

# Contributions of Soil Fauna to Decomposition and Mineralization Processes in Semiarid and Arid Ecosystems

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**Abstract** *This review examines the following questions: (1) do soil fauna play an important regulatory role in decomposition and mineralization processes in arid and semiarid ecosystems? (2) if important, what are the mechanisms of the rate regulation, and (3) what are the management implications of these relationships? Because termites process more than half of the surface litter in hot deserts, this review focuses on faunal effects on buried litter and roots. Elimination of soil arthropods reduced rates of mass loss and coupled mass loss to soil moisture. With arthropods present soil moisture accounted for less than 50% of the variation in mass loss. Other experiments demonstrated that regulation of mass loss results from predatory mites regulating the population density of grazers, thereby preventing overgrazing of the fungi and bacteria. The regulation of microbial grazers by soil microarthropods also affects rates of mineralization and nutrient immobilization. Populations of small fungus grazing mites (*Tarsonomidae*) affect mineralization directly. Microarthropods tend to uncouple mineralization from abiotic constraints. Fluctuations in microbial populations and soil fauna are more a function of substrate availability than of abiotic regulation. Pulses in organic matter inputs result in periods of nutrient immobilization, the extent of which is a function of the rate of recovery of populations of key soil microarthropods.*

## Introduction

Desertification is an ever-increasing problem in semiarid areas of the earth. In these areas, water is not necessarily the most important factor limiting primary production (Penning de Vries and Djiteye 1982). These workers and others (Ettershank *et al.* 1978, Floret *et al.* 1982) point to nutrient deficiencies (especially nitrogen) as factors reducing primary production. Indeed, in the semiarid regions of the world that are most severely impacted by desertification, drought only exacerbates the gradual deterioration of these ecosystems. Because nitrogen appears to be an important factor limiting productivity, we have concentrated much of our work on nitrogen mineralization and immobilization processes and the roles of microflora and fauna in these processes. Here we review the data obtained in these studies.

The causes of degradation (desertification) of semiarid lands are beyond the scope of this work, but it is certain that a lack of understanding of the processes maintaining equilibrium in such systems is a major contributor. The degradation of semiarid lands involves both soil and vegetation, although most work has focused on the vegetation. In this article, we emphasize the necessity of taking a whole system approach to understanding the contributions of the soil biota to the stability of semiarid ecosystems and in the development of technology utilizing this biota to reverse the desertification process. It is our view that it is necessary to approach such a problem in an ecosystem context. In the ecosystems paradigm, microorganisms and microbial processes are viewed as system components that use and transform energy and chemicals in their life processes. The rates of energy flow and nutrient transformation are regulated by a number of abiotic parameters, e.g., moisture, temperature, soil chemistry, soil structure, etc., and by biotic interactions among microorganisms and between microorganisms and other biota.

Taking that paradigm one step further, we can view the soil as a subsystem of the whole ecosystem, in which the other system components provide inputs and to which the outputs of the soil subsystem flow (Fig. 1). In a stable system the processes within the soil subsystem are maintained at rates that balance inputs and outputs. In this equilibrium model, the internal rate regulators of the subsystem play an important role because imbalances in these components affect the equilibrium of the entire system. One can view

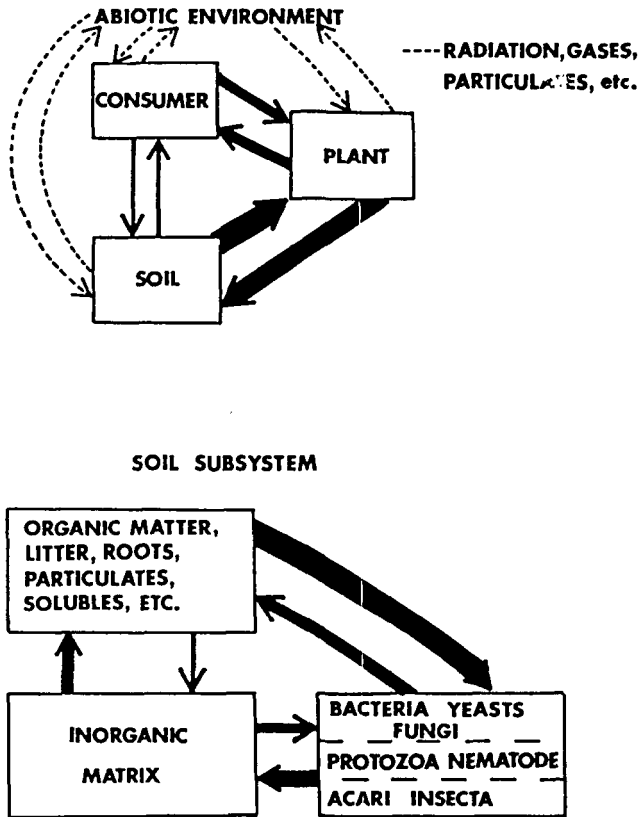


Figure 1. Diagrams of the ecosystem paradigm. The upper figure shows the exchanges from the atmospheric abiotic environment that act as driving variables and general input-output relationships. The lower figure provides information on exchanges within the soil subsystem.

desertification as perturbation or series of perturbations that affect one or more components of the system pushing those components above or below the normal boundaries of variation within which they operate. The perturbations thus produce a change of state of the system that affects rates of processes. An imbalance in rates of key processes then creates "bottlenecks," which affect the flow of energy or cycling of nutrients. If some outside agent does not perturb the system, forcing it in the opposite direction, the system may stabilize at a new equilibrium point with a structure very different from that of the original system.

