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A COMPARISON OF SURFACE AND BURIED *LARREA TRIDENTATA* LEAF LITTER DECOMPOSITION IN NORTH AMERICAN HOT DESERTS[1]

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Abstract. We conducted studies of mass losses from surface and buried litter bags in four North American hot desert areas to test the following hypotheses: (1) leaf litter disappearance in hot deserts is independent of actual evapotranspiration, (2) buried litter disappearance is a function of actual evapotranspiration, (3) the pattern of microarthropod colonization of buried leaf litter is a function of the stage of decomposition, and (4) elimination of microarthropods results in reduced rates of decomposition and increased numbers of free-living nematodes. Mass losses from surface *Larrea tridentata* leaf litter bags ranked highest to lowest: Chihuahuan desert, Sonoran desert, Mojave desert, Coloradan desert. Mass losses from buried litter bags were essentially equal, ≈40%, in each of the deserts for bags buried from March to October. There was low correlation between rainfall and mass loss of buried litter and surface litter in the North American hot deserts. Mass losses from insecticide-treated buried bags were lower than from untreated bags. There was a greater abundance of nematodes in insecticide-treated bags than in untreated bags. Tarsonemid mites were found only in litter bags from the Chihuahuan desert. The most abundant microarthropods in buried leaf litter in the other deserts were predatory raphignathids, tydeids, and arctacarids. Decomposition (litter disappearance) in North American hot deserts was highly correlated with long-term rainfall patterns, which we hypothesize have served as the selective agents for the soil biota active in the decomposition process. Thus litter disappearance does not respond to annual fluctuations in rainfall amounts.

Key words: decomposition; desert; Larrea tridentata; *microarthropods; nematodes; North America; rainfall.*

INTRODUCTION

The data on leaf litter decomposition in deserts has largely been limited to studies in the northern Chihuahuan desert (Fowler and Whitford 1980, Santos and Whitford 1981, Elkins and Whitford 1982, Whitford et al. 1982). Data from these studies have been used to test hypotheses about the relationship of decomposition to actual evapotranspiration and lignin (Whitford et al. 1981*a*, Elkins et al. 1982). These studies have demonstrated that, in the northern Chihuahuan desert, the rate of decomposition is relatively independent of actual evapotranspiration. It has been suggested that the relative independence of decomposition from environmental constraints is due to the activity of soil fauna that are active in desert soils even in the absence of available free water (Whitford et al. 1981*b*). If this is a general relationship, then rates of decomposition in other North American hot deserts should also be relatively independent of actual evapotranspiration. A portion of the studies reported here were designed to test this hypothesis.

Studies of soil fauna in North American deserts have shown that these desert soils are usually dominated by prostigmatid mites (Santos et al. 1978, Franco et al. 1979, Santos and Whitford 1981), but in one area by mesostigmatid mites (Elkins and Whitford 1982). Santos and Whitford (1981) followed microarthropod succession in buried creosotebush (*Larrea tridentata*) leaf litter and found tydeid and tarsonemid mites predominated in the leaf litter in early stages of decomposition. There are no comparable data for fauna in surface litter during stages of decomposition. Whitford et al. (1981*b*) found that oribatid mites predominated in surface litter in the early morning hours, but few if any mites were found in litter collected at midday. Those collections were made in natural litter accumulations, which included all stages of litter breakdown in the sampled material. We hypothesized that the patterns of microarthropod colonization would be related to the stage of decomposition of the buried leaf litter in other North American hot deserts.

Santos and Whitford (1981) showed that litter treated with the insecticide Chlordane had a slower rate of disappearance than untreated litter, and further that the Chlordane-treated litter had higher populations of free-living nematodes. Santos et al. (1981) suggested that the elimination of a nematode predator, tydeid mites, allowed this increased population of nematodes to overgraze the bacteria (or yeasts), thereby reducing

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the rate of decomposition. We hypothesized that the exclusion of prostigmatid nematode predators would result in increased densities of free-living nematodes, and that exclusion of arthropods would result in reduced rates of litter disappearance similar to that reported in the Chihuahuan desert. Here we report the studies designed to test these hypotheses. We conducted studies of mass losses from surface and buried litter bags in four North American hot desert areas to test the following hypotheses: (1) leaf litter disappearance in hot deserts is independent of actual evapotranspiration, (2) buried litter disappearance is independent of actual evapotranspiration, (3) the pattern of microarthropod colonization of buried leaf litter is a function of the stage of decomposition, and (4) elimination of microarthropods results in reduced rates of decomposition and increased numbers of free-living nematodes.

