

## Decomposition Patterns of Surface Leaf Litter of Six Plant Species Along a Chihuahuan Desert Watershed

JORGE G. CEPEDA-PIZARRO<sup>1</sup> AND WALTER G. WHITFORD

*Department of Biology, New Mexico State University, Las Cruces 88003*

**ABSTRACT.**—Mass losses from litter bags of surface creosote bush litter placed along a Chihuahuan Desert watershed were measured to answer the following questions: (1) Do edaphic factors affect organic matter losses? (2) Are there differences in mass losses between the litter of the site-dominant plant species and creosote bush leaf litter? We hypothesized that (1) mass losses of all litter types would be higher at the base of the watershed and lower on the upper portions of the watershed and (2) mass losses of the litter of the site-dominant plants would be higher than those of creosote bush leaf litter in the same site.

Mass losses from creosote bush leaf litter did not follow the moisture-organic matter gradient present in the watershed. Mass losses were higher at mid-slope run-on areas than in upper-slope erosional sites and the dry lake basin. Mass losses were highest where subterranean termite activity was the highest. There were differences between losses from the litter of the site-dominant and creosote bush leaf litter in some instances, but these differences were not attributable to differences in lignin content nor C:N ratio. Mass losses of litter of site-dominant species were not always higher than that of creosote bush leaf litter in the same site. Mass losses were best described by the double exponential model.

### INTRODUCTION

Considerable variation in decomposition rates of litter has been reported for different types of ecosystems (Swift *et al.*, (1979). Values of the decay constant (K) range from 0.03 year<sup>-1</sup> (tundra) to 6.0 year<sup>-1</sup> (tropical forests). Site variations in climate, topography, physicochemical soil properties and vegetational cover can produce different patterns of decomposition rates, mineralization and soil organic matter accumulations (Seastedt *et al.*, 1983; Day, 1982; Schinner, 1982; Santos *et al.*, 1978). While climate places upper and lower limits to potential decay, the fine control at the local level is determined by litter quality and factors of the edaphic complex (Swift *et al.*, 1979).

The chemical composition of litter affects decomposition rates and patterns. McClaugherty *et al.* (1985) found that litter rich in soluble material lost mass rapidly during early stages of decomposition. Initial losses due to leaching are frequently observed in decomposition studies (Seastedt and Crossley, 1980). Because of this two-step nature, mass losses over time may be well-described by a double exponential decay model (Wieder and Lang, 1982).

Most of the current information on decomposition in terrestrial ecosystems comes from studies conducted in mesic environments. Recent studies have shown that some explanatory hypotheses, which apply to moister environments, are not applicable to decomposition processes in hot deserts (MacKay *et al.*, 1987; Whitford, 1986; Whitford *et al.*, 1986; Elkins *et al.*, 1982; Whitford *et al.*, 1982).

Studies performed on the northern Chihuahuan Desert have reported higher litter decay rates than those predicted from current models (*e.g.*, Meentemeyer's model, Meentemeyer,

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<sup>1</sup> Present address: Departamento de Biología y Química, Universidad de La Serena, Casilla 599, La Serena, Chile

1978). Discrepancies are attributed to continual mechanical and physical weathering (*e.g.*, high solar radiation, sheet run-off, wind scouring) (Schaefer *et al.*, 1985) and to a rapid and efficient litter breakdown by the soil community (Elkins *et al.*, 1982; Santos and Whitford, 1981).

Most studies of litter decomposition in arid systems have assessed the effect of climatic factors on mass disappearance (Whitford *et al.*, 1986; Schaefer *et al.*, 1985; Santos *et al.*, 1984). Studies that have considered litter chemistry and/or soil chemistry failed to provide conclusive evidence that these variables affect litter decomposition (Schaefer *et al.*, 1985; MacKay *et al.*, 1987). Dwyer and Merriam (1981) reported that litter decomposition in a hardwood forest varied as a function of topography. Since the topography of desert ecosystems varies greatly, we hypothesized that litter decomposition would reflect that variability.

In the southwestern U.S. a desert watershed varies greatly with respect to soil water availability and retention (a function of run-off, run-on patterns), soil organic matter distribution, dominant vegetation and soil structure (Wierenga *et al.*, 1987). Litter decomposition should vary as a function of several of these factors, especially soil water storage, soil structure and soil organic matter. We designed a study of litter decomposition on a desert watershed in southern New Mexico in order to examine topographic position-decomposition rate relationships of *Larrea tridentata* litter. *Larrea tridentata* occurs as a dominant in a virtual monoculture on part of the watershed, and as scattered shrubs on the remainder of the watershed except for the lake bottom. Quantities of *L. tridentata* litter are washed into the lake during large run-off events. Thus, *L. tridentata* litter occurs over the entire watershed.

In order to evaluate the relative importance of topographic position and litter quality, we compared the decomposition of *Larrea tridentata* litter with that of the site-dominant plant species. The aim of this study was to compare the effect of microsite characteristics on decomposition patterns of surface creosote bush leaf litter, and to compare patterns of mass losses of leaf litter of the site-dominant and creosote bush leaf litter across a Chihuahuan Desert watershed.

