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Effects of simulated rainfall and litter quantities on desert soil biota: nematodes and microarthropods

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With 6 figures

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1. Introduction

Desert soil fauna, eg. microarthropods and nematodes, are patchily distributed with the diversity and density varying as a function of leaf litter distribution and soil organic matter (Santos *et al.* 1978; Freckman & Mankau 1977). The accumulation of plant debris in patches of varying size appears to be a factor in the breakdown of surface litter in desert ecosystems. Whitford *et al.* (1982) and Whitford *et al.* (1980) found relationships between quantities of surface litter accumulations and rate of litter breakdown. Whitford *et al.* (1982) also found that suppression of soil microarthropods by chemical means reduced the rate of litter disappearance and concluded that soil microfauna were important in litter break down. Microarthropods are active in surface litter accumulations for 2—4 hours in the early morning even during periods when the soil has no measureable moisture (Whitford *et al.* 1981), but when the soil and litter are wet, more individuals and more taxa can be extracted from both soil and litter. In our earlier work (Whitford *et al.* 1981) we found that simulated rainfall affected the proportions of the nematode population that were anhydrobiotic but found no changes in numbers following water addition such as that exhibited by soil microarthropods. However that study was based on a single simulated rainfall event (Whitford *et al.* 1981) which resulted in large numerical responses of microarthropods in surface litter and in soil under litter accumulations.

Noy-Meir (1974) emphasized that water is the factor of overriding importance in desert ecosystems and stated that rainfall pulses must be important stimulators of soil biotic activity. The studies of distributions of soil fauna (Santos *et al.* 1978; Franco *et al.* 1979) and litter disappearance — soil fauna relationships (Santos & Whitford 1981; Whitford *et al.* 1982; Whitford *et al.* 1983) suggest that for soil organisms, an adequate energy and nutrient supply in the form of plant litter is more important than water as a factor affecting numerical responses of soil fauna. The experiments reported here were designed to test the hypothesis that numerical responses of soil fauna to simulated rainfall would occur only in soils having an adequate leaf litter cover.

2. Method

These studies were conducted at the base of an alluvial plain approximately 5 km ESE of Las Cruces, NM. The soils are deep sandy loams with a vegetative cover of creosote bush, *Larrea tridentata* with scattered mesquite, *Prosopis glandulosa*, along drainages.

We selected 36 *L. tridentata* shrubs of approximately the same size: 70—100 cm height and 100 cm canopy diameter. All leaf litter was cleared. The shrubs were assigned at random to one of the following litter replacement regimes: 0 g, 30 g or 150 g of litter m^{-2}. The replacement litter was col-

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lected from under creosotebushes in the area. The litter treatments were further divided equally to receive 12 mm supplemental water every third day for a period of 30 days during August 1980 (wet) or a control of the natural rainfall (dry). Simulated rainfall was provided by a sprinkler head situated above the shrub canopy. This provided a complete factorial design for examining responses of desert soil biota to soil moisture and litter quantity.

Three soil cores (4.5 cm diameter and 8 cm deep) were taken from each plot (1 m^{-2} area at the base of individual creosote bushes) at six day intervals between 0600 and 0800 hrs., prior to water amendment. One set of cores from each treatment was placed in plastic bags and shipped to University of California, Riverside for nematode extraction. Nematodes were extracted from soil by modified sugar flotation (Freckman *et al.* 1975). Nematodes were identified, counted and placed in one of the following trophic groups: (1) fungal feeders, (*Aphelenchus avenae* Bastian, *Aphelenchoides* sp., *Ditylenchus* sp.), (2) Microbial feeders (mainly Cephalobidae, some Rhabditidae), (3) Omnivore — predators — (Dorylaimina), (4) Plant parasites (*Tylenchorhynchus* spp., *Merlinius* spp.). Those nematodes which were damaged or unidentifiable comprised a fifth group, or were not included in total counts. Statistical analyses, ANOVA and Duncan's Multiple Range, were performed on the log ($N + 1$, N = number of nematodes).

