

PLANT-FEEDING NEMATODES IN DEEP-ROOTING DESERT ECOSYSTEMS¹

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Abstract. In the Chihuahuan Desert of southern New Mexico, mesquite (*Prosopis glandulosa*) occurs in a variety of landscape positions where water may accumulate to varying depths. The structure of Chihuahuan Desert landscapes has changed dramatically in the past 100 yr with mesquite expanding from its original distribution (playa, arroyo) into grassland and dune ecosystems. Our objective was to examine spatial and seasonal distribution of plant-feeding nematodes and the potential importance of herbivory in four mesquite communities (playa, arroyo, dunes, grassland) hypothesized to differ in rooting depth and distribution. These sites were compared to a more shallow-rooted creosote bush (*Larrea tridentata*) community. Intact soil cores were recovered to depths of 13 m beneath the canopies of mesquite or creosote bush using a continuous sampling tube drilling system in the winter, spring, and fall on the Jornada LTER site, Las Cruces, New Mexico.

Nematode density and root mass decreased with depth. Nematodes were found to the maximum depth of recovered roots only at the playa (11–12 m) and occurred as deep as 5–6 m at the arroyo, 2–3 m at the dunes, and 1–2 m at the grassland and creosote bush sites. At the playa, 75% of the nematodes and 90% of the roots were below 0.5 m, whereas, in the creosote bush system 79% of the roots and 99.7% of the nematodes were recovered in the upper 0.5 m of soil. Nematode diversity (seven genera) and endoparasite densities were greatest at the playa. Only ectoparasites (three genera) were found at the creosote bush system. Total nematodes across all sites were highly correlated with total soil N, NH_4^+ , and PO_4^{-3} , but not NO_3^- . Nematodes were not positively correlated with soil moisture. Potential herbivory was best described by nematode numbers per gram root or an herbivory index (based on nematode density weighted by an impact factor for each genus), rather than the ratio of endoparasite:ectoparasite numbers. The herbivory index decreased in the order playa > creosote bush > dune > grassland > arroyo.

The movement of mesquite into new habitats (grassland, dunes) is associated with shallow rooting, and relative to the playa, a greater allocation of roots to the upper 0.5 m soil layer, a decrease in nematode herbivory and diversity, and, a failure of the nematodes to be distributed throughout the entire rooting zone. The densities of ecto- and endoparasites varied with site, thus, plant-feeding nematodes should not be treated as a single guild since they have different effects on roots. Our study shows that in some ecosystems the majority of herbivory may occur at soil depths rarely studied. Although technically difficult to examine in ecosystems where deep-rooted plants occur, the potential importance of deep soil biota and their effects on plant growth and nutrient cycling should be considered.

Key words: creosote bush; deep soil; desert; herbivory; mesquite; nematode; roots; soil fauna.

INTRODUCTION

Nematodes are dominant soil invertebrates in most ecosystems and influence nutrient cycling by grazing on plant roots and on soil microfauna and microflora (Sohlenius 1980, Ingham et al. 1985, Freckman 1988). Although the contribution of nematodes to total soil metabolism (CO_2) is estimated to be <2%, they may have large effects on plant production through feeding

on roots. Estimates of decreased plant production due to nematode herbivory range from 6–13% in grassland ecosystems (Ingham and Detling 1984) to 1–10% in agricultural systems (Sohlenius et al. 1988).

Nematodes are abundant in arid and semiarid soils (Freckman 1982, Steinberger et al. 1984, Freckman and Mankau 1986). The distribution, abundance, and functional significance of nematodes associated with deep roots (>1 m) in deserts has not been examined, although nematodes have been associated with deep roots (1.5 m) of some agricultural perennials (Ferris

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and McKenry 1976). Plants rooting to soil depths of ≥ 50 m occur in many ecosystems, especially deserts, grasslands, and savannas (Weaver and Darland 1949). These roots provide access to deep soil moisture and may increase nutrient uptake by the plant, particularly if infected by root symbionts such as rhizobia (Jenkins et al. 1988) and mycorrhizal fungi (Virginia et al. 1986). If nematodes and other fauna are not capable of dispersing and surviving at such soil depths, then deep roots have escaped herbivory, and this may increase the relative contribution of these deep roots to total plant production.

Roots of the woody legume mesquite (*Prosopis glandulosa*) have been reported as deep as 53 m (Phillips 1963). Cannon (1925) noted that of all the plants of the southern Sonoran Desert, the root system of mesquite was capable of the widest adjustment to varying soil conditions by penetrating to depths of ≥ 5 m, remaining close to the surface, or assuming distributions between these extremes. The plasticity of rooting depth exhibited by this plant provides an excellent model for comparison of root distribution, soil properties, and their influences on plant-feeding nematodes.

The structure of Chihuahuan Desert landscapes has changed dramatically in the past 100 yr. Large areas of black grama (*Bouteloua eriopoda*) grassland have been replaced by plant communities dominated by shrubs, especially mesquite and creosote bush (*Larrea tridentata*). In the Chihuahuan Desert of southern New Mexico, mesquite occurs in a variety of landscape positions where water may accumulate: at depth from channeling and concentration of water into low-lying areas (playas, arroyos); in high infiltration soils which permit deep infiltration and limit evaporation (dunes); and, as scattered individuals expanding into former grasslands where rooting is limited to the depth of infiltration of incident rainfall (Buffington and Herbel 1965). We hypothesized that *P. glandulosa* growing in these systems would vary considerably in root distribution and maximum rooting depth. The creosote system was expected to be more shallow rooted, and unlike mesquite, the nematode communities have been well characterized (Freckman and Mankau 1986). The objectives of this study were to examine the temporal (seasonal) and spatial (depth) distribution of plant-feeding nematodes associated with shallow and deep-rooting mesquite and to compare these results with creosote bush. We also measured soil parameters known to affect root growth and activity such as water content and nutrient concentration to examine relationships between nematodes and soil factors.

MATERIALS AND METHODS

Study site

A series of communities was examined in the northern Chihuahuan Desert on the Jornada Long-Term Ecological Research site, located 40 km north-north-

east (32°30' N, 106°45' W) of Las Cruces, New Mexico, USA. The 100-yr annual precipitation is 211 mm \pm 1 SD \pm 77 mm, with 60% of the annual precipitation occurring between July and October (Houghton 1972). Maximum temperatures in summer range from 36° to 40°C and winter minimum temperatures regularly drop below 0°. The *P. glandulosa* communities studied were: grassland, dune, arroyo, and playa. The playa is fringed with a dense stand of mesquite and floods at irregular intervals; during flooding the soil profile may be recharged to depths of many metres. The dunes are dominated by low-growing coppice mesquite which have accumulated windblown sand, forming dunes 1–3 m tall. The grassland sites contain widely scattered mesquite and shrubs (*Yucca*, *Gutierrezia*) and grasses (*Bouteloua*, *Aristida*, *Erioneuron*). An adjacent site dominated by the shallow-rooted creosote bush (*Larrea tridentata*) was chosen as a reference system, since the nematode spatial and seasonal distribution associated with *L. tridentata* were known from previous studies (Freckman et al. 1975, Whitford et al. 1981, Freckman and Mankau 1986). Isolated plants at each site were selected for sampling; however, herbaceous roots may have been present at the *P. glandulosa* grassland sites especially in the upper 50 cm. The soil at the playa, grassland, and creosote bush sites is a Haplargid, the arroyo a Torrifluent, and the dunes a Torrispsament. The general classification of the soils at the study sites on the Jornada have been reported by Gile et al. (1981) and Wierenga et al. (1987).

