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THE EFFECTS OF MICROARTHROPODS ON LITTER DECOMPOSITION IN A CHIHUAHUAN DESERT ECOSYSTEM[1]

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Abstract. We compared decomposition of surface and buried, untreated, mixed desert shrub litter to that of insecticide- and fungicide-treated litter. Suppression of fungi reduced decomposition by ≈29%; exclusion of microarthropods reduced decomposition by ≈53%. Approximately 55% of the organic mass of the untreated litter disappeared during the 6-mo growing season and 23–29% disappeared in the winter months (November through March).

There was a consistent pattern of microarthropod colonization of buried litter that was related to the percent organic matter lost. This sequence was tydeid mites, tarsonemid and pyemotid mites, gamasina and predatory Prostigmata, Collembola and Psocoptera, and oribatids. After 1 yr, large numbers of enchytraeid worms were extracted from buried litter. Decomposition of insecticide-treated litter varied directly with rainfall and soil temperature while abiotic factors accounted for <50% of the variation in decomposition of untreated buried litter. We hypothesize that microarthropods affect litter decomposition in desert ecosystems by inoculating litter with fungal spores, by grazing on fungi, and in a heretofore undescribed mode, by preying on free-living nematodes.

Key words: buried litter; Collembola; decomposition; desert; enchytraeids; fungi; insecticides; mites; nematodes; predation; Psocoptera.

Most energy fixed as organic matter by autotrophs of most terrestrial ecosystems becomes input to the soil-litter subsystem and is ultimately acted on by decomposer organisms (Weigert and Evans 1967, Whittaker 1970, Witkamp 1971). Decomposition processes within soil involve interactions between the microflora and fauna (Macfadyen 1963, Crossley 1970, McBrayer 1977). The recent emphasis on nutrient cycling as a means of quantifying ecosystem processes (Waide et al. 1974), indicates the need for study of the role of microarthropods and microflora in litter decomposition in different terrestrial ecosystems. Most of the available information on the role of soil microarthropod populations is based on studies of areas where the soil fauna is predominantly composed of oribatid mites and collembolans. However, some terrestrial ecosystems have lower densities of soil microarthropods, with prostigmatid mites being the dominant taxon (Leetham 1977, Santos et al. 1978).

There are a few studies of the soil microarthropods in deserts (Wood 1971, Wallwork 1972, Edney et al. 1976, Santos et al. 1978). In a Chihuahuan desert ecosystem, prostigmatid mites are most abundant, with oribatid mites and collembolans making up a very small portion of the total soil microarthropod population. Microarthropod densities are directly correlated with surface litter accumulation (Santos et al. 1978). Litter constitutes an important storage reservoir of nutrients in desert ecosystems and the litter fauna may control the rate of mineral turnover.

Several workers have addressed the succession of microarthropod communities associated with the stage of decomposition of plant material (Anderson 1975, Eitminaviciute et al. 1976). These studies fail to provide unequivocal evidence for succession since the faunal changes could also have been seasonal.

Attempts to evaluate the role of microarthropods in decomposition processes have often relied on exclusion of organisms by chemicals (Kurcheva 1960, Witkamp and Crossley 1966). Macauley (1975) demonstrated the efficacy of using selected insecticides and fungicides to assess the relative importance of arthropods and fungi in decomposition processes.

In most deserts, significant quantities of litter are buried by the action of sheet-flow water during intense rain storms and by aeolian sand. In addition, roots of annual plants, which remain belowground after death, may be available only to the meso- and microfauna and microflora. Therefore, studies of the fate of litter in desert ecosystems must account not only for the surface materials but also for the buried litter.

By using selected chemical inhibitors and overlapping sequence of litter placement, we addressed the following questions: (1) Do microarthropods affect the rate of plant litter decomposition in a Chihuahuan desert ecosystem? (2) What is the relative contribution of

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bacteria, fungi, and microarthropods to decomposition? (3) Is there a predictable pattern of microarthropod succession related to stage of litter decomposition or are the faunal changes primarily seasonal effects? (4) What are the differences in decomposition of surface and buried litter in a desert ecosystem?

Study Site

These studies were conducted on the Jornada International Biological Program Validation Site on the New Mexico State University Experimental Ranch 40 km north-northeast of Las Cruces, Dona Ana County, New Mexico. The Jornada Validation Site is a desert watershed which drains into a small, dry, lake bed (playa). The watershed varies in elevation from ≈1200 to 2000 m. The 100-yr annual rainfall average ±1 SD at the New Mexico State University Station, Las Cruces, New Mexico, is 211 ± 77 mm (Houghton 1972), with most of that rainfall occurring during late summer from convectional storms. Maximum summer temperatures reach 40°C and freezing temperatures are recorded from October through mid-April (data from the Jornada Validation Site Weather Station).

The site is a bajada (alluvial piedmont sloping from Mt. Summerford on the west to the Jornada basin on the east and north) with creosote bush (*Larrea tridentata* [D.C. Cov.]) as the dominant shrub. The bajada is drained by a large ephemeral wash (arroyo) which flows south to north. The soils are gravelly to sandy loams. Creosote bushes average 1 m or more in height and the caliche layer is >1.2 m below the surface.