We address three questions here. (1) Do soil fauna play an important regulatory role in decomposition and mineralization processes in semiarid and arid ecosystems? (2) If soil fauna are important, what are the mechanisms by which this rate regulation is achieved? (3) What considerations of soil fauna need to be made when using organic amendments, mycorrhizae, cyanobacteria, etc., in attempts to reverse effects of desertification processes in semiarid environments?

### Experimental Approaches

If we are to understand the contributions and interrelationships of organisms in the soil, we must design experiments that allow us to dissect out parts of the system and then examine how the system works in the absence of that part. In order to eliminate certain biota from the system under study, we have used selected biocides alone or in combination. Based on the literature evaluation of effects on nontarget organisms, we used chlordane, a persistent chlorinated hydrocarbon insecticide, in combination with fungicides (Santos and Whitford 1981, Parker *et al.* 1984, Parker *et al.* 1985). We also used a soil sterilant, Nemagon, that eliminated both nematodes and microarthropods (Santos *et al.* 1981).

In our experiments, we have attempted as far as possible to estimate population sizes of all major groups of soil biota and to measure changes in nitrogen and carbon pools. By relating changes in rates of decomposition and mineralization to experimentally induced changes in soil biota, we have been able to examine relationships between soil fauna and microorganisms not heretofore possible.

Another approach that has elucidated relationships between soil organisms is the microcosm or gnotobiotic systems (Anderson *et al.* 1978, 1979, 1981, Coleman *et al.* 1978, Elliot *et al.* 1979a,b). In this approach, systems are simplified in that a single species of bacteria, fungi, protozoan, or nematode is generally used. The point of reference may be a sterile root in a sterile soil, or sterile plant materials, chitin, cellulose, etc., that provides the energy base for the system. More complex microcosms have been used in which whole groups of organisms are inoculated into the sterile substrate (Coleman *et al.* 1984, Parker *et al.* 1985). This approach has the advantage of providing a clear picture of relationships between taxa and the teasing out of feeding relationships not possible in the field situation. It also avoids use of chemicals that may affect nontarget organisms, thus confusing the interpretation of the experiment. However, microcosms do not mimic the real world in either the abiotic fluctuations or the complex fauna and microflora that are found in a soil. In systems where abiotic constraints on processes are very important, microcosms have limited utility.

### The Fauna

In a 1982 book, Wallwork reviewed the status of our knowledge of soil faunas in arid and semiarid ecosystems. The fauna of such regions contains representatives of most of the

major taxa found in soils of mesic areas. However, it is here that similarities between mesic and arid systems stop.

In arid regions, soil animals exhibit a patchy distribution, which is a function of the distribution of litter and organic material. The relationship between litter and soil fauna is well documented for nematodes (Freckman and Mankau 1977) and microarthropods (Santos *et al.* 1978, Franco *et al.* 1979, Santos and Whitford 1983). Dead roots of annual and perennial plants also serve as foci for populations of soil organisms (Parker *et al.* 1984a, Whitford *et al.* 1988).

The largest fraction of the biomass of soil animals in most arid and semiarid ecosystems is that of termites (Lee and Wood 1971, Johnson and Whitford 1975). Most termites harbor a complex assemblage of microorganisms as gut symbionts that are essential for these insects to utilize dead plant material (Breznak 1984). Because these insects move through galleries in the soil, they can harvest materials from the surface even when soils are dry (MacKay *et al.* 1986). The materials consumed by termites include dead stems, leaves, roots, and dung (Whitford *et al.* 1981, Silva *et al.* 1985, MacKay *et al.* 1987, Whitford *et al.* 1988). Thus a large fraction of materials on the soil surface are decomposed and mineralized by the symbiotic microorganisms in the gut of these insects. In this article, we emphasize decomposition and mineralization of dead plant materials that are buried by physical processes or roots that are in the soil and processed primarily by soil biota other than termites.

Most of the soil fauna feed directly on bacteria, yeast, or fungi. In organic matter patches protozoans are common. The desert soil protozoan fauna is dominated by amoeboid forms, although some ciliates are part of the protozoan community (Parker *et al.* 1984b). The protozoans are dependent upon soil moisture for their activity, and remain inactive as cystic forms in dry soils (Parker *et al.* 1984b). The protozoans feed on both bacteria and yeasts, which are especially abundant on litter and roots in the early stages of decomposition.

The nematode fauna is dominated by bacteriophagous species, which account for approximately 48% of the nematode biomass in our Chihuahuan desert soils (D. Freckman, personal communication). Bacteriophagous nematodes may feed on yeasts and protozoans in addition to bacteria. The other group that constitutes a major part of desert soil nematode fauna is composed of omnivore predators. These nematodes are equipped to feed on bacteria, fungi, yeast, protozoans, and other nematodes. When we examined the nematode fauna around decomposing annual plant roots, we found a shift from bacteriophagous to fungiphagous forms through time (Parker *et al.* 1984a).

Microarthropods form a diverse group of organisms, but by far the most numerous and most important in desert soil processes are the acari (mites). One mite family, the Nanorchestidae, is relatively abundant even in bare soils. Santos and Whitford (1983) even found a nanorchestid *Spelorchestes* in the unvegetated dunes in the center of a gypsum dune field in southern New Mexico. These mites are thought to feed on cyanobacteria or other soil algae. Other than the nanorchestids, soil mites are generally found associated with plant litter and roots. In North American hot deserts, tydeid mites were numerous in buried litter (Santos *et al.* 1983) and are abundant in both buried and surface litter in the Negev Desert in Israel (Steinberger and Whitford, unpublished data) and in mulga, *Acacia aneura*, woodlands in northwestern New South Wales, Australia (Noble and Whitford, unpublished data). In the Chihuahuan desert, small fungus feeding tarsonemid and pyemotid mites are extremely abundant on roots and in buried litter. Desert soil microarthropod faunas are dominated by prostigmatid mites in contrast to more mesic systems in which cryptostigmatid (oribatid) mites predominate (Santos *et al.* 1978,

Franco *et al.* 1979). In semiarid regions cryptostigmatid mites are found in surface litter accumulations. Many of the prostigmatids are small fungus feeding forms like tarsonemids and pyemotids or are larger predatory forms like Bdellids. These predators may feed on small mites or on nematodes (Elkins and Whitford 1982).