#### STUDY AREA

The work was conducted on the Jornada Long-Term Ecological Research Site (30°30'N, 106°45'W), 40 km NNE of Las Cruces, New Mexico. The long-term average rainfall is 225 mm yr<sup>-1</sup>. Summers are hot with maximum air temperature between 35–40 C from mid-May to mid-September. Rainfall is predominantly summer rainfall from convectional storms. Freezing temperatures frequently occur at night between October and March (Houghton, 1972).

At the study site, two 3-km transects (nitrogen-fertilized and control) extend on a NE-facing slope of the Dona Ana Mountain range, elevation 1501 m, downward into a dry lake (playa), elevation 1318 m, crossing seven perennial vegetation zones (sites). From the lower end of the transects to the upper end, these zones are identified as (1) playa—dry lake; (2) playa fringe; (3) basin slope; (4) bajada; (5) lower piedmont; (6) upper piedmont, and (7) sotol rockland (Fig. 1). Details of soil and vegetational characteristics across the transects are in Wierenga *et al.*, 1987; Nash, 1985; and Stein and Ludwig, 1979.

#### MATERIALS AND METHODS

We studied surface leaf-litter decomposition of the following species, which are common in one or more of the zones of the watershed: vine mesquite grass (*Panicum obtusum* H.B.K.), mesquite (*Prosopis glandulosa* Torr.), desert marigold (*Baileya multiradiata* Harv. and Gray), creosote bush (*Larrea tridentata* (DC) Cov.), fluffgrass (*Erioneuron pulchellum* (H.B.K.) Takeoka) and black grama grass (*Bouteloua eriopoda* Torr.). Leaves (creosote bush and

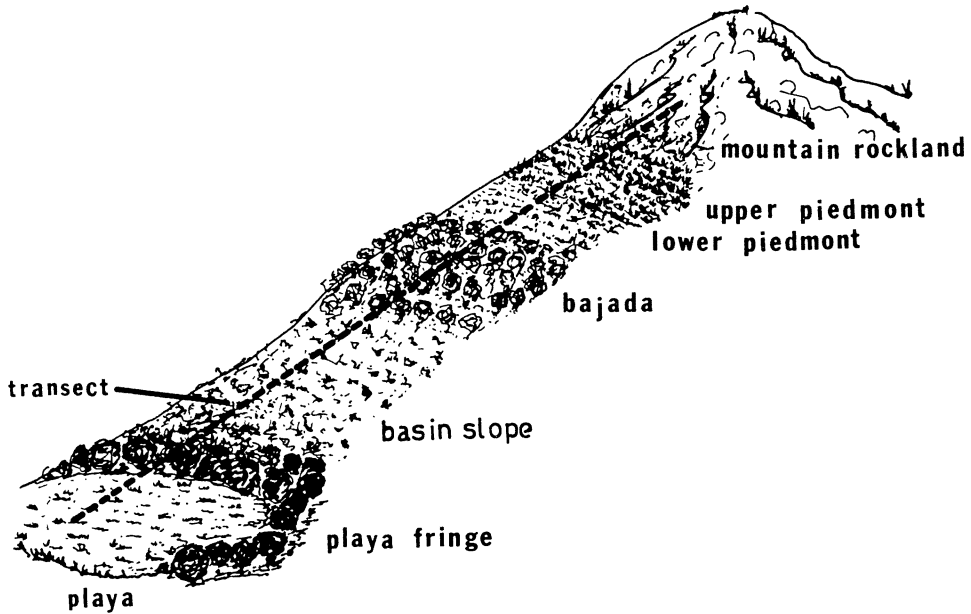


FIG. 1.—A diagrammatic representation of the spatial relationships of the vegetation zones on the Chihuahuan Desert watershed on which decomposition studies were conducted. The transects are 3 km in length. The elevation of the playa is 1318 m and the top of the transects is at 1501 m

mesquite) and aboveground parts (the remaining species) were harvested in fresh condition during July 1984, and sun-dried for a week. The drying material was turned over daily to assure homogeneous desiccation.

Mass losses were measured using 930 pairs of 15 cm × 15 cm litter bags (fiberglass mesh 1.5 mm) filled with  $10.35 \pm 0.15$  g of air-dried litter. In each zone, groups of bags were placed under the canopy of shrubs or adjacent to grass clumps selected at random. The pairs (155 per zone) were a bag with creosote bush leaf litter and a bag with litter of the plant species dominant at each site, *i.e.*, vine mesquite grass (playa), mesquite (playa fringe), desert marigold (basin slope), creosote bush (bajada), fluffgrass (lower piedmont) and black grama grass (upper piedmont). Immediately after placement of the litter bags, a sample of five pairs per site was collected to estimate moisture content and spillage due to handling.

Five randomly selected pairs of litter bags per site were retrieved biweekly in the growing season (July through September), and monthly during the remaining time. Twenty-two sets of samples were collected from August 1984 to December 1985. After collection, the litter was oven-dried at 60 C for 5 days, weighed and ashed in a muffle at 600 C for 8–10 h. Cumulative mass losses were estimated using the equation developed by Santos and Whitford, 1981, as modified by Elkins and Whitford, 1982.

$$d = \frac{I + A - Y}{S_i} - F; \quad \%d = \frac{d \times 100}{I - Y}$$

Where:

$d$  = estimated organic matter loss

$Y$  = mass of initial inorganic content of sample

- I = initial dry mass of sample
- A = final ash weight of sample
- Si = estimated soil organic matter content
- F = final dry mass of sample

Three decay models were fitted to the percent mass remaining through time: (1) single exponential ( $B_0$  fixed and  $B_0$  estimated from the data); (2) double exponential, and (3) asymptotic model (Wieder and Lang, 1982). Curve-fitting was conducted with nonlinear regression procedure of SAS-version 5 (method Gauss; SAS, 1985). The criterion to select the "best model" was the smallest residual mean squares (RMS). Once selected, the model was checked by lack-of-fit test (level of significance at  $P < 0.01$ ) and graphical analysis of the behavior of residuals.