The differentiation in soils and drainages produces distinct assemblages of perennial vegetation. Non-arroyo areas have an essentially monotypic cover of creosote bush. The arroyos on the east side of the large wash are lined with mesquite (*Prosopis glandulosa* Torr.), tarbush (*Flourensia cernua* D.C.), desert willow (*Chilopsis linearis* (Cav.) Sweet), soaptree yucca (*Yucca elata* Engelm.), and banana yucca (*Yucca baccata* Torr).

Methods and Materials

Naturally mixed litter samples were collected from the study site and consisted of *L. tridentata, Y. elata,* Apache plume (*Fallugia paradoxa*), *P. glandulosa,* and annual plant samples were oven dried at 60°C for 72 h. Pre-weighed, 30 ± 0.01 g (precision of balance) samples of litter were placed in 20-cm² fiber glass mesh bags (mesh = 1.5 mm). To prevent loss of material or the escape of microarthropods due to transportation, each fiberglass bag containing litter was placed in a plastic Ziploc® bag.

We used the following treatments: (1) Control (C), water containing 1% Tween 20®, a wetting agent, (2) Insecticide-treated (I), 1% (by volume) Chlordane® plus wetting agent in water to eliminate arthropods, (3) Fungicide-treated (F), 0.1% (by mass) suspension of Benomyl® in combination with 0.2% (by mass) of Dexon® plus wetting agent in water, and (4) Fungicide-insecticide treated (FI), a combination of the Chlordane, Benomyl, and Dexon in the concentration of the insecticide and fungicide treatments, plus wetting agent in water. Litter bags were soaked for 2 h then dried at room temperature for 25 h. This is a modification of a method described by Macauley (1975).

In order to separate seasonal changes from effects due to degree of decomposition of the substrate, we buried bags in the field and removed them at 30-, 60-, 90-, and 180-d intervals with retrieval of complete sets on a single date. In the non-growing season, November–March, the bags were buried for 80 or 107 d with overlap in December and January. Additional sets of eight to 10 bags per treatment were placed on the surface under creosote bushes. Surface bags were left in the field for 90 d during the growing season and 120 d during the nongrowing season in November–March.

Litter bags returned from the field were immediately emptied into Tullgren funnels and extracted for 72 h. All control and fungicide-treated bags and three to five of the insecticide-treated bags and fungicide-insecticide treated bags were extracted from each set. The initial gradient in the extractors was from 38°C at the top of the sample to ≈25°C at the bottom. The microarthropods were collected in water and counted immediately. Representatives of the different microarthropods were mounted on slides in Hoyer's mounting medium and identified to family (Krantz 1975).

The litter was carefully removed from the extractors, dried at 60°C for a minimum of 5 d, weighed, and burned in a muffle furnace at 700°C for 12 h to obtain organic matter content by mass. Since the buried bags were infiltrated with varying quantities of mineral soil, it was necessary to correct the dry masses of litter for this soil. We developed the following equation to estimate the change in organic matter content in the litter:

$$d = \bar{Z}_i + \bar{f}(I_f - \bar{I}_i) + I_f - M_f \quad \%d = \frac{d \times 100}{\bar{Z}_i},$$

where:

d = estimated organic matter loss from each sample;

$\bar{Z}_i$ = estimated mean of the initial organic content from 10 samples of each treatment;

$\bar{f}$ = site-specific correction factor, to compensate for different ammounts of soil entering bags within the same treatment. $\bar{f}$ determined for each sample date; $\bar{f} = (\phi_o/\phi_i)$, where ϕ_o is the estimated organic content of the soils and ϕ_i is the inorganic content of the soil (mean of 10 samples);

I_f = final inorganic content (ash masses) of each collected sample (700°C/1–2 h);

$\bar{I}_i$ = estimated mean of the initial inorganic content from 10 samples of each treatment;

TABLE 1. Pairwise statistical comparisons (Bayes exact test) of the decomposition of variously treated creosote bush litter in surface (S) or buried (B) litter bags. The comparisons are between untreated (C), fungicide-treated (F), insecticide-treated (I), and fungicide-insecticide treated (FI) bags. Statistical significance is shown by ** = $P < .01$, * = $P < .05$, NS = $P > .05$.