Collembola and Psocoptera appear to be important during certain times of the year when the soil is wet. These organisms are very dependent upon soil moisture for their activity (Poinsot-Balaguer 1976, Poinsot 1968); hence their importance in decomposition and mineralization may be limited.

In arid and semiarid ecosystems the relationship between soil moisture and the growth and activity of organisms is of extreme importance. Bacteria and yeast require water for growth, but because of their small size and short time requirements for cell division they may be capable of growing on leaf and root surfaces even in dry soils due to water films on these surfaces. It is also possible that bacteria and yeast populations may be able to grow in surface litter during the short period each day when litter moisture is high (Whitford *et al.* 1981), but this has yet to be confirmed. In contrast to bacteria and yeasts, fungi grow at low soil moisture tensions  $< -40$  MPa (Griffin 1981). Of all the desert soil fauna only microarthropods are active all or most of the time (Santos and Whitford 1981, Whitford *et al.* 1981, MacKay *et al.* 1986). Some acari are active in surface leaf litter accumulations during the early morning hours even when the soils are oven dry (Whitford *et al.* 1981). In contrast, nematodes, protozoans, and collembolans are active only when soils are wet (Greenslade 1982, Freckman and Womersley 1983). The result of these soil moisture limitations is that during most of the year mass loss and mineralization processes occur via the interactions of fungi and soil acari.

Studies in Africa, Australia, Israel, and North America have pointed to the taxonomic similarities in soil microarthropods from these deserts (Santos *et al.* 1978, Franco *et al.* 1979, Greenslade 1981, Coineau and Seely 1983) even at the generic level. Why should genera of microarthropods tend to be cosmopolitan in the arid regions of both hemispheres, and what does this suggest about the rest of the soil biota? We suggest that the soil biotas of the arid and semiarid regions of the world will be found to be very similar. Arid region soil organisms generally have resistant stages in their life cycle, i.e., cysts, or enter some cryptobiotic state, i.e., anhydrobiosis in nematodes (Freckman and Womersley 1983) and collembola (Greenslade 1983).

The sparse vegetation and sandy soils of semiarid regions contribute to soils being transported aloft by winds (jet stream, etc.). Strong winds at certain times of the year are characteristic of arid and semiarid regions. There is a high probability that strong winds will pick up not only soil particles and organic debris but also spores, cysts, anhydrobiotic, and cryptobiotic soil fauna and eggs of these forms. The anhydrobiotic forms would certainly survive transport in the upper atmosphere as would spores and cysts and possibly eggs also. These particles settle out with the inorganic dust after having moved a half hemisphere or more aloft resulting in constant inoculation of semiarid and arid regions with the soil fauna from other regions. Because this is a likely scenario, we suggest that soil fauna and soil processes in arid and semiarid regions will be very similar regardless of the geographic location.

## Soil Fauna and Decomposition

In this article we make a clear distinction between mass loss from dead plant material and the metabolism of that material to CO<sub>2</sub>, water, and other molecular elemental constit-

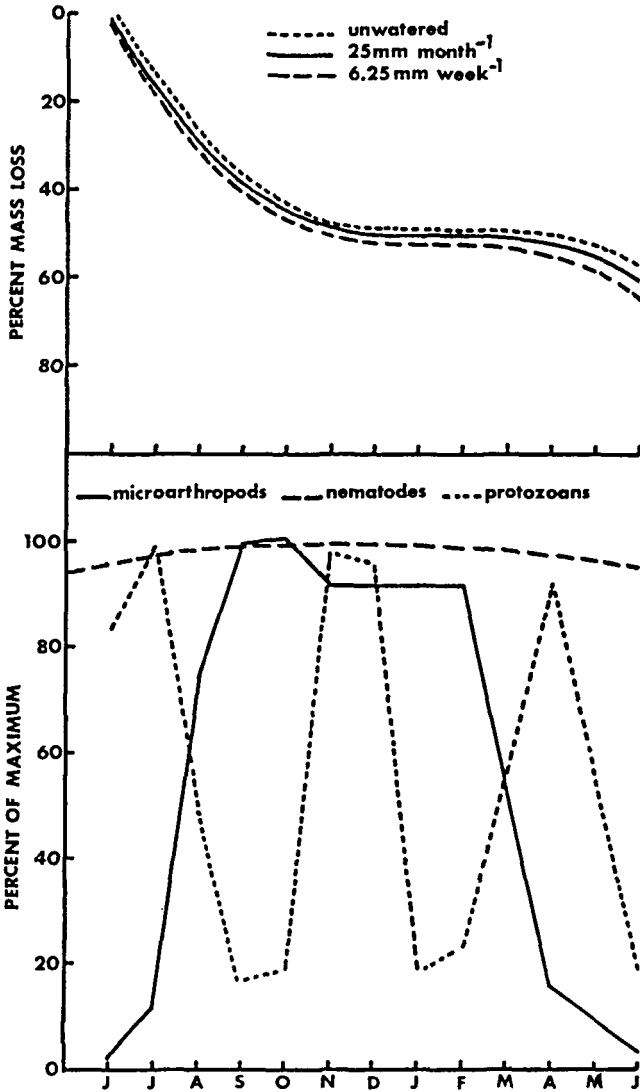
uents. Most papers do not distinguish between these two processes, which are generally referred to as decomposition. Indeed, in most systems these two processes occur simultaneously and continuously and may be considered together. One major difference between arid and semiarid ecosystems and more mesic systems is that mass loss and mineralization often occur at different rates because these processes are regulated by different abiotic parameters. The separation of these processes and regulation of rates by different abiotic factors has important implications in considering microbiological processes in arid lands for control of desertification and increasing productivity.

