

## Soil biota and soil properties in the surface rooting zone of mesquite (*Prosopis glandulosa*) in historical and recently desertified Chihuahuan Desert habitats

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**Summary.** The woody legume, mesquite (*Prosopis glandulosa*), has expanded from its historical habitats (playas and arroyos) to recently occupied grassland and dune habitats during the desertification of perennial grasslands in the Chihuahuan Desert. We studied historical and recently occupied sites, having hypothesized that the trophic structure and population density of soil microarthropods and nematodes associated with the surface root system of mesquite would differ in sites representing historical and recent habitats, and that the N mineralization potential would be lower in the recent habitats. Our results showed that net N mineralization potential did not differ significantly among the sites, even though soil nutrient concentrations and texture varied widely. Concentrations of organic C, N, and P were lowest in the recent dune habitat and highest at the playa. Very low concentrations of P in the dune and grassland soils implicated P as a limiting factor in these systems. The bacterial-feeding and omnivore-predator functional groups made up the largest fraction of the nematode community at most of the sites. The high density of plant-feeding nematodes at the playa indicated that herbivory is potentially most important at this site. Total microarthropod densities did not vary significantly among habitats, with Collembola densities highest in the mesquite dunes. Grazers were the dominant microarthropod functional group. While both C and N pool sizes were higher in the historical habitats, a higher substrate lability in the recent habitats appeared to support biota populations and N mineralization rates equivalent to those in the playa and arroyo. Differences in soil properties and biota among historical and recent mesquite habitats may be important for understanding the changes that have occurred in Chihuahuan Desert ecosystems during desertification.

**Key words:** Desertification – *Prosopis glandulosa* – Soil properties – Mites – Collembolans – Nematodes – Nitrogen mineralization – Chihuahuan desert

During the past 130 years the woody legume, mesquite (*Prosopis glandulosa*), has dramatically colonized new habitats and landscape positions in association with desertification in the Chihuahuan Desert (Schlesinger et al. 1990). Before the introduction of domestic livestock by European man in the late 1800 s, mesquite grew predominantly in locations where run-on water accumulated, such as the edges of ephemeral streams (arroyos) and temporary lakes (playas) (Buffington and Herbel 1965; York and Dick-Peddie 1969). These habitats are supplied with organic matter and nutrients by fluvial transport, which presumably increases soil nutrient availability. Following increased grazing and periodic drought, mesquite, and in some cases creosote bush (*Larrea tridentata*), expanded into large areas that were previously perennial grassland dominated by black grama (*Bouteloua eriopoda*). In locations with coarse textured soils, mesquite establishment often resulted in the formation of extensive coppice sand dunes (Hennessy et al. 1983). In these habitats there has been extensive soil redistribution and loss from aeolian processes, probably resulting in a decline in soil organic matter and nutrient concentrations.

Desert soils are typically characterized by low concentrations of N, P, and organic matter (West 1981). While the productivity of arid and semiarid ecosystems is primarily water-limited (Noy-Meir 1973), several studies have shown that N may limit production when water is available (Ludwig and Flavill 1979; Floret and Rambal 1982; Fisher et al. 1988; Sharifi et al. 1988). Terrestrial consumer populations, (i.e., soil microarthropods and nematodes) are among the many factors thought to affect soil nutrient cycles by altering the equilibrium between immobilization and mineralization of nutrients essential to plants (Kitchell et al. 1979; Ingham et al. 1985; Hunt

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et al. 1987). Grazing of the rhizosphere microflora by nematodes and microarthropods increased the mineralization of N and P in microcosms, even when bacterial populations were reduced (Anderson et al. 1981; Baath et al. 1981; Coleman et al. 1984; Setälä and Huhta 1991). The importance of soil microfauna in N mineralization has been emphasized in field studies in the Chihuahuan Desert (Santos et al. 1981; Whitford et al. 1983; Parker et al. 1984).

Numerous studies have examined soil biota associated with *Larrea tridentata* (creosote bush) in the Chihuahuan Desert of southern New Mexico, but much less is known about the soil biota associated with mesquite and the relationship between soil biota and nutrient availability for this plant. Steinberger and Whitford (1984) found little difference in the seasonal population dynamics of soil microarthropods under mesquite in three landscape positions along a Chihuahuan Desert watershed. In other studies the soil biota associated with mesquite and creosotebush was compared in recent and historical habitats to depths of in 13 m (Jenkins et al. 1988; Freckman and Virginia 1989; Silva et al. 1989). These studies showed that deep soil microarthropod and nematode assemblages were absent or poorly represented in recent habitats in comparison to the areas of historical mesquite occupation. Samples were collected at 50- or 100-cm depth increments, and therefore these studies did not examine soil fauna and soil property relationships in the soil zone of highest nutrient availability (i.e., 0–20 cm).

The objective of the present research was to determine whether there have been changes in the structure and function of the surface (0–20 cm) soil system, the zone most affected by litter decomposition, which is associated with the rapid movement of mesquite from historical habitats (arroyo and playa fringe) into recent habitats (grassland and dunes). We hypothesized that the soil biotic communities would be poorly developed in the recent mesquite habitats because of lower soil C and nutrient concentrations. As a result of these differences we predicted lower rates of net N mineralization in the soils from recent mesquite habitats.

## Materials and methods

### Study site

This study was conducted in the Jornada del Muerto Basin, 40 km NNE of Las Cruces, Dona Ana County, New Mexico, USA. The area is near the northern limits of the Chihuahuan Desert. The elevation of the area varies from 1200 to 2000 m. The climate is semiarid, with a 100-year mean annual precipitation of 211 mm (Houghton 1972), 60% occurring as late summer rainfall from brief convective storms. Summer maximum air temperatures reach 40°C, while freezing temperatures have been recorded from October to mid-April (data from the Jornada Validation Site Weather Station). The study region has three well-defined seasons during the year, the hot and wet summer from July to October; the cool and dry winter from November to March; and the hot and dry spring from April to June.

Four habitat types previously examined by Jenkins et al. (1988), Silva et al. (1989), and Freckman and Virginia (1989) were sampled: (1) playa, within a dense stand of large (3–5 m tall) mesquite growing along the edge of a large playa; (2) arroyo, with widely spaced mesquite trees (3–5 m tall) along the margin of temporary water courses; (3)

dunes, which are dominated by low-growing coppice mesquite; the dunes are formed of wind-transported sand from which the clay and silt fractions have been stripped, as eroded soil was trapped by the mesquite plants; the dunes vary in height from 1.5 to 4.0 m above the interdune soil, which forms a layer 10–20 cm thick over an indurated CaCO<sub>3</sub> (caliche) layer through which roots of mesquite penetrate; and (4) grassland, at the base of a watershed with widely scattered mesquite, 2–3 m tall, many of the plants being multiple-stemmed. The dune site is located on the USDA Jornada Experimental Range, while the other three sites are located on the New Mexico State University College Ranch.