Six simultaneous regression equations (double exponential decay model) were calculated to compare mass losses of creosote bush leaf litter among sites. The curves (one per site) were compared by pair-wise tests for overlap trends. The decomposition rates (proportion remaining per day) were compared by asymptotic 95% confidence interval (SAS, 1985). The same steps and procedures described above were used to compare mass losses between creosote bush leaf litter and site-dominant litter type. Five double exponential equations were calculated (one per litter type) and inspected with lack-of-fit tests and graphical examination of residuals. Each equation was contrasted against the respective creosote bush double exponential fit for overlap trend.

Data on the chemical characteristics of the litter were obtained from the literature or from laboratory analyses done for other studies. Plant nitrogen content was measured by a micro-kjeldahl technique (Bremner and Mulvaney, 1982). Lignin content was measured by the Van Soest method (Van Soest, 1963); plant carbon content was estimated from data summarized by Schlesinger, 1977.

## RESULTS

Decay models yielded different goodness-of-fit. The double exponential decay model consistently gave the lowest residual mean square (RMS) and the single exponential model with intercept fixed at 1.0 yielded the highest RMS. Based on the lack-of-fit tests and examination of residuals, we decided that the double exponential model satisfactorily described the observed trends in mass reduction. Here, both the decomposition rate of the "labile" ( $k_1$ ) and "recalcitrant" ( $k_2$ ) fraction are expressed as proportion remaining of litter mass per day.

The estimated "labile" fraction of creosote bush leaf litter ranged from 27% to 33%. This percentage may represent the fraction easily reducible under the abiotic and biotic conditions prevailing in the watershed. No significant differences in  $k_1$  were detected across the sites, but it ranged from 0.0255 (playa) to 0.1451 (basin slope) (Figs. 1–5).

Creosote bush litter  $k_2$  was highest at the playa fringe site (0.015) and lowest in the playa and the bajada sites (0.0007). Pairwise comparisons showed the following combinations of significant differences: playa (0.0007)–playa fringe (0.0015); playa fringe (0.0015)–bajada (0.0007); playa fringe (0.0015)–upper piedmont (0.0008); basin slope (0.0010)–bajada (0.0007); bajada–lower piedmont (0.0013); lower piedmont–upper piedmont. The highest asymptotic 95% confidence interval was observed in the basin slope site.

The expected trends of mass loss of creosote bush leaf litter set in the bajada and in the lower piedmont sites were nearly equal (Fig. 2). For all sites the double exponential predicts high initial mass losses of all species. Whereas the highest initial decrement is predicted for

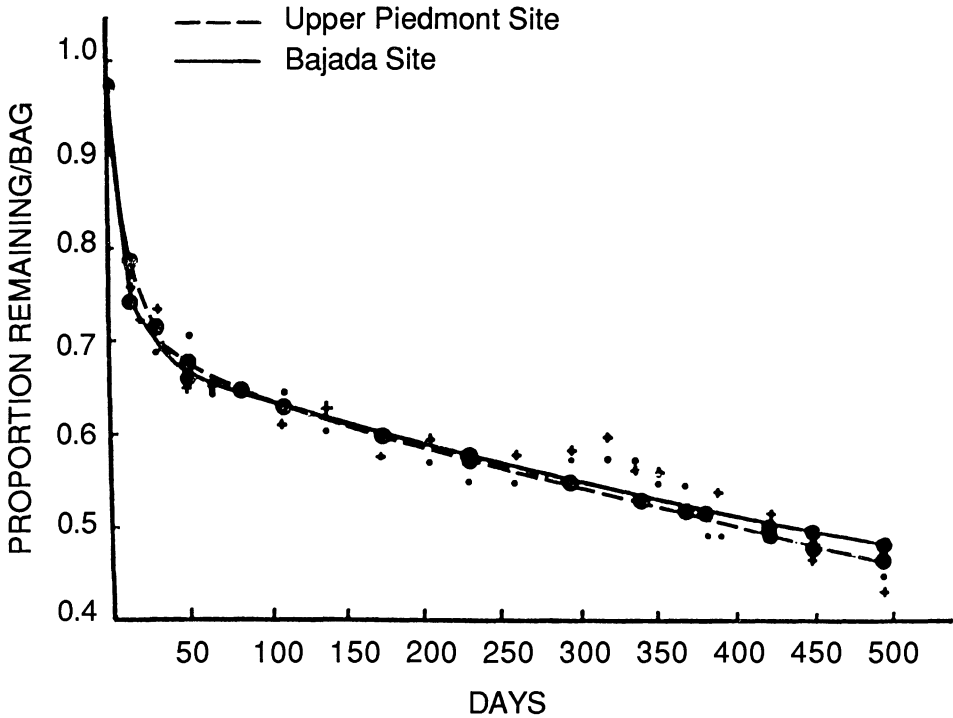


FIG. 2.—Mass loss of surface creosote bush (*Larrea tridentata*) leaf litter. Each observed value represents the mean of five litter bags. The mean expected mass loss values calculated by regressions are shown as large solid circles. Actual data are (+) means for the bajada site and (•) means for the upper piedmont site. The regression equations are:  $X_{up} = 0.303e^{-0.076t} + 0.697e^{-0.0008t}$  and  $X_{bajada} = 0.296e^{-0.111t} + 0.704e^{-0.0007t}$ .

litter at the playa fringe site, the lowest is predicted for the playa, despite the spatial proximity of the sites (Figs. 2–6).

