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# Loss of phenolic compounds from leaf litter of creosotebush [*Larrea tridentata* (Sess. & Moc. ex DC.) Cov.] and tarbush (*Flourensia cernua* DC.)

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**Abstract**

We examined loss of organic matter (OM) and phenolics from leaf litter of two shrubs that are invasive in the Chihuahuan Desert. Fiberglass bags (1-mm mesh) containing creosotebush [*Larrea tridentata* (Sess. & Moc. ex DC.) Cov.] or tarbush (*Flourensia cernua* DC.) leaf litter were placed below shrubs in two positions (soil surface and 5 cm below-ground) and removed at several intervals up to 90 days during winter (creosotebush and tarbush) and spring (creosotebush). Over the 90-day sampling interval, OM loss from creosotebush and tarbush during the winter sampling period was low for both surface and buried litter, ranging from 1.7% to 5.2%. Losses of OM from creosotebush litter during the spring were much greater (75.1% and 33.5% for buried and surface samples, respectively). Total phenolic losses after 90 days were 1.6%, 4.8%, 21.6%, 13.5%, 87.1%, and 43.5% for winter buried creosotebush, winter surface creosotebush, winter buried tarbush, winter surface tarbush, spring buried creosotebush, and spring surface creosotebush litter, respectively, while losses of condensed tannins for the same samples were 45.8%, 56.1%, −34.0%, −41.8%, 91.1%, and 67.4%. Nordihydroguaiaretic acid loss from creosotebush litter was 25.4%, 18.3%, 95.2%, and 66.7% for winter buried, winter

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surface, spring buried, and spring surface samples, respectively, over the 90-day interval. Losses of OM and phenolics were generally greater in buried vs. surface and spring vs. winter samples, and losses typically occurred during the last 30–45 days.


*Keywords:* Condensed tannins; *Flourensia cernua*; *Larrea tridentata*; Litter; Nordihydroguaiaretic acid; Shrubs; Total phenolics

## 1. Introduction

Grasslands have been undergoing replacement by shrubs in the arid south-west for the last 150 years (Buffington and Herbel, 1965). Two shrubs that have become dominant in large areas of the northern Chihuahuan Desert are creosotebush [*Larrea tridentata* (Sess. & Moc. ex DC.) Cov.] and tarbush (*Flourensia cernua* DC.). Creosotebush is evergreen and loses leaves yearlong but abscission peaks during fall and spring (Burk, 1970; Syvertsen and Cunningham, 1977; Lajtha and Whitford, 1989). Tarbush has also been described as evergreen (Stubendieck et al., 1992), but in this region it has a deciduous behavior. Tarbush loses the majority of its leaves in late fall after freezing temperatures occur, although some desiccated leaves may remain on the plant into the following spring (Zak and Freckman, 1991; P.W. Hyder, pers. obs.). Leaves from both shrub species contain substantial levels of phenolic compounds. The leaf surface of creosotebush has a resinous exudate (approximately 8–12% of dry weight) composed primarily of phenolics, with nordihydroguaiaretic acid (NDGA) being the predominant component of this fraction (Mabry et al., 1977). Tarbush also has a resinous leaf surface (8–12% of dry matter; Estell et al., 1994) and an abundance of total phenolics (TPs) in the leaves (6.5–8.1% of dry matter; Estell et al., 1996).

Litter accumulation and subsequent release of compounds through decomposition and leaching can affect nutrient recycling, carbon balance, microfaunal community composition, seed germination and establishment, and many other processes (Facelli and Pickett, 1991). Although nutrient flow and redistribution would be expected to influence competition among plants, the significance of nutrient cycling in arid environments has been downplayed because of the common assumption that water is the only critical limiting driver in arid ecosystems (Whitford, 2002). A few studies have quantified the rate and extent of organic matter (OM) loss from litter of Chihuahuan Desert shrubs (Fowler and Whitford, 1980; Whitford et al., 1982; Santos et al., 1984), but loss of secondary compounds from litter during decomposition (other than lignin; Schaefer et al., 1985) has not been examined. Our objective was to quantify the release of phenolic compounds from leaf litter of creosotebush and tarbush during decomposition.

## 2. Materials and methods

The study site was in the northern Chihuahuan Desert on the USDA, Agricultural Research Service, Jornada Experimental Range approximately 16 km north of Las

Cruces, New Mexico, USA. The site consists of an area of sandy loam soil on a 2° east-facing slope. Depth to the first calcic layer is approximately 0.9 m. Gravel and sand at this site were derived from andesites, monzonites, and rhyolites eroded from the nearby Doña Ana Mountains. Elevation at the site is 1322 m. Long-term (1915–1999) mean annual and growing season (July, August, and September) precipitation for the area is 246 and 133 mm, respectively. Long-term mean monthly temperatures for the coldest (January) and warmest (July) months are 6 and 26 °C, respectively.

The two sites (creosotebush and tarbush) were within 200 m of each other and were similar in all respects except relative abundances of accompanying plant species. The creosotebush-dominated site had tarbush, mesquite (*Prosopis glandulosa* Torrey), yucca (*Yucca elata* Engelm.), and Mormon tea (*Ephedra trifurca* Torrey, *E. torryana* Wat.) present as minor components. Grasses present included burrograss (*Scleropogon brevifolius* Phil.), fluffgrass (*Dasyochloa pulchella* (Kunth) Steudel), black grama (*Bouteloua eriopoda* (Torr.) Torr.), and bush muhly (*Muhlenbergia porteri* Scribn.). The tarbush-dominated site had creosotebush, mesquite, burrograss, and fluffgrass present.

Creosotebush and tarbush leaves were collected in early winter to coincide as closely as possible to natural leaf fall. Approximately 100 tarbush plants were clipped at the base and leaves were removed from leaders by hand and air-dried at room temperature (approximately 21 °C). Creosotebush branches were collected from approximately 200 plants and air-dried with leaves intact on screens for 10–16 days, and then leaves were removed by shaking branches. Leaves from both species were cleaned using a fan separator.

Simulated litter samples (10 g) were placed in 15.24 $cm^2$ mesh (1 mm