soil; (2) abundance of omnivore-predator (OP), plant-parasitic (PP), fungal-feeding (FF) and bacterial-feeding (BF) nematodes (trophic structure) (Steinberger and Sarig 1993; Pen-Mouratov et al. 2003; Pen-Mouratov et al. 2004); (3) Wasilewska index (WI), $WI = (FF + BF) / PP$ (Wasilewska 1994); (4) fungivore/bacterivore ratio (F/B), $F/B = FF/BF$ (Twinn 1974); (5) trophic diversity (T), $T = 1 / \sum Pi^2$ where Pi is the proportion of the i -th trophic group in the nematode community (Heip et al. 1988); (6) Shannon-Weaver index (H'), a species diversity measure that gives more weight to rare species, $H' = [-\sum Pi(\ln Pi)]$, where P is the proportion of individuals in the i -th taxon (Shannon and Weaver 1949 322 /id); (7) maturity index (MI), $MI = \sum v_i \rho_i$ where v_i is

Table 1 Univariate analysis of variance (GLM) of the soil properties, nematode communities and ecological indices under the canopy of *P. praecox* and *P. laevigata* in the west part of the Tehuacán-Cuicatlán Valley

	Sampling sites		Plants		Depth		Plant × depth	
	<i>F</i> test	<i>P</i> value	<i>F</i> test	<i>P</i> value	<i>F</i> test	<i>P</i> value	<i>F</i> test	<i>P</i> value
1. Soil moisture (SM)	8.3	0.0009	0.95	NS	16.9	0.0001	0.73	NS
2. Total organic carbon (C_{org})	7.53	0.002	0.34	NS	23.21	0.0001	2.77	0.01
3. Total nematode abundance (Tnem)	12.16	0.0001	6.34	0.02	25.68	0.0001	8.35	0.0001
1. Trophic structure								
Bacterial-feeding (BF)	6.79	0.0027	3.87	0.05	9.58	0.0001	4.41	0.0005
Fungal-feeding (FF)	7.22	0.0019	6.41	0.02	7.14	0.0002	5.09	0.0002
Plant parasitic (PP)	4.32	0.0192	0.71	NS	11.05	0.0001	2.98	0.0092
Omnivores-predators (OP)	4.03	0.0245	3.66	0.05	11.66	0.0001	3.78	0.0018
2. Indices								
Wasilewska index (WI)	2.38	NS	0	NS	1.91	NS	1.63	NS
FF to BF ratio (F/B)	6.36	0.0037	5.27	0.03	4.66	0.0031	2.76	0.0144
Trophic diversity (<i>T</i>)	13.33	0.0001	0.02	NS	14.87	0.0001	1.52	NS
Shannon index (<i>H'</i>)	6.61	0.003	1.16	NS	24.07	0.0001	1.79	NS
Maturity index (MI)	4.08	0.0235	5.1	NS	16.63	0.0001	7.03	0.0001

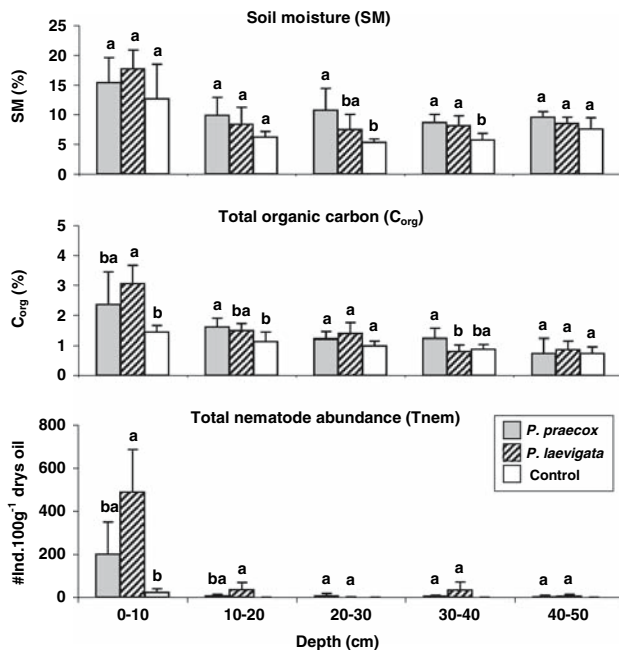


Fig. 2 Changes in percentage of soil moisture, organic carbon, and total number of soil free-living nematode communities collected under the canopy of *P. praecox* (filled square), *P. laevigata* (cross-lined square), and inter-plant spaces (open square) in different soil layers. Significant differences ($P < 0.05$) between sampling terraces are indicated by different letters (*a*, *b*, *c*)

the c - p value of the i -th genus in the nematode and ρ_i , the proportion of the genus in the nematode community. The c - p values describe the nematode life strategies and range from 1 (colonizers, tolerant to disturbance) to 5 (persisters, sensitive to disturbance) (Bongers 1990 136 /id)(Freckman and Ettema 1993 141 /id).