Soil sampling

A continuous sampling tube drilling system of a type frequently employed for soil environmental contamination studies (e.g., Wilson et al. 1983) was used to remove undisturbed soil cores from the rooting zone of plants in each of the five study sites. Replication of samples was limited to three cores per site per sampling date because of the expense of the drilling equipment. The drilling corer consisted of a split-steel, continuous sampling tube, 1.56 m long with an inner diameter of 6.5 cm. The split-tube bit fit into an outer, rotating auger bit which served as a continuous casing to prevent cave-in (Virginia and Jarrell 1987, Caldwell and Virginia 1989). As the outer bit cut through the soil, the inner, nonrotating bit was pressed into the soil. Cores were collected near the edge of the *P. glandulosa* canopy and under the canopy of creosote shrubs. The sampling tube was flame-sterilized with ethanol before being used and after each soil depth increment was sampled. Soil sample increments were 0–0.5 m, 0.5–1.0 m, and in 1.0 m increments to the depth of drilling. The final depth increment was determined by either the absence of roots in two consecutive 1.56 m coring tubes or by the presence of coarse, dry, loose soil which fell from the coring tube as it was being lifted out of the core hole. Sampling dates were selected to correspond with major phenological stages of mesquite: (1)

aboveground quiescence—winter (January 1986); (2) peak aboveground biomass—spring (late May 1986); and (3) early senescence—following the summer rains (early October 1986). The grassland ecosystem was sampled only spring and fall.

Soil samples were removed from the corer using flame-sterilized trowels and spatulas, placed into plastic bags, stored in ice-cooled insulated chests, and transported within 48 h to the University of California, Riverside, where nematodes and roots were extracted.

Soil analysis

Gravimetric water content of the soil samples was determined ≈ 2 –4 d after soil collection, immediately before nematode extraction. Soil used for chemical analyses was air-dried in a glasshouse, ground to break up clay and caliche aggregates, and passed through a 2-mm mesh sieve. For each soil depth increment, a single soil saturation extract (United States Salinity Laboratory Staff 1954) was prepared and electrical conductivity (EC) measured with a temperature-compensating conductivity meter. KCl-extractable $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ (Keeney and Nelson 1982), and NaHCO_3 -extractable P (Olsen and Dean 1965) were measured colorimetrically for a single subsample from each depth increment using a Technicon Autoanalyzer.

Nematode and root analyses

In the initial winter sampling, three nematode extraction techniques were compared to maximize isolation of each nematode species from the deep soil cores (Freckman 1982). Living and dead nematodes were recovered from two flotation methods, the centrifuge (Jenkins 1964) and semi-automatic elutriator with sugar flotation-sieving (Byrd et al. 1976). For each depth increment, one 700–800 g soil sample was elutriated. The Baermann funnel was used for extracting actively moving nematodes. A higher percentage of plant feeder species was extracted by the elutriator and centrifuge (D. Freckman, *personal observation*). Results presented are for the semi-automatic elutriator, which was used for root and nematode extraction for the remainder of the study.

Nematodes were counted and identified to genus. Only genera whose feeding habits as obligate plant feeders have been confirmed experimentally were classified as endo- or ectoparasitic nematodes (Norton 1978). Nematode species whose feeding habits are unknown or who feed both on plant roots and fungi, usually designated as facultative root feeders (Sohlenius 1980), were not considered in this analysis. Nematode data were corrected for soil moisture content, but were not adjusted for extraction efficiency due to the variability in soil textures within cores and between sites. Data were transformed to $\log(X + 1)$ for statistical analyses and graphical presentation. Species were determined for diversity of nematodes only at the fall sampling, so only these data are reported.

It is very difficult to quantify the effect of nematode herbivory on plants directly (Stanton 1983, Seastedt et al. 1988). Consequently, indirect approaches are necessary to assess the relative impact of the nematode on the plant under various environmental conditions. In this study, the impact of nematode herbivory in the various sites was estimated by an approach for determining the potential effects of nematodes on plant yield in agronomic systems (Ferris 1980). A pathogenic damage rating, or “impact factor,” was assigned to each genus based on literature accounts (Ferris 1980, 1982) or our estimate, with *Meloidogyne* and *Meloidodera* assigned the maximum impact value of 1.0. This factor was multiplied by the density of each genus. Summation of values for all genera within an ecosystem yielded an “herbivory index” based on the different combinations of potential feeding damage by the genera and overall nematode densities among the systems.

Roots and organic debris were elutriated for two sampling times only, spring and fall, from each soil sample used for nematode extraction and were collected on a 425 μm -mesh sieve. Roots were separated by handpicking and fresh root masses determined. Further analyses for infection by vesicular–arbuscular mycorrhizal fungi and rhizobia (Jenkins et al. 1988) were performed using fresh roots. Therefore, root dry masses were not determined.

RESULTS

Nematodes and root distribution

In general, nematode density and root mass decreased with increasing depth at all sites (Fig. 1). Peak nematode densities for all sites were in the surface 0–0.5 m. Nematodes were found to the maximum depth of recovered roots only at the playa (11–12 m), but occurred as deep as 5–6 m at the arroyo, 2–3 m at the dunes, and 1–2 m at the grassland and creosote sites. Roots at all sites penetrated one or more distinct caliche (CaCO_3) layers, indicating caliche was not a barrier to root extension and nematodes in these systems.

The recovered root mass for replicate cores within a site was highly variable with depth and time. Since there were no statistically significant (ANOVA) differences in root mass recovered for the spring and fall samplings, data for these dates were averaged to produce the mean root mass depth profiles shown in Fig. 1. Despite the high variation in root mass, distinct root distributions were apparent for each site. Although the playa and arroyo had the most deeply rooted *P. glandulosa* systems, root mass for these systems was only $\approx 50\%$ that of the more shallow-rooted dunes, grassland, and creosote bush systems. Root mass decreased with depth at all sites with the exception of the playa and dunes, where increases in root mass occurred at 9–12 and 3–5 m, respectively. Although root mass at the playa was similar at 0.5–3 and 9–12 m, nematode density was considerably lower at the 9–12 m depth.