The soils were sampled in October 1986 at the end of the hot, wet, summer season when surface soil biota in the Chihuahuan Desert reach their maximum densities (Elkins and Whitford 1982; Santos et al. 1984; Steinberger and Whitford 1984; Silva et al. 1985; Whitford et al. 1988; Cepeda and Whitford 1989; Cepeda-Pizarro and Whitford 1989). At each habitat type location (playa, arroyo, grassland, and dune) soil samples were collected from the midcanopy beneath six mesquite plants at two depths (0–10 and 10–20 cm), using a bucket auger soil corer (7.5 cm diameter, 10 cm depth). The samples were placed in plastic bags, stored in a portable cooler, and then transported to the laboratories. These samples were later divided into subsamples for root mass, microarthropod, and nematode extractions, and soil moisture and soil chemical analyses.

### Soil analysis

The gravimetric water content of the soil samples was determined 2–4 days after the soil sample collection, immediately before nematode extraction. Samples used for texture, pH, total organic C, total N, and total P analyses were air-dried in a glasshouse, ground to break up the clay and caliche aggregates, and passed through a 2-mm mesh sieve. N mineralization and inorganic N analyses were made on field-moist soil. Total C was determined by dry combustion following pretreatment with acid to remove carbonates (Nelson and Sommers 1982). Inorganic C was determined by gravimetric loss of CO<sub>2</sub> (U. S. Salinity Laboratory Staff 1954). Particle-size distribution was determined by a hydrometer method following pretreatment in the dispersant sodium hexametaphosphate (Gee and Bauder 1986).

Total N and total P were determined by a Kjeldahl digestion-block technique (Bremner and Mulvaney 1982). Soil NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N were extracted in a 2 N KCl solution, and analyzed using an automated salicylate procedure (Technicon Industrial method No. 329–74W/B). Available P was analyzed as NaHCO<sub>3</sub>-extractable PO<sub>4</sub><sup>3-</sup>-P (Olsen and Sommers 1982). The N mineralization potential was estimated using a batch incubation procedure on freshly collected soil as described by Fisher et al. (1987). Two sets of 25-g soil subsamples were incubated at 29°C for 4 weeks. The moisture content was adjusted to 0.1 g g<sup>-1</sup> (field capacity) at weekly intervals. The soils were extracted with 2 N KCl (Keeney and Nelson 1982) and NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N were determined as above. Net N mineralization was calculated as the net change in N occurring from the beginning to the end of the incubation period.

### Soil biota and root analyses

Microarthropods and Collembola were extracted in modified Tullgren funnels into water (Santos et al. 1981), counted, and identified to species, and placed in functional groups based on information from Christiansen (1964), Krantz (1978), and Walter (1987). The functional groups were (1) grazers (fungal and algal feeders), which include most of the Cryptostigmata, some Prostigmata, and Collembolans; (2) omnivores, which include some Prostigmata and some Collembola; and (3) predators, which include all Mesostigmata and some Prostigmata.

Nematodes and roots were recovered from soil samples of 700–900 g using a semi-automatic elutriator with sugar flotation-sieving (Byrd et al. 1976). This method was selected from a comparison with the Baerman Funnel technique (Freckman and Virginia 1989). The nematodes were counted, and separated into functional groups of (1) fungal feeders, (2) bacterial feeders, (3) omnivore-predators, and (4) plant feeders (Freckman et al. 1987; Freckman and Baldwin 1990). Nematode densities were corrected for soil moisture content, but were not adjusted for extraction efficiency due to the variability in soil textures between sites (Table 1).

Roots and organic debris were eluted from each soil sample used for nematode extraction and collected on a 425  $\mu\text{m}$ -mesh sieve. The roots were separated by hand into three size classes, fine (< 2 mm), intermediate (2–5 mm), and tap roots (> 5 mm), and the fresh root mass was determined for each. Dry root weights were not determined because the roots were stained and examined for mycorrhizal infection.

### Statistical analysis

Microarthropod and nematode data were transformed to  $\log(X+1)$  to normalize the data prior to analysis. A factorial analysis of variance model was used to test for differences between sites, depths, and depths within sites (PROC GLM, SAS Institute, Inc. 1985). Planned mean comparisons of variables with significant analyses of variance were made using least-square means pairwise comparisons. The relationships between nematode or microarthropod abundance and root mass, soil moisture, and soil chemical properties were examined using Spearman correlation coefficients.

## Results

### Soil properties and roots

There was significant variation in soil properties between sites and soil depths (Table 1). The playa soil had significantly higher clay and silt content and significantly higher gravimetric water content in the upper 10 cm than the

other habitats. The aeolian mesquite dunes had the highest sand content (> 90%).

Soils from the playa had higher concentrations of nutrients and organic C than the leached arroyo soils and the more recently established grassland and dune systems. Playa concentrations of extractable N and P, total N, and organic C were three- to eightfold higher than the dune and grassland habitats. The mesquite dunes had the lowest nutrient concentrations, especially in the 10–20 cm depth where the organic C level was only 0.2% and the total P concentration was 70  $\text{mg kg}^{-1}$ . Comparable values for the playa soil were 1.27% and 870  $\text{mg kg}^{-1}$ , respectively. Many soils at the Jornada contain high concentrations of carbonates (Gile et al. 1981). Inorganic C concentrations were lowest for the leached arroyo soil, and the wind-deposited dune sand. At each site, soil nutrient levels were either the same (arroyo, grassland, dune) or significantly lower (playa) with increasing depth (Table 1). The root mass increased significantly with soil depth only for the playa, where the root mass recovered from a depth of 10–20 cm was 10 times greater than at 0–10 cm. The water-collecting playa and arroyo sites had the greatest total root mass. Fine roots made up 80% of the total roots from the arroyo. Fine root values for the