Time in field		F value	r^2	C × F	F × I	I × FI	N
Apr–May	B	17.02	.61	NS	**	NS	9
May–Jun	B	47.50	.79	**	**	*	10
Jun–Jul	B	72.56	.85	**	**	*	10
Apr–Jul	B	38.15	.76	**	**	*	10
Jul–Aug	B	41.76	.79	**	**	NS	9
Aug–Sep	B	98.04	.90	**	*	**	9
Sep–Oct	B	14.97	.61	**	NS	**	8
Jul–Oct	B	48.17	.83	**	**	**	8
Apr–Oct	B	22.09	.70	*	*	*	8
Nov–Feb	S	175.11	.94	**	**	**	8
	B	52.44	.84	**	**	**	8
Dec–Mar	S	101.16	.91	**	**	*	8
	B	37.31	.79	**	**	**	8

M_f = final dry mass of each sample (60°C for 72 h);
M_i = initial dry mass = (30 g − $\bar{x}$) where $\bar{x}$ = average mass loss (by handling) from 10 bags in each treatment;

$$M_i = \bar{Z}_i + \bar{I}_i.$$

To compare the microarthropod faunas of buried litter bags with naturally buried litter, we collected five samples of naturally buried litter at different times from October through March. Microarthropods were extracted from 30 g of this material. Nematodes were extracted from litter bags by a combination of the Cobb sieving method and the Oostenbrinck cotton-wool filter (Nicholas 1975).

Decomposition data (in percentages) were normalized by arcsine transformation. The Bayes exact test (BET) was used to compare treatment means because the observed F values were relatively large ($F = 15$ to $F = 175$). Carmer and Swanson (1973) demonstrated that BET procedure is more sensitive than other pairwise methods when the observed F values are large. A factor analysis (Morrison 1976) was used to examine the relationships among microarthropod taxa from the litter bags. A stepwise multiple regression model was used to examine the effects on organic matter loss of elapsed time, season, and mean monthly air temperature and precipitation (Barr et al. 1976).

RESULTS

There were significant differences in mass loss due to treatment in nearly all of the experimental periods (Table 1). The treatments accounted for between 61% and 90% of the variance in mass loss from the buried bags and >90% of the variance in mass loss of surface bags (Table 1).

The loss of organic matter was consistently higher in the controls than in any of the treatments. The amount lost (highest to lowest) was always in sequence: untreated, fungicide-treated, insecticide-treated, fungicide-insecticide treated (Figs. 1–5). The loss of organic matter was highest in the 1st 30 d with the rate of decomposition apparently declining after this initial loss (Fig. 1). More than 50% of the initial organic matter present disappeared over the frost-free growing season, April–October (Fig. 1).

No microarthropods were extracted from the insecticide-treated and fungicide-insecticide treated bags. We did find large numbers of free-living nematodes in the insecticide- and fungicide-treated bags. However, there were fungal hyphae present in the fungicide- and fungicide-insecticide treated bags. Although there were few mycelia visible in the fungicide treatments in comparison to controls in which the litter was covered with mycelia, we were able to isolate *Alternaria* spp., *Rhizopus* spp., and *Cunninghamella* spp. from treated bags.

A comparison of seasonal variation in organic matter loss and microarthropod communities in the 30-d buried bags is presented in Figs. 2 and 3. Tydeid mites were the initial colonizers of buried litter, representing virtually the only mites present in untreated bags which lost <30% of the initial organic matter.

In untreated bags that lost 30% of the initial organic matter, tarsonemids and pyemotids were present in large numbers, with tarsonemids being the early summer group and pyemotids the late summer group. Gamasina (Arctacaridae, Rhodacaridae, Laelapidae, and Ascidae) and Prostigmata mites (Raphignathidae and Bdellidae) were found in 30-d bags in which organic matter loss exceeded 30% of original mass and collembolans were found only in the August–September bags in which organic matter loss was nearly 40% of the original mass (Figs. 2 and 3).

A comparison of the June–July and September-October 30-d bags (Figs. 2 and 3) with the 90-d bags collected in July and October (Fig. 4) reveals that the microarthropod fauna is dependent on the degree of decomposition and is independent of season. Collem-

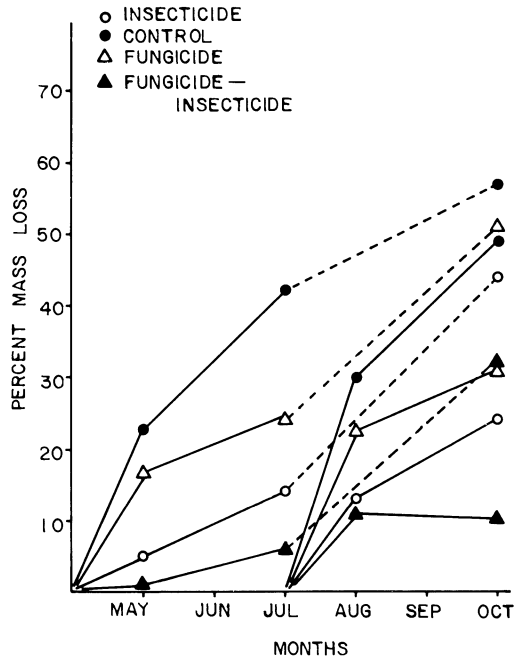


FIG. 1. Mean percent mass loss of buried litter bags over the growing season. The lines are extrapolations based on mass losses for the separate 30-, 90-, and 180-d experiments over the time periods indicated on the abscissa.

bola and Psocoptera which were absent in the 30-d bags were a major fraction of microarthropod fauna in the 90-d bags (Fig. 5). Bags in the field for 6 mo had a fauna similar to that of the 90-d bags (Fig. 4).