There were only small differences in the lignin content of the plant materials but there were large differences in C:N ratios (Table 1).

Six out of 15 comparisons of curve-overlap indicated different patterns in litter disappearance (Table 2), three in the playa fringe, and three at the lower piedmont site. No differences were observed between the playa fringe and the lower piedmont sites.

TABLE 1.—A comparison of the characteristics of the litter of plant species used in this study. ND indicates no data available. Data from Schaefer *et al.*, 1985, and this study

	C:N ratio	Lignin %
<i>Baileya multiradiata</i>	24.2	6.9
<i>Bouteloua eriopoda</i>	37.6	7.0
<i>Erioneuron pulchellum</i>	59.9	7.6
<i>Larrea tridentata</i>	26.7	10.6
<i>Panicum obtusum</i>	ND	7.9
<i>Prosopis glandulosa</i>	16.1	7.85

TABLE 2.—F values of pair-wise curve-overlap tests for mass-loss trends (double exponential model) of surface creosote bush leaf litter across six vegetation zones of the LTER-Jornada Site (control-transect). \* Significantly different at  $P < 0.01$

Site comparisons	F
Playa versus:	
Playa fringe	7.29*
Basin slope	0.95
Bajada	3.95
Lower piedmont	4.53*
Upper piedmont	2.53
Playa fringe:	
Basin slope	3.94
Bajada	9.97*
Lower piedmont	2.35
Upper piedmont	8.52*
Basin slope:	
Bajada	0.79
Lower piedmont	1.46
Upper piedmont	0.28
Bajada:	
Lower piedmont	7.26*
Upper piedmont	1.61
Lower piedmont:	
Upper piedmont	5.00*

The estimated “labile” fraction of vine mesquite (*Panicum obtusum*) grass litter (0.15) was lower than the respective value of creosote bush leaf litter (0.33) ( $P < 0.05$ ). However, there were no differences between  $k_1$  and  $k_2$  of these litter types (Fig. 3).

Dry-weight reduction of creosote bush litter and vine mesquite grass were clearly different ( $F_{(2,27)} = 8.00$ ;  $P < 0.01$ ) (Fig. 3). Most of the observed differences in decay took place during a short time after the litter was placed in the field (before day 150). After day 150 the curves tended to converge (Fig. 3). These differences were probably due to differences in the “labile” to “recalcitrant fraction” ratio. The ratio of vine mesquite litter was close to 0.18, whereas that of creosote bush litter was near to 0.49.

No significant differences were detected between the “labile” fractions of creosote bush and mesquite litter. Similarly,  $k_1$  was the same. However,  $k_2$  was different. It was higher in creosote bush (0.0015) than in mesquite litter (0.0010). The patterns of mass losses over time were different ( $F_{(3,43)} = 7.58$ ;  $P < 0.01$ ) (Fig. 3). Differences are due to the higher decomposition rate of the “recalcitrant” fraction of creosote bush leaf litter.

Compared to other portions of the watershed, estimations of mean litter disappearance both for desert marigold and for creosote bush exhibited the highest intrasite variability in the basin slope site (Fig. 5). Additionally, the litter bags set in this site showed the highest infiltration of mineral soil, with many of the bags buried under 1–2 cm of soil during the summer rains of 1984. The variability was, however, higher in desert marigold than in creosote bush. The “labile fraction” of desert marigold litter, as estimated by the double exponential model, was significantly different from that of creosote bush litter (0.61 and