All data were subjected to statistical analysis of variance using the SAS model (GLM, Duncan's test and Pearson correlation coefficient) and were used to evaluate differences between separate means. Differences obtained at levels of $P < 0.05$ were considered significant.

Cluster analysis was performed using PC-Ord[®] software version 4 for Windows[®] (McCune and Mefford 1999). The program was set up for Euclidean distance determination, and linkage was estimated by Ward's method. Values representing the sum of individuals found in the four repetitions were used for cluster analysis. Rows with no nematode detected accounted for "zero" values and were deleted before clustering, in this case the interspace soil at depths from 10 to 50 cm.

Results

Soil moisture (SM) and total organic carbon

Soil moisture (SM) values were found to be significantly different between plants and inter-plant space ($P < 0.0009$, $n = 60$), and among soil layers ($P < 0.0001$, $n = 60$); but no differences were observed between plants (Table 1). The maximal SM values were found in the upper (0–10 cm) soil layer under plants as well as in the inter-plant spaces, and then they followed a decreasing pattern with depth (Fig. 2).

The total organic carbon pattern was similar to SM, differing between plants and inter-plant spaces ($P < 0.002$, $n = 60$) and reaching maximal values in the upper (0–10 cm) soil layer and decreasing with depth ($P < 0.0001$, $n = 60$). No differences were observed between plants (Fig. 2, Table 1).

Nematode communities

The total number of soil free-living nematodes during the study period ranged from 0 to 675 individuals per 100 g dry soil (Fig. 2). The nematode community density was found to be significantly different between plants ($P < 0.02$; Table 1, "Plants") and control soil