Microarthropod fauna in the bags in the winter months, November–February, consisted of two groups, tydeids and collembolans (Fig. 5). The early spring bags had higher organic matter loss than the winter bags and a microarthropod fauna similar to late summer and 90-d bags (Figs. 2, 3, and 5). Although the November–February organic matter loss was low (≈23%) collembolans were present in the bags.

With the exception of the July–August 30-d bags, the numbers of individuals and families were greater in the control bags than in the fungicide-treated bags. The pattern of taxa in the fungicide-treated bags paralleled that of the control bags, with tydeids associated with low organic matter loss followed by tarsonemids or pyemotids and predatory mites associated with successively greater amounts of organic matter loss (Figs. 2–6).

When we compared the density and diversity of microarthropods extracted from naturally buried litter to microarthropods from buried bags we found lower densities of each taxon per unit mass of naturally buried leaf litter but higher diversity. Taxa extracted from naturally buried litter but not from litter bags were raphygnathids, tetranychids, and oribatids.

Surface bags left in the field for 3 or 4 mo were dominated by nanorchestid and oribatid mites. The percent organic matter lost from surface bags (57.4 ± 7.7) in the August–October period was significantly higher than in buried bags (40.0 ± 2.7%) for the comparable period. All of the surface bags contained termite gallery carton (chambers of cemented soil particles produced by termite workers) and even the fine-

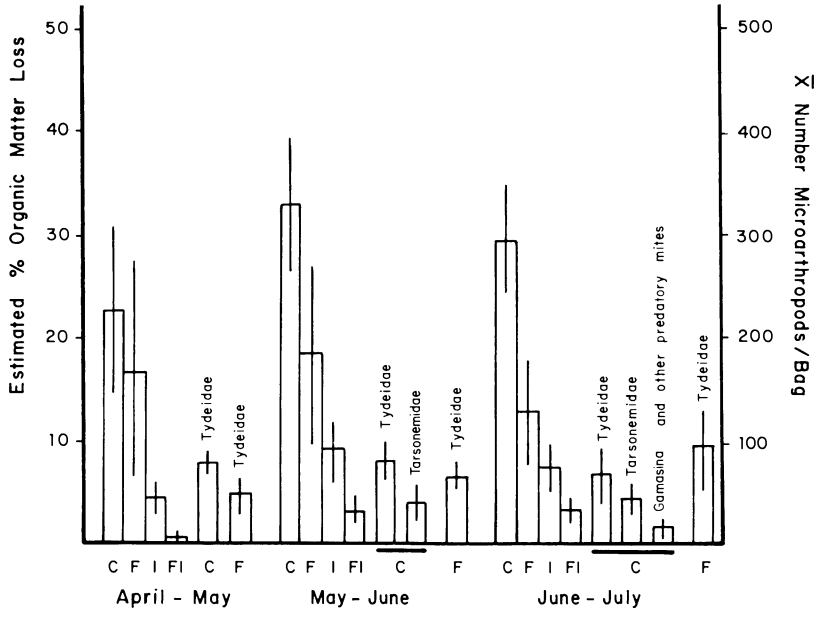


FIG. 2. Mean percent mass loss of control (C), fungicide (F), insecticide (I), and fungicide-insecticide (FI) treated buried litter bags and mean numbers of microarthropods extracted from (F) and (C) bags. The vertical lines in the center of the bars represent ±1 SD.

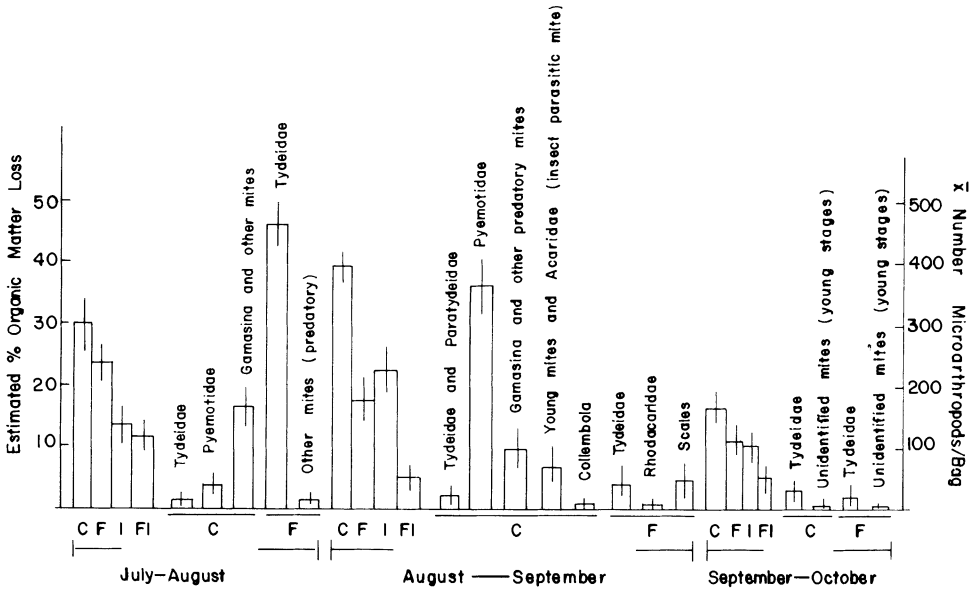


FIG. 3. Mean percent mass loss and mean number of microarthropods extracted from 30-d buried litter bags. Method of presentation the same as in Fig. 2.

mesh bags used to exclude termites were cut through by termites; therefore, the data are lumped. The organic matter loss from the surface bags November–February (23.7 ± 1.8%) and December–March (39.3 ± 5.8%) was not significantly different from the organic matter loss from buried bags for the same periods (Fig. 5).