It has been well documented that rates of disappearance of dead plant materials in arid regions are considerably higher than predicted on the basis of models relating decomposition to actual evapotranspiration and lignin content (Whitford *et al.* 1981, Santos *et al.* 1983, Steinberger and Whitford, 1988). In addition, the correlations between soil moisture and mass losses are very low and in multiple regression models soil moisture accounted for less than 50% of the variation in mass loss. However, when arthropods were removed from the system by an insecticide, soil moisture accounted for 80–90% of the variation in mass loss (Santos and Whitford 1981). These microarthropods appear to uncouple the process of organic matter loss from abiotic constraints (soil moisture). Whitford *et al.* (1981) found that soil acari were active in litter for a short period each day even when soils contained 0 gravimetric water. The soil acari feeding on the microorganisms on and in dead plant material fragment the plant material resulting in mass losses and transport materials into the upper soil layers. Although this activity reaches a maximum rate during wet periods, in the Chihuahuan desert it is continuous over the warm season, May through October.

Changes in population sizes of soil acari are seasonal and related to the periods of high probability of soil-wetting rainfalls. Mass loss in North American hot deserts was found to be correlated with long-term average rainfall but not with the water inputs of the year that measurements were made (Santos *et al.* 1983). This relationship suggests that the soil biota key on seasonal rainfall and are unresponsive to the occasional seasonal storm. We confirmed this in studies using artificial rainfall and found that mass losses from leaf litter and reproduction in the soil acari were seasonal and that neither population size nor mass loss changed when water was supplied in the normally dry season (Wallwork *et al.* 1983, Whitford *et al.* 1986) (Fig. 2). Steinberger and Whitford (1988) confirmed this pattern in the Negev Desert, Israel.

Evidence that microarthropods are primary rate regulators of mass loss is based on use of chemical inhibitors that prevent arthropods from consuming the plant material or entering the material. These studies demonstrate that except for subterranean termites, arthropods have no effect on the rates of decomposition of dead plant materials on the soil surface (Silva *et al.* 1985). In a number of studies in a variety of arid and semiarid ecosystems, elimination of arthropods resulted in a substantial reduction in the rate of mass loss of materials buried in the soil (Fig. 3) (Santos and Whitford 1981, Elkins and Whitford 1982, Santos *et al.* 1983, Whitford *et al.* 1983, Parker *et al.* 1984a). Arthropods account for a significant percentage of the mass loss according to these studies. Plant mass ingested by arthropods, passed through the gut or fragmented and mixed with the inorganic soil, is then mineralized during periods of favorable soil moisture.

In early stages of decomposition of buried litter, Santos *et al.* (1981) documented a mechanism by which the soil fauna can affect mass loss indirectly. Using combinations of chemicals, they were able to study mass loss and populations of bacteria and yeasts and fungi in the absence of microarthropods and both microarthropods and nematodes. In



**Figure 2.** The relationship between mass losses and supplemental water (upper panel) and the responses of the soil fauna to water amendments (lower panel). Because there were no differences in population sizes of the soil fauna, the population sizes for all water treatments have been averaged together.

the absence of microarthropods, nematode populations increased rapidly and grazed the bacteria and yeast to extremely low levels. This overgrazing appeared to be the factor causing reduced mass loss. With microarthropods that prey on nematodes present, the nematode population remained at moderate levels as did the biomass of bacteria and yeast and the resulting mass loss was significantly higher. With both microarthropods and nematodes removed, mass loss was reduced from 30% to 3% with an increase in bacteria and yeast from  $10^6$  to  $10^9$  (Santos 1979). This study demonstrated that regulation of mass loss can occur by a predator that regulates the populations size of a grazer (bacteriophagous nematodes), thereby preventing overgrazing of the primary decomposers.

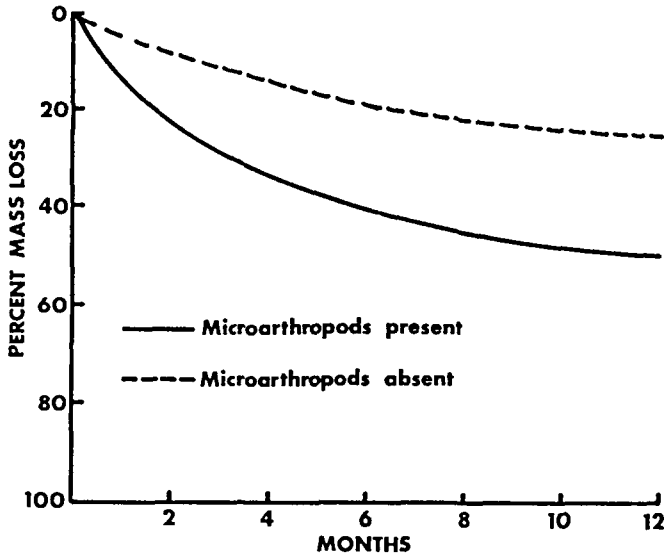


Figure 3. The effect of removing microarthropods on mass losses of buried and surface leaf litter in a variety of desert ecosystems.