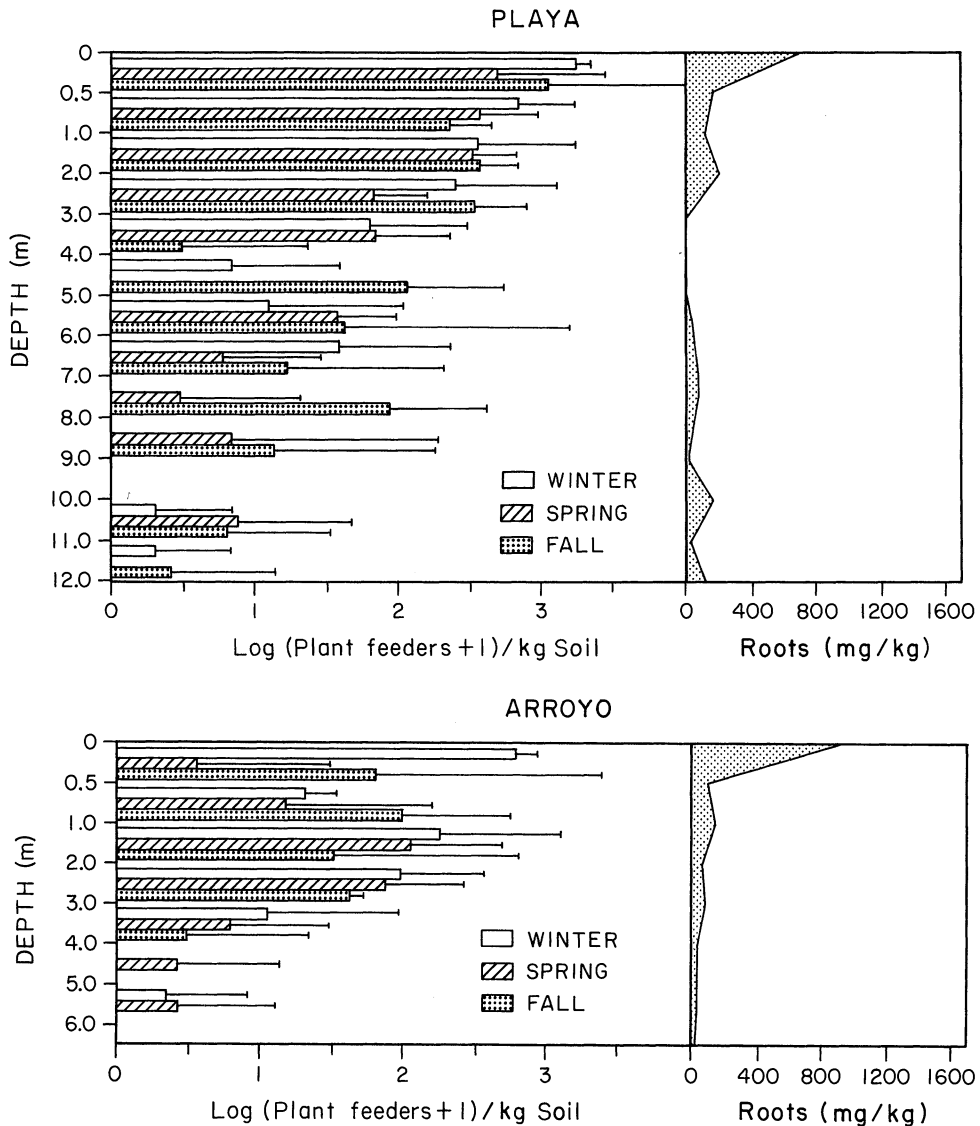


FIG. 1. Seasonal depth distribution of plant-feeding nematodes and root fresh mass for five Chihuahuan Desert sites. Nematode values are means of the three sampling dates ± 1 SD, $n = 3$. Root mass values are the means of spring and fall sampling dates combined ($n = 2$). Absence of bars indicates none recovered from that depth.

Nematodes were recovered in all seasons from the upper 7 m at the playa, 4 m at the arroyo, 2 m at the dunes, 2 m at the grassland, and 1 m at the creosote bush site. Recoveries below these depths were sporadic. The highest nematode densities at each site occurred at the winter sampling for the deep-rooting playa and arroyo systems and in the fall for the more shallow-rooted systems. In the spring, the pattern of nematode distribution at the mesquite sites indicated that nematode densities were either reduced at the 0–0.5 m depth and increased to 2–3 m depth (Fig. 1, see dunes and arroyo), or remained relatively stable from 0–2 m depth (Fig. 1, see grassland and playa), and then decreased below these depths. *L. tridentata* nematode abundance declined with depth throughout the year. The playa

had relatively stable populations from 0 to 3 m during all seasons, which gradually declined with depth. Nematode abundance at depths below 4 m at the playa was higher in the fall sampling than in the winter and spring.

Nematode community structure varied among the five sites at the fall sampling. Phytophagous nematodes found at the mesquite sites included major agronomic economic pests previously undescribed at the Jornada LTER site (Freckman et al. 1975, Whitford et al. 1981). Species abundance distributions were best described by exponential curves (May 1981). The *P. glandulosa* systems were similar in the relative abundances of three dominant nematode genera, with the dunes having the least genera (three) of all the mesquite ecosystems (Fig.