STUDY SITES

Study sites were chosen to provide as similar an aspect, slope, soil type, and dominant vegetation (*Larrea tridentata*) as possible in each of the hot deserts. The Chihuahuan site had a rain gauge within 0.5 km of the litter bag location. Precipitation data for the other sites were obtained from the nearest National Oceanic and Atmospheric Administration reporting station. For long-term precipitation data for the Coloradan desert we had to use the Yuma, Arizona, data because the Gold Rock Ranch, California, station has not been in existence long enough to accumulate a long-term record. We used the term Coloradan desert in sensu Burk (1977) to distinguish between the biseasonal rainfall eastern Sonoran desert site near Casa Grande, Arizona, and the winter rainfall western Sonoran desert site in eastern California.

Chihuahuan

The Chihuahuan desert site was located on the New Mexico State University Ranch ≈40 km north-northeast of Las Cruces, New Mexico. The area is an alluvial piedmont of 3–4% slope with a vegetative cover of creosotebush. The long-term average annual precipitation is 225 mm, most of which falls July through October in convectional storms. Midsummer temperatures reach 40°C and temperatures below 0° occur regularly from November through February. The soils are sands with a calcium carbonate deposition layer 20–40 cm below the surface.

Sonoran

The Sonoran desert site was located 17 km west-southwest of Casa Grande, Arizona, near the base of a piedmont of <2% slope, sloping to the east. The long-term average annual precipitation is 206 mm. Summer maxima reach 43° and winter temperatures rarely fall to 0°. The vegetation is predominately creosotebush (*Larrea tridentata*) with palo verde (*Cercidium* spp.) and saguaro cacti (*Carnegia gigantia*) along the small drainages. The soils are medium sands with some coarse sands and gravels along the washes.

Mojave

The Mojave desert site was 25 km east-southeast of Boulder City, Nevada, on an east-facing alluvial piedmont of ≈4% slope. The long-term average precipitation is 131 mm, most of which falls between November and April as a result of frontal storms. Summer maxima reach 42° and temperatures below 0° occur from November through March. The dominant vegetation is creosotebush (*Larrea tridentata*) with scattered Joshua trees (*Yucca brevifolia*) and other small shrubs (*Atriplex* sp. and *Gutierrezia* sp.). The soils are loose medium to fine sands with a highly fractured calcium carbonate deposition layer at 20–30 cm.

Coloradan

The Coloradan desert site was located east of Glamis, California, on a broad, highly braided sheet wash plain with <2% slope. The nearest long-term National Oceanic and Atmospheric Administration reporting station is Yuma, Arizona, ≈70 km south-southeast, where the long-term mean average precipitation is 68 mm, most of which falls in December through March as a result of frontal storms. In our analysis we used the precipitation data from Gold Rock Ranch, California, which is ≈5 km from our study site. Summer maxima reach 43° and winter temperatures rarely drop to 0°. The soils are hard-packed silts and fine sands with a calcium carbonate deposition layer at <10 cm.

METHODS

We studied decomposition of creosotebush, *Larrea tridentata*, leaf litter confined in fiberglass mesh bags. The leaf litter was collected from creosotebushes on the New Mexico State University Ranch, air dried, and subsamples oven dried at 60° for 72 h to obtain oven dry mass. Each litter bag (20 × 20 cm fiberglass, screen mesh size 1 mm) contained 20 g of dried leaf litter. One-half of the litter bags that were to be buried were soaked in a 1% (by volume) Chordane plus wetting agent solution (1% Tween 20). The other half of the bags were soaked in water with the wetting agent. All bags were air dried and then placed in individual plastic bags for transport to the field. The sequence of bag placement and retrieval was designed to allow separation of seasonal variation in microarthropods in buried litter from variation due to degree of litter decomposition.