The generalized relationships between percent organic matter loss from control bags and structure of the buried litter microarthropod community are pre-

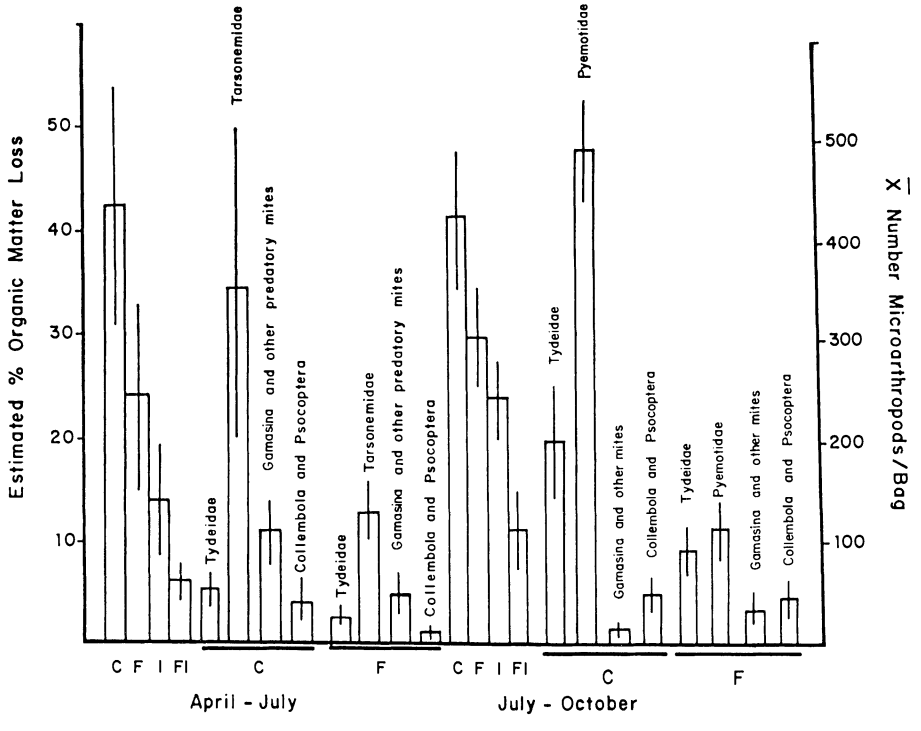


FIG. 4. Mean percent mass loss and mean number of microarthropods in 90-d buried bags. Method of presentation the same as in Fig. 2.

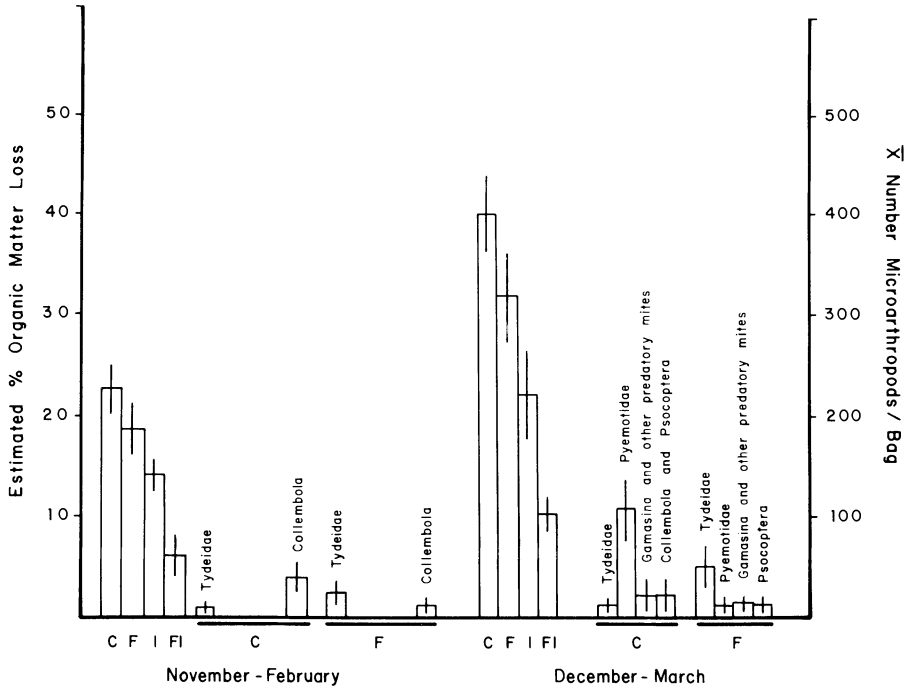
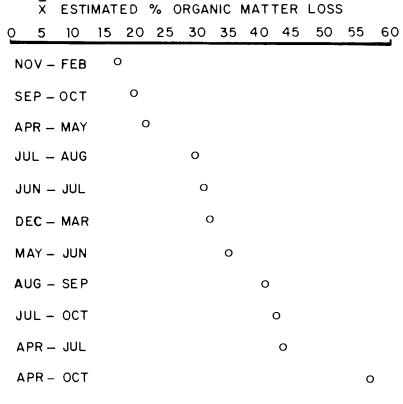