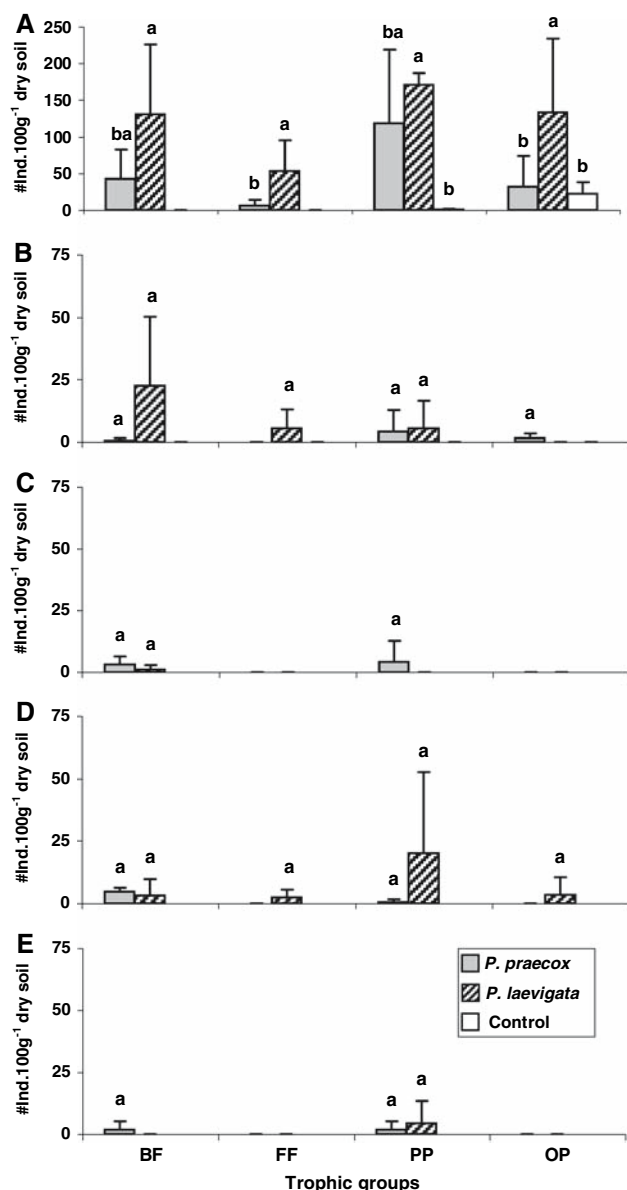


Fig. 3 Density of soil free-living nematode trophic groups in soil samples collected under the canopy of *P. praecox*, *P. laevigata*, and inter-plant spaces at different soil layers (where A, B, C, D, E are 0–10, 11–20, 21–30, 31–40, 41–50 cm, respectively). BF bacterial feeders, FF fungal feeders, PP plant parasites, OP omnivore-predators. Significant differences ($P < 0.05$) between sampling terraces are indicated by different letters (a, b, c)

samples ($P < 0.0001$) as well as between soil layers ($P < 0.0001$) (Table 1 “Depth”). The total number of nematodes reached maximal values in the upper (0–10 cm) soil layer, with a sharp decrease in the deeper (10–20 cm) soil layer (Fig. 2). The variation in the nematode density between soil layers under the plants was found to be higher (amounting to 90–98 times) than in the inter-plant (17 times) control area. Moreover, the total number of nematodes was more than twice as high under *P. laevigata* as under *P. praecox*.

The total number of soil free-living nematodes was found to be closely correlated with SM and C_{org} (Table 2).

Nematode trophic and genus diversity

The trophic groups, similarly to the total number of nematodes, were most abundant in the upper (0–10 cm) soil layer and decreased with depth (Fig. 3). All trophic groups were correlated with SM and C_{org} (Table 2).

Among the 28 genera found in the study area, 9 belonged to bacteria-feeding (BF), four to fungi-feeding (FF), seven to plant-parasite (PP) and six to omnivore-predator (OP) nematodes (Table 3). Moreover, the nematode community under the plants was represented by all four trophic groups, whereas the nematode community in the inter-plant area was represented only by OP and two plant-parasite species (Fig. 3, Table 3). The abundance of trophic groups under *P. laevigata* was higher than under *P. praecox* (Fig. 3, Table 3). However, the number of genera was not different between the two plants: 15 genera were found under *P. praecox* and 16 genera were found under *P. laevigata*. Nonetheless, the BF exhibited the highest generic richness among all observed trophic groups, and the total number of PP nematodes was higher than in the other trophic groups. *Acrobeloides*, *Tetylenchus*, and *Tylenchorhynchus* were the most abundant genera under *P. praecox*, whereas *Panagrolaimus*, *Tylenchorhynchus*, and *Dorylaimus* were the most abundant under *P. laevigata* (Table 3). *Dorylaimus* genus was the most abundant in the inter-plant soil spaces (Table 3).

On the whole, the nematode distribution differed at the different soil layers under the canopy of observed plants and the inter-plant area (Table 4). Significant difference in bacteria-feeding composition under two plants and the inter-plant-area (Table 4) was found. *Aphelenchoides* and *Aphelenchus*, which belong to the fungi-feeding trophic group, were found only under *P. laevigata*, while *Tylencholaimus* was discovered only under *P. praecox* (Table 4). *Longidorus* and *Pratylenchus*, which belong to the plant-parasite trophic group, were found only under *P. laevigata*, while *Heterodera*, *Rotylenchus* and *Tetylenchus* were found under *P. praecox* (Table 4). *Aporcelaimellus* and *Nyngolaimoides* were not found under *P. laevigata* or the inter-plant area, and *Microdorylaimus* was not found under *P. laevigata* (Table 4). *Tetylenchus* was found to be dominant at the upper soil layer and absent at the deeper soil layers under *P. praecox*, where *Dorylaimus* was found to be dominant at the upper soil layer under *P. laevigata*. However, the nematode community composition in the inter-plant space (control) was found to be different in comparison to samples taken from the vicinity of the plants, while no free-living nematodes were found in the upper and the deeper soil layers (Table 4).