Sets of litter bags were placed in the field on 14 March, 5 June, and 7 August 1979. Collections were made on 5 June, 7 August, and 2 October 1979. There were 5 litter bags in each set of surface bags and 10 untreated and 10 insecticide-treated bags in each set of buried bags. On each collection date the surface bags, 5 insecticide-treated and 5 untreated buried bags

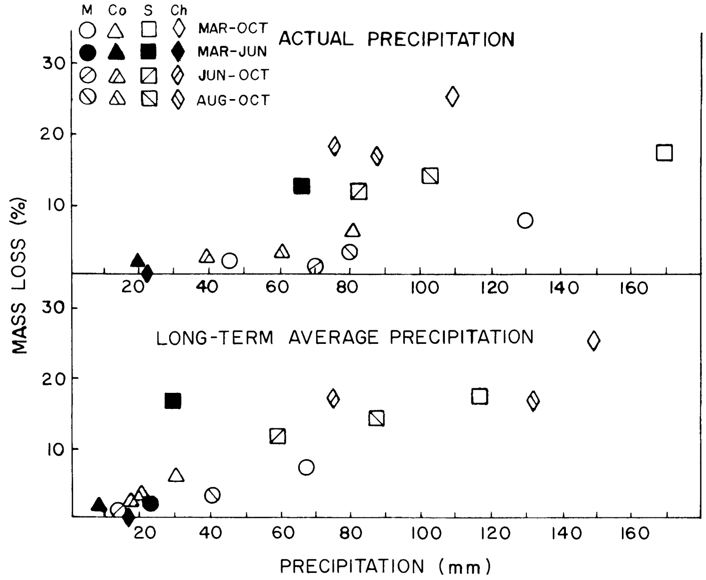

FIG. 1. Percent mass loss from creosotebush (*Larrea tridentata*) leaf litter in fiberglass mesh bags on the soil surface in four North American hot desert sites as a function of actual precipitation and long-term average precipitation. M = Mojave; Co = Coloradan; S = Sonoran; Ch = Chihuahuan.

were placed on modified Tullgren funnel extractors (Santos et al. 1978) and the mites extracted onto water. The extractors provide both a temperature (60°–25°) and humidity gradient. Mites and insects were identified and counted immediately after extraction using keys in Krantz (1975) and Borror et al. (1976). Nematodes were extracted from the remaining bags in each treatment using the Oostenbrink cotton wool filter and sieving (Nicholas 1975). After mites had been extracted from the litter, the litter was oven dried, weighed, combusted in a muffle furnace and the ash mass was determined. Organic matter loss was calculated using the equation developed by Santos and Whitford (1981) to correct for infiltration of soil into buried litter bags.

Data were analyzed for each collection date by ANOVA and Tukey's *Q*. Because some marking tags were lost, we did not recover all litter bags placed in the field. Where there were insufficient bags for the minimal sample sizes described above, the reduced sample sizes are noted on the summary tables. Climate data were obtained from National Oceanic and Atmospheric Administration (1979).

RESULTS

Mass loss

In the time period 14 March–5 June, the only significant mass loss from surface bags was at the Sonoran desert site, where there was also significant rainfall during that period (Fig. 1). However, there was no correlation between rainfall and mass loss ($r^2 = 0.8$, $P > .4$). The highest mass loss from buried bags also was recorded at the Sonoran site ($F_{3,16} = 16.6$, $P < .0001$) and the untreated buried bags had significantly higher mass losses at all sites than the insecticide-treated bags ($F_{3,16} = 61.5$, $P < .0001$) (Table 1).

In litter bags left in the field for 6 mo, March–October, the highest mass losses from surface bags were in the Chihuahuan desert; these losses were significantly higher ($F_{3,16} = 27.5$, $P < .0001$) than the mass losses from bags at the Sonoran site. There were no significant differences in mass losses from the surface at the Mojave and Coloradan sites (Fig. 1) nor was there a correlation between rainfall during the period and mass loss ($r^2 = 0.5$, $P > .3$). Although the buried bags in the Coloradan desert had significantly higher mass loss ($F_{3,16} = 4.1$, $P < .01$) than buried bags in the other deserts, this difference was very small (Table 1). The significant differences between insecticide-treated and untreated litter were found only in buried bags at sites with low rainfall (Table 1).

