

Interactions among Soil Biota in Desert Ecosystems

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ABSTRACT

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In desert systems, the availability of soil nitrogen can be the single most limiting factor controlling plant growth during periods of adequate soil moisture. Decomposition and nitrogen-mineralization rates prior to or during peak periods of plant growth can therefore be critical. Decomposition rates in deserts are generally high, and are relatively independent of rainfall. These high rates can be attributed to a combination of abiotic weathering, the types of microflora and microfauna associated with plant litter, and the adaptations of the soil biota to moisture pulses.

The factors controlling litter decomposition and subsequent nitrogen mineralization are dependent upon the location of the organic matter in the habitat. The breakdown of surface litter occurs primarily through either abiotic weathering or by termite consumption. Microarthropods do not appear to have any role in the decomposition of surface litter owing to abiotic constraints on activity. The decomposition of roots, and buried litter, however, has been shown to be dependent on the presence of soil microarthropods. Microbial-microfaunal activity in the root region of desert plants may also have a significant effect on the short-term cycling of nitrogen in arid systems.

INTRODUCTION

Plant growth in desert environments is regulated primarily by rainfall patterns and seasonal temperature maxima. Fisher et al. (1988a) found that shoot and fruit production in *Larrea tridentata*, (creosotebush) the dominant evergreen shrub in the Chihuahuan Desert, was highest in late spring, before the summer drought, with a second pulse in primary production during the late summer rainy season. During those years when there is an abundance of moisture in the winter months, annual plant production in the Chihuahuan Desert can be very high (Ludwig and Whitford, 1981) equaling perennial plant production. When two wet seasons occurred in succession, Parker et al. (1984) found that shrub and/or annual plant production was reduced in the second year (Table 1). Parker et al. (1984) hypothesized that the large pulse of or-

TABLE 1

The responses of net primary production to different rainfall patterns in the northern Chihuahuan Desert

Vegetation	Biomass (kg ha ⁻¹)	
	Above-ground	Below-ground
Creosotebush		
2 wet years ¹	636	347
2 dry years	2226	1213
Winter-Spring annuals		
2 wet years	63	63
2 dry years	2	2

¹Wet year = rainfall during all seasons; dry year = summer rainfall only, data from Parker et al. (1984).

TABLE 2

Effects of supplemental rainfall on net above-ground primary production of creosotebush and potential nitrogen mineralization of soils by laboratory incubation¹

Supplemental water	Production ² (g m ⁻² year ⁻¹)	Soil nitrogen, NH ₄ + NO ₃ ³ (mg N kg ⁻¹ soil)
0 mm	196 ^a	17.2 ^a
6 mm week ⁻¹	262 ^a	6.1 ^b
25 mm month ⁻¹	248 ^a	7.4 ^b
Fertilization		
- N	179 ^a	
+ N	291 ^b	

¹Numbers followed by different superscripts are significantly different at $P=0.005$.

²Data from Fisher et al. (1988a).

³Data from Fisher et al. (1987).

ganic matter entering the system from the annual plants after the first growing season resulted in soil nitrogen depletion during the wet season, as a consequence of N immobilization by fungi. They speculated that the fungi were better competitors for available soil N than plant roots. Ettershank et al. (1978) had also found that low nitrogen availability could reduce plant growth during periods of adequate soil moisture.

A series of 10 × 10-m plots was established in the creosotebush zone of the Jornada LTER site to examine the interactions between water and nitrogen availability on plant growth and nitrogen mineralization. Shrub production was estimated by measuring growth increments of tagged branches and dry weights at the end of the 9-month growing season.

Supplemental rainfall did not increase total shoot biomass significantly (Table 2). The lack of response to additional moisture may have resulted from low nitrogen mineralization (Table 2) limiting plant growth. In plots receiving nitrogen fertilizer, shoot production was greater ($P \leq 0.05$) than in nonfertilized plots.

Studies by Fisher et al. (1988a) with creosotebush and by Gutierrez and Whitford (1987) on the effects of supplemental water on annual plant growth have supported the hypothesis that, in the Chihuahuan Desert, the availability of soil nitrogen can be the single most limiting factor controlling plant growth during periods of adequate soil moisture. Abiotic and biotic constraints on decomposition and nitrogen mineralization rates prior to or during peak periods of plant growth can therefore be critical and may limit primary production.