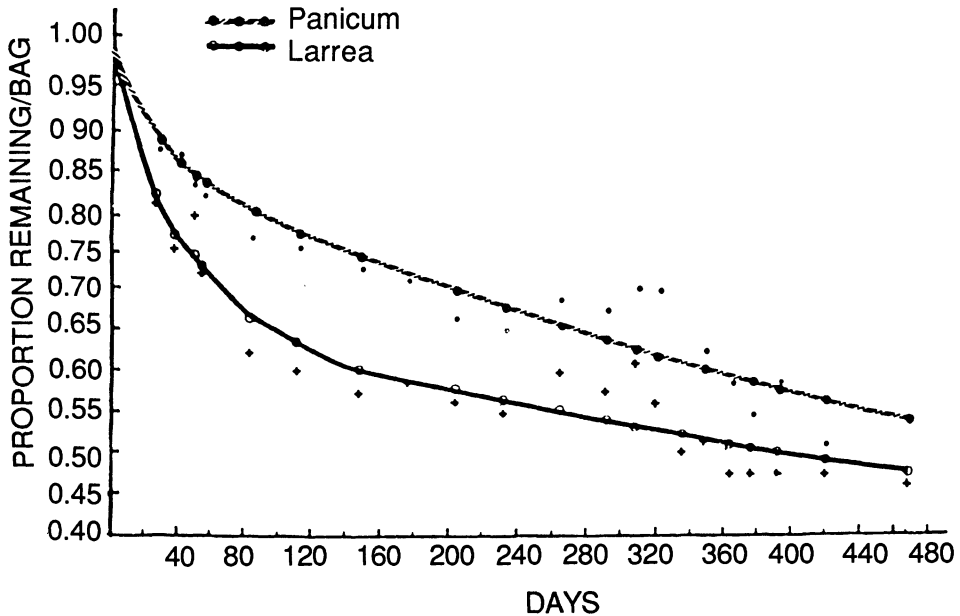


FIG. 3.—Comparison of organic matter losses of surface leaf litter of *Panicum obtusum* and *Larrea tridentata* at the playa site. The mean expected mass losses calculated by the regressions are shown as large solid or open circles. Each observed value represents the mean of five litter bags. (●) *Panicum obtusum* and (+) *Larrea tridentata* are mean values of five litter bags. The regression equations are:  $X_{Larrea} = 0.3335e^{-0.0255t} + 0.6664e^{-0.0007t}$  and  $X_{Panicum} = 0.1497e^{-0.0378t} + 0.8502e^{-0.009t}$

0.27, respectively). While  $k_1$  was the same,  $k_2$  was different: very close to zero for desert marigold and 0.0010 for creosote bush. Desert marigold and creosote bush exhibited different patterns of litter disappearance ( $F_{(3,430)} = 8.49$ ;  $P < 0.01$ ) (Fig. 4). Mass losses of desert marigold were high within the 1st 50 days, then remained quite constant. For creosote bush, the mass loss was more gradual. After day 50, both curves tended to follow the same trend.

Mass losses of fluffgrass and creosote bush litters were the same across sampling dates (Fig. 6). By the end of the year, both litter types had lost 55%. At the end of the study (day 498), mean mass losses were close to 70%. The estimated “labile fraction” of fluffgrass, based on fitting the double exponential decay model, was 0.23 ranging from 0.12–0.35. Neither the rate of decomposition of this fraction nor that of the “recalcitrant fraction” was different from those estimated for creosote bush placed in the same site. Similar trends in dryweight reduction ( $F_{(3,43)} = 2.81$ ;  $P > 0.01$ ) were displayed by both litter types (Fig. 6).

Mass losses from black grama litter were consistently lower than those from creosote bush litter set in the upper piedmont site (Table 2). Within the 1st 6 mo, cumulative litter disappearance was 43% in creosote bush, but only 18% in black grama grass litter. After 1 yr in the field, the losses increased to 47% and 31%, respectively. At day 498 (end of the study), total mass losses were 41% for black grama grass, and 55% for creosote bush leaf litter.

#### DISCUSSION

Microsite differences on the watershed affected the rate of organic matter loss from surface creosote bush leaf litter. These microsite differences include soil edaphic factors and structural

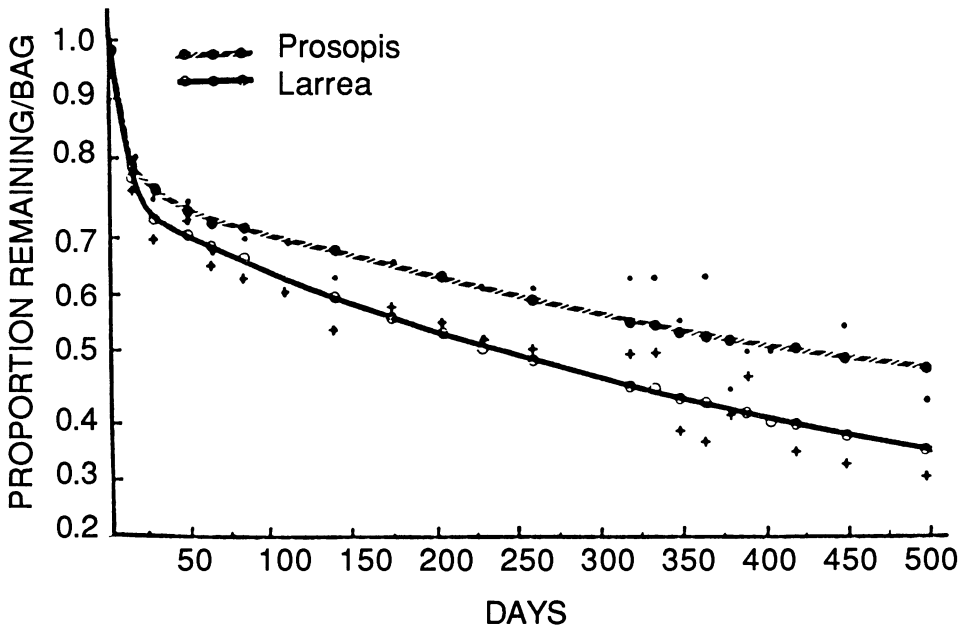


FIG. 4.—Comparison of organic matter losses of surface leaf litter on the playa fringe site. The mean expected mass loss calculated by the regressions are shown as large solid or open circles. The small dots (●) are means of five litter bags of *Prosopis glandulosa* leaves and the (+) are means of five litter bags of *Larrea tridentata*. The regression equations are:  $X_{Larrea} = 0.2779e^{-0.0938t} + 0.7221e^{-0.0015t}$  and  $X_{Prosopis} = 0.2443e^{-0.0924t} + 0.7557e^{-0.0010t}$

features that affect microclimate. The analyses only partially supported the expectation that mass losses would be higher at sites on the lower part of the transect, *i.e.*, the sites with higher soil organic matter and moisture. Larger mean mass losses were recorded in some higher elevations, *e.g.*, the lower piedmont site as compared to the playa site.