The second series of cores was placed in modified Tullgren funnels (Sanros *et al.* 1978); microarthropods extracted for 72 hrs. into water, and counted immediately after. The third set of cores was processed for enumeration of fungal, bacterial and protozoan activity and biomass (Parker *et al.* 1983). Numbers of organisms were expressed as number per m^2 at 0—8 cm depth.

3. Results

On days 9, 12 and 19 there were natural rains of 20, 30 and 5 mm respectively. The field capacity (—0.33 bar ≙ 33 hPa) of the soil was 9% water. Samples collected on day 12 were collected in the rain. Total accumulated rainfall (day 9 plus day 12) at the time of sampling was 45 mm and produced high soil moisture values (Table 1) that eliminated differences between wet and dry treatments during the middle of the study.

Microarthropods Populations of microarthropods increased during the experiment in all treatments in response to artificial water supplementation and to natural rainfall events (Fig. 1—3). Tydeids, pyemotids, nanorchestids (Prostigmata) and *Cosmochthonius* sp. and *Passalozetes* sp. (Cryptostigmata, Oribatei) were present at every date and were treated separately. There was considerable variation in population numbers and on most sampling dates the minimum population was zero for every microarthropod taxon encountered in at least one sample from each treatment. There were no significant differences in population sizes of mite taxa in soils with different quantities of litter within the litter treatments (all F's < 1.0, $p > 0.05$). Also, there were no significant water effects within the water treatments with the exception of population size of the cryptostigmatid genus *Cosmochthonius* ($F = 3.71$, $p < .05$). However, there were significant water-litter interactions: the population densities of some taxa were higher in the wet, 150 g m^{-2} litter treatment (F's between 3.53 and 5.86, $p < .05$) eg. tydeids, pyemotids, nanorchestids, and *Cosmochthonius* (Fig. 4).

There were also significant water and water-litter interactions on the numerical responses of collembolans (F is 4.2 and 6.4, $p = 0.001$: Fig. 5). Highest numbers of microarthropods reflected the responses seen in individual taxa, eg. that there were significant differences only in the 150 g m^{-2} wet (Fig. 3). Peak numbers of microarthropods reached 13,000

Table 1. The effect of simulated rain on soil moisture content

Rain	Days								
	0	3	6	12	18	21	24	27	30
Wet									
before	0.5[a]	2.1[b]	2.8[b]	8.6[a]	3.4[a]	3.9[b]	3.4[b]	4.7[b]	4.1[a]
after	8.2[b]	—	12.2[c]	—	7.8[b]	8.6[c]	10.3[c]	12.2[c]	—
Dry	0.5[a]	0.5[a]	0.5[a]	8.5[a]	3.7[a]	3.3[a]	2.8[a]	3.6[a]	4.2[a]

Note: Values in a column followed by the same letter are not significantly different at the P = 0.05 level.