Table 2 Correlation coefficient between indices of soil organisms and soil condition under canopy of plants in the west part of the Tehuacán-Cuicatlán Valley, Mexico

	Tnem	BF	FF	PP	OP	WI	FB	T	H'	MI
SM	0.58***	0.61***	0.49***	0.42***	0.52***	0.39**	0.43***	0.68***	0.65***	0.52***
C _{org}	0.79***	0.64***	0.68***	0.72***	0.68***	0.41***	0.66***	0.69***	0.66***	0.39**

Soil properties: *SM* soil moisture, *OM* organic matter

Indices: *Tnem* total number of nematodes (per 100 g dry soil)

Trophic structure: *BF* bacterial-feeding, *FF* fungal-feeding, *PP* plant parasitic, *OP* omnivores-predatores

Ecological indices: *WI* Wasilewska index, *FB* fungivore/bacterivore ratio, *T* trophic diversity, *H'* Shannon index, *MI* maturity index

*, **, *** Correlation coefficient significant at $P < 0.05$, 0.01 and more than 0.001, respectively

Table 3 Abundance (individuals per 100 g dry soil) of soil nematode genera under 2 shrubs and inter-plant area in the western part of the Tehuacán-Cuicatlán Valley, Mexico

Trophic groups/ genus/family ^a	<i>c-p</i> value ^b	<i>P. praecox</i>		<i>P. laevigata</i>		Control	
		Min–max (v) ^c	Mean (stdev)	Min–max (v)	Mean (SD)	Min–max (v)	Mean (SD)
Bacterivores							
<i>Acrobeles</i>	2	0–21 (37.1)	2.0 (6.1)	0	0	0	0
<i>Acrobelloides</i>	2	0–37 (86.7)	5.0 (9.3)	0–40 (83.4)	3.8 (9.1)	0	0
<i>Cervidellus</i>	2	0	0	0–35 (77.4)	2.7 (8.8)	0	0
<i>Chiloplacus</i>	2	0–59 (173.9)	3.6 (13.2)	0–53 (285)	6.9 (16.9)	0	0
<i>Eucephalobus</i>	2	0	0	0–20 (19.8)	1.0 (4.4)	0	0
<i>Heterocephalobus</i>	2	0	0	0	0	0	0
<i>Monhystera</i>	2	0	0	0–11 (5.6)	0.5 (2.4)	0	0
<i>Panagrolaimus</i>	1	0	0	0–68 (423)	11.9 (20.6)	0	0
<i>Rhabditis</i>	1	0	0	0–90 (419)	6.3 (20.5)	0	0
Fungivores							
<i>Aphelenchoides</i>	2	0	0	0–45 (213)	6.8 (14.6)	0	0
<i>Aphelenchus</i>	2	0	0	0–20 (21)	1.3 (4.5)	0	0
<i>Nothotylenchus</i>	2	0–9 (4.2)	0.5 (2.1)	0–40 (132)	4.2 (11.5)	0	0
<i>Tylencholaimus</i>	4	0–16 (12.2)	0.8 (3.5)	0	0	0	0
Plant-parasites							
<i>Heterodera</i>	3	0–4 (0.97)	0.2 (1.0)	0	0	0	0
<i>Longidorus</i>	4	0	0	0–4 (0.82)	0.3 (0.9)	0	0
<i>Pratylenchus</i>	3	0	0	0–68 (407)	8.3 (20.2)	0	0
<i>Rotylenchus</i>	3	0–7 (2.5)	0.4 (1.6)	0	0	0	0
<i>Tetylechus</i>	2	0–109 (663.6)	7.6 (25.8)	0	0	0	0
<i>Tylenchorhynchus</i>	2	0–250 (3127)	17.7 (55.9)	0–159 (2887)	31.9 (53.7)	0–2 (0.23)	0.1 (0.5)
<i>Xiphinema</i>	5	0	0	0	0	0–2 (0.25)	0.1 (0.5)
Omnivores-predators							
<i>Aporcelaimellus</i>	4	0–16 (12.2)	0.8 (3.5)	0	0	0	0
<i>Discolaimus</i>	4	0–15 (14.5)	1.3 (3.8)	0–68 (228)	3.7 (15.1)	0–29 (53)	2.5 (7.3)
<i>Dorylaimus</i>	4	0–15 (17.3)	1.5 (4.2)	0–139 (2039)	20.0 (45.2)	0–5 (2.1)	0.7 (1.5)
<i>Microdorylaimus</i>	4	0–16 (12.2)	0.8 (3.5)	0	0	0–2 (0.23)	0.1 (0.5)
<i>Nygolaimoides</i>	5	0–16 (12.2)	0.8 (3.5)	0	0	0	0
<i>Nygolaimus</i>	5	0–31 (48.9)	1.6 (7.0)	0–68 (228)	3.7 (15.1)	0–11 (8.8)	1.1 (3.0)