### Soil Fauna and Mineralization

Desert soils are generally considered to be nutrient poor and thus competition for essential plant nutrients and water is high (Parker *et al.* 1982). The rapid mineralization of essential plant nutrients stored in soil organic matter and dead plant material is essential for maintaining a productive system (Gutierrez and Whitford, 1987a,b, Gutierrez *et al.* 1988). Conversely, processes that immobilize nutrients dramatically reduce plant production. The directional flow of essential plant nutrients (immobilization-mineralization) in soils is highly dependent on the organic carbon status of the soil. The major organic carbon inputs into soils are: throughfall, litter, dead roots, and exudation. These inputs are supplied by both annual and perennial plants and contain not only carbon but other nutrients (N,P,S,K, etc.) as well. If the ratios of carbon to other nutrients in these inputs is high, then the decomposing microflora will immobilize nutrients other than C from the surrounding soil and the mineralization of carbon has to occur before substantial mineralization of other nutrients can occur (Fig. 4).

The mineralization of carbon in decomposing plant material makes up only a small portion of the total mass loss; however, the degree of mineralization is dependent on the type of plant material and its location in the soil. The proportion of mineralized C- in buried material (27–42%) is higher than that in surface material (14%) (Parker *et al.* 1983). Within the soil matrix, environmental conditions are more mesic than in the soil surface; cooler temperatures and higher humidity result in slower drying of plant debris after rain events. Even when surface litter is maintained at higher water contents by application of supplemental rainfall, mineralization comprised only a small proportion of the total mass loss (Parker *et al.* 1983). C-mineralization in soil and litter increases with supplemental rainfall (Parker *et al.* 1983) (Figs. 5,6); however, C-mineralization is poorly correlated with soil moisture ( $r^2 = 0.16$  and  $0.45$  for soil and litter, respectively) (Parker *et al.* 1984a). C-mineralization in the Chihuahuan desert is thus only poorly



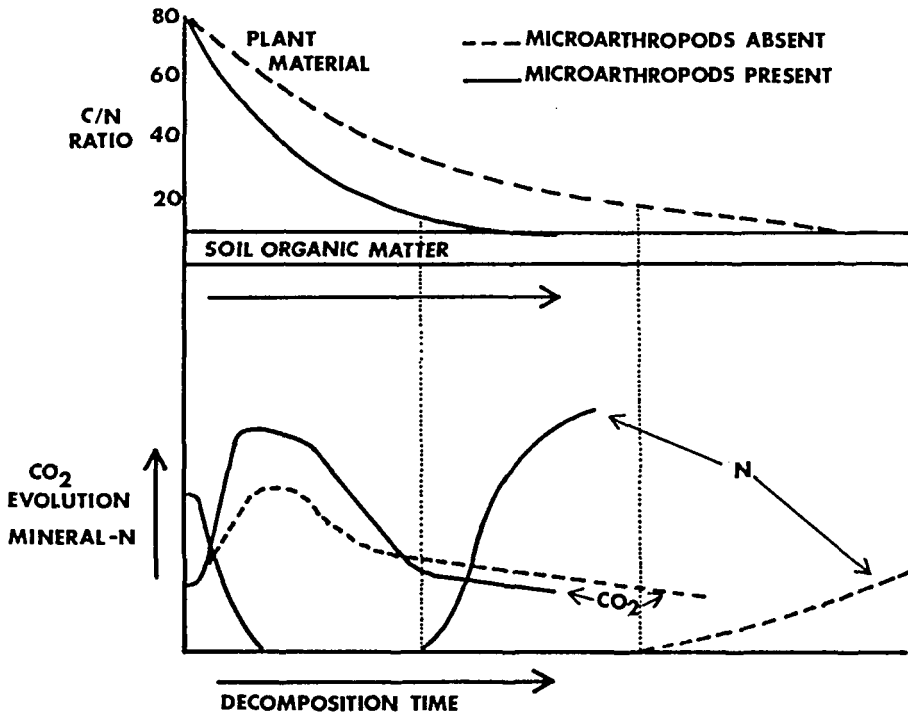
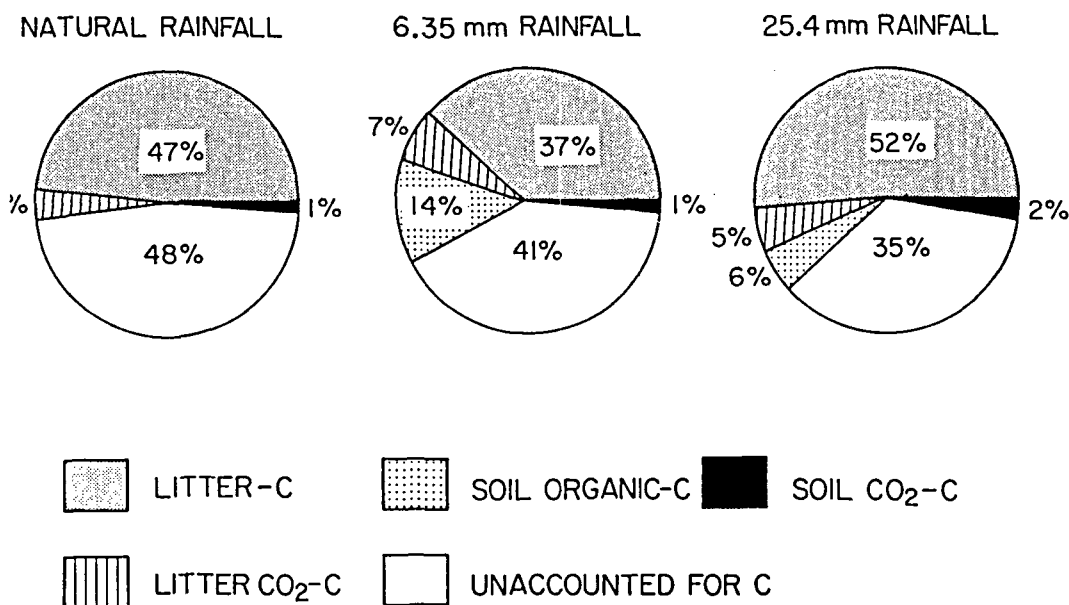