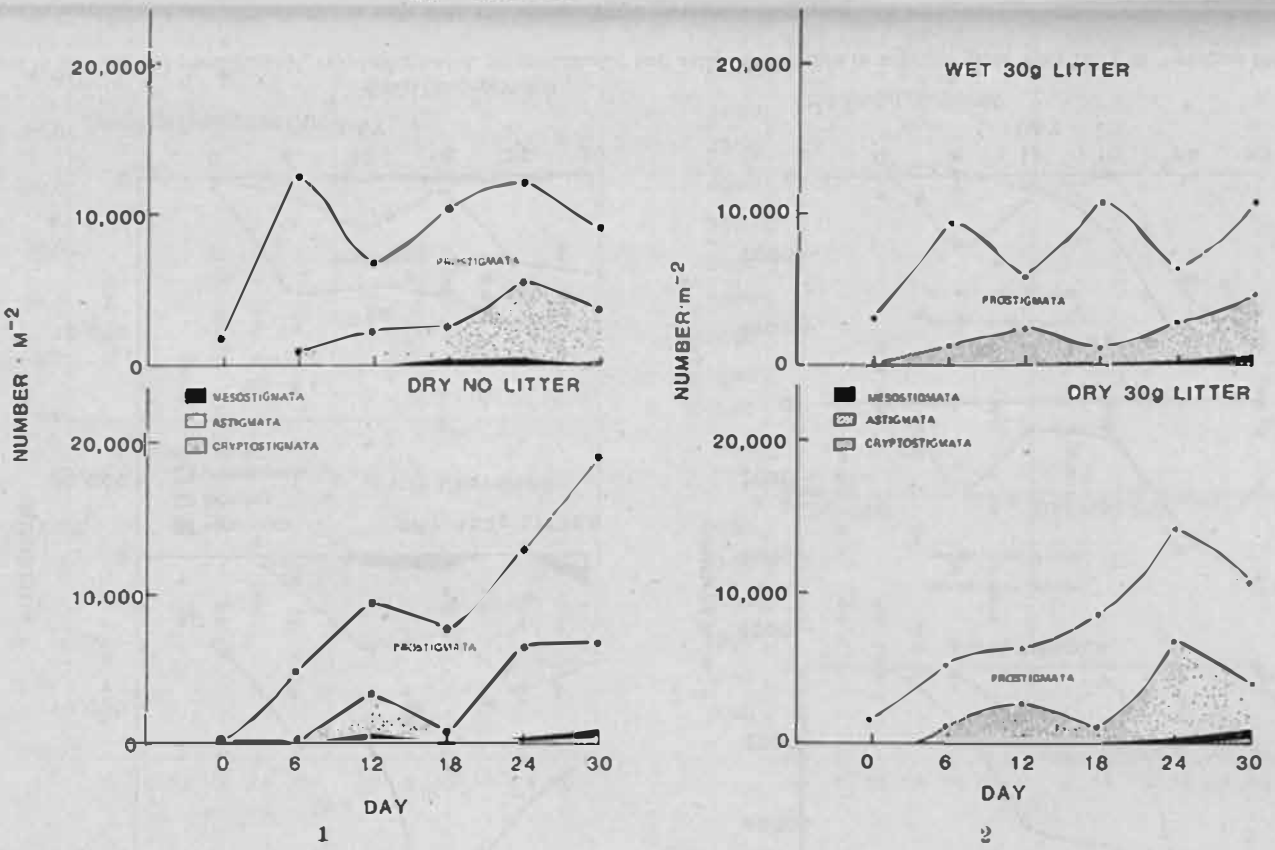
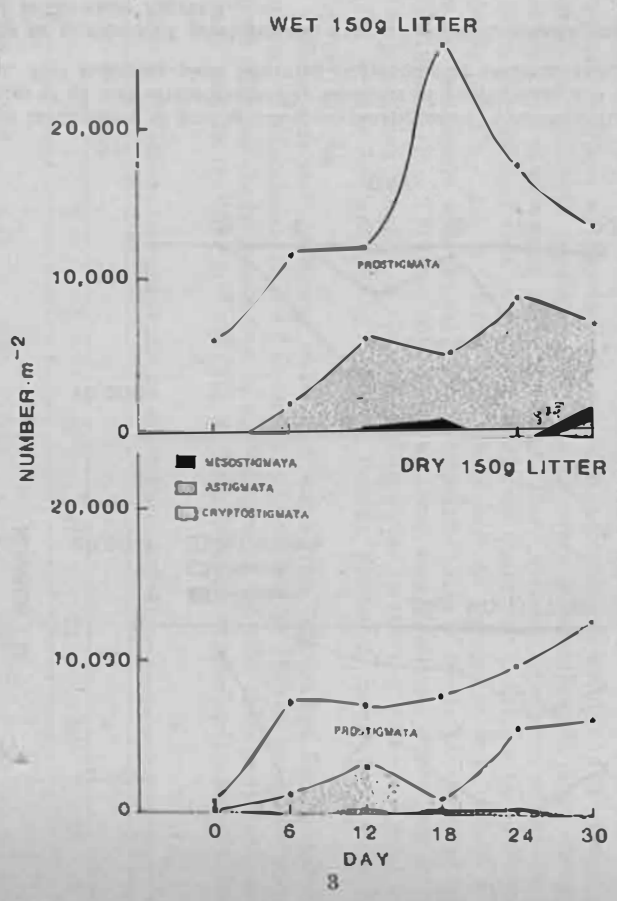