^a By classification Yeates and King (1997)

^b Values taken from Bongers (1990)

^c Variance value

Ecological indices

All ecological indices (except for the Wasilewska index (Wasilewska 1994)) exhibited significant differences between plants and inter-plant spaces (Table 1) and were positively correlated with SM and C_{org} values (Table 2). Values of all ecological indices (except the Wasilewska index) were significantly different between soil layers (Table 1). However, only the fungivore/bacterivore ratio (F/B) was significantly different between plants as well as between plants and inter-plant spaces at the different

soil depths (Tables 1, 5). In this study, the F/B ratio varied between 0–0.07, 0–0.32, and 0.0, with mean values amounting to 0.015, 0.10, and 0 under *P. praecox*, *P. laevigata*, and the inter-plant spaces, respectively.

Analyzing the nematode community composition in the soil layers, it was found that the surface layer (0–10 cm) of *P. laevigata* and *P. praecox* clustered together with about 65% similarity (Fig. 4). *P. praecox* showed chaining clustering from the 20 to 50 cm soil layers, whereas *P. laevigata* showed wider variances of the nematode community along its root system. The

Table 4 Nematode genera distribution under two shrubs and inter-plant area in the west part of the Tehuacán-Cuicatlán valley, Mexico

Trophic groups/genus/family	<i>P. praecox</i>	<i>P. laevigata</i>	Control
Bacterivores			
<i>Acrobeles</i>	U	A	A
<i>Acrobelloides</i>	C	B	A
<i>Cervidellus</i>	A	U	A
<i>Chiloplacus</i>	C	U	A
<i>Eucephalobus</i>	A	U	A
<i>Heterocephalobus</i>	A	U	A
<i>Monhystera</i>	A	D	A
<i>Panagrolaimus</i>	A	C	A
<i>Rhabditis</i>	A	B	A
Fungivores			
<i>Aphelenchoides</i>	A	C	A
<i>Aphelenchus</i>	A	C	A
<i>Nothotylenchus</i>	U	C	A
<i>Tylencholaimus</i>	U	A	A
Plant-parasites			
<i>Heterodera</i>	D	A	A
<i>Longidorus</i>	A	D	A
<i>Pratylenchus</i>	A	C	A
<i>Rotylenchus</i>	D	A	A
<i>Tetylelenchus</i>	U	A	A
<i>Tylenchorhynchus</i>	C	C	U
<i>Xiphinema</i>	A	A	U
Omnivores-predators			
<i>Aporcelaimellus</i>	U	A	A
<i>Discolaimus</i>	C	B	U
<i>Dorylaimus</i>	B	U	U
<i>Microdorylaimus</i>	U	A	U
<i>Nygolaimoides</i>	U	A	A
<i>Nygolaimus</i>	U	B	U

A absent in the sampling area, B found both at the upper and deeper soil layers with different proportion in the nematode composition, C found both at the upper and deeper soil layers with same proportion in the nematode composition, U found only at the upper soil layer, D found only at the deeper soil layers

vertical distribution in the control soil layers was found to be entirely different from the vertical distribution of the nematode community in the soil layers in the vicinity of the plants at the 0–10-cm layer, sharing less than 50% similarity with the nematode community under the shrubs.

Discussion

Desert ecosystems are characterized by extreme spatial heterogeneity of soil nutrients and temporal inequity of scarce soil water availability (Xie and Steinberger 2001). Plants are, essentially, the local ecological factor, creating niches that moderate environmental surroundings (Milton and Dean 1995; Rohner and Ward 1999; Pen-Mouratov et al. 2004), determining soil communities along root areas. The abundance of the total nematodes in the current study reached maximal values in the upper (0–10 cm) soil layer, with a sharp decrease in total free-living communities with depth, as reflected in the vertical rooting dispersion. These changes were followed by changes in soil moisture and