**Table 1.** Comparisons of soil properties among mesquite habitats and by soil depth

Soil property	Depth (cm)	Mesquite habitat			
		Playa	Arroyo	Grassland	Dunes
Soil moisture (g H <sub>2</sub> O 100 g <sup>-1</sup> soil)	0–10	14.9Ba	4.78Aa	5.55Aa	4.27Aa
	10–20	7.9Ab	4.97Aa	3.53Aa	3.62Aa
pH	0–10	8.05Ba	9.03Aa	8.58Ca	8.15Ba
	10–20	8.42Bb	9.10Aa	8.50Ba	8.33Ba
Sand (%)	0–10	32.8Aa	80.5Ba	81.1Ba	92.4Ca
	10–20	38.5Aa	78.2Ba	76.1Ba	91.3Ca
Silt (%)	0–10	39.4Ca	14.1Ba	10.4Ba	2.6Aa
	10–20	38.8Ca	15.4Ba	12.3Ba	3.2Aa
Clay (%)	0–10	27.8Ca	5.4Aa	8.5Bb	5.0Aa
	10–20	22.7Cb	6.5Aa	11.6Ba	5.5Aa
Organic C (%)	0–10	2.06Ba	0.52Aa	0.31Aa	0.28Aa
	10–20	1.27Cb	0.63Ba	0.33ABa	0.20Aa
Inorganic C (%)	0–10	0.38Ba	0.05Aa	0.38Ba	0.002Aa
	10–20	0.37Ba	0.08Aa	0.56Cb	0.005Aa
Total N (mg kg <sup>-1</sup> )	0–10	2491Ba	540Aa	346Aa	354Aa
	10–20	1396Bb	646Aa	338Aa	266Aa
NO <sub>3</sub> <sup>-</sup> -N (mg kg <sup>-1</sup> )	0–10	37.92B	8.53A	13.33A	8.62A
	10–20	18.52A	11.94A	9.34A	5.20A
NH <sub>4</sub> <sup>+</sup> -N (mg kg <sup>-1</sup> )	0–10	8.30B	4.53AB	1.01A	3.05A
	10–20	5.16A	4.94A	2.78A	4.42A
N mineralization potential (mg kg <sup>-1</sup> )	0–10	5.7Aa	5.5Aa	12.5Aa	11.7Aa
	10–20	-0.9Aa	-1.9Aa	2.0Ab	3.9Aa
Total P (mg kg <sup>-1</sup> )	0–10	1060Ca	558Ba	193ABa	95Aa
	10–20	874Db	595Ca	216Ba	71Aa
PO <sub>4</sub> <sup>+</sup> -P (mg kg <sup>-1</sup> )	0–10	28.18Ba	6.37Aa	5.33Aa	5.08Aa
	10–20	13.68Bb	6.82Aa	2.27Aa	2.62Aa
Fine roots (fresh weight, mg kg <sup>-1</sup> )	0–10	35Aa	844Ba	182Aa	123Aa
	10–20	763Bb	1262Ba	153Aa	135Aa
Total roots (fresh weight, mg kg <sup>-1</sup> )	0–10	123Aa	1026Ba	289ABa	302ABa
	10–20	1158BCb	1581Ca	308Aa	476ABa

Means of five or six soil samples. Comparisons are given only for significant main effects. Small case letters are comparisons between depths, and capital letters are comparisons between sites. Numbers within the same row with different capital letters are significantly different from each other ( $P < 0.05$ ). Numbers within the same column with different small letters are significantly different from each other ( $P < 0.05$ ).

other sites ranged from 33% in the dunes to 62% on the playa.

### Soil nitrogen and nitrogen mineralization potential

The level of N mineralized during the 4-week incubation period did not vary significantly among the sites, despite large initial differences in total N, inorganic N, P concentration, and root mass of the soils (Table 1).  $\text{NH}_4^+$  concentrations decreased during incubation for both depths and for all sites, and the mineralized N accumulated as  $\text{NO}_3^-$ . Net N mineralization did not vary significantly with soil depth, except in the grassland site where most of the N mineralized was in the surface 0–10 cm. There was net N immobilization at 10–20 cm for sites from the historical mesquite habitats, in contrast to the net N mineralization found for sites from the recent mesquite habitats.

The relationship between net N mineralization and soil properties varied with site (Table 2). N mineralization in the playa soil was not significantly correlated with soil properties that can be associated with this process (e.g., total N, organic C, P). A negative correlation was found between these properties and mineralization in the arroyo soil. Extractable soil P was correlated with N mineralization for the more recently established grassland and dune sites (Table 2), where the concentrations of soil P were the lowest (Table 1).

### Nematodes

The sites differed significantly in total nematode densities (Table 3). The grassland site had the lowest total density and the playa site the highest total nematode density. Total nematode densities did not vary significantly as a function of soil depth by site, but there was significant variation among the sites in density by functional groups. The nematode community structure, with the exception of the playa, was dominated by bacterial-feeding and omnivorous groups (Fig. 1). Plant-feeding (plant parasitic) nematode densities were highest for the playa. Bacterial-feeders were the most numerous group in all other sites, comprising 35%–55% of the total population in the upper 0–10 cm of soil (Fig. 1). The bacterial-feeding nema-

Table 2. Spearman correlation coefficients between net N mineralization potential and soil properties by habitat

Soil property	Mesquite habitat			
	Playa	Arroyo	Grassland	Dunes
$\text{NO}_3^-$ -N	-0.57*	-0.66*	NS	NS
$\text{NH}_4^+$ -N	-0.62*	-0.61*	NS	NS
Total N	NS	-0.70*	NS	0.50+
Total P	NS	-0.60*	NS	NS
Extractable $\text{PO}_4^{3-}$ -P	NS	-0.52+	0.82**	0.67*
Organic C	NS	-0.53+	NS	0.51+
Inorganic C	NS	NS	NS	NS
Total root mass	NS	NS	NS	NS

Each correlation is based on 12 values, six replicates, and two depths per habitat. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ; +  $P < 0.1$

Table 3. Comparisons of densities (numbers  $\text{kg}^{-1}$  soil dry weight) of nematode functional groups between habitats and by soil depth

Functional group	Depth (cm)	Mesquite habitat			
		Playa	Arroyo	Grassland	Dunes
Fungal-feeders	0–10	453B	47A	277B	530B
	10–20	523B	199A	279B	339B
Bacterial-feeders	0–10	1633a	1482a	1041a	1408a
	10–20	978a	716a	461b	761b
Omnivore-predators	0–10	402A	746B	480AB	1051C
	10–20	460A	895B	440A	889B
Plant-feeders	0–10	2055Ca	663BCa	68Aa	431Ba
	10–20	2802Ba	1055Aa	449Ab	996Ab
Total nematodes	0–10	4543B	2938AB	1866A	3420B
	10–20	4763B	2865A	1629A	2985A

See footnotes to Table 1

tode densities decreased significantly and plant-feeding nematode numbers increased significantly as a function of soil depth in the recent habitat sites. No significant depth variation in functional groups was found for the historical habitat sites. There were significantly fewer fungal-feeding nematodes in the arroyo site, and fewer omnivore-predators in the playa and grassland sites than in the other systems (Table 3).