Fig. 1. Changes in numbers of prostigmatid, cryptostigmatid, mesostigmatid and astigmatid mites in soils on plots with no surface litter. The top line represents the sum of all microarthropods. The numbers of prostigmatids is obtained by subtracting the cryptostigmatids, astigmatids and mesostigmatids from the total. Wet indicates plots receiving supplemental artificial rainfall at 3 day intervals and dry indicates plots receiving only natural rainfall.

Fig. 2. Changes in numbers of prostigmatid, cryptostigmatid, mesostigmatid and astigmatid mites in soils on plots with 30 g m^{-2} surface litter method of presentation is the same Figure 1.



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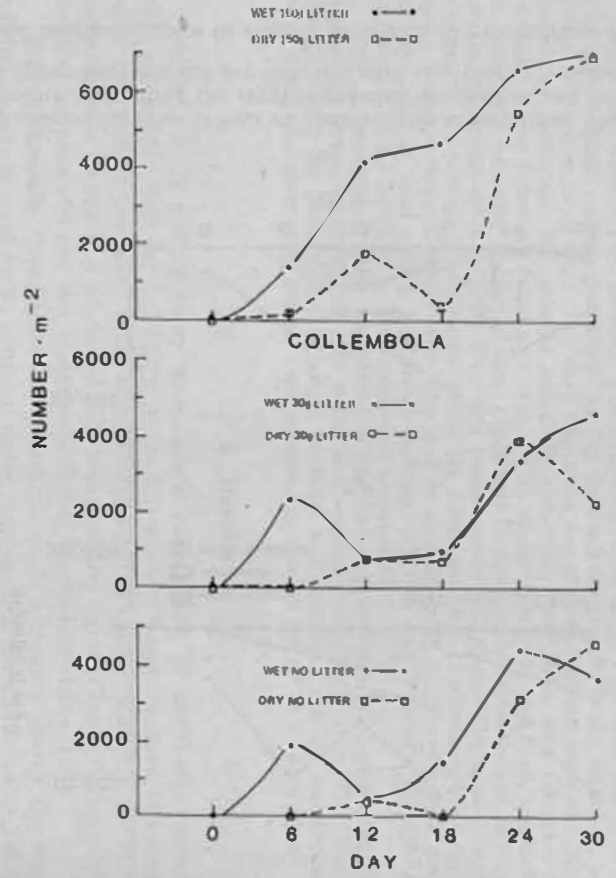

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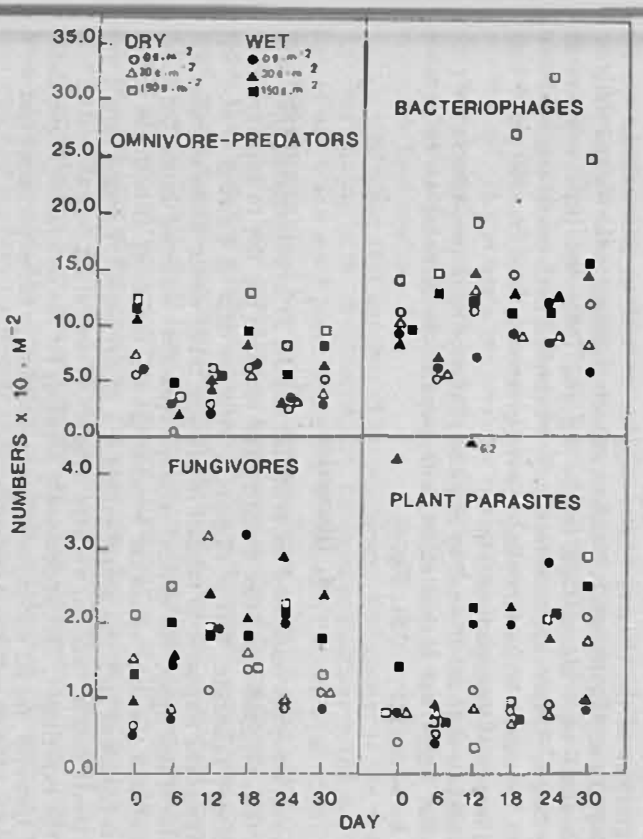
Fig. 3. Changes in numbers of prostigmatid, cryptostigmatid, mesostigmatid and astigmatid mites in soils on plots with 150 g m^{-2} surface litter. Method of presentation in the same as Figure 1.