The highest mass losses of creosote bush leaf litter were at the playa fringe site. That site is characterized by numerous dense stands of mesquite and other shrubs that produce shade and litter layers that should favor longer and more intense activity of decomposers, partially releasing decomposition from the abiotic constraints. Additionally, the dense shrubs form barriers that reduce the erosive impact of run-off from the watershed, protecting the litter and the decomposer community from major physical disturbances.

The piedmont and bajada sites, with slopes between 2–10°, are erosional surfaces of the watershed, as a part of an alluvial fan system. The soils are shallow, less complex and less protected by plant cover. The lower piedmont site, where arroyos and gullies are common, has a slope above 5%, and was the least protected site studied. The remaining sites are depositional surfaces. Abiotic factors, especially water loss from erosional sites, may account for much of the variance in mass loss of the leaf litter on these sites. Water movement across erosional surfaces can contribute to fragmentation and transport of litter. Unfortunately, we are unable to separate the effects of abiotic variables from those of biological activities.

The largest differences between expected and observed mass loss were in desert marigold and creosote bush litter set in the basin slope site. This is an expression of the high intrasite variability resulting from termite activity and partial to complete burial of bags by sediment



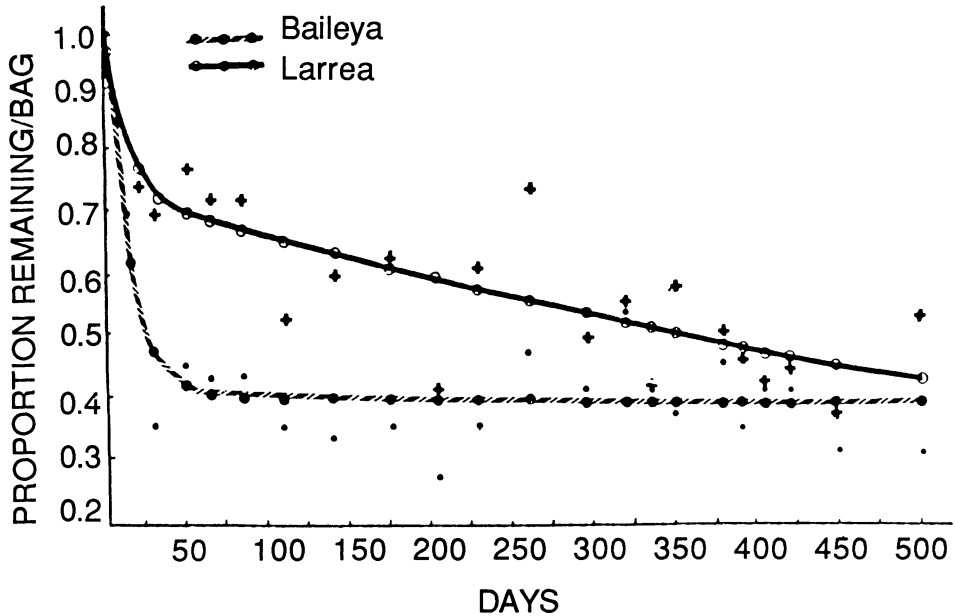


FIG. 5.—Comparison of organic matter losses of surface leaf litter on the basin slope site. The mean expected mass losses calculated by the regressions are shown as large solid or open circles. The small symbols (●) are means of five litter bags of *Larrea tridentata* and (+) are means of five litter bags of *Baileya multiradiata* litter. The regression equations are:  $X_{Larrea} = 0.2714e^{-0.1452t} + 0.7286e^{-0.0010t}$  and  $X_{Baileya} = 0.06089e^{-0.0633t} + 0.3911e^{-0.0006t}$

movement. Based on the assumption that nutrients, particularly nitrogen, are commonly limiting the activity of decomposers, Swift *et al.* (1979) postulated that the C:N ratio has regulatory effects on decomposition. However, Schaefer *et al.* (1985) found no correlations between rates of mass loss and lignin percentage, C:N ratio, or lignin:N ratio in northern Chihuahuan Desert. They suggested that the observed differences may have been due to photo-oxidation of lignin or to undetected chemical differences among litter types. Indeed, the species differ both in the lignin, and fiber content and in the content of some micronutrients (Nelson *et al.*, 1970). Despite the high C:N ratio, mass losses of fluffgrass were the highest recorded and there was no relationship between C:N ratio and/or lignin content of other litter types and mass losses.

As mentioned before, subterranean termites are important litter consumers in this ecosystem. They consume as much as 45% of desert marigold and fluffgrass litter (Whitford *et al.*, 1982; Silva *et al.*, 1985). Termite feeding activities were observed in both of these litter types in September through November. These activities were more intense during the 1st yr of the study, at the time nutritious leaf tissues were more abundant. These insects probably account for much of the mass losses of desert marigold and fluffgrass observed in this work. The data support the idea that litter quality is less important than presence or absence of some soil biota (*e.g.*, termites) and modification of the litter microclimate by shading and/or burial as factors affecting decomposition. Additionally, soil sheet flow affected the litter bags at these sites because they were highly infiltrated by mineral soil. Many were also buried 1–2 cm thus affecting the microclimate for the soil biota and the precision of mean mass loss estimations (Schaefer *et al.*, 1985).