FIG. 5. Mean percent mass loss and mean number of microarthropods in 80- and 107-d buried bags from November 1977 to February 1978 and December 1977 to March 1978, respectively. Method of presentation the same as in Fig. 2.

sented in Fig. 7. Tydeid and occasional paratydeids were the only mites in litter in which up to 30% organic matter was lost. Tarsonemids and pyemotids reached peak populations in litter in which 30–40% of the initial organic matter was lost. The predatory Gamasina mites were included in the microarthropod community when 40–45% of the initial organic matter was lost. Thus, there was a successional sequence and increase in microarthropod diversity which was related to the stage of decomposition of buried organic matter (Fig. 6).

One set of untreated bags initially containing 30 g of creosote bush litter was left in the field for 1 yr (July 1978–July 1979). Ten bags were extracted by Baerman funnel and 10 by Tullgren funnel. The mean numbers of microarthropods ±1 SD were: Acarina—Arctacaridae 398 ± 134.6, Collembola—Entomobryidae 598.8 ± 164.8, oribatid mites 86.4 ± 28.6, other mites 21.5 ± 10.8. Baerman funnel extraction produced an average of 670.6 ± 329.5 enchytraeid worms per bag. We were unable to obtain mass loss from these bags because the material was inadvertently thrown out.



TYD	TAR	GAM	PSO	COL
O				±
O				
O				
O	O	±		
O	O	±		
O	O	±		
O	O	±		
O	O	O	O	
O	O	O	O	O
O	O	O	O	O
O	O	O	O	O

FIG. 6. Mean percent mass loss of untreated bags and the major groups of microarthropods extracted from those bags. O indicates always present and (±) indicates present or absent. TYD = Tydeidae, TAR = Tarsonemidae and Pyemotidae, GAM = Gamasina, PSO = Psocoptera, and COL = Collembola.

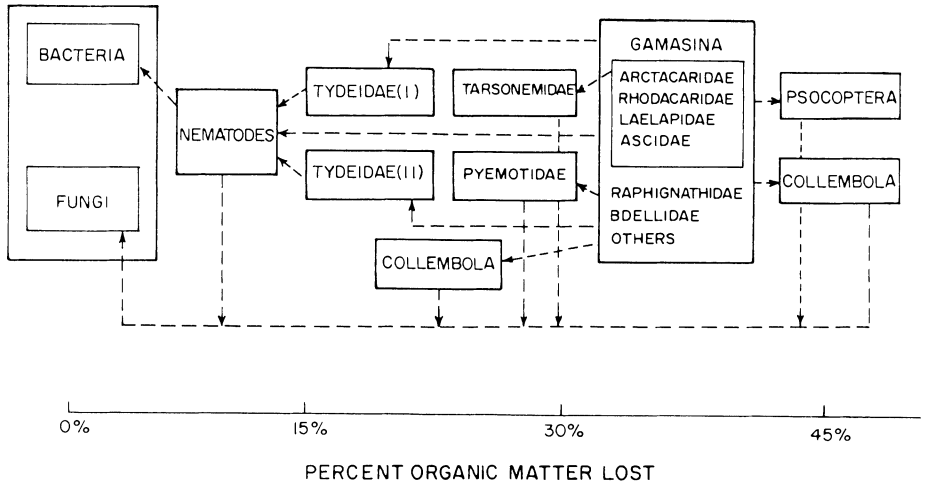


FIG. 7. An hypothesized colonization sequence in relation to percent organic matter lost, and hypothesized trophic relationships of microarthropods, nematodes, and microflora in buried litter in a Chihuahuan desert ecosystem. Arrows point from predators to prey groups.

Using a stepwise (variable addition) multiple regression to evaluate the effect of abiotic factors on decomposition, we found that abiotic factors explained 80–90% of the variation in the (I) and (FI) bags but <50% of the variation in the untreated bags. The seven parameters examined were precipitation (millimetres per month), average minimum air temperature, average maximum air temperature, maximum air temperature of the month, minimum air temperature of the month, length of time bags were in the field, and the time of the year. Precipitation was the most important parameter for all treatments, explaining between 40% and 75% of the variance in organic matter loss.