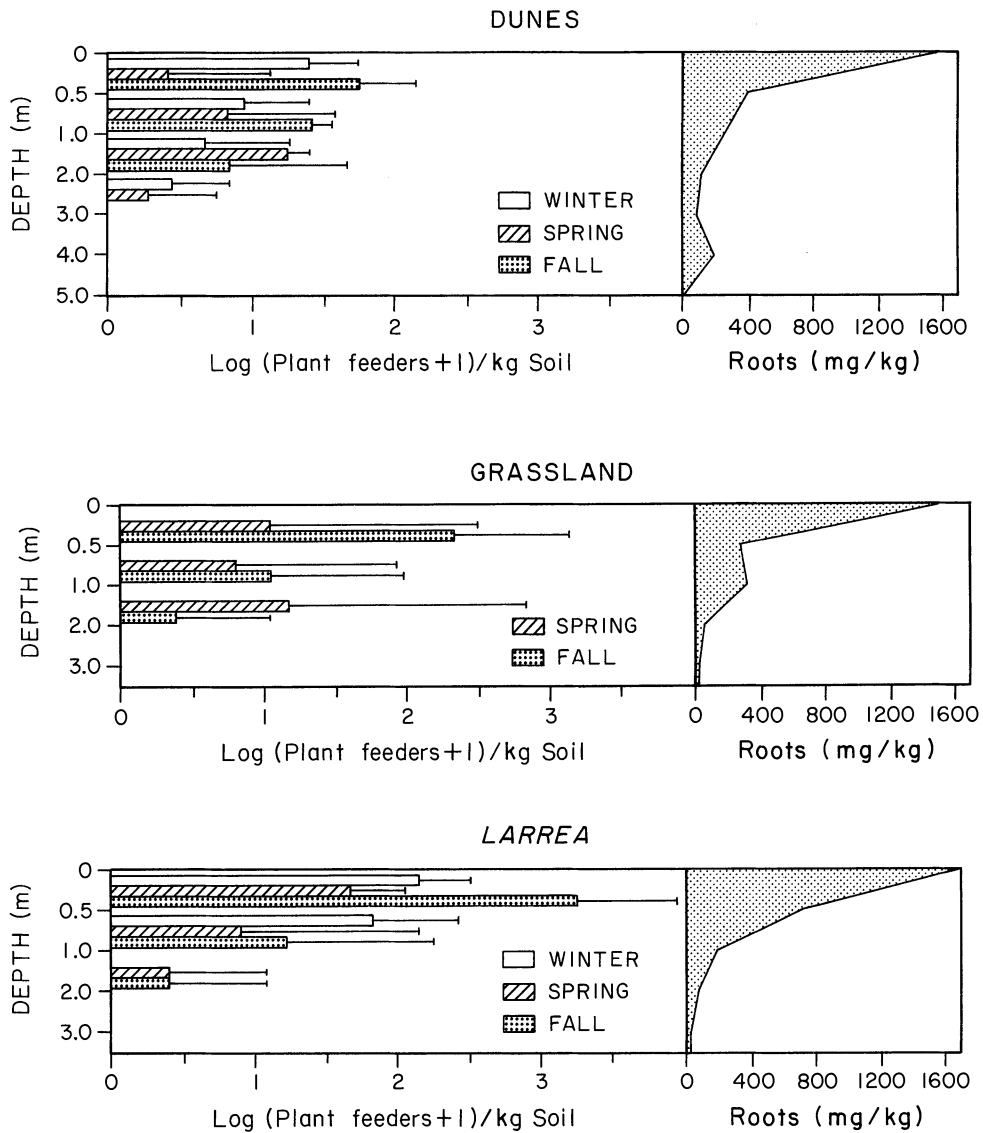


FIG. 1. Continued.

2). The playa and arroyo had the most diverse community structure, resulting from the recovery of relatively rare species with relative abundance <1. *L. tridentata* differed from the *P. glandulosa* ecosystems in having fewer genera and a dominance of one genus.

The relative distribution of the nematode species and root mass by depth varied among the systems (Table 1). Total plant parasites were greatest in the creosote bush system followed by playa, arroyo, dune, and grassland. Seventy-five percent of the total plant parasites at the playa occurred below 0.5 m, as well as 90% of the root mass. For the arroyo, most of the plant parasites were also located below 0.5 m, although 66% of the root mass was recovered above that depth. Most

of the plant parasites and roots for the remaining systems were concentrated in the 0–0.5 m increment.

The abundance of endoparasites at the sites decreased in the following order: playa > dune > grassland > arroyo > creosote (Table 1). The distribution of *Meloidodera charis* Hopper (1960) was variable at the mesquite sites, with the greatest numbers recovered at the playa ($1.16 \times 10^6/m^2$), where 62% of the population was below 0.5 m. *Meloidodera charis* was the only species originally described from mesquite (Hopper 1960). The other endoparasites, *Meloidodera* and *Meloidogyne*, and root mass, were also more abundant at depths from 0.5 to 12 m at the playa. In contrast, >50% of the endoparasites at the dunes and arroyo

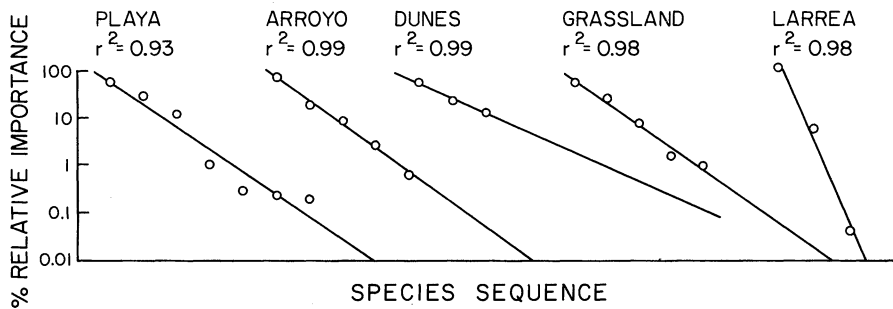


FIG. 2. Relative abundance of plant-feeding nematode genera at five Chihuahuan Desert sites for the fall sampling.

TABLE 1. Distributions of seven nematode genera and root fresh mass (g/m²) by depth (0–0.5 m and >0.5 m depth) at four *Prosopis glandulosa* sites and a *Larrea tridentata* site in the northern Chihuahuan Desert (Jornada Long Term Ecological Research site [LTER], New Mexico). Values are means of three cores collected in fall. Values of mean root mass followed by the same superscript letter do not differ significantly from each other according to Duncan's multiple range test and analysis of variance ($P < .05$).

Nematode abundance	Endoparasitic genera				Ectoparasitic genera				Total nematode plant parasites	Root mass	
	<i>Meloidogyne</i>	<i>Meloidodera</i>	<i>Pratylenchus</i>	Total	<i>Helicotylenchus</i>	<i>Paratylenchus</i>	<i>Tylenchorhynchus</i>	<i>Xiphinema</i>			
Playa site											
% < 0.5 m	0	38	19	37	100	16	100	33	20	25	10
% > 0.5 m	100	62	81	63	0	84	0	67	80	75	90
10 ⁵ individuals/m ² to 15 m depth	0.1	11.6	0.4	12.2	0.1	24.2	1.0	4.9	29.4	41.5	
Total root fresh mass (g/m ²)											1792 ^b
Arroyo site											
% < 0.5 m	0	92	0	92	0	21	100	0	28	40	66
% > 0.5 m	0	8	0	8	100	79	0	100	72	60	34
10 ⁵ individuals/m ² to 9 m depth	0	1.3	0	1.3	0.2	5.0	0.6	0.05	5.8	7.1	
Total root fresh mass (g/m ²)											1824 ^b
Dune site											
% < 0.5 m	0	52	0	52	0	51	93	0	78	63	53
% > 0.5 m	0	48	0	48	0	49	7	0	22	37	47
10 ⁵ individuals/m ² to 5 m depth	0	3.5	0	3.5	0	0.8	1.5	0	2.3	5.9	
Total root fresh mass (g/m ²)											3477 ^a
Grassland site											
% < 0.5 m	100	100	0	100	0	90	100	64	85	94	56
% > 0.5 m	0	0	0	0	0	10	0	36	15	6	44
10 ⁵ individuals/m ² to 4 m depth	0.05	3.0	0	3.0	0	1.4	1.0	0.4	1.9	5.0	
Total root fresh mass (g/m ²)											2104 ^b
Larrea site											
% < 0.05 m	0	0	0	0	0	99.8	97	0	99.7	99.7	79
% > 0.05 m	0	0	0	0	100	0.2	3	0	0.3	0.3	21
10 ⁵ individuals/m ² to 4 m depth	0	0	0	0	0.04	86.6	4.7	0	91.3	91.3	
Total root fresh mass (g/m ²)											5279 ^a

and 100% of the endoparasites at the grasslands were in the surface soils, as was over half of the root mass. No endoparasites were associated with *L. tridentata*, despite a large root mass in the surface depth increment.