organic carbon contents. The findings of this study were found to be similar to studies of Liang et al. (2002) and Pen-Mouratov et al. (2003), who studied soil systems in the Negev Desert. In those studies, the total number of soil free-living nematodes beneath plants was found to be significantly more abundant than in inter-plant spaces, with both soil moisture and organic carbon being dominant drivers of this spatial heterogeneity. The under-canopy environment of *P. laevigata* was found to be more favorable for soil free-living nematodes than the under-canopy environment of *P. praecox*, as reflected by the total count of nematode communities. The mean values of the total number of nematodes amounted to up to 113 individuals per 100 g dry soil beneath *P. laevigata* and was half that amount (45 individuals per 100 g dry soil) under the canopy of *P. praecox*, and 25 and 10 times lower, respectively, compared to samples collected from the inter-plant spaces (4.6 individuals per 100 g dry soil). These numbers were found to be lower than those reported by Freckman and Mankau (1986), with 912 individuals per 100 g soil in samples taken from the Mojave Desert, but were found to be similar to results reported by Steinberger and Loboda (1991) and Liang et al. (2002) for the Negev Desert, with values ranging from 74 to 272 individuals per 100 g dry soil under plants. This illustrates the difference between the Mojave and Tehuacán ecosystems, showing that the plants along the alluvial terrace in the Tehuacán ecosystem are exposed to a more xeric environment.

In the upper (0–10 cm) soil layers, the abundance of all trophic groups was found to be higher than in the deeper soil layers. However, the highest diversity was found in the vicinity of plants in comparison to the control samples. These results are in accordance with data obtained by Freckman et al. (1987), Steinberger et al. (1984, 1989), and Steinberger and Loboda (1991).

Whitford (2002) showed that, under the more favorable environmental conditions in the soil upper layers, the abundance and trophic composition of soil mesofauna were higher than in more xeric or deeper soil layers. He also showed the importance of litter accumulation beneath shrubs as an important factor in prolonging moisture and nutrient availability, having a positive effect on soil biota distribution.

P. laevigata is known to contribute gum exudates, which contain several amino acids, carbohydrates [sacrose, glucosidated flavonoids, pipercolic acids, and pinitol (poly-alcohol)], and this may be one of the main effects that contributes to changes in soil biota composition together with the shedding of leaves (Anderson et al. 1985; Harbone and Baxter 1993; Orozco-Villafuerte et al. 2003; Garcia-Bores 2003).

Gum exudates produced by *P. praecox* typically contain the sugars arabinose (9%) and xylose (59%), together with β -O-glucuronic acid and its 4-ortho-methyl analogue (32%) (dePinto et al. 1993, 1994). However, research on the gum properties of *P. praecox* has been limited, and there have been no studies on this plant species in the Tehuacán region.

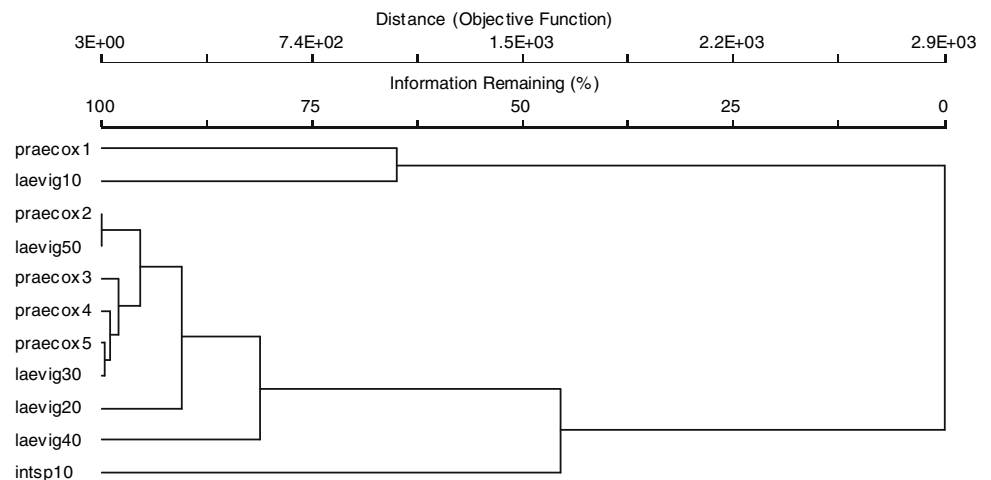
Table 5 Mean values of ecological indices obtained for observed plants and inter-plants (control) plots in the study area