Among the nematode functional groups, the bacterial-feeding nematodes were most highly correlated with soil properties (Table 4). The density of bacterial-feeding nematodes was positively correlated with soil total N, organic C, and extractable P for the playa and dune sites.

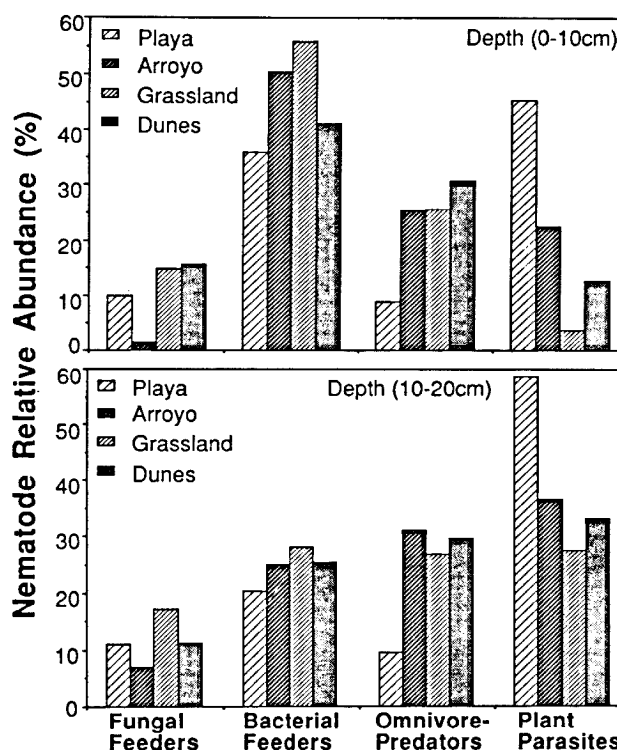


Fig. 1. Nematode community structure in the four habitats at two soil depths, (a) 0–10 cm, and (b) 10–20 cm. ▨, Playa; ▩, Arroyo; ▤, Grassland, □, Dunes

**Table 4.** Spearman correlation coefficients between densities of nematode functional groups and soil properties

Functional group	Soil properties	Mesquite habitat			
		Playa	Arroyo	Grassland	Dunes
Fungal-feeders	Total N	0.15	-0.44	-0.02	0.41
	Total roots	0.08	-0.11	0.18	0.52
	Organic C	0.42	-0.25	-0.04	0.44
	PO <sub>4</sub> <sup>-</sup> -P	0.15	-0.53	0.04	0.69*
Bacterial-feeders	Total N	0.80**	0.37	0.15	0.83***
	Total roots	-0.67*	-0.22	-0.07	0.17
	Organic C	0.89***	0.13	-0.22	0.82***
	PO <sub>4</sub> <sup>-</sup> -P	0.82**	0.43	0.73**	0.82***
Omnivore-predators	Total N	0.07	0.38	-0.29	0.65*
	Total roots	0.07	-0.03	-0.53*	0.24
	Organic C	0.14	0.58*	-0.54*	0.58*
	PO <sub>4</sub> <sup>-</sup> -P	-0.07	0.38	0.06	0.48
Plant-feeders	Total N	-0.29	-0.13	0.06	-0.07
	Total roots	0.22	0.07	-0.26	0.29
	Organic C	-0.29	-0.10	0.10	-0.13
	PO <sub>4</sub> <sup>-</sup> -P	-0.37	-0.23	-0.65*	-0.28

See footnotes to Table 2

Fungal-feeding nematodes were poorly related with soil properties in all sites, with the exception of extractable P in the dune site. Relationships between omnivore-predators and soil properties were not consistent among the sites. Plant-feeding nematode densities were not correlated with root mass or soil properties, with the exception of P in the grassland.

### Microarthropods

Total microarthropod densities did not vary significantly among sites or with depth, but the densities of some microarthropod taxonomic groups did (Table 5). Among the Acari, prostigmatid mites (mostly omnivores, some predators) occurred at the highest densities, but there were no significant differences in their densities among mesquite sites. Cryptostigmatid mites and Collembola were the only microarthropods that showed significant density differences by site and soil depth. The density of cryptostigmatid mites was significantly higher in the playa than the other sites. Collembolan densities ranged from a low of 6 kg<sup>-1</sup> soil at the playa to nearly 200 kg<sup>-1</sup> soil at the dune site. The highest densities were in the surface depth.

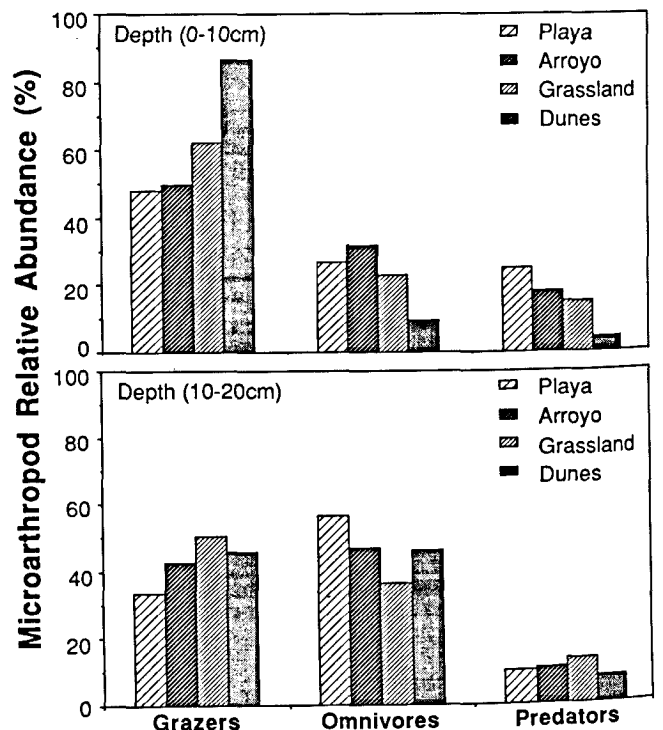
Grazers (including algal- and fungal-feeders) were the most abundant microarthropod functional group in each habitat site in the surface depth (Table 6). The density of grazers in the recent dune habitat site was up to four times higher than in the other sites, due to a significantly higher density of Collembola. No significant intersite variation was found for the omnivore and predator functional groups. Across all sites there was a change in community structure with increasing soil depth. The surface depth was dominated by grazers at all sites, forming from about 45% of the total microarthropod population at the playa to 85% at the dunes. At 10–20 cm the omnivores had a relative abundance comparable to the grazers (Fig. 2).