The mass losses recorded for the shorter time intervals in the field exhibited patterns similar to those seen in the longer time intervals. If low amounts of rainfall were recorded, there were virtually no mass losses from surface bags. However, there was no correlation between rainfall and mass loss (r^2 between 0.0 and 0.5, $P > .25$) in surface bags (Fig. 1).

A regression analysis of all of the data for surface litter decompsition vs. actual precipitation for the field periods from the nearest reporting station yielded the following relationship: $y = -2.2 + 0.14x$, where y = percent mass loss and x = millimetres of precipitation. The r^2 for this relationship was 0.46 (Fig. 1). When the same analysis was performed using the long-term average precipitation for the field periods (data

TABLE 1. Percent mass losses from litter bags containing *Larrea tridentata* leaf litter buried below the canopy of *L. tridentata* in North American hot deserts. Cumulative rainfall is from the nearest National Oceanic and Atmospheric Administration reporting station for the time period indicated. Within an exposure period, mass loss values with different superscript letters are significantly different at $P < .05$ (Tukey's Q). Numbers in parentheses indicate sample sizes <5. ND = no data.

Measure	Mojave	Coloradan	Sonoran	Chihuahuan
		14 March–5 June		
Mass loss (%)				
Buried untreated	28.3 ± 4.3^{a} (3)	25.7 ± 3.8^{c}	43.2 ± 0.9^{d}	23.0 ± 3.0^{c}
Buried insecticide-treated	18.2 ± 0.7^{e}	11.0 ± 6.5^{e}	32.4 ± 1.5^{f}	6.6 ± 4.9^{c}
Cumulative rainfall (mm)	45.8	20.0	66.6	22.1
		14 March–2 October		
Mass loss (%)				
Buried untreated	37.8 ± 2.0^{d}	48.1 ± 2.6^{e}	43.0 ± 3.8^{e} (4)	43.1 ± 3.6^{e}
Buried insecticide-treated	ND	36.3 ± 4.8^{f} (4)	43.4 ± 2.0^{e}	43.5 ± 1.8^{e}
Cumulative rainfall (mm)	125.4	81.3	170.5	110.1
		2 August–2 October		
Mass loss (%)				
Buried untreated	33.0 ± 0.1^{c}	47.1 ± 8.0^{f}	44.9 ± 3.9^{f}	46.7 ± 1.7^{f}
Buried insecticide-treated	28.9 ± 6.4^{g}	31.6 ± 3.9^{g}	44.6 ± 1.5^{f}	37.8 ± 4.3^{g}
Cumulative rainfall (mm)	64.4	38.9	82.6	77.9
		5 June–2 October		
Mass loss (%)				
Buried untreated	27.5 ± 5.1^{d}	41.3 ± 1.1^{e}	44.1 ± 3.0^{e} (4)	39.7 ± 3.4^{e}
Cumulative rainfall (mm)	79.6	61.3	103.9	96.4

from nearest National Oceanic and Atmospheric Administration reporting station) the regression equation was $y = -0.6 + 0.17x$, with an r^2 of 0.82. Thus litter disappearance was better correlated with long-term average precipitation than with actual precipitation for the periods the litter bags were in the field (Fig. 1).

Microarthropods

The only consistent data on microarthropods in surface bags were tydeids extracted from surface litter bags on 5 June. There were no significant differences between sites, and average numbers per bag (± SD) ranged from 5.5 ± 3.5 to 2.5 ± 1.8 across the desert sites. Since collections of litter bags were made mid-morning to late afternoon, the data on microarthropods in surface bags is unreliable because of diurnal migration patterns (Whitford et al. 1981*b*).