Fig. 4. Changes in numbers of soil collembolan in soils with the surface litter quantities indicated and with (wet) or without (dry) supplemental water.



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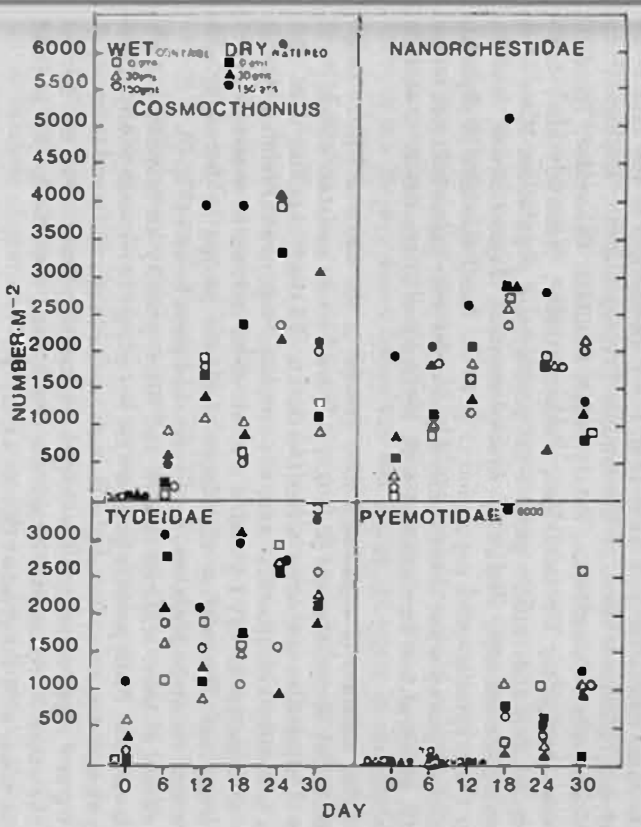

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Fig. 5. Changes in numbers of the trophic groups of soil nematodes in soils with the surface litter quantities indicated and with (wet) or without (dry) supplemental water.

Fig. 6. Changes in numbers of selected taxa of soil microarthropods in soils with surface litter quantities indicated and with (wet) or without (dry) supplemental water.

to 15,000 ind. m^{-2} in all of the treatments except for the 150 g m^{-2} wet where average numbers reached 30,000 ind. m^{-2}. There was a relatively constant ratio of prostigmatid to cryptostigmatid mites in all treatments. Mesostigmatid and astigmatid mites made up a minor part of the total microarthropod fauna (Fig. 1—3). In addition to the taxa of prostigmatids previously discussed, mites of the families Cryptoguatbidae, Raphignathidae, Tarsonemidae, Stigmaeidae, Teneriffiidae, Paratydeidae, Bdellidae, Cunaxidae, Trombidiidae, Erythraeidae, Anystidae, Linotetranidae, Paehygnathidae, Nematalyeidae, Scutacaridae, made up a small and variable part of the prostigmatid population. Mites of the genera *Aphelacarus*, *Passalozetes*, *Joshuella*, *Brachychthonius*, *Haplochthonius*, and *Galumna* made up the cryptostigmatid population (Fig. 1—3). Small numbers of diplurans, family Japygidae, and psocopterans of the family Liposcelidae were extracted from samples during the study, albeit at low numbers and with no trend as to treatment or sampling date.