**Table 5.** Comparisons of densities (numbers kg<sup>-1</sup> soil dry weight) of microarthropod taxonomic and functional groups between habitats and by soil depth

Taxa	Depth (cm)	Mesquite habitat			
		Playa	Arroyo	Grassland	Dunes
Cryptostigmata	0–10	58Aa	9Ba	14Ba	8Ba
	10–20	14Aa	6Ba	4Ba	4Ba
Mesostigmata	0–10	9	11	8	7
	10–20	3	4	13	5
Prostigmata	0–10	77	40	51	59
	10–20	63	49	86	100
Total Acari	0–10	144	60	73	74
	10–20	80	59	103	109
Insecta:	0–10	6Cb	38BCa	45BCa	198Aa
	10–20	4Bb	5Bb	10Ba	22Ab
Total microarthropods	0–10	150	98	118	272
	10–20	84	64	113	131

Means of six samples; for other explanations, see footnotes to Table 1

Unlike the nematodes, very few significant correlations were found between microarthropod density and functional group and soil properties. Across all sites, cryptostigmatid mites were the only group that was significantly correlated with soil properties. Their density was positively correlated with NO<sub>3</sub><sup>-</sup> ( $r = 0.52$ ,  $P < 0.05$ ), total P ( $r = 0.48$ ,  $P < 0.05$ ), total N ( $r = 0.47$ ,  $P < 0.05$ ), and extractable P ( $r = 0.41$ ,  $P < 0.05$ ). In the grassland, grazing ( $r = -0.89$ ,  $P < 0.001$ ) and predatory microarthropods ( $r = -0.56$ ,  $P < 0.05$ ) were negatively correlated with total soil N.

**Fig. 2.** Microarthropod relative abundance in the four habitats at two soil depths, (a) 0–10 cm, and (b) 10–20 cm. For explanation of symbols, see Fig. 1

**Table 6.** Comparisons of densities (numbers  $\text{kg}^{-1}$  soil dry weight) of total microarthropods by functional groups between habitats and by soil depth

Functional group	Soil depth (cm)	Mesquite habitat			
		Playa	Arroyo	Grassland	Dunes
Grazers	0–10	72B	48B	74B	235A
	10–20	28A	27A	57A	60A
Omnivores	0–10	40	31	27	25
	10–20	48	30	41	61
Predators	0–10	38a	17a	18a	11a
	10–20	9b	7b	15a	10a

Means of six samples; for other explanations, see footnotes to Table 1

## Discussion

### Soil properties

The accumulation of nutrients in the surface soil beneath woody plant canopies is a common feature of arid and semiarid systems, leading to the development of "islands of fertility" (Garcia-Moya and McKell 1970; West and Klemmedson 1978; Barth and Klemmedson 1982; Virginia and Jarrell 1983; Lajtha and Schlesinger 1986). The extent of this accumulation is largely determined by plant productivity, root activity, decomposition processes, and the duration of shrub interaction with the soil (Virginia 1986). Soils from the recent habitat sites (especially the dunes), which now form most of the range of mesquite, had lower concentrations of organic C, N, and P. This is probably related to the length of time since the establishment of mesquite in each habitat site and the balance between aeolian and fluvial inputs and losses of soil and organic matter. We were not able to determine the ages of the individual trees beneath which we collected soil. Mesquite was recorded as established in the area of the grassland site during the 1950s (Buffington and Herbel 1965). The dune systems began forming about 80 years ago following intensive grazing and drought (Buffington and Herbel 1965). The larger basal diameters of the main stems of mesquite found around the perimeter of the playa and along the arroyo suggest that these plants are considerably older than those of the grassland and dune sites.

Virginia and Jarrell (1983) found that the soil N accumulation beneath mesquite in the California Sonoran Desert varied with soil type and water regime. N (total and inorganic) was highest in the surface soils with a high clay content, where mesquite was growing as a phreatophyte, using groundwater (similar to the playa), and lowest in sites with coarse-textured surface soils subjected to flooding and leaching (arroyos) or where the soils were aeolian sands with a very low N content (dunes). A similar pattern of soil N accumulation was found in the present study, with highest soil N concentrations in the playa site with the finer textured soils, and lower N concentrations in the dune and arroyo sites where the sand content was highest.

Our initial hypothesis proposed that rates of N mineralization would be lowest in the more recent sites.

While the absolute rates were not significantly different among sites, there was a clear increase in the fraction of total N in surface soil which was mineralized in the laboratory test. With both soil layers combined, the percentage of total N mineralized in the surface 0–20 cm was 0.08% for the playa, 0.36% for the arroyo, 2.10% in the grassland and 2.39% in the dunes. Although the absolute soil concentrations of N in the recent habitats tended to be lower than in the historical mesquite habitats, we suggest that the higher bioavailability of this N is a factor in maintaining plant production in more recent, nutrient-poor environments.

The very low concentrations of total and extractable P in the dunes suggest that this element may be limiting dune productivity and nutrient cycling. Below the 2-m depth in the dunes, extractable P concentrations were only about  $0.1 \text{ mg kg}^{-1}$  (Jenkins et al. 1988). Lajtha and Schlesinger (1988) found no evidence of P limitations in soils along the watershed encompassing the arroyo and playa and grassland sites. However, they did not examine the mesquite dunes where soil P concentrations are lower. The positive correlation between soil P concentrations and N mineralization, as well as with soil biota (e.g., collembolans, and fungal- and bacterial-feeding nematodes), suggest that P availability may have limited N cycling and productivity in the dunes.

### Nematodes

The numbers of nematodes found in the surface soil zone beneath the mesquite are within the range of values reported for woody species in other desert systems (Wood 1971). The total density of nematodes under mesquite (0–10 cm) was higher than reported for creosote bush on the Jornada (Freckman et al. 1987). Densities beneath mesquite decreased in the order of playa ( $590\,500 \text{ m}^{-2}$ ), dunes ( $444\,700 \text{ m}^{-2}$ ), arroyo ( $382\,000 \text{ m}^{-2}$ ), and grassland ( $242\,700 \text{ m}^{-2}$ ). Freckman et al. (1987) found a mean nematode density of  $106\,400 \text{ m}^{-2}$  for creosote bush (0–10 cm) over a 1-year study on the Jornada. In the Mojave Desert, Freckman and Mankau (1986) found that the nematode density in the upper 30 cm of soil ( $1\,243\,000 \text{ m}^{-2}$ ) was two to five times higher than in any of our sites (0–20 cm). The densities we found beneath mesquite are somewhat higher than those found in Australian semiarid areas (0–10 cm), which ranged from  $17\,600 \text{ m}^{-2}$  to  $313\,500 \text{ m}^{-2}$  (Wood 1971).