DECOMPOSITION DYNAMICS

Surface litter

Plant litter accumulates either directly under shrubs, in rodent excavations (Steinberger and Whitford, 1983), or in debris dams in arroyos following rain events. Recent work (Loring et al., 1988a) has shown that woody litter may be concentrated primarily in wood-rat middens. Mass loss of surface litter in the Chihuahuan Desert is affected significantly by subterranean termites (Silva et al., 1985; Whitford et al., 1982). Termite grazing accounted for 50% of the mass loss from litter of *Baileya multiradiata*, *Erioneuron pulchellum*, *Eriastrum diffusum* and *Lepidium lasiocarpum* during the 2 months of maximum surface activity (September–October) in the Chihuahuan Desert (Whitford et al., 1982). Silva et al. (1985) estimated that termites accounted for 90% of the mass loss of fluffgrass, *E. pulchellum*, litter (Fig. 1). Mass loss of creosotebush wood (Zak et al., 1988) was also significantly greater with termite grazing than without. Preliminary analysis indicated that creosotebush wood (1–2-cm diameter) occurring on the soil surface may take up to 100 years to decompose fully, unless grazed by termites.

Grazing of surface litter could also affect subsequent decomposition indirectly, through nitrogen additions during gallery construction and by altering the species composition of fungal assemblages associated with the litter. Termite carton is composed of soil particles, mud and fecal material (MacKay et al., 1985). The addition of nitrogen from termite feces could provide sufficient nitrogen, following grazing, to increase fungal activity and subsequent decomposition rates. Isolations made from grazed and ungrazed creosotebush wood (Table 3) revealed that the structure and composition of the fungal assemblages were altered following grazing. By altering the fungal species composition of litter, either through selective grazing or by changing the nutrient status of the material as a result of gallery construction, subterranean termites may

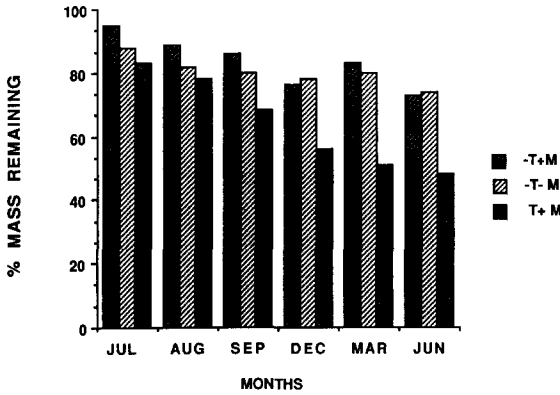


Fig. 1. The effects of termites and mites on mass losses of fluff grass *Erioneuron pulchellum* (data from Silva et al., 1985).

TABLE 3

Dominant fungi associated with grazed and ungrazed creosotebush wood¹

Taxa	Percentage frequency of occurrence ($\bar{x} \pm SD$)	
	Ungrazed	Grazed
<i>Alternaria alternata</i>	9 ± 2	0
Basidiomycete	0	6 ± 2
<i>Coleophoma</i> sp.	84 ± 4	25 ± 25
<i>Coniothryium</i> sp.	8 ± 4	43 ± 27
<i>Fusarium acuminatum</i>	8 ± 6	14 ± 20
Sterile hyaline (G-024)	0	15 ± 20
Sterile dark (W-007)	8 ± 13	0

¹J. Zak, unpublished data (1988).

be important regulators of microbial activity associated with surface litter in the Chihuahuan Desert.

Studies by Silva et al. (1985), MacKay et al. (1986), and Whitford et al. (1986) have shown that although surface litter accumulations are colonized by a diverse group of microarthropods, the soil microfauna have no apparent effect on rates of decomposition. Silva et al. (1985) concluded that microarthropod densities in fluffgrass litter were too low to have a measurable effect on decomposition rates. Furthermore, even at higher densities, MacKay et al. (1986), also found no effect of the soil microarthropods on creosotebush surface-litter decomposition rates. Whitford et al. (1986) suggested that at the low moisture tensions characteristic of surface litter during most of the day, microarthropod activity would be severely limited. Even with supplemental