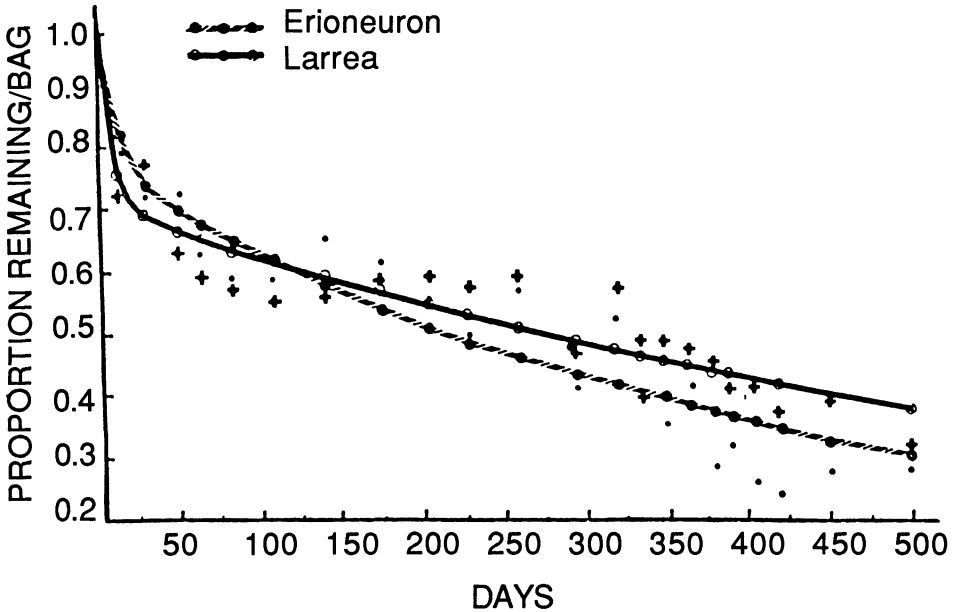


FIG. 6.—Comparison of organic matter losses of surface leaf litter on the lower piedmont site. The small symbols (●) represent mean values of five litter bags of *Larrea tridentata* and (+) five litter bags of *Erioneuron pulchellum* litter. The regression equations are:  $X_{Larrea} = 0.2722e^{-0.1199t} + 0.7218e^{-0.0013t}$  and  $X_{Erioneuron} = 0.2336e^{-0.0813t} + 0.7664e^{-0.0019t}$

The expected trend was not found in the bajada and in the upper piedmont sites. Litter bags set on the bajada zone were not affected by sheet flow because of the soil mounds at the base of creosote bush shrubs. This may explain why mass losses of creosote bush litter were among the lowest recorded. Organic matter losses in the upper piedmont site showed a slightly different pattern from that exhibited by litter set in the lower piedmont site. We saw no evidence of disturbance due to water run-off in the upper piedmont site. This was probably a result of the density of grass at this site.

The playa site, at the other extreme of the watershed, acts as a sink for much of the sediment being carried down slope by water run-off. As a result of the summer thunderstorms of 1984, the playa flooded and became a temporary desert pond. After the water evaporated, a favorable combination of soil moisture, temperature, plant cover and soil organic matter persisted for several months. After flooding, therefore, higher decay rates were expected. However, rates of mass loss were not among the highest recorded. Water logging during flooding, lag in recolonization of soil by microflora and microfauna and certain physico-chemical properties of the soil may account for this result, particularly the high clay content (Anderson *et al.*, 1983; Stevenson, 1982).

In sum, while the components of resource quality that are more important in controlling mass losses from litter in a hot desert are still obscure, our results support the hypothesis that microsite location and factors affecting physical fragmentation are important factors affecting mass losses from litter on this desert watershed. The results do not support the initial hypothesis that losses from litter of the site-dominant plant species would be higher than those of creosote bush leaf litter. They suggest that the effect of abiotic factors across the watershed may be as important for litter disappearance as differences due to physical

and chemical properties of litter. Additionally, our study shows that microsite characteristics are important factors controlling mass loss of surface creosote bush leaf litter. Some of the most important factors are: (1) the degree of exposure of the litter to seasonal disturbances and (2) physicochemical characteristics of the edaphic complex, which in turn may be related to the decomposer community. Parallel studies on soil microarthropods may provide further insights into variables affecting decomposition on this watershed.