Nematodes: Total numbers of nematodes were greater in the 150 g m^{-2} litter supplement than in the 0 and 30 g treatments ($P < 0.01$). There were no moisture effects on the total population of nematodes comparing across treatments at a single sampling date. There were differences in density with time that were not correlated with natural rainfall. Average population size was greatest at day 24, and is a result of an increase in nematodes in the dry 150 g m^{-2} treatment. The relative abundance of trophic groups in decreasing order was bacterial feeders, omnivore-predators, fungivores, and plant feeders (Fig. 6).

Analysis of effects of time, artificial rainfall and litter quantity on individual trophic groups was quite variable. Plant parasite numbers did not change in response to any of these parameters. Population density of the fungivores was greater in the 150 g m^{-2} litter supplement than the 0 g m^{-2} supplement, but the 30 g m^{-2} litter supplement was not different from either of the other 2 treatments. Fungivore density was not affected by moisture, but did vary with time, with the greatest density at day 24.

The largest changes occurred in bacterial feeders and omnivore-predators. Bacterial feeders exhibited differences with litter supplement, litter-water interactions and time. Numbers were greatest in the 150 g m^{-2} litter supplement with no difference in numbers between the 0 and 30 g m^{-2} supplements. Numbers of bacteriophages in the 0 g and 150 g m^{-2} dry litter supplements were higher than in the 0 g and 150 g wet litter supplements, whereas in the 30 g m^{-2} litter supplements, density was highest in the water amended treatment ($P = 0.05$). Numbers of bacteriophages were greatest in the dry 150 g m^{-2} litter supplement and increased through time (Fig. 6).

Omnivore-predators were not affected by moisture, but were more numerous in 150 g m^{-2} litter amendments. There was a time effect, with populations declining at 12 days and then increasing by 24 days ($P = 0.01$; Fig. 6).

4. Discussion

The soil microarthropods responded to artificial rainfall as hypothesized, that is, the most abundant taxa responded to litter quantity and moisture but not to moisture in the absence of sufficient substrate. This is consistent with the data of Franco *et al.* (1979) who observed numerical responses to rainfall in samples taken under shrub canopies with varying quantities of leaf litter. The natural rainfall events that occurred during the middle of this study confound the data somewhat because the soil moistures of both the treated and control plots remained high and nearly equal for a 12 day period. Because shrubs were assigned to the treatments at random, we were not able to control for organic matter prior to initiation of the experiment. This undoubtedly accounts for the differences in population sizes at time 0. However, initial differences disappeared during the experiment and we do not feel they confounded the results of the study.

The immediate numerical response to artificial rainfall by the collembolans suggest that those arthropods are present in the dry soil in some kind of cryptobiotic state that is quickly reversed when the soils are wetted. Poinsot-Balaguer (1976) reported such a process in

two species of Collembola from a semi-arid area. GREENSLADE (1981) also reported that this behavior is common in Australian and African arid zone Collembola. The responses of the collembola in differing from that of the acari suggests that either cryptobiosis is absent in the acari or if present, requires a longer time period for reversal.

The moisture-litter quantity relationships point out the difficulty of assessing soil processes in deserts. The biota are dependent upon organic matter that is patchy in distribution. In the absence of sufficient organic material, water elicits no response by most taxa of soil microarthropods. At a litter concentration of 30 g m^{-2} there are no accumulations in which the microarthropods can feed and scattered litter is apparently of little use to the microarthropod fauna.

Average population densities of microarthropods recorded in this study following simulated and natural rainfall are equal to maximum densities reported by FRANCO *et al.* (1979) in the Mojave desert during the wet season. However in the rainfall supplemented 150 g m^{-2} litter treatments, peak microarthropod populations were double the maximum reported by FRANCO *et al.* (1979) and approach the population density reported for lowland grassland by WALLWORK (1970). It is likely, therefore that soils under heavier litter accumulations would have populations more numerous than found in this study.