Abundance of ectoparasites in the study sites decreased in the following order: creosote > playa > arroyo > dunes > grassland (Table 1). Most of the ectoparasites found at the playa and arroyo occurred at depths below 0.5 m, whereas at the other three sites they were in the surface soils. *Paratylenchus* was the most abundant of all plant parasites. It occurred in large numbers in the surface 0.5 m at the *L. tridentata* site ($8.7 \times 10^6/\text{m}^2$) and below 0.5 in the playa system ($2.4 \times 10^6/\text{m}^2$). At all sites, >90% of *Tylenchorhynchus* was found in the surface depth increment. Although these two species were the dominant ectoparasites in most sites, *Xiphinema* was also abundant at the playa, particularly to depths of 12 m. *Helicotylenchus* occurred in low densities both in the surface 0.5 m (playa) and at greater depths (arroyo and creosote) but was absent from the dune and grassland sites.

Herbivory

The sites varied markedly in the ratio of endoparasite numbers to ectoparasite numbers (Table 2). The creosote system lacked endoparasites, whereas the dune and grassland systems were dominated by endoparasites ($\text{En}/\text{Ec} > 1$). The deep-rooted playa and arroyo were between these extremes.

The herbivory index at the playa was >4 times as high as the other mesquite sites. The playa also had the highest number of nematodes per gram root (Table 2). The creosote bush system had the next highest herbivory index. Nematode impact at the playa resulted from a high density of the endoparasitic *Meloidodera* (impact factor = 1). In contrast, at the creosote bush site, nearly all of the nematode herbivory was accounted for by the ectoparasite, *Paratylenchus*, which occurred at very high density, although it had a low impact factor (0.05). The low herbivory index at the arroyo was associated with a low En/Ec ratio and low densities. Nematode herbivory indices in the dune and grassland systems were comparable; these systems were unique in being dominated by endoparasitic nematodes ($\text{En}/\text{Ec} \sim 1.5$).

Soil factors

The relationships between nematode abundances and soil depth, root mass, soil moisture, and soil chemical properties were examined using correlation statistics (Table 3). Total nematode population densities, particularly ectoparasites, were inversely related to depth at all sites. However, at the arroyo and grassland, endoparasites were not significantly correlated with depth. Total nematodes were not correlated with soil water content across all sites collectively, although significant

TABLE 2. Expressions of nematode herbivory for five communities in the northern Chihuahuan Desert, New Mexico, USA.

Ecosystems	10^5 nematodes/g root	(Endoparasites/Ectoparasites)	Herbivory index*
Playa	2.31	0.41	16.63
Arroyo	0.39	0.22	1.70
Dunes	0.17	1.52	3.67
Grassland	0.24	1.58	3.45
Creosote bush	1.73	0	4.68

* Weighted factor calculated as $\sum[(\text{no./genus}) \times \text{impact factor}]$, where impact factor is *Meloidogyne* = 1.0 (Ferris 1980), *Meloidodera* = 1.0, *Paratylenchus* = 0.5 (Ferris 1980), *Helicotylenchus* = 0.4, *Paratylenchus* = 0.05, *Tylenchorhynchus* = 0.05 (Ferris 1980), *Xiphinema* = 0.7.

negative correlations occurred at the arroyo, dunes, and creosote bush sites.

Nematode abundances were always positively correlated with root mass, but the correlation was not significant at the playa and was lower at the arroyo than for the more shallow-rooted systems. The correlation of nematode numbers with mesquite root mass was highest for endoparasites at the grassland, and ectoparasites associated with creosote bush.

Total nematode numbers treated collectively across all sites were highly correlated with three soil chemical properties: concentrations of total N, NH_4^+ , and PO_4^{3-} , but not NO_3^- (Table 3). Relationships between soil factors and nematodes for individual sites were variable in the sign and magnitude of the correlation coefficient. Examination of individual sites showed that of the soil variables measured, total plant feeders were significantly correlated with four soil variables at the playa: two at the arroyo, grasslands, and *L. tridentata*, and only one at the dunes. At the playa, nematodes were highly correlated with total N and PO_4^{3-} , and to a lesser degree, NO_3^- and NH_4^+ . Nitrogen (total N and NO_3^-) concentrations were also related to nematodes at the arroyo, grasslands, and creosote bush sites. Nematode relationships with soil NO_3^- were inconsistent. Soil nitrate was positively correlated with endoparasites at the arroyo and playa, and negatively correlated with ectoparasites at *L. tridentata* and the grasslands. Phosphorus seemed to be the key variable at the dunes ($r = 0.83$) since, unlike the other sites, nematodes were not significantly related to soil N (total, NO_3^- , or NH_4^+). Neither the arroyo nor *L. tridentata* nematodes were correlated with PO_4^{3-} .

DISCUSSION

The causes of the changing vegetation from grassland to shrub-dominated ecosystems are complex and not well understood (Fisher 1977). Grazing disturbance is thought to be a primary factor, and drought may also play a role (Herbel et al. 1972). In New Mexico the number of cattle grazed on black grama grasslands in-

TABLE 3. Correlation coefficients for relationships between ectoparasitic, endoparasitic and total plant parasitic nematodes and soil properties (including depth), and for relationships between soil depth and soil properties, for sites in the northern Chihuahuan Desert. Data are from fall sampling only. *N* is the total number of samples collected per site.