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#### LITERATURE CITED

- ANDERSON, J. M., J. PROCTOR AND H. W. VALLACK. 1983. Ecological studies in four contrasting lowland rainforests in Gunung Mulu National Park, Sarawak. III. Decomposition processes and nutrient losses from leaf-litter. *J. Ecol.*, **71**:503–527.
- BREMNER, J. M. AND C. S. MULVANEY. 1982. Nitrogen—total, p. 595–624 *In*: C. A. Black (ed.). Methods of soil analysis. Am. Soc. Agron., Madison, Wisconsin.
- DAY, F. JR. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. *Ecology*, **63**:670–678.
- DWYER, L. M. AND G. MERRIAM. 1981. Influences of topographic heterogeneity on deciduous litter composition. *Oikos*, **37**:228–237.
- ELKINS, N. Z. AND W. G. WHITFORD. 1982. The role of microarthropods and nematodes in decomposition in a semi-arid ecosystem. *Oecologia*, **55**:303–310.
- , Y. STEINBERGER AND W. G. WHITFORD. 1982. Factors affecting the applicability of the AET model for decomposition in arid environments. *Ecology*, **63**:579–580.
- HOUGHTON, F. E. 1972. Climatic guide, New Mexico State University, Las Cruces, New Mexico 1851–1971. *New Mexico State Univ., Agric. Exp. Stn. Res. Rep.* 230. 1–20 p.
- MACKEY, W. P., F. M. FISHER, S. I. SILVA AND W. G. WHITFORD. 1987. The effects of nitrogen, water and sulfur amendments on surface litter decomposition in the Chihuahuan Desert. *J. Arid Environ.*, **223**–232.
- MCCLAUGHERTY, C. A., J. A. PASTOR AND J. M. MELILLO. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology*, **66**:266–275.
- MEENTEMEYER, V. 1978. Microclimate and lignin content of litter decomposition rates. *Ecology*, **59**:465–472.
- NASH, M. H. H. 1985. Numerical classification, spatial dependence, and vertical kriging of soil sites in southern New Mexico. Master's Thesis, New Mexico State Univ., Las Cruces. 194 p.
- NELSON, A. B., C. H. HERBEL AND H. M. JACKSON. 1970. Chemical composition of forage species grazed by cattle on an arid New Mexico Range. *N.M. Agric. Exp. Stn. Bull.* 561. New Mexico State University, Las Cruces.
- SANTOS, P. F., E. DEPREE AND W. G. WHITFORD. 1978. Spatial distribution of litter and microarthropods in a Chihuahuan Desert ecosystem. *J. Arid. Environ.*, **1**:41–48.
- , N. Z. ELKINS, Y. STEINBERGER AND W. G. WHITFORD. 1984. A comparison of surface and buried *Larrea tridentata* leaf-litter decomposition in North American Deserts. *Ecology*, **65**:278–284.
- AND W. G. WHITFORD. 1981. The effects of microarthropods on litter decomposition in a Chihuahuan Desert ecosystem. *Ecology*, **62**:654–663.
- SAS INSTITUTE INC. 1985. SAS user's guide: statistics. Version 5 Ed. SAS Inst. Inc., Cary, North Carolina. 922 p.
- SCHAEFER, D., Y. STEINBERGER AND W. G. WHITFORD. 1985. The failure of nitrogen and lignin decomposition in a North American Desert. *Oecologia*, **65**:383–386.
- SCHINNER, P. 1982. Soil microbial activity and litter decomposition related to altitude. *Plant Soil*, **65**:87–94.

- SCHLESINGER, W. H. 1977. Carbon balance in terrestrial detritus. *Annu. Rev. Ecol. Syst.*, **8**:51-81.
- SEASTEDT, T. R. AND D. A. CROSSLEY, JR. 1980. Effects of microarthropods on the seasonal dynamics of nutrients in forest litter. *Soil Biol. Biochem.*, **12**:337-342.
- , ———, V. MEENTEMEYER AND J. B. WIEDE. 1983. A two-year study of leaf-litter decomposition as related to microclimate factors and microarthropod abundance in the Southern Appalachians. *Holarctic Ecol.*, 11-16.
- SILVA, S. I., W. P. MACKAY AND W. G. WHITFORD. 1985. The relative contributions of termites and microarthropods to fluffgrass disappearance in the Chihuahuan Desert. *Oecologia*, **67**: 32-34.
- STEIN, R. A. AND J. A. LUDWIG. 1979. Vegetation and soil patterns on a Chihuahuan Desert Bajada. *Am. Midl. Nat.*, **100**:28-37.
- STEVENSON, F. J. 1982. Humus chemistry: genesis, composition, reactions. John Wiley and Sons, Ltd., New York. 443 p.
- SWIFT, M. J., O. W. HEAL AND J. M. ANDERSON. 1979. Decomposition in terrestrial ecosystems. Univ. Calif. Press., Berkeley and Los Angeles. 372 p.
- VAN SOEST, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *J. Assoc. Off. Anal. Chem.*, **49**:546-551.
- WHITFORD, W. G. 1986. Decomposition and nutrient cycling in deserts, p. 93-117. In: W. G. Whitford (ed.). Patterns and processes in desert ecosystems. Univ. New Mexico Press, Albuquerque. 139 p.
- , R. REPASS, L. W. PARKER AND N. Z. ELKINS. 1982. Contributions of subterranean termites to the "economy" of Chihuahuan Desert ecosystems. *Oecologia*, **55**:298-302.
- , Y. STEINBERGER, W. P. MACKAY, L. W. PARKER, D. FRECKMAN, J. A. WALLWORK AND D. WEEMS. 1986. Rainfall and decomposition in the Chihuahuan Desert. *Oecologia*, **68**:512-515.
- WIEDER, R. K. AND G. E. LANG. 1982. A critique to the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, **53**:1636-1642.
- WIERENGA, P. J., J. M. N. HENDRICK, M. H. NASH, J. LUDWIG AND L. A. DAUGHTERY. 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. *J. Arid Environ.*, **13**:53-63.

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