Figure 4. The theoretical effect of microarthropods on the C/N ratio and C-mineralization of decomposing plant material and N-immobilization and mineralization.

related to abiotic constraints. This may be complicated by C incorporation into calcium carbonate and subsequent deposition in caliche layers.

Mineralization, like mass loss, is regulated by soil fauna (Waksman, 1916, Coleman *et al.* 1978, Hanlon and Anderson 1979; Parker *et al.* 1984a). In desert ecosystems, microarthropods are the major regulators of C-mineralization of decomposing litter (Parker *et al.* 1984a). Microarthropods achieve this regulation by grazing on fungi and the small forms like tarsonemid mites may graze on bacteria and yeast. Depending upon their population numbers, microarthropods may either stimulate mineralization rates by maintaining microorganisms in an active growth phase, depress mineralization by over-grazing the microorganisms, or have no effect if their populations are too low (Hanlon and Anderson 1980, Parker *et al.* 1984a). Since microarthropods can be active in extremely dry soils (moisture potentials  $> -40$  MPa), they tend to uncouple mineralization from abiotic constraints (Parker *et al.* 1984a). When microarthropods are removed by the use of biocides, C-mineralization becomes more closely a function of soil moisture ( $r^2 = 0.62$ ) and regulated by nematodes and protozoa, which are dependent upon soil moisture for their activity ( $r^2 = 0.99$ ) (Parker *et al.* 1984a).

Figure 7 is a simplified nitrogen cycle showing the importance of predators in regulators in regulating major flows of N. We have separated the predators into two groups: the microarthropods and the nematodes and protozoa, the former being relatively independent of water and the latter dependent on water for activity as described in detail in an earlier section. The work of Coleman *et al.* (1978), etc. has demonstrated the importance of nematodes and protozoa in mineralizing N and P immobilized by the rhizosphere



**Figure 5.** The effect of supplemental water on the partitioning of carbon during the decomposition of *Larrea tridentata* leaf litter. Values are the percent of initial litter carbon (800 g/m<sup>2</sup>) after 12 months of decomposition.

microflora, thereby increasing the available soil-N pool. Coleman *et al.* (1984) have elucidated on a number of mechanisms by which nematodes and protozoa enhance mineralization. By grazing on the microflora these predators maintain the microflora in a more active physiological state by reducing competitive pressures between microflora and excreting essential nutrients. The average C/N ratio for the soil microflora, protozoa, and nematodes is approximately 10/1. A portion of the prey ingested by protozoans and nematodes is respired as CO<sub>2</sub> (21% and 39%, respectively) (Heal 1967; Sohlenius 1980). The net result is a surplus of N and P, which must be excreted by the predators in order to maintain a proper balance between carbon and nitrogen. A major portion of the excreted nitrogen is as NH<sub>4</sub><sup>+</sup> -N (62%) (Lee and Atkinson 1977). Thus, whereas carbon is primarily mineralized by the microflora, N and P are mineralized by the predators of the microflora: protozoans, nematodes, and some mites.

Semiarid regions by definition are water stressed. It is, therefore, not unusual to find that yeasts and fungi are major decomposer microflora in desert soils. Fungi can be active at a moisture potential of > -40 MPa (Griffin 1981). At this moisture potential protozoans and nematodes are encysted or anhydrobiotic and only microarthropods are active (Whitford *et al.* 1981). Fungi, through their pattern of growth, are able to utilize a considerable area around decomposing plant debris and immobilize essential plant nutrients. The turnover of this fungal biomass through death and grazing is undoubtedly the single most important process regulating the rate at which these nutrients are made available to the plants. Results of studies by Parker *et al.* (1984a) indicate that grazing on fungi hyphae by microarthropods is probably the most important mechanism for the recycling of N immobilized by fungi during the decomposition of annual plant roots (Table 1); in the absence of microarthropods N immobilization can be considerable.

The nitrogen budgets in Parker *et al.* (1984a) (Table 1) were based on a radius of a