There were some important and consistent differences in the microarthropod fauna extracted from buried litter bags. Tarsonemid mites were found only in litter bags in the Chihuahuan desert, and these were found on all collection dates (Table 2). On the 5 June collection, liposcelid psocopterans were abundant in bags buried at the Sonoran, Coloradan, and Mojave desert sites, but they were absent in the Chihuahuan (Table 2). The August collection was the only time period when the density and number of taxa of microarthropods was highest in a desert other than the Chihuahuan. On all other collection dates, the highest densities and number of taxa were in the Chihuahuan desert samples. In the Mojave in August most of the microarthropods were isotomid and sminthurid collembolans. On that collection date gravimetric soil moistures were: Sonoran 3.1%, Coloradan 0.6%, Chihuahuan 2.3%, and Mojave 7.5%. When litter bags were collected in June, gravimetric soil moistures were: Sonoran 1.1%, Coloradan 0.4%, Chihuahuan 1.2%, and Mojave 0.9%. In October, soil moistures were: Sonoran 0.5%, Coloradan 0.5%, Chihuahuan 5.4%, and Mojave 0.7%. We also extracted collembolans from Chihuahuan desert buried bags in October (Table 2).

Although there was a correlation between number of taxa ($r^2 = 0.9$, $P < .05$) and soil moisture at the time of collection, there was no correlation between density of microarthropods and soil moistures at the time of collection ($r^2 = 0.1$–0.4, $P > .1$) (Table 2). Psocopterans were predominant in buried litter in the October samples, and these soil animals were numerous in litter bags collected in June in all but the Chihuahuan desert site (Table 2).

Nematodes

There was a consistent pattern of higher nematode numbers in the insecticide-treated bags in comparison to the untreated buried litter bags except in the 14 March–5 June Coloradan desert bags. The differences were highly significant ($t = 3.9$–8.9, $P < .01$) for all of the pairs indicated as significantly different in Table 3.

DISCUSSION

This study provides the first comparative data on decomposition in North American hot deserts. The data provide additional support to the suggestion of Whitford et al. (1981*b*), that the failure of actual

TABLE 2. Mean numbers of microarthropods per bag (±SE) extracted from buried *Larrea tridentata* leaf litter bags in the North American hot deserts. Bags had been buried in the soil for the time periods indicated.

Taxon	Mojave	Coloradan	Sonoran	Chihuahuan
		14 March–5 June		
Tydeidae	8.3 ± 5.9	3.3 ± 1.8	17.3 ± 4.2	156.7 ± 36
Tarsonemidae	0	0	0	7345 ± 1681
Raphignathidae	19.3 ± 13.5	1.3 ± 1.2	17 ± 4.1	0
Arctacaridae	0	0	0	0
Gamasina	0.1 ± 0.2	0	.02 ± .02	461 ± 167
Psocoptera	126 ± 75.3	12.3 ± 3.5	153.3 ± 12.4	0
Sminthuridae	0	0	0	0
Isotomidae	0	0	0	0
		5 June–7 August		
Tydeidae	21 ± 7	10 ± 4	144 ± 18	15 ± 4
Tarsonemidae	0	0	0	94 ± 36
Raphignathidae	0	0	20 ± 11	0
Arctacaridae	37 ± 31	7 ± 5	0	625 ± 433
Gamasina	21 ± 13	16 ± 12	0	18 ± 13
Psocoptera	.05 ± 1	7 ± 8	0	0
Sminthuridae	129 ± 130	0	0	0
Isotomidae	393 ± 253	0	0	0
		2 August–2 October		
Tarsonemidae	0	0	0	367 ± 186
Paratydeidae	0	0	0	7 ± 3
Gamasina	0	0	0.3 ± 1.5	5 ± 3
Psocoptera	6 ± 3	163 ± 131	32 ± 6	87 ± 31
Isotomidae	0	0	0	10 ± 5
Others	0	0	0	7 ± 6
		5 June–2 October		
Tarsonemidae	0	0	0	221 ± 99
Paratydeidae	0	0	0.5 ± 1.0	3 ± 2
Gamasina	0	0	1.0 ± 2.0	12 ± 7
Psocoptera	4 ± 2	147 ± 51	20 ± 4	71 ± 14
Isotomidae	0	0	0	19 ± 12
Others	0	0	0	3 ± 2
		14 March–2 October		
Tarsonemidae	0	0	0	77 ± 20
Paratydeidae	0	0	0	2 ± 2
Gamasina	0	0	0	16 ± 12
Psocoptera	7 ± 3	127 ± 124	10 ± 3	11 ± 6
Isotomidae	0	0	0	53 ± 24
Others	0	0	0	2 ± 1.5

evapotranspiration to serve as a predictor of decomposition in deserts is a function of the adaptations of desert soil biota. In the present study we found that the percent of surface litter that disappeared was better correlated with long-term average rainfall than with the actual rainfall during the period of study. Some of the data, i.e., litter disappearance between March and June, suggest that rainfall that produces some minimal level of soil moisture is necessary for measurable litter disappearance. In the two winter rainfall deserts, the

TABLE 3. Numbers ± 1 SD of nematodes extracted from three buried untreated and three buried insecticide-treated litter bags. Significant differences between treated and untreated are shown by different letters. ND = no data.