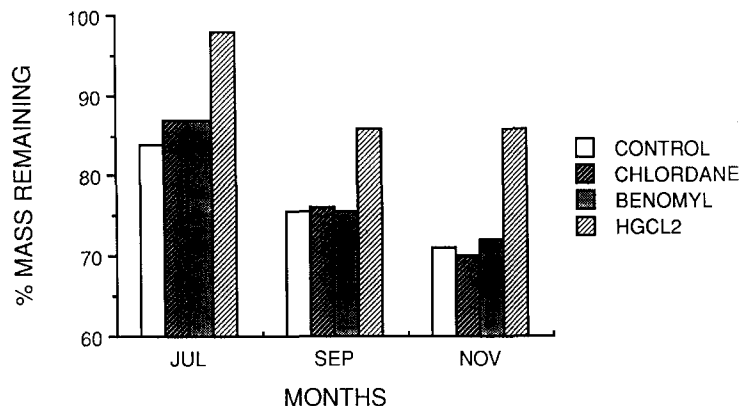


Fig. 2. The effects of excluding groups of soil biota on mass losses of creosotebush, *Larrea tridentata* litter (chlordane eliminated microarthropods, benomyl reduced fungi, and HgCl_2 eliminated virtually all biota resulting in abiotic mass loss) (data from Loring et al., 1988b).

rainfall, rates of creosotebush litter decomposition, and biomass of the soil biota were not significantly altered (Whitford et al., 1981). These results indicate that decomposition rates of surface litter are independent of rainfall (Whitford and Freckman, 1988) and mass loss may be the result of abiotic weathering and termite grazing.

Surface litter in desert systems is exposed to intense ultraviolet radiation and high temperatures during summer months, which can result in loss of structural integrity and subsequent fragmentation (Pauli, 1964). Vossbrinck et al. (1979) reported that abiotic factors accounted for 3–5% of the mass loss of surface litter in a shortgrass prairie. Using selected biocides, Loring et al. (1988b) examined the roles of fungi, microarthropods and abiotic weathering on mass loss of creosotebush litter during the summer months in the Chihuahuan Desert. Their results (Fig. 2) indicated that abiotic weathering accounted for 15% of the mass loss in creosotebush litter over a 5-month period. Silva et al. (1985) also reported significant mass loss from fluffgrass litter during the summer months even when termites and mites were excluded from the litter. Although the HgCl_2 - CuSO_4 -treated litter lost less mass than the other treatments, the net mass loss rate for the period July–September was similar to that in the other treatments. The higher air and soil temperature and levels of ultraviolet radiation during the summer months coupled with summer rains also occurring during this period, could have resulted in increased fragmentation and subsequent mass loss from the litter. These results indicate that abiotic weathering can have a major role in regulating mass loss and subsequent decomposition of surface litter in desert systems.

Wood-rat middens

Dead wood can be a significant component of the total carbon pool and may be an important nutrient sink in desert systems (Ettershank et al., 1978; Bam-

TABLE 4

Average quantities of dead wood in wood rat (*Neotoma* spp.) nests and in the common habitats in the Chihuahuan and Sonoran Deserts¹

Habitat	Wood in midden (kg ha ⁻¹)	Surface + standing dead (kg ha ⁻¹)	Percentage in midden
Chihuahuan Desert	95.8	1208	7.9
Upper Bajada			
Playa (Mesquite Fringe) ²	2447.6	7187	34.0
	471.8		7.0
Playa (Mesquite-Atriplex Fringe)	756.0		
Sonoran Desert			
Upland Cercidium- Saguaro	1435.0	3460	41.5

¹Data from Loring et al. (1988a).

²Values are for the highest and lowest density estimates per sector.

TABLE 5

Micro- and macrofauna associated with wood-rat middens in the Chihuahuan and Sonoran Deserts¹

Class: Insecta	
Orders:	
Siphonaptera	(fleas)
Psocoptera	(psocids, "book lice", "bark lice")
Orthoptera	(grasshoppers, crickets, mantids)
<i>Gryllus</i> spp.	
<i>Ceuthophilus pallidus</i>	
Hymenoptera	
Formicidae	(ants)
Isoptera	(termites)
Coleoptera	(beetles)
Tenebrionidae	(darkling beetles)
Carabidae	(ground beetles)
Curculionidae	(snout weevils and others not yet identified)
Collembola	
Myriapoda	
Class: Diplura	
Japygidae	
Class: Chilopoda	(centipedes)
Scolopendramorpha	
Arachnida	
Acarina	(mites)
Aranida	(spiders)
Scorpiones	(scorpions)

¹Data from Loring et al. (1988a).