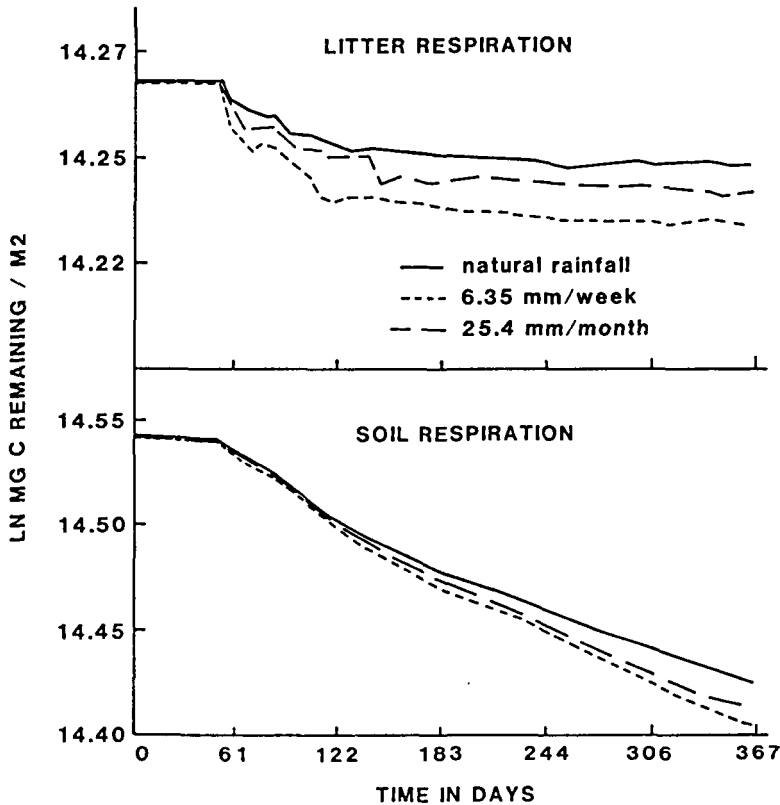


Figure 6. The effect of supplemental water on the mineralization of carbon from decomposing *Larrea tridentata* leaf litter and bare soil.

fungal colonization around decomposing roots of 1.25 cm. This is a highly conservative estimate. An estimate of 7 cm may be more appropriate (Swift *et al.* 1979). The revised net increases in Table 1 would be 421% where microarthropods are present (control) and 946% where they are absent (insecticide treatment). This not only emphasizes the importance of microarthropods in the turnover of fungal biomass but also the importance of the annual plant carbon input on the nitrogen economy of this system. In the Chihuahuan desert, we estimate that between 3.7 and 7.4 g N m<sup>-2</sup>y<sup>-1</sup> will be available for plant growth. This is based on a 1 and 2% turnover, an average of soil organic N content of 325 mg g<sup>-1</sup> (Parker *et al.* 1982), a bulk density of 1.62 g cm<sup>-3</sup>, and a surface to caliche depth of 70 cm. Nitrogen uptakes (Table 2) are based on the data of Ludwig and Flavill (1979) for *Larrea tridentata* and Parker *et al.* (1982) for the annual plants. The carbon content of *L. tridentata* was 54% and a C/N ratio of 22:1 for above ground leaves and stems and 60:1 for roots. The carbon content of annual plants was 60% and a C/N ratio of 27:1 for above ground and 60:1 for below ground plant parts. The soil microflora production is based on Parker *et al.* (1984a) and the above revision of their data.

The estimates of nitrogen uptake fall within the ability of the soil to supply N (Table 2). In years of wet autumns and springs, N uptake falls within the lower range of nitrogen supply, whereas in dry falls and springs nitrogen uptake approaches the maximum. These uptakes do not account for the carbon input from fall annual plants that die during the winter and they are based on gross estimates of below ground *L. tridentata* production.

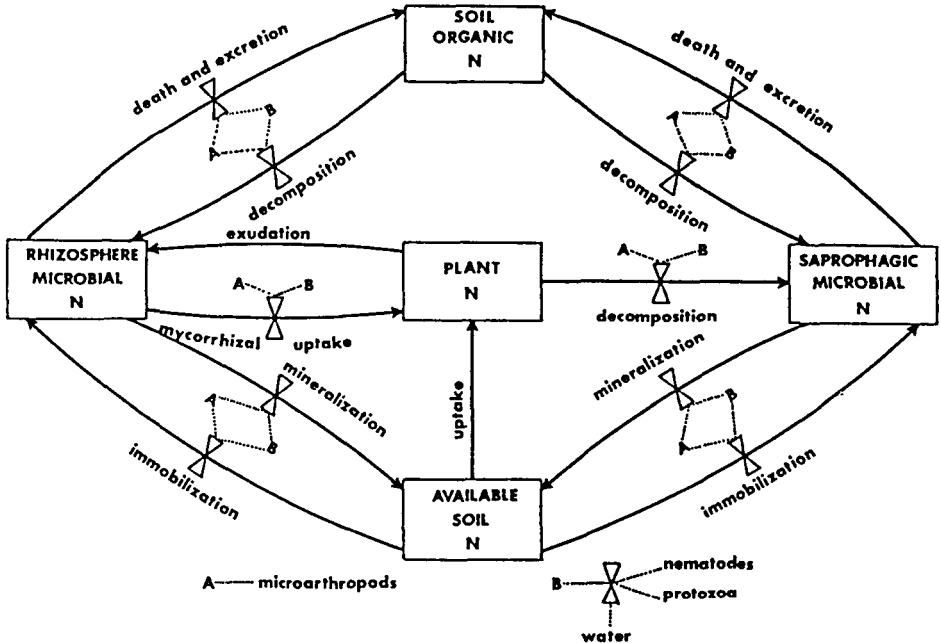


Figure 7. A schematic representation of the major flows of N and their regulation by soil fauna in a desert ecosystem.