Bag treatment	Mojave	Coloradan	Sonoran	Chihuahuan
		14 March–5 June		
Untreated	3963 ± 132^{a}	2096 ± 2374^{a}	722 ± 464^{a}	105 ± 78^{a}
Insecticide-treated	12 104 ± 430^{b}	1009 ± 58^{a}	8780 ± 3372^{b}	2046 ± 154^{b}
		5 June–2 October		
Untreated		2226 ± 1209^{a}	723 ± 195^{a}	749 ± 98^{a}
Insecticide-treated	ND	7636 ± 6834^{b}	8728 ± 1547^{b}	4739 ± 1753^{a}
		2 August–2 October		
Untreated	187 ± 60^{a}	593 ± 837^{a}	2359 ± 1040^{a}	1343 ± 118^{a}
Insecticide-treated	9392 ± 3634^{b}	11 007 ± 1918^{b}	12 415 ± 7583^{b}	3098 ± 324^{b}

Mojave and Coloradan, the rates of litter disappearance were lowest and nearly equal, while mass loss from surface litter in the Sonoran desert was intermediate, and that in the summer rainfall Chihuahuan desert the highest. This pattern of litter disappearance is predictable if we assume that the soil biota in the respective deserts is the biota adapted to the long-term "average" conditions. Unfortunately we have no data on the soil biota involved in the breakdown of surface litter in any of the hot deserts except for the Chihuahuan where oribatid mites appear to be important components of the soil fauna in surface litter accumulations.

Meentemeyer (1978) provided a model to predict decomposition as a function of actual evapotranspiration and lignin content. We used this model to calculate the expected percent mass loss using both the actual precipitation for the period of the study and the long-term average annual precipitation for the desert areas studied. Using the actual precipitation and lignin content of creosotebush leaves (Elkins and Whitford 1982) we would expect mass losses of 4.3% in the Coloradan (actual 6.8%), 7.9% in the Mojave (actual 7.4%), 11.1% in the Sonoran (actual 17.3%), and 6.7% in the Chihuahuan (actual 26.4%). Using the long-term average annual precipitation, we would expect 3.64%, 8.24%, 13.71%, and 15.1%, respectively, in the deserts, ranked from lowest to highest precipitation. In most cases the Meentemeyer (1978) model underestimated the mass loss, even though the estimates were for only 6 mo in the field. This is the same pattern discussed by Whitford et al. (1981*a*). In this study we found a good correlation between percent mass loss and long-term average precipitation. The equation for this relationship: y(percent mass loss) $= -0.6 + 0.17x$ (precipitation in millimetres) provides an alternate model that needs to be tested in desert areas having very different rainfall regimes.

Some of the data, i.e., surface litter disappearance between March and June, suggest that rainfall producing some "threshold" level of soil moisture is necessary for measurable litter disappearance. However, without additional data we cannot determine what the threshold level of rainfall is. Some soil moisture is probably necessary if water vapor movement in the soil (Jury and Letey 1979) is to occur, and this moisture may be necessary for surface activity of microarthropods (Whitford et al. 1981*b*). However, it would be necessary to make repeated measurements at each of the hot desert sites in order to determine if there is moisture stored in the soil following rains that subsequently moves upwards as water vapor in amounts sufficient to wet surface litter.

The data on buried litter decomposition showed few significant differences between deserts. In the 6-mo warm season, there was a mass loss of ≈40% in the buried litter in each of the deserts, comparable to mass losses reported by Santos and Whitford (1981). There were significant differences in decomposition during the 1st 3 mo that appeared to be related to the higher rainfall in the Sonoran desert during that period, and there was no difference in mass loss in the Sonoran desert between bags buried from March to June and those left from March to October. This may be a function of temperature and moisture, or loss of ≈40% of the mass of creosotebush leaves may simply represent the loss of readily decomposable material. If ≈60% of the mass of creosotebush leaf litter is recalcitrant and breaks down slowly, that fact could account for the apparent anomaly in these data.