The high relative abundance of plant-feeding nematodes under the playa mesquite agrees with the results of Freckman and Virginia (1989), who also reported a decrease in the density and diversity of plant-feeding nematodes in deeper soils of the recent mesquite habitats. We found significantly lower plant-feeding nematode densities in the surface soils of recent habitat sites. This result and those of Freckman and Virginia (1989) suggest that plant-feeding nematodes may have less effect on root growth and root-related rhizosphere processes in the recent mesquite habitats. This may be an important habitat site difference, since plant-feeding nematodes are known to affect plant nutrient uptake and nutrient cycling (Freckman and Caswell 1985).

Freckman and Virginia (1989) examined the distribution of plant-feeding nematodes to depths of 13 m in the same habitats we studied and found that the density of plant-feeding nematodes was significantly correlated with total N,  $\text{NH}_4^+$ , and extractable P. We obtained similar results. For all sites combined, nematodes were correlated with total N, extractable P, and  $\text{NH}_4^+$  ( $r = 0.65$ ,  $P < 0.001$ ;  $r = 0.62$ ,  $P < 0.001$ ; and  $r = 0.79$ ,  $P < 0.0001$ , respectively). However, in contrast to the Freckman and Virginia (1989) study of deeper soils, the plant-feeding nematodes in the surface soils of our historical habitats were not correlated with soil properties.

### *Microarthropods*

The microarthropod densities (Table 4) can be compared with those found in a study of a semiarid area in Australia by Wood (1971), where soil organic C values are similar to the Chihuahuan Desert soils we examined. There, acarine densities were 4700 and 680  $\text{m}^{-2}$  for Prostigmata and Mesostigmata, respectively. The densities of soil-dwelling prostigmatid and mesostigmatid mites at our mesquite sites were of the same order of magnitude. The densities of cryptostigmatid and astigmatid mites were combined by Wood (1971), and the value obtained (1350  $\text{m}^{-2}$ ) is similar to those for our sites except for the playa, where our density estimate was much higher (cryptostigmatid mites, 7500  $\text{m}^{-2}$ ).

In the playa, where microarthropod densities were highest, the soil water content, organic C, and total N were also highest. Santos et al. (1978) reported that in the Chihuahuan Desert total microarthropod densities were directly related to the amount of litter accumulation. Wallwork et al. (1985) found fewer cryptostigmatid mites in the playa than any other site, which was attributed to physical disturbance from flooding, a factor to which cryptostigmatids are very sensitive (Holt 1985). However, like Cepeda (1986), we found that the densities of cryptostigmatid mites (fungivores-detritivores) were greatest at the playa site. Our study was conducted 13 months after the last flooding of the playa (August 1985), perhaps providing sufficient time for the acarine populations to recover from any effects of the flooding.

Prostigmatid mites were the most abundant Acari at all sites. The majority of prostigmatid mites found were tarsonemids (fungivores) and tydeids (fungivorous nematode predators) (Santos et al. 1981). Walter (1987) reported that these groups of prostigmatid mites are probably generalists and capable of feeding on a variety of fungi and/or nematodes, characteristics that enhance their ability to survive in all the mesquite habitats studied.

Collembola were unique among the soil biota examined in reaching very high densities only in the mesquite dunes. Santos et al. (1978) reported that collembolans were associated only with the main drainage arroyos of the Jornada Long Term Ecological Research (LTER) watershed where we also sampled. Cepeda-Pizarro and Whitford (1989) found that collembolans were more abundant in the playa fringe, particularly during the wet season. They suggested that improved soil moisture conditions were responsible for the increased collembola

densities. Our sampling was in mid-October, following 2 weeks in which rain events occurred every 2–4 days, totaling 24 mm (unpublished Jornada LTER weather data). The soils from all sites were moist at the time of collection, but only the dune soil had abundant collembola. Apparently moisture alone cannot account for the large intersite variation in collembola that we observed.

### *N mineralization*

We hypothesized that the recent mesquite habitat sites would have a lower net N mineralization than the historical habitat sites, reflecting lower overall levels of N and organic matter and lower populations of the soil biota that influence mineralization in the Chihuahuan Desert (Whitford and Parker 1989). We did not observe this pattern. The net N mineralization rates under mesquite were low and did not differ significantly by site even though the mean N mineralization rates were about twice as high in the recent dune and grassland habitats. Whitford et al. (1987) reported higher rates of net N mineralization in soils collected under mesquite at the edge of the same playa (120  $\text{mg kg}^{-1}$ , 16-week incubation) and high rates (20  $\text{mg kg}^{-1}$ , 16-week incubation) for dune soils also. These differences are attributable to seasonal effects of rainfall in desert ecosystems and their effect on labile C pools and N mineralization processes (Whitford et al. 1987; Fisher et al. 1988). Rates of N mineralization are highest following rains that break extended periods of drought, for example immediately following the first summer rains. By October, at the end of the summer rains and the growth period for C4 grasses, most of the labile organic N has been mineralized and taken up by plants. The remaining organic N and C probably represent the recalcitrant fraction, which should release only small amounts of N during mineralization incubations. Thus, any large differences in N mineralization among mesquite habitat sites that may have occurred before the summer rainy season (Whitford et al. 1987) could have disappeared by the end of the summer rains when we collected our soils. A seasonal study of N mineralization will be necessary to determine whether the total amount and timing of N availability is significantly different between historical and recent mesquite habitats.

In the Chihuahuan Desert, N is the primary nutrient limiting primary productivity, after water (Ludwig and Flavill 1979; Fisher et al. 1988). However, we found P in very low concentrations, especially in the dune soil. At this site, low P availability may directly or indirectly control primary productivity. Fungivorous collembolans and bacterivorous nematodes in the dune soil were positively correlated with extractable P, and extractable P was positively correlated with net N mineralization. This result suggests that numbers of fungivores such as Collembola and fungivorous and bacterivorous nematodes may be related to N mineralization in stressed, nutrient-poor systems such as the mesquite dunes. Parker et al. (1984) conclude from studies conducted on the Jornada site that microarthropod grazing on fungi is the most important mechanism for recycling N that has been immobilized by fungi during decomposition of roots.

## Conclusions

Associated with desertification in the Chihuahuan Desert, mesquite has now spread to soils that have lower levels of organic matter and N than its historical habitat such as the playa. We originally proposed that soil biota numbers and N availability would be considerably lower in recent mesquite habitats. We found that biota densities and the N mineralization potential did not vary significantly with habitat, although total C, N, and P concentrations were lower in the recent habitats. This suggests that soil biota numbers are more closely related to the availability/accessibility of soil nutrients like N than to total nutrient pool sizes.