	WI	F/B	<i>T</i>	<i>H'</i>	MI
<i>P. praecox</i>	0.30 ± 0.71 ^a	0.015 ± 0.06 ^b	1.11 ± 0.82 ^a	0.48 ± 0.57 ^a	2.47 ± 0.83 ^b
<i>P. laevigata</i>	0.29 ± 0.59 ^a	0.10 ± 0.09 ^a	1.15 ± 1.25 ^a	0.63 ± 0.72 ^a	2.21 ± 0.99 ^b
Control	0	0	0.23 ± 0.48 ^b	0.21 ± 0.44 ^b	4.25 ± 0.20 ^a

Different letters indicate significant differences between site sampling

WI Wasilewska index, F/B ratio fungivores/bacterivores, *T* trophic diversity, *H'* Shannon-Weaver index, MI maturity index

Fig. 4 Cluster analysis of the nematode community in the 0–50-cm soil layers under *P. laevigata* and *P. praecox* in the Tehuacán Desert, Mexico. Abbreviations: *praecox*, *P. praecox*; *laevig*, *P. laevigata*. Soil layers: 1 and 10, 0–10 cm; 2 and 20, 10–20 cm; 3 and 30, 20–30 cm; 4 and 40, 30–40 cm; 5 and 50, 40–50 cm



The contribution of these compounds may be a key factor in determining the difference between the nematode communities found in the vicinity of plants in the 0–10-cm layer, being able to supply a more diverse source of energy that may sustain a greater richness of microorganism species with a different trophic composition.

Such a diversity of compounds is absent in the inter-plant spaces, and therefore the nematode community there is represented mainly by few omnivore and predator nematodes, which may reflect an instable condition in the soil food web as mentioned by Freckman and Mankau (1986). These observations are compatible with the conclusion reached by Porazinska et al. (1999) about using the omnivore-predator group to define the soil ecosystem status. Trophic groups and nematode abundance were strongly dependent on soil moisture and organic matter availability (Table 2). However, different qualities of organic matter affecting the bacterial and fungal association may lead to an alteration in the trophic and species structure of the nematode communities.

All the ecological indices used in the present study were found to be very dependent on soil moisture and organic carbon availability (Table 2). The values obtained for the F/B reflect the structure of the microflora community and are in agreement with the findings of Ingham et al. (1985) and Liang et al. (2001) for Mediterranean agroecosystems, where the mean values were found to be lower than those found by Neher et al. (2005) in different soil types in North Carolina

(0.37–0.54), in soil samples collected in the Negev Desert by Pen-Mouratov et al. (2003) (0.1–0.2), and in agricultural soils observed by Porazinska et al. (1999) (0.1–1.1).

All the indices used confirm that these plants, which grow on the alluvial terraces, were under increased environmental stress, and their biological activity retarded the process of transformation of these terraces into badlands. Therefore, their activity as “islands of fertility” gained more importance before the increase in stressing environmental conditions that typically lead to the formation of badlands in the western part of the Tehuacán Valley.

On the other hand, we can conclude that the visible ecophysiological difference between both shrubs was clear only in the 0–10-cm soil layer, where the differences in the nematode assemblages can be attributed to littering and washouts from plants, as discussed above. However, cluster analysis also refers to differences in the way both species may function underground. The nematode communities under *P. praecox* exhibited gradual changes from the 10- to 50-cm soil layers that can be attributed to a steep decrease in available food at this part of the root system, while the nematode community along roots of *P. laevigata* exhibited greater differences between the same soil layers. Such variations may be a consequence of minute differences in the functioning of both root systems. Xu and Li (2006) showed that the root system structure of phreatophytic desert shrubs were closely related to their aboveground functioning

and that their surface area of feeder roots increased with depth, making them dependent on subsurface waters rather than on surface surplus. *P. laevigata* and *P. praecox* are both phreatophytic shrubs. However, the differences in root functioning evidenced by changes in the nematode community may account for the observed difference in littering time, where *P. laevigata* clearly functioned as a phreatophytic shrub, and *P. praecox* functioned more as a non-phreatophytic plant.

The present study, undertaken in a rainy shadow desert, elucidates the importance of plant ecophysiological adaptation and moisture vertical distribution on the density and structure of soil free-living nematode communities. In turn, the free-living nematode community was found to be a very sensitive tool, reflecting negligible ecophysiological differences between desert plants.

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