DISCUSSION

The rate of litter decay is an important factor governing the cycling time for vital elements in terrestrial ecosystems. Earlier workers suggested that nutrient cycling, litter decomposition, and mineralization are slow in arid regions (Rodin and Basilevich 1965, West and Klemmedson 1978). However, the overall rate of litter disappearance from buried or surface bags in a Chihuahuan desert, within the growing season, is high (56.6%/6 mo), and falls within the range of decay rates reported for mesic grassland herbage, (59–70%/6 mo) (Curry 1969*a*). In our study, between 19% and 39% of the litter in buried bags disappeared in the 1st 30 d, 42% in 90 d, and 56.6% in 180 d during the growing season. Decomposition rates for winter months November through March varied between 23% and 39% which is still higher than rates of decomposition (29%/9 mo) reported for blue grama grass litter in a semiarid grassland (Vossbrinck et al 1979).

No termites or termite activity were observed in any of the buried bags. However, termites were observed in all surface untreated bags from August through October, which undoubtedly accounts for the higher rate of organic matter loss from these bags. Termite surface foraging is the greatest from late August through October (Johnson and Whitford 1975). Based on our comparisons of organic matter loss, termites removed at least 20% of the organic matter present. Fowler and Whitford (1980) have shown that termites do not eat creosote bush leaves; therefore the 20% organic matter loss attributed to termites is probably from annual plant parts and grasses. The lack of termite activity in buried bags adds further evidence to the contention of Ettershank et al. (1980) that Chihuahuan desert subterranean termites, *Amitermes wheeleri* (Desneux) and *Gnathemitermes tubiformans* (Buckley) feed only on surface litter.

The exclusion of microarthropods from buried and surface bags by the insecticide Chlordane indicates that microarthropods have a marked effect on the rate of litter decomposition. The reduction in organic matter loss we attribute directly to the absence of microarthropods and not the direct effects of Chlordane on fungi and bacteria. In a similar experiment using creosote bush litter in mesh bags buried for a period of 30 d (Santos et al. 1981) we found no measurable effect of Chlordane on fungal density. Martin et al. (1959) reported no measurable effect of Chlordane on numbers of bacteria or fungi in five annual applications of 11.1 kg/ha to two fields. CO_2 evolution did not decline in soils receiving high concentrations of Chlordane (Alexander 1969). However, Witkamp and Crossley (1966) showed that large doses of Chlordane increased soil respiration. Therefore we conclude that microbial populations are not inhibited by Chlordane and that the reduction in decomposition rates is due to the absence of microarthropods.

Suppression of fungal populations by the combina-

tion of Benomyl and Dexon had less effect on decomposition rates than did the exclusion of microarthropods. Although Benomyl affects a wide range of fungi (Delp and Klopping 1968) we were unable to eliminate all the hyphal growth in the litter using Benomyl alone or in combination with Dexon. Macauley (1975) found that supressing the fungal population with Benomyl decreased the rate of decomposition of *Eucalyptus* leaves much more than did the elimination of arthropods with DDT or Dieldrin. Although we found a great reduction in mycelial density in the fungicide-treated bags compared with control bags, *Alternaria* spp., *Rhizopus* spp., and *Cunninghamella* spp. were isolated from treated bags.

Benomyl has been reported to have acaricidal and insecticidal effects (Reyes and Stevenson 1975), miteovicidal effects (Delp and Klopping 1968), and toxicity to three collembolan species (Tomlin 1977). However, microarthropod populations were present in all extractions from Benomyl-Dexon treated bags. The exclusion of microarthropods and fungi together resulted in a significant reduction in the decay rates of litter, suggesting that these soil biota are very important in decomposition processes in a desert soil ecosystem.

As stated by Weigert (1974), the litter fauna is a transient subset of a larger and possibly more diverse soil fauna. Microarthropods extracted from litter bags represent an active portion of that subset at the time of collection. This active subset present in surface bags differed in number of individuals and group composition from that in buried bags collected at the same time. Thus the nanorchestids, oribatids, caeculids, erythraeids, neophillobids, and trombiculids were found almost exclusively in surface litter bags, while rhodacarids, arctacarids, laelapids, ascids, and raphignathids were confined almost exclusively to buried bags. Tydeids and tarsonemids that were present in surface and buried bags were always more numerous in buried bags. The moist, rich organic environment and moderate temperature of buried bags allowed development of more stable populations of arthropods. The surface bags supported transient populations of active mites that are capable of moving out of the bags back to the soil if conditions are not favorable. Most mites in the surface bags were predatory with nanorchestids and oribatids probably fungivorous (Krantz 1975). The low number of microarthropods extracted makes it difficult to interpret their role in surface bags.

The microfauna in litter bags buried for 1 yr was surprising. We had not expected to find enchytraeid worms in the desert because O'Conner (1979) stated that drought appeared to be the main factor limiting their distribution and abundance. Buried litter accumulations retain moisture and provide an organic island in an inorganic sea of mineral soil. The colonization of such an island should be a function of the population density, distance from source, mobility of potential colonizers, and suitability of the habitat. The absence of oribatids in earlier stages of decomposition may be a function of their low density in Chihuahuan desert soils or their requirement for partially decomposed litter. We did find fairly high numbers of oribatids in naturally buried litter. Enchytraeids probably occur in islands of naturally buried litter but this remains to be examined. The mesofauna of litter which had been buried for a long period was more like a forest litter fauna than that expected in a desert.