Site	Nematode	<i>N</i>	Depth	Gravi- metric H ₂ O	Root fresh mass	Nutrient concentrations			
						Total <i>N</i>	NO ₃ ⁻	NH ₄ ⁺	PO ₄ ⁻³
Playa	depth	43		-0.35*	-0.12	-0.69***	-0.48***	-0.50***	-0.72***
	endoparasites		-0.56***	0.02	0.18	0.66***	0.58***	0.35*	0.59***
	ectoparasites		-0.62***	0.23	0.25	0.49***	0.33*	0.42**	0.47***
	total		-0.70***	0.13	0.18	0.56***	0.44**	0.44**	0.55***
Arroyo	depth	26		0.67***	-0.45**	-0.65***	-0.42*	0.02	-0.52**
	endoparasites		-0.36	-0.31	0.29	0.44*	0.84***	0.10	0.28
	ectoparasites		-0.66***	-0.48**	0.53**	0.64***	0.41*	0.25	0.18
	total		-0.72***	-0.50**	0.52**	0.70***	0.48**	0.25	0.24
Dunes	depth	18		0.59**	-0.55**	-0.60**	-0.32	-0.01	-0.82***
	endoparasites		-0.77***	-0.72***	0.59**	0.27	-0.13	-0.13	0.78***
	ectoparasites		-0.83***	-0.69***	0.73***	0.34	0.10	-0.05	0.83***
	total		-0.84***	-0.72***	0.65**	0.35	0.06	-0.06	0.83***
Grassland	depth	14		-0.56*	-0.46*	-0.97***	0.26	-0.66**	-0.78***
	endoparasites		-0.45	0.01	0.92***	0.44	-0.23	0.16	0.34
	ectoparasites		-0.76***	0.19	0.58*	0.77***	-0.50*	0.35	0.68**
	total		-0.74***	0.16	0.70**	0.75***	-0.48*	0.33	0.64
Creosote	depth	15		0.70**	-0.73***	-0.86***	0.95***	-0.51*	-0.17
	endoparasites		...†
	ectoparasites		-0.75***	-0.51*	0.87***	0.91***	-0.60**	-0.05	-0.22
	total		-0.75***	-0.51*	0.87***	0.91***	-0.60**	-0.05	-0.22
All sites	depth	116		0.05	-0.35***	-0.63***	-0.18	0.07	-0.41***
	endoparasites		-0.27**	-0.04	0.30**	0.44***	-0.10	0.31**	0.53***
	ectoparasites		-0.42***	-0.01	0.47***	0.50***	-0.20	0.28***	0.40***
	total		-0.40***	-0.04	0.45***	0.52***	-0.22	0.34***	0.46***

* $P \leq .05$; ** $P \leq .01$; *** $P \leq .001$.

† No endoparasitic nematodes were found at the creosote bush site.

creased nearly 10-fold to over a million animals from 1870 to 1886 (Ares 1974). During this same period the portion of the Jornada classified as grassland declined from 90 to 25%, while mesquite shrublands increased from ≈ 5 to 50% (Buffington and Herbel 1965). This rapid change in plant communities occurred as mesquite, which prior to intensive grazing was largely confined to the margins of arroyos and playas, dispersed into former grasslands. On the Jornada, extensive sand dunes dominated by low-growing multistemmed coppice mesquite were also formed (Wright 1982, Wright and Honea 1986) in response to the desertification of the Jornada Basin.

The distribution of plant-feeding nematodes was generally related to root distribution in this study. At all systems except the dunes, and one depth at the playa, nematodes were found with the entire sampled root zone. Substantial quantities of roots were located between 3 and 5 m in the dunes and 9 and 10 m at the playa, yet no nematodes were recovered. Reasons for the lack of nematodes at these depths are not clear. Significant populations of mesquite-nodulating rhizobia were isolated from 3 to 5 m at the dunes (Jenkins et al. 1988, 1989), indicating conditions for microbial activity and root nodulation were favorable. However, mites and collembola were also essentially absent below 3 m at the dunes, yet occurred in low numbers to

depths of 13 m in the playa (W. G. Whitford, *personal communication*). This suggests that as *P. glandulosa* moved into the dune habitat the complete assemblage of soil fauna associated with this plant in the well-established playa system did not disperse to the dunes, or that the soil fauna found the deep soil environment of the dunes unfavorable. The dunes were also distinct from the other mesquite systems with only three nematode genera, all with high relative abundance. The high species diversity of the playa resulted from a few additional rare species. The most numerous nematode genera at the playa were also found at the dunes, again suggesting the failure of part of the rarer genera associated with the playa to disperse to the dunes.

Our results indicate there are major differences in the distribution of roots and root-feeding nematodes in the pregrazing-type habitats of mesquite (playa and arroyo) and in the younger mesquite ecosystems formed in response to grazing disturbance. The mesquite found along the margin of the playa were the deepest rooted, followed by the arroyo. The *P. glandulosa* plants in these systems have greater canopy volume, biomass, and higher productivity than mesquite in the other systems (Whitford 1973). The mesquite dunes and the playa have a bimodal root distribution, with increases in root biomass at depths which were associated with increased soil moisture (Jenkins et al. 1988). Both root

mass and soil moisture decreased markedly with increasing depth in the arroyo, grasslands, and creosote sites, with the latter two systems having similar rooting patterns. The grasslands and creosote bush systems probably receive the smallest amounts of rainfall concentrated from runoff and should have lower infiltration rates than the mesquite dunes.

Surprisingly, the greatest root mass to the depth of coring was not in the deeper rooted playa and arroyo systems, but in the *L. tridentata* system. About 80% of the root mass at the creosote bush site was found in the upper 0.5 m of soil, indicating that this plant is well suited to take advantage of small, intermittent rainfalls. The dunes had the greatest root mass among the *P. glandulosa* systems, while the remaining systems had roughly equal root biomass. Relative to the *L. tridentata* community, the proportion of root mass recovered below 0.5 m in the mesquite systems was high, ranging from 34% for the arroyo to 90% for the playa. These results suggest that the large differences between the creosote bush and *P. glandulosa* systems in regard to such parameters as production, aboveground biomass, and phenology (Whitford 1973) are more easily related to the distribution of roots in soil than the total root mass. The playa, the most productive of the systems (Whitford 1973), actually had the lowest root mass recovery, expressed as all roots recovered to a depth of 15 m. The root mass relationships between the sites would change if there were significant variation in the lateral extent of root systems, since our sampling scheme only allowed root assessment at one location relative to the plant canopy. Also, we did not distinguish between living and dead roots. Nonetheless, the most productive mesquite habitats, which were also the dominant pregrazing disturbance habitats, had the largest fraction of roots recovered below 0.5 m (Table 1).

Deserts are characterized by large spatial variations in soil physical and chemical properties. Much of this heterogeneity is induced by the activities of perennial plants which accumulate nutrients beneath their canopies, forming the "islands of fertility" typical of desert shrub ecosystems (Charley and West 1975, Virginia and Jarrell 1983, Lajtha and Schlesinger 1986, Virginia 1986). Surface soil fauna are closely tied to patterns of plant distribution and litter accumulation (Steinberger et al. 1984). Deep-soil nematode communities are also characterized by high heterogeneity, likely induced by the activities of plants.