Our evidence suggests that soil P may be an important limiting element in the recent mesquite habitats and may influence N availability in these systems where soil N and P concentrations are very low. The density and trophic structure of soil biota in the recent grassland and dune sites suggest a shift toward fungal-feeding strategies and a lower abundance of belowground herbivores. These differences may be important factors in the changes in plant production and nutrient cycling beneath mesquite canopies that have occurred during desertification of the Chihuahuan Desert.

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## References

- Anderson RV, Coleman DC, Cole CV (1981) Effects of saprotrophic grazing on net mineralization. In: Clark FE, Rosswall T (eds) Terrestrial nitrogen cycles. *Ecol Bull (Stockholm)* 33:201–216
- Baath EBL, Rosswall T, Soderstrom B, Sohlenius A (1981) Impact of microbial-feeding animals on total soil activity and nitrogen dynamics: A soil microcosm experiment. *Oikos* 37:257–264
- Barth RC, Klemmedson JO (1982) Amount and distribution of dry matter, nitrogen, and organic carbon in soil-plant systems of mesquite and palo verde. *J Range Manage* 5:412–418
- Bremner JM, Mulvaney CS (1982) Nitrogen-Total. In: Page AL, Miller RH, Keeney DR (eds) *Methods of soil analysis. Chemical and microbiological properties*. Agron 9, Am Soc Agron, Madison, Wisconsin, pp 595–694
- Buffington LC, Herbel CH (1965) Vegetational changes on a semidesert grassland range from 1958 to 1963. *Ecol Monogr* 35:139–164
- Byrd DW Jr, Barker KR, Ferris H, Nusbaum CJ, Griffin WE, Small RH, Stone CA (1976) Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. *J Nematol* 8:206–212
- Cepeda J (1986) Spatial and temporal patterns of decomposition and microarthropod assemblages in decomposing surface leaf-litter on a Chihuahuan Desert watershed. PhD Thesis, New Mexico State University, Las Cruces, New Mexico
- Cepeda JG, Whitford WG (1989) The relationships between abiotic factors and the abundance patterns of soil microarthropods on a desert watershed. *Pedobiologia* 33:79–86
- Cepeda-Pizarro JG, Whitford WG (1989) Spatial and temporal variability of higher microarthropod taxa along a transect in a northern Chihuahuan Desert watershed. *Pedobiologia* 33:101–111
- Christiansen K (1964) Bionomics of Collembola. *Annu Rev Entomol* 9:147–178
- Coleman DC, Ingham RE, MacClellan JF, Trofymow JA (1984) Soil nutrient transformations in the rhizosphere via animal-microbial interactions. In: Anderson JM, Rayner ADM, Walton DWH (eds) *Invertebrate-microbial interactions*. Cambridge University Press, Cambridge, pp 35–58
- Elkins NZ, Whitford WG (1982) The role of microarthropods and nematodes in decomposition in a semi-arid ecosystem. *Oecologia* 55:303–310
- Fisher FM, Parker LW, Anderson JP, Whitford WG (1987) Nitrogen mineralization in desert soil: Interacting effects of soil moisture and nitrogen fertilizer. *Soil Sci Soc Am J* 51:1033–1041
- Fisher FM, Zak JC, Cunningham GL, Whitford WG (1988) Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *J Range Manage* 41:387–391
- Floret CRP, Rambal S (1982) Measurement and modelling of primary production and water use in a south Tunisian steppe. *J Arid Environ* 5:77–90
- Freckman DW, Baldwin JG (1990) Nematoda. In: Dindal DL (ed) *Soil biology guide*. John Wiley and Sons, New York, pp 155–200
- Freckman DW, Caswell EP (1985) The ecology of nematodes in agroecosystems. *Annu Rev Phytopathol* 23:275–296
- Freckman DW, Mankau R (1986) Abundance, distribution, biomass and energetics of soil nematodes in a northern Mojave Desert ecosystem. *Pedobiologia* 29:129–142
- Freckman DW, Virginia RA (1989) Plant-feeding nematodes in deep-rooting desert ecosystems. *Ecology* 70:1665–1678
- Freckman DW, Whitford WG, Steinberger Y (1987) Effects of irrigation on nematode population dynamics and activity in desert soils. *Biol Fertil Soils* 3:3–10
- Garcia-Moya E, McKell CM (1970) Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51:81–88
- Gee GW, Bauder JW (1986) Particle-size analysis. In: Page AL, Miller RH, Keeney DR (eds) *Methods of soil analysis. Chemical and microbiological properties*. Agron 9, Am Soc Agron Madison, Wisconsin, pp 383–411
- Gile LH, Hawley JW, Grossman RB (1981) Soils and geomorphology in the basin and range area of southern New Mexico: Guidebook to the desert project. *Memoir 39*, New Mexico Bureau of Mines and Mineral Resources, Socorro, New Mexico
- Hennessy JT, Gibbens RP, Tromble JM, Cardenas M (1983) Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *J Range Manage* 36:370–374
- Holt JA (1985) Acari and Collembola in the litter and soil of three north Queensland rainforests. *Aust J Ecol* 10:57–65
- Houghton FE (1972) *Climatic guide*, New Mexico State University, Las Cruces, New Mexico, 1851–1971. *Agric Stn Res Rep* 230:1–20
- Hunt HW, Coleman DC, Ingham ER, Ingham RE, Elliott ET, Moore JC, Rose SL, Reid CPP, Morley CR (1987) The detrital food web in a shortgrass prairie. *Biol Fertil Soils* 3:57–68
- Ingham RE, Trofymow JA, Ingham ER, Coleman DC (1985) Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecol Monogr* 55:119–140
- Jenkins MB, Virginia RA, Jarrell WM (1988) Depth distribution and seasonal populations of mesquite-nodulating rhizobia in warm desert ecosystems. *Soil Sci Soc Am J* 52:1644–1650
- Keeney DR, Nelson DW (1982) Nitrogen-Inorganic forms. In: Page AL, Miller RH, Keeney DR (eds) *Methods of soil analysis. Chemical and microbiological properties*. Agron 9, Am Soc Agron, Madison, Wisconsin, pp 643–698
- Kitchell JE, O'Neil RV, Webb D, Gallepp GW, Bartell SM, Koonce JF, Ausmus BS (1979) Consumer regulation of nutrient cycling. *Bio Science* 29:28–34
- Krantz GW (1978) *A manual of acarology*, 2nd edn. Oregon State University, Corvallis