TABLE 6

Effect of wood-rat middens on organic matter and nitrogen content of Chihuahuan Desert soil¹

	Under midden	3-m away
NO ₃ -N (mg kg ⁻¹)		
Black grama grassland	8.3** ± 3	0.7 ± 0.4
Playa	121.5** ± 14.8	9.3 ± 2.3
NH ₄ -N (mg kg ⁻¹)		
Black grama grassland	6.5 ± 4.5	0.4 ± 0.9
Playa	17.0** ± 0.2	1.2 ± 0.02
Total N (mg kg ⁻¹)		
Grassland and playa combined	1334** ± 835	537 ± 67
Percentage soil organic matter ($\bar{x} \pm SD$)		
Grassland and playa combined ²		
0-5 cm	2.3 ^a ± 0.4	1.0 ^b ± 0.4
5-10 cm	2.0 ^a ± 0.4	1.3 ^a ± 0.6

¹Data from Loring et al. (1988a).²For each depth, means with different superscripts are significantly different at $P \leq 0.01$.** = $P \leq 0.01$.

berg et al., 1980). Wood on the soil surface, unless grazed by termites, decomposes at an extremely slow rate. Any mechanism which concentrates woody litter and stimulates microbial decomposition is extremely important in these habitats. Recent studies in the Chihuahuan and Sonoran Deserts suggest that wood rats (*Neotoma* spp.) may play a major role in wood decomposition as a result of their midden-building activities.

Wood-rat middens are significant features of these desert landscapes (Table 4). The interior of a nest usually contains a large organic duff, similar to the litter layer in mesic woodlands, which is colonized by a rich macro- and micro-fauna (Table 5). While these arthropods can be found in other habitats, their densities are far greater in middens than reported previously for other desert habitats. Total soil N, NO₃ and NH₄ concentrations and organic-matter content (Table 6) are higher ($P < 0.01$) under middens than 3 m away. Wood-rat middens may represent islands of intense microfaunal and microbial activity and could significantly affect nutrient decomposition in habitats where they are numerous.

Buried litter and plant roots

Decomposition rates of surface litter, translocated below ground as a result of wind and water action, and of plant roots, have been found to be regulated

by microarthropod activity. Santos and Whitford (1981) reported that the soil microfauna uncoupled decomposition from abiotic constraints, thereby resulting in a higher rate of decomposition. When buried creosotebush litter was treated with selective biocides to eliminate either microarthropods, fungi and/or nematodes, Santos et al. (1981) found that decomposition was reduced significantly in all litter with biocide treatments but particularly in those treatments where fungi, nematodes and/or microarthropods were removed or reduced (Fig. 3). When microarthropods were excluded, decomposition rates varied directly with rainfall.

During decomposition of buried creosotebush litter, Santos and Whitford (1981) showed, by using an overlapping sequence of litter bags, that as the material decomposed specific groups of microarthropods were associated with the litter. The initial colonizers of buried litter were tydeid mites, regardless of the season of burial. Tarsonemid mites were the next group of colonizers and reached peak population levels after 30–40% of the initial mass was lost. The tarsonemids associated with the litter bags were primarily fungal feeders and apparently entered the litter as fungal biomass increased. The predatory gamasid mites and the more generalist collembolans and psocopterans were the last group associated with the litter. Following establishment of the predatory mites, Gamasidae and Prostigmata, densities of tarsonemids and pygmephorid (pyemotid) mites declined, suggesting a food-web relationship existed between fungi, tarsonemids and the predatory mites. By using selected biocides, Santos et al. (1981) examined the trophic interactions between the soil microflora and microfauna during decomposition of buried creosotebush litter. They concluded that microarthropods regulated decomposition rates by preying upon nematodes, which in turn graze upon bacteria. When mites were eliminated, densities of bacterial-feeding nematodes increased and resulted in a 40% decrease in mass loss compared with litter bags with only mites.

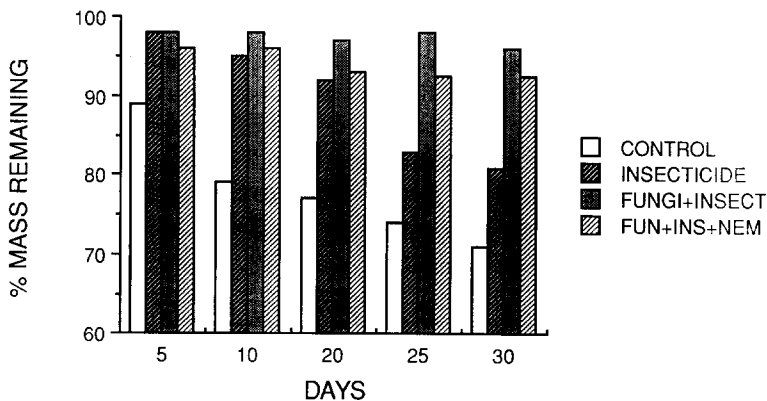


Fig. 3. The effects of excluding and/or reducing various groups of soil biota on mass losses of buried creosotebush leaf litter (data from Santos et al., 1981).