The absence of numerical responses to water in nematodes is surprising. We expected soil nematodes to respond like the microarthropods based on distributional patterns described by FRECKMAN & MANKAU (1977). The higher numbers of bacteriophages in the dry 150 g m^{-2} litter treatments could have resulted from the leaching of soluble organics deeper than 8 cm resulting in a reduction in a readily available carbon source and thus a decrease in bacteria through predation & death in the wet treatments on days 18 and 24 (PARKER *et al.* 1983). Protozoa, (PARKER *et al.* 1983) another possible food source for the bacteriophages, could have influenced the increased nematode response to 150 g m^{-2} dry litter. Actual numbers of protozoa in the 150 g m^{-2} dry and wet litter supplements were not different. However, all the protozoa in 150 g m^{-2} wet treatments were cystic, and it is not known if they are an adequate food source for nematodes in this state. In the 150 g m^{-2} dry litter protozoans were active, and peaked at day 18 and then declined sharply. This could be related to the steadily increasing numbers of bacteriophagous nematodes on day 18, 24 and 30. Either of the two hypotheses concerning the higher numbers of bacteriophages in the 150 g m^{-2} dry litter is possible, ie. a decline in the bacterial food source because of organic leaching, and a higher level of trophic protozoa. Nematodes feed on both protozoa and bacteria. This presents two areas for further investigation of this group in desert soils: (1) the examination of both bacteria and protozoa as alternate food sources for bacteriophagous nematodes in desert soils and, (2) examination of both cystic and active protozoa as possible food sources.

It is interesting that numbers of bacteriophages were greater in the wet 30 g m^{-2} litter supplements than in the dry counterpart. Bacterial populations in the wet treatments were high at day 6 and much lower in the dry treatments (PARKER *et al.* 1983), and could have provided an initial food base for the bacteriophages on day 6. The natural rainfall on days 12 and 13 would have brought the nematodes in the dry treatments out of anhydrobiosis and in the absence of additional rain pulses, these nematodes could have reentered anhydrobiosis before a population increase could have been assessed. Nematodes can enter anhydrobiosis in a relatively short time period if soil moisture and monomolecular layers of water around the soil particles decrease rapidly (DEMEURE *et al.* 1979). Results of these studies present some interesting questions. For example, does decomposition really accelerate with rainfall pulses, or is it more a combination of a large accumulation of litter and alternate drying and wetting over a long time period? The faunal-microfloral interactions are even more intriguing. The large population of yeasts, rather than filamentous fungi, could be a food source for the bacterial feeding nematodes, and thus could explain the lower percentage of fungivorous nematodes in desert soils. The fungivorous nematodes are characterized by having short, needle-like stylets, which are used for piercing hyphae. The yeasts coulder be more easily consumed by the bacteriophages that have a morphology that is better adapted for ingesting these globose microflora.

This study re-emphasizes the importance of the energy source as the principal regulator of population size in desert soil fauna. In the absence of an adequate or abundant source of carbon, populations of desert soil fauna are unable to increase and this accounts for the patchy distribution of soil fauna. However, we need data on seasonal reproductive responses to rainfall by the various soil taxa in order to resolve the moisture, numerical response relationships but as yet these data are not available.

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We used a complete factorial designed experiment to examine the population responses of soil nematodes and soil microarthropods in desert soils having no litter, litter at 30 g m^{-2} and at 105 g m^{-2} and receiving either natural rainfall or 12 mm supplemental water at 3 day intervals. Populations of several microarthropod taxa (tydeids, pyemotids, nanorchestids, and *Cosmochthonius* sp.) achieved higher densities in the 150 g m^{-2} litter with supplemental water. Nematode population densities were highest in the 150 g m^{-2} with no differences attributable to supplemental water. This study demonstrates that water is of less importance than adequate organic matter for the population growth of desert soil nematodes and microarthropods.

Key words: numerical responses, Prostigmata, Cryptostigmata, anhydrobiosis, simulated rainfall, Chihuahuan Desert.