- Lajtha K, Schlesinger WH (1986) Plant response to variations in nitrogen availability in a desert shrubland community. *Biogeochemistry* 2:29–37
- Lajtha K, Schlesinger WH (1988) The biogeochemistry of phosphorus cycling and phosphorus availability along a desert soil chronosequence. *Ecology* 69:24–39
- Ludwig JA, Flavill P (1979) Productivity patterns of *Larrea* in the northern Chihuahuan desert. In: Lopez EC, Mabry TJ, Tavizon SF (eds) *Larrea*. Centro de Investigacion en Quimica Aplicada, Saltillo, Mexico, pp 130–150
- Nelson DW, Sommers LE (1982) Total carbon, organic carbon, and organic matter. In: Page AL, Miller RH, Keeney DR (eds) *Methods of soil analysis. Chemical and microbiological properties*. Agron 9, Am Soc Agron, Madison, Wisconsin, pp 539–579
- Noy-Meir I (1973) Desert ecosystems: Environment and producers. *Annu Rev Ecol Syst* 5:195–214
- Olsen SR, Sommers LE (1982) Phosphorus. In: Page AL, Miller RH, Keeney DR (eds) *Methods of soil analysis. Chemical and microbiological properties*. Agron 9, Am Soc Agron, Madison, Wisconsin, pp 403–430
- Parker LW, Santos PF, Phillips J, Whitford WG (1984) Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual, *Lepidium lasiocarpum*. *Ecol Monogr* 54:339–360
- Santos PF, DePree E, Whitford WG (1978) Spatial distribution of litter and microarthropods in a Chihuahuan Desert ecosystem. *J Arid Environ* 1:41–48
- Santos PF, Phillips J, Whitford WG (1981) The role of mites and nematodes in early stages of buried litter decomposition in a desert. *Ecol* 62:664–669
- Santos PF, Elkins NZ, Steinberger Y, Whitford WG (1984) A comparison of surface and buried *Larrea tridentata* leaf litter decomposition in North American hot deserts. *Ecology* 65:278–284
- SAS Institute Inc (1985) *SAS user's guide: Statistics, Version 5*. SAS Institute Inc, Cary, North Carolina
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247:1043–1048
- Setälä H, Huhta V (1991) Soil fauna increase *Betula pendula* growth: Laboratory experiments with coniferous forest floor. *Ecology* 72:665–671
- Sharifi MR, Meinzer FC, Nilsen ET, Rundel PW, Virginia RA, Jarrell WM, Herman DJ (1988) Effect of resource manipulation on the quantitative phenology of *Larrea tridentata* (creosote bush) in the Sonoran Desert of California. *Am J Bot* 75:1163–1174
- Silva SI, MacKay WP, Whitford WG (1985) The relative contributions of termites and microarthropods to fluff grass litter disappearance in the Chihuahuan Desert. *Oecologia* 67:31–34
- Silva SI, Whitford WG, Jarrell WM, Virginia RA (1989) The microarthropod fauna associated with a deep rooted legume, *Prosopis glandulosa*, in the Chihuahuan Desert. *Biol Fertil Soils* 7:330–335
- Steinberger Y, Whitford WG (1984) Spatial and temporal relationships of soil microrthropods on a desert watershed. *Pedobiologia* 26:275–284
- US Salinity Laboratory Staff (1954) *Methods for soil characterization (Alkaline-earth carbonates by gravimetric loss of carbon dioxide)*. In: Richards LA (ed) *Diagnosis and improvement of saline and alkali soils*. Agric Handb no 60, USDA, US Government Printing Office, Washington, DC
- Virginia RA (1986) Soil development under legume tree canopies. *For Ecol Manage* 16:69–79
- Virginia RA, Jarrell WM (1983) Soil properties in a mesquite-dominated Sonoran Desert ecosystem. *Soil Sci Soc Am J* 47:138–144
- Wallwork JA, Kamill BW, Whitford WG (1985) Distribution and diversity patterns of soil mites and other microarthropods in a Chihuahuan Desert site. *J Arid Environ* 9:215–231
- Walter DE (1987) Trophic behavior of “mycophagous” microarthropods. *Ecology* 26:226–229
- West NE (1981) Nutrient cycling in desert ecosystems. In: Goodall DA, Perry RA (eds) *Arid land ecosystems: Structure, functioning and management*, vol 2. Cambridge University Press, Cambridge, pp 301–324
- West NE, Klemmedson JO (1978) Structural distribution of nitrogen in desert ecosystems. In: West NE, Skujins JJ (eds) *Nitrogen in desert ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp 1–16
- Whitford WG, Reynolds JF, Cunningham GL (1987) How desertification affects nitrogen limitation of primary production on Chihuahuan Desert watersheds. In: Moir WH, Gonzales-Vicente CE, Adon EA (eds) *Proc Symp on Strategies for Classification and Management of Natural Vegetation for Food Production in Arid Zones*. Gen Tech Rep RM-150. U.S. Forest Service, Fort Collins, CO, pp 143–153
- Whitford WG, Parker LW (1989) Contributions of soil fauna to decomposition and mineralization processes in semiarid and arid ecosystems. *Arid Soil Res Rehabil* 3:199–215
- Whitford WG, Freckman DW, Parker LW, Schaefer D, Santos PF, Steinberger Y (1983) The contributions of soil fauna to nutrient cycles in desert systems. In: Lebrun P, Andre HM, DeMedts A, Gregoire-Wibo C, Wauthy G (eds) *New trends in soil biology*. Dieu-Brichart, Ottignies-Louvain-la-Neuve, Belgium, pp 45–59
- Whitford WG, Reynolds JF, Cunningham GL (1987) How desertification affects nitrogen limitation of primary production on Chihuahuan Desert watersheds. In: Moir WH, Gonzales-Vicente CE, Adon EA (eds) *Proc Symp on Strategies for Classification and Management of Natural Vegetation for Food Production in Arid Zones*. Gen Tech Rep RM-150. U.S. Forest Service, Fort Collins, CO, pp 143–153
- Whitford WG, Stinnet K, Steinberger Y (1988) Effects of rainfall supplementation on microarthropods on decomposing roots in the Chihuahuan Desert. *Pedobiologia* 31:147–155
- Wood TG (1971) The distribution and abundance of *Folsomodes deserticola* (Collembola: Isotomidae) and other microarthropods in arid and semi-arid soils in Southern Australia, with a note on nematode populations. *Pedobiologia* 11:446–468
- York JC, Dick-Peddle WA (1969) Vegetation changes in southern New Mexico during the past hundred years. In: McGinnies WG, Goldman BJ (eds) *Arid lands in perspective*. Univ Arizona Press, Tucson, Arizona, pp 157–166