Differences in the season of peak nematode numbers among the sites, and between surface and deep soil within sites, may indicate differences in root phenology and other processes linked with root activities such as mineralization. Plant root distribution and growth varies seasonally and is not always synchronized with shoot growth (Montenegro et al. 1982). In multispecies, shallow-rooted systems such as the grassland site, root overlap between shrubs and herbaceous plants having

different seasons of peak root activity, e.g., winter and summer annuals, may act to stabilize nematode populations by maintaining a continuous resource availability. This situation might be exploited by generalist feeders, capable of migrating from one host species to another. In contrast to the surface root systems, the deep soil environment would contain fewer species of host plants, subsequently greater temporal variation in root growth patterns. We would predict more specialized root feeders in the deep soil systems, whose feeding modes, survival, and life cycle would be synchronized with the deeply rooted host; our results to the genus level did not confirm this, however.

Soil factors

Although plant productivity in deserts is closely related with patterns of moisture availability (Noy-Meir 1973), soil biotic populations and decomposition processes are not as closely related to soil water status as might be expected (Whitford et al. 1986). Soil organic matter and litter quality may exert greater control on nematode distribution and activity (Steinberger et al. 1984, Whitford et al. 1986). We found that nematode numbers were either not correlated or were negatively correlated with gravimetric soil moisture, which was surprising since nematodes require water films for their activity. However, Ingham et al. (1982) published similar results in the shortgrass prairie. Even in soils with low gravimetric water content, microsites with a water potential favorable for soil biota may occur. Freckman et al. (1987) noted that 40% of the nematodes beneath creosote bush on the Jornada were apparently active in soil microsites even when bulk soil moisture was <4.7 g/100 g soil. In addition, nematodes may migrate to a more favorable soil moisture environment (Whitford et al. 1981), enter anhydrobiosis, or remain within plant roots during dry conditions (Freckman 1986).

Phytophagous nematodes have been often related to soil physical and chemical factors as well as soil moisture (Norton 1979, Noe and Barker 1985). Soil texture, bulk density, and aggregation can influence nematode population size and distribution (Wallace 1968, Jones et al. 1969). In general, phytophagous nematode populations are greatest in coarse-textured soils (Ingham et al. 1982, Noe and Barker 1985, Shane and Barker 1986) and in soils where pores >30 μm in diameter are found (Wallace 1968, Jones et al. 1969, Jones and Thomasson 1976). Soil texture did not seem to be related to nematode numbers and distribution for the systems we examined. For example, nematode population densities were much higher at 0–0.5 m in the finer textured depositional playa soil than in the dunes, which have a sand content >80% (Wright and Honea 1986). In addition, we found that nematodes penetrated soil layers in the playa varying in texture from sand to clay and also were found beneath well-developed caliche layers in each ecosystem. Apparently natural channels are present in the soil or nematodes fol-

low developing roots deep into the soil profile. The conventional view that larger nematodes are limited in vertical distribution by pore space (Jones et al. 1969) is not supported by our observations. The large (2–5 mm) nematode *Xiphinema* occurred to 12 m depths in the playa. Our findings indicated that soil physical properties did not exert direct control on the presence or absence of nematodes in the Chihuahuan Desert ecosystems studied. Plant host root quality and root morphology (Yeates 1987) and mode of nematode feeding (Atkinson 1985), along with soil pore size, are factors that may affect size distribution of nematodes.

Nematode populations were negatively correlated with depth at each site. The soil properties measured with a few exceptions (e.g., nitrate at the creosote site) were also negatively correlated with soil depth. This is expected since in most soils the concentrations of soil nutrients usually decrease with increasing depth. Thus, when examining the distribution of soil biota, it is frequently difficult to separate the effects of depth from other soil factors. However, if nematode numbers were responding solely to soil depth (and correlated soil parameters) then the direction and degree of nematode correlation with specific soil properties and root mass should be very similar across all sites. Departures from this pattern (Table 3) indicate differences among the plant communities in the important soil parameters that are associated with or determine nematode distribution and abundance.

Across all sites, nematodes were positively correlated with root mass, total soil N, NH_4^+ , and P, but they were not correlated with soil moisture and nitrate. Systems differed in the magnitude and direction of the correlation between soil properties (including root mass) and nematodes. At the playa, nematodes were negatively correlated with depth, yet root mass and depth were not correlated, suggesting other factors affected nematode distribution in this system. Playa nematodes were more closely related with soil properties influenced by previous root activity such as total N than with the present distribution of roots.

The dunes were distinct from the other systems since nematodes were not related with soil N, but had a strong positive correlation with soil P. The absence of plant-feeding nematodes below 3 m at the dunes was correlated with the low P availability of the dune soil. Overall, the dunes had the lowest NaHCO_3 -extractable P concentrations among the sites. P concentrations below 3 m were <0.1 mg/kg soil (Jenkins et al. 1988) while the highest concentration was only 3.4 mg/kg for the surface 50 cm of dune soil. It is unclear why available P or related factors might affect the numbers of nematodes in soil with coarse texture and roots. Lajtha and Schlesinger (1988) examined the same systems, with the exception of the dunes, and found that P concentrations in shrubs did not reflect total soil P, and that P was not the limiting element for plant production in these systems.

Nematode diversity

This study presents the first detailed quantitative accounting of nematodes associated with *Prosopis*, an important and widespread rangeland plant. Previous work on plant-feeding nematodes in the Chihuahuan Desert have been mainly restricted to *L. tridentata* (Steinberger et al. 1984, Freckman et al. 1987). The nematode community structure of the mesquite and creosote bush sites was very different. The deep-rooted and presumably old playa system had the most diverse nematode community, and the young invasive dune and the *L. tridentata* sites the least. The creosote bush ecosystem was dominated by the small (190–600 μm length) ectoparasitic nematode *Paratylenchus* (Freckman et al. 1975), which feeds primarily on root hairs and usually does not affect root function as severely as *Meloidogyne* or the larger *Xiphinema* both found on mesquite (Wyss 1981, Ferris 1982). The low diversity of nematodes associated with creosote bush could, until this study, be explained by the harsh environmental conditions (low and fluctuating soil moisture, high soil temperatures) limiting nematode function and survival (Whitford et al. 1981, Freckman 1986, Freckman et al. 1987). However, we suggest that plant host factors, such as the differences in resource quality of mesquite and creosote, are a larger factor in determining nematode diversity. The roots of mesquite are expected to have a higher N concentration than creosote bush since it is a symbiotic N_2 -fixing species. The distribution and abundance of rhizobia in the mesquite ecosystems indicates active N_2 -fixation at some or all of the sites (Jenkins et al. 1988). The higher quality of mesquite roots might be expected to favor a greater diversity of nematodes. In addition, creosote roots may contain secondary plant compounds such as terpenes or other compounds, which are known to inhibit nematode feeding (Gomers et al. 1980, Yeates 1987).