TABLE 7

The importance of microfloral-microfauna interactions on root-decomposition dynamics¹

Treatment	Mass loss (Kw) day ⁻¹	Carbon mineralization (Km) day ⁻¹	Biomass carbon 96 days (g m ⁻²)
Control ²	0.0043 ^a	0.0048 ^a	32.5 ^a
Insecticide	0.0019 ^b	0.00036 ^b	27.8 ^b
Fungicide plus insecticide	0.0016 ^b	0.00016 ^c	13.5 ^c

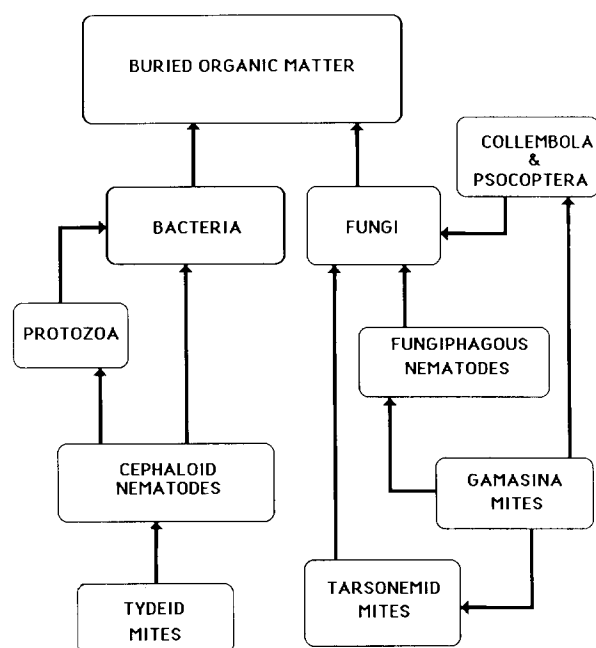
¹Data from Parker et al. (1984).²For each column, means with different superscripts are significantly different at $P \leq 0.05$.

Fig. 4. Trophic relationships among soil biota in buried litter (data from Santos and Whitford, 1981).

The importance of microfloral-microfaunal interactions in regulating decomposition and C and N mineralization rates was examined by Parker et al. (1984) using biocide-treated litter and the roots of a desert annual, *Lepidium lasiocarpum*. Parker et al. (1984) found that decomposition rates, C mineralization and biomass C were reduced significantly when microarthropods were

eliminated (Table 7) and that these processes were reduced even further when fungi were eliminated together with soil microarthropods. They used a stepwise regression to account for variation in total soil N and $\text{NH}_4\text{-N}$ ($r=0.53$, $P\leq 0.001$). In chlordane treatments, $\text{NH}_4\text{-N}$ was correlated with nematode and protozoan populations ($r=0.86$, $P\leq 0.009$).

Interrelationships between the soil biota during the decomposition of buried litter in the Chihuahuan Desert are summarized in Fig. 4. Data from Santos and Whitford (1981) and Parker et al. (1984) have emphasized the importance of grazing by soil microarthropods and nematodes of fungi and bacteria, as regulators of decomposition and nitrogen fluxes in desert systems. These processes are especially important following years of high ephemeral plant production with attendant nitrogen immobilization by bacteria and fungi during decomposition. Without grazing of the microflora by the soil microfauna, primary production of perennial plants would be reduced significantly owing to decreased nitrogen availability.

ROOT-REGION INTERACTIONS

The root region or rhizosphere represents an important center of microbial activity, affecting nutrient availability and the nutrient-uptake process (Parkinson, 1967; Bowen and Roviera, 1976; Coleman, 1976). Microcosm studies by Anderson et al. (1981) Baath et al. (1981) and Coleman et al. (1984) have shown that grazing of the rhizosphere microflora by microarthropods and nematodes, may increase the rates of N mineralization within the root region and thus affect plant growth. Ingham et al. (1985) suggested that in semi-arid habitats, the effects of microbivores grazing on the microflora and mineralizing nitrogen may be particularly important when nutrient demand by the plant exceeds the rate of mineralization by the microflora alone.