Tydeid mites were the first group to colonize the buried litter bags. Members of that family are mainly predators or conceivably both predators and phytophages (Brickhill 1958, Baker 1965). Some species are reported to eat fungi, honeydew, and dead arthropods (Krantz 1975). Tydeid mites found in litter bag studies have been thought to be mainly fungivorous (Crossley and Hoglund 1962). Those reported here are probably new species (E. W. Baker, *personal communication*) and fungi are probably not the main food source in this case since tydeids were present in all fungicide-treated bags. As discussed before, fungal hyphae were not completely eliminated from those bags, but the fungicide treatments actually resulted in increased tydeid numbers on several of the dates. Tydeids extracted from control bags ate bacteriophagic nematode eggs in the laboratory. When groups of 30 tydeid mites were added to nematode cultures and examined at 2-d intervals for 1 mo, there were significant reductions in numbers of nematodes and eggs. Based on these observations, we hypothesize that tydeid mites affect the rate of decomposition by preying on bacteriophagic nematodes. The relationship between tydeid mites and bacteriophagous nematodes is examined in detail in another paper (Santos et al. 1981).

The second group of colonizers were mites belonging to the families Tarsonemidae and Pyemotidae. The tarsonemids and pyemotids in the litter bags appeared to be mainly fungivorous. They were absent from all fungicide-treated bags buried for 30-d periods and numbers were reduced in 90-d buried bags when compared with control bags. They were cultured in the laboratory with *Fusarium* spp. for a 4-mo period. If litter was buried from March to June, tarsonemids were present, but if the experiment was conducted from July to December, pyemotids dominated. However, in bags buried from April to October, only tarsonemids were present. Once one population was established, the other did not develop in the bags, suggesting the use of a common resource. When high densities of tarsonemids or pyemotids were achieved, there was colonization by predatory Gamasina and predatory prostigmatids. The Gamasina were represented by families: Arctacaridae, Rhodacaridae, Laelapidae, and Ascidae. The main predatory Prostigmata were Raphignathidae and Bdellidae.

After the Gamasina and predatory Prostigmata were established in the bags, there was a marked drop in the numbers of tarsonemid or pyemotid mites, sug-

gesting the latter species were prey. Gamasina and predatory Prostigmata may prey on both mites and nematodes (Price 1973, Muroaka and Ishibashi 1976).

Collembola and Psocoptera were the last groups to colonize together with the first colonizers. Collembola are considered general feeders utilizing fungi, algae, microorganisms, humus, leaf litter, and living vegetation (Gist and Crossley 1975, Butcher et al. 1977). They also can feed on nematodes (Brown 1954, Murphy and Doncaster 1957, Gilmore 1970). Psocoptera occurred only in late stages of decomposition. The Liposcelidae were the only family present in this experiment. They are reported to eat fungi (Borror et al. 1976).

There were repeatable colonization sequences of microarthropods in buried litter which were a function of the degree of decomposition of the litter not in season (Fig. 7). The overlapping litter bag placement and removal sequence allowed us to document this relationship clearly. In Fig. 7 we summarize not only the colonization sequence but also provide suspected trophic relationships. The predominance of predatory microarthropods and the absence of detritus-feeding oribatids at least in the 1st 6 mo of decomposition suggest a heretofore undescribed mode of action of microarthropods in buried litter in a desert ecosystem, as nematode carnivores.

The stepwise multiple regression analysis showed that abiotic factors had a greater effect on decomposition of treated bags than on the controls. The ranking with respect to effect of the abiotic environment on organic matter loss was insecticide-treated > fungicide-insecticide treated > fungicide-treated > untreated. Since all treatments (in buried bags) were exposed to the same environment, the variation in effect of abiotic factors must be due to biotic interactions. In the control bags, the seven parameters examined explained only half of the variation, but explained almost all of the variation in the bags where microarthropods were excluded. This suggests that decomposition was relatively independent of the environment in buried bags.

Removal of most of the fungi did not have a large effect on initial organic matter loss, suggesting that the principal interactions affecting organic matter loss in early stages of buried litter decomposition are between mites, nematodes, and bacteria. To support this idea further, we have documented potential food chain links between bacteria, nematodes, and tydeid mites (Santos et al. 1981). Treatments which simplify the biota and which eliminate microarthropods cause decomposition to fluctuate with the abiotic environment. The action of these predatory microarthropods is that of environmental integrators. Their presence partially uncouples decomposition from environmental constraints. These relationships have profound implications for the stability of communities.

Here we demonstrated that despite their low density in a desert ecosystem, if microarthropods are excluded the rate of litter decomposition is drastically reduced. The effect of microarthropods on buried litter decomposition in the Chihuahuan desert is probably through control of the microbial population, directly, by grazing on fungi and dispersing microrganisms, and indirectly, by preying on microbivorous nematodes.

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