The high diversity of plant-feeding nematode genera at the playa contrasts with *L. tridentata*, but is similar to other ecosystems. The number of genera at the playa was equal to the Great Basin International Biological Program (IBP) site, Curlew Valley, Utah, and greater than the Mojave Desert Rock Valley, Nevada, (3 genera), and Sonoran Desert Silverbell, Arizona (2 genera) IBP sites (Freckman et al. 1975, Freckman and Man-kau 1986) and the Namib Desert (Procter 1982). Other ecosystems have a greater diversity than the deserts. Grassland sites, such as the Central Plains Experimental Range, Colorado, USA, have 10 genera (Smolik and Dodd 1983), Wind Cave, South Dakota, 9 genera (R. E. Ingham, *personal communication*) and the Konza Prairie, Kansas, 9 genera (T. Todd, *personal communication*).

Herbivory

The effect of these nematodes on plant production at the Jornada is difficult to estimate if “lumped” only

by the designation "plant feeders." The recent proposal (Walter et al. 1988) that analysis of soil fauna processes be based on grouping of organisms into guilds or functional groups may not be appropriate since little is known about the feeding behaviors of these organisms. Rather than group plant parasites into a single functional group, we used the categories of ecto- and endoparasites to further identify possible interactions with other soil factors and biota (Freckman 1982). Endoparasites spend a majority of their life cycle in the root, protected somewhat from the soil abiotic environment, while ectoparasites rely on well-developed survival mechanisms to endure desert soil extremes. Many nematodes in desiccating soils enter a resistant state, anhydrobiosis, while other species have evolved specific survival mechanisms (Freckman 1986). The fourth-stage juvenile of the ectoparasite *Paratylenchus*, recovered from mesquite, creosote, and grasslands (Yeates 1978), is resistant to desiccation and is triggered to moult by specific plant root exudates (Fisher 1966, Ishibashi et al. 1975).

The two categories of "ectoparasite" and "endoparasite," while referring to life style, also provide information on the effect of nematode herbivory on the plant root. The overall effect of plant-feeding nematodes is physical and physiological disruption of roots, particularly young roots, with subsequent reduction in root biomass and aboveground function (Stanton 1983, Ingham and Detling 1984). Endoparasites, which were only found on mesquite, are considered to be more detrimental to roots, via disruption of new cortical and stelar tissues (Freckman and Chapman 1972, Anderson 1987), and generally have a narrower host range than ectoparasites. However, the En/Ec ratio alone is probably not a good indicator of total herbivory, because it is independent of nematode density, which in our systems varied widely (Table 1). The En/Ec ratio appears better related to host plant factors or edaphic differences between systems, which affect endo- and ectoparasites differently. Clearly, nematodes in these two classes contribute differently to herbivory across these sites.

Quantification of nematode herbivory in the field is difficult unless production can be measured in control and nematicide-treated plots (e.g., Seastedt et al. 1987). This is impractical for all but very shallow-rooted ecosystems. Expressions of nematode numbers relative to root mass or calculation of an index weighted for nematode density and potential root damage by genera or species may provide an understanding of differences among systems in the importance of herbivory to plant production and nutrient cycling (Table 2). Using these measures, nematodes appear to have the greatest impact on the older deep-rooted playa ecosystem. However, rooting depth was not the primary factor controlling herbivory, since creosote had the second highest herbivory index, and the arroyo the lowest. The newer systems, dunes and grassland, although differing in

number of nematodes per gram root and En/Ec ratio, had herbivory indices between those of the deeper rooted systems. The creosote system shows that high densities of nematodes, even those with very low impact factors, can potentially result in significant herbivory.

Plants have evolved mechanisms to cope with their environment, of which herbivorous nematodes are a part. Evidence that herbivory actually benefits plant growth or fitness is controversial (Belsky 1986, McNaughton 1986, Seastedt et al. 1988). However, beyond the negative effects typically associated with nematodes feeding on plant roots, plants may tolerate nematodes and show little or no reduction in plant production (Shane and Barker 1986), or may even increase root production. The rapid growth of many legumes and their ability to fix N may also allow them to escape herbivory by replacing roots faster than nematodes destroy them (Reay and Wallace 1981). The occurrence in *Prosopis* sites of these nematode genera, which are known to cause economic losses in agricultural crops (Freckman and Caswell 1985), suggests that nematode herbivory should affect *Prosopis* production. However, Wallace (1987) has suggested that native plants are more resistant and tolerant to nematode infection than agricultural plant species and if so, *P. glandulosa* may be relatively unaffected by, or may even benefit from, nematode herbivory.

Nematode herbivory can affect plant nutrient uptake and nutrient cycling. A frequent response to nematode herbivory is lateral root production and increased root exudation (Van Gundy et al. 1977, Shane and Barker 1986, Yeates 1987), which may result in increases in plant growth and nematode numbers (Woods et al. 1982, Coleman et al. 1984). Ingham and Coleman (1982) noted higher bacterial populations in soils with the ectoparasitic nematode *Tylenchorhynchus claytoni*, which they attributed to increased root exudation in treatments with nematodes. Nematode herbivory may have significant effects on nutrient accumulation and production in *P. glandulosa* through interactions with root symbionts. Nematode feeding, by stimulating lateral root development, might increase the number of possible infection sites for rhizobia. Rhizobia enter *P. glandulosa* roots via root hairs and lateral root junctions (Baird et al. 1985). Huang (1987) suggested that plant-feeding nematodes might be used to stimulate N fixation since in some cases they have been shown to increase nodulation and N fixation. N₂-fixing root nodules have been recovered as deep as 7 m at the playa (Jenkins et al. 1988). Similarly, nematode wounding of roots might provide infection sites for vesicular-arbuscular mycorrhizal fungi. Conceivably, some levels of nematode herbivory could enhance nutrient uptake especially from nutrient-poor deep soil layers.

CONCLUSION

The movement of mesquite into new habitats (grassland, dunes) has been associated with shallow rooting,

and, relative to the playa, a much greater allocation of roots to the surface soil layer (0–0.5 m), a decrease in nematode herbivory and diversity, and a failure of the nematodes to be distributed throughout the entire rooting zone (i.e., dunes). Plant-feeding nematodes should not be treated as a single guild or functional unit since En/Ec varied with plant host and ecosystem type, and since the feeding mechanisms of these nematodes have different effects on plant function.

Conceptual models of belowground herbivory have been based on studies of shallow root systems. Our study shows that in some ecosystems the majority of herbivory may occur at soil depths rarely studied. Although technically difficult to examine in ecosystems where deep-rooted plants occur, the potential importance of deep soil biota and their effects on plant growth and nutrient cycling should be considered.

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