The significant reductions in mass losses of buried leaf litter treated with insecticide demonstrate the importance of arthropods in mass loss in all of the North American hot deserts. The significant increases in nematodes in the insecticide-treated litter could be a response to the elimination of predatory mites, as discussed by Santos et al. (1981), or simply a response of nematodes to the Chlordane insecticide. Since we have no data on microflora, we are unable to determine if there was significant reduction of microflora in the litter bags treated with Chlordane. Without data on microflora, we can only assume that the relationships described by Santos et al. pertain, and that the higher numbers of nematodes are related to the reductions in mass loss. These data allow us to conclude that the elimination of arthropods adversely affects mass loss in buried creosotebush leaf litter, but we can only speculate as to the mechanism.

The microarthropods extracted from buried leaf litter in this study, with the exception of the collembolans, psocopterans, and tarsonemid mites, are forms generally considered to be predators (Krantz 1975, Santos and Whitford 1981). The predatory taxa may prey on other mites or upon nematodes. Nematodes in dry soils are generally anhydrobiotic (Freckman et al. 1977, Whitford et al. 1981*b*) and probably are not preyed upon in this state. However, the buried leaf litter was perceptibly moist in all deserts on each collection date, which may account for the presence of active nematodes and also account for the presence of nematode predators. The only collections of collembolans were made when litter bags were removed from moist soils. This pattern is consistent with the idea that soil collembolans in arid and semiarid regions may be adhydrobiotic when the soil is dry (Poinsot 1968, Poinsot-Balaguer 1976).

The microarthropods extracted from buried litter bags represent a subset of the soil microarthropod fauna. We know that many other taxa occur in soils of the Mojave desert (Wallwork 1972, Franco et al. 1979), including genera of oribatid mites that are probably involved in comminution of leaf litter. Surface litter accumulations have populations of active microarthropods for only short time periods each day (Whitford et al. 1981*b*), which accounts for the lack of data on surface litter microarthropods in this study.

We used an overlapping sequence of bag placement and retrieval in order to examine the generality of the sequence of colonization of buried litter described by Santos and Whitford (1981). The microarthropods extracted from buried litter in this study did not present the same pattern seen by Santos and Whitford (1981). For example, psocopterans occurred in litterbags in early stages of decomposition in all deserts except the Chihuahuan. Tydeids were present in buried litter in June and August, but not in September. Tydeids have been implicated as regulators of early stages of buried litter decomposition by preying on bacteriophagous nematodes (Santos et al. 1981), and reduction in mass loss in the insecticide-treated bags in this study may be attributable to this relationship. The Chihuahuan desert site was the only area where tarsonemid mites were extracted from buried litter. These small fungiphagous mites were numerically important, and second-stage colonizers in the study of Santos and Whitford (1981). The presence of large predatory mites and psocopterans in early-stage buried litter in deserts other than the Chihuahuan indicate that the colonization sequence described by Santos and Whitford (1981) is peculiar to that Chihuahuan desert site and not applicable to other desert sites.

An important generalization suggested by this study is the inapplicability of the "pulse-reserve" paradigm proposed by Noy-Meir (1973) for desert processes. The "pulse-reserve" paradigm states that a trigger (rainfall) sets off a pulse of activity, i.e., production or decomposition, and that the pulse is rapidly lost or depleted, but some of the energy goes into a reserve, i.e., seeds, spores, anhydrobiotic forms, eggs, etc. This study documents the independence of both surface litter and buried litter decomposition from rainfall. As discussed earlier, some moisture may be necessary to initiate activity, but above some threshold, soil organisms act independently of soil moisture. The long-term climatic patterns are obviously more important as selective forces shaping the structure of desert soil communities than are the short-term yearly fluctuations. These soil organisms determine rates of litter disappearance; hence the pattern of surface litter disappearance is related to long-term rainfall patterns in the North American hot deserts.

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