A series of field studies was begun at the Jornada LTER site in the northern Chihuahuan Desert, in November 1986, in conjunction with Dr. Diana Freckman, U.C. Riverside. Selected biocides were used to examine the effects of microbial grazing by rhizosphere microfauna, and predation of nematodes by microarthropods, on the structure and composition of the root-region microflora of a desert grass, *Erioneuron pulchellum* (fluffgrass), and plant and root-region nutrient dynamics. The treatments included an insecticide (chlordane), a nematicide (nema-cur) and a control. Two months following biocide application, nematode and microarthropod densities and trophic groups were assessed, species numbers and composition of rhizosphere and root surface fungi estimated, along with shoot and root biomass and plant and soil nitrogen status.

Fungal densities were significantly higher on the root surface than in the rhizosphere (Table 8). The rhizosphere is defined here as the soil within the root region of the plant. The higher density of fungal hyphae on the root surface may reflect a more favorable habitat than the rhizosphere soil and suggest that for desert plants, the root surface rather than the rhizosphere may be the

TABLE 8

Relative density of fungi isolated from the rhizosphere and root surface of fluffgrass

Treatment	Number of particles producing colonies (\bar{x} (%) \pm SD)	
	Rhizosphere	Root surface
Initial (October 1986) 2 months following biocide application	4.2 \pm 10.7	88.2 \pm 11.1
Control	2.5 \pm 3.6	79.5 \pm 8.5
Chlordane	4.7 \pm 6.3	83.8 \pm 6.7
Nemacur	3.5 \pm 3.1	72.0 \pm 6.3

For rhizosphere soil and root segments, 50 particles were plated per treatment following ten 2-min washes.

center of microbial activity. Elliott et al. (1984) have suggested that, in general, root surface microflora may play a more important role in microbe-plant interactions than the rhizosphere. Although there were no quantitative differences between treatments, preliminary identification of the fungal isolates indicates that species composition had been altered.

The lack of quantitative changes in the root surface fungi following application of the insecticide or nematicide suggest that although microfaunal grazing may affect fungal species composition, grazing may have no effect on overall fungal activity. With a large fungal species pool in the root region to draw upon, the loss of one species, as a result of selective grazing, may simply allow an equivalent species which is not grazed to colonize the root surface. The consequences of these interactions are no measurable effects on nutrient dynamics, and a steady rate of mineralization, unless the system is severely stressed.

Total numbers of nematodes per 100 g dry weight of soil were not significantly different among the treatments 2 months after application of the chemicals. However, the densities of bacteriovores and omnivore-predators were reduced in the chlordane and nemacur treatments. Whether these differences were sufficient to cause changes in nutrient dynamics in the root system is unclear at this time.

Preliminary identification of microarthropods has indicated that numbers of species and their composition were similar in the nemacur and control plots at the 2-month sampling period. Densities of microarthropods were, as expected, lowest in the chlordane-treated plots. However, these plots did contain the highest number of species, but at low frequencies of occurrence.

CONCLUSIONS

The Chihuahuan Desert is characterized as a water-regulated, nitrogen-limited system. Although primary production is dependent on rainfall pattern and

soil moisture, availability of soil nitrogen can severely limit plant growth. During peak periods of plant growth, abiotic and biotic factors controlling decomposition and mineralization rates became critical. For surface litter, mass loss occurs through a combination of termite grazing during the summer rainy season, July–October, and by abiotic weathering. Owing to temperature and moisture constraints on activity, the soil microfauna did not appear to be important in the decomposition of surface litter.

Wood-rat middens may represent islands of intense microfloral and microfaunal activity in desert systems and may be important sites of wood decomposition. These collections of organic material are colonized by a large assemblage of microflora and microfauna at densities not previously found in desert systems. Soil organic-matter content, total N and levels of $\text{NO}_3\text{-N}$ and NH_4 are higher under the middens and decrease with increasing distance from the middens. By concentrating nutrients and organic matter, wood rats may have a significant effect on plant spatial patterns and primary productivity.

The decomposition and mineralization rates of roots and surface litter translocated below ground is regulated by trophic interactions between the soil biota. Microarthropods are the top trophic group, preying upon nematodes and also grazing directly on bacteria and fungi. Nematodes exert their control by feeding on protozoans, bacteria and fungi.

The importance of root-region microfloral–microfaunal interactions in short-term nutrient dynamics has only recently been examined in desert systems. Preliminary results indicate that microfloral activity is confined to the root surface. As a consequence of low soil moisture occurring for a considerable portion of the year in desert systems, and the ameliorating effect of root exudates, the root surface, rather than the rhizosphere, may be the center of intense microbial activity.

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