The immobilization of nitrogen by the saprophagic soil microflora appears to be important in regulating primary plant production in the Chihuahuan desert (Parker *et al.* 1984a; Gutierrez and Whitford 1987a) and the mineralization of that microbial-N by microarthropods is essential (Fig. 4). The above data elucidates the hypothesis proposed by Parker *et al.* (1984a), which is graphically presented in Figure 8. When the timing of rain events is sufficient to establish a significant annual plant biomass (wet fall and spring), then a significant carbon input into the system occurred placing a stress on the available N pool as a result of microbial growth and immobilization of N (Figs. 4,8). Competition between the perennial plants rhizosphere microflora and the saprophagic microflora reduced perennial plant uptake of N. When hydrologic conditions are unfavorable for an-

Table 1

The effect of microarthropod removal and fungal inhibitor on the nitrogen budgets for annual plant root decomposition at 90 days

Compartment	Untreated	Chlordane	Chlordane + Captan and Benomyl
Plant	30	77	57
Microflora	13	13	18
Protozoa + nematode	0.3	0.8	1.0
Microarthropod	0.02	0.0	0.0
Soil organic-N	86	172	92
Soil mineral-N	3	7	6
Total accounted for	132	270	174
Net increase	32	170	74

**Table 2**  
Estimated nitrogen uptake for the canopy area of *Larrea tridentata* dominated Chihuahuan desert ecosystem

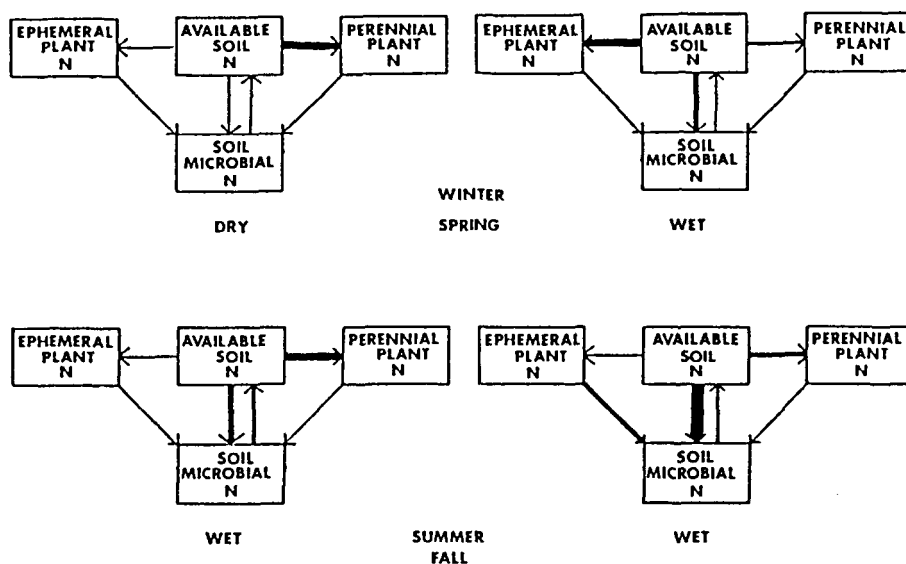
Compartment		Uptake			
		Wet fall-spring		Dry fall-spring	
		g N m <sup>-2</sup> y <sup>-1</sup>			
<i>L. tridentata</i>	above ground	1.5		5.3	
	below ground	0.3		1.1	
Annual plant	above ground	0.53		0.02	
	below ground	0.37		0.01	
Soil microflora		0.12 <sup>a</sup>	1.56 <sup>b</sup>	0.003 <sup>a</sup>	0.04 <sup>b</sup>
Total		2.82 <sup>a</sup>	4.26 <sup>b</sup>	6.43 <sup>a</sup>	6.47 <sup>b</sup>

<sup>a</sup> Assuming a fungal colonization of 1.25 cm radius around decomposing roots.

<sup>b</sup> Assuming a fungal colonization of 7 cm radius around decomposing roots.

nual plant production (dry falls and springs), a carbon input as annual plant roots does not occur and without a carbon source a significant saprophagic microflora is not established. Under these conditions major uptake of N will be by the perennial plants.

It should be clear from this review that soil fauna plays an important role as regulators of decomposition and mineralization in arid and semiarid ecosystems. This regulation is achieved primarily by the fauna feeding on the microorganisms, thereby affecting the physiological state of the microorganism populations. Regulation may also occur through predatory forms that regulate population sizes of the grazers (protozoa, nematodes, small microarthropods), thereby preventing overgrazing. There are many other potentially important functions of the soil fauna that have yet to be examined. Algal crusts are common in many deserts and probably are significant in N fixation (Snyder and Wullstein



**Figure 8.** The effect of climate on the seasonal flows of nitrogen from a dry winter-spring followed by a wet summer-fall and for a wet winter-spring followed by a wet summer-fall.

1973a,b, Eskew and Ting 1978, Rychert *et al.* 1978, Klubek and Skujiņš 1980). In some preliminary surveys of the fauna of algal/lichen crusts, we found large populations of collembolans and nanorchestid mites. Ghabbour *et al.* (1980) in laboratory studies of algal crusts found that protozoans and nematodes stimulated nitrogen fixation by cyanobacteria (blue-green algae). Is a complete soil fauna necessary to maintain maximum N fixation and N mineralization in algal/lichen crusts? This is a question we plan to answer in future experiments. Another important relationship that requires examination is that of mycorrhizae in desert systems. Do soil fauna especially nematodes and mites affect the growth and physiology of mycorrhizal fungi? It seems unlikely that fungiphagous mites and nematodes living in the rhizosphere would not feed on the mycorrhizal hyphae, and therefore this fauna needs to be considered in evaluation of the role of mycorrhizae in these systems.

Finally, reversing desertification will probably involve some or all of the following: organic amendments, seeding, direct planting of shrubs and trees, contouring, and other modifications of topography. The ultimate success or failure of these measures may depend upon an understanding of the soil ecosystem, not just the specific microflora involved in nitrogen fixation or nutrient uptake. Balanced rates of decomposition and mineralization require an intact fauna. Even with an intact ecosystem, "bottlenecks" can occur when climatic fluctuations allow rapid proliferation of some organisms (short life cycle) and escape from regulation by the longer life cycle organisms. Thus as shown in the model of N availability to perennial plants, the soil fauna may be important in affecting the physiological status of plants and thereby affect the susceptibility to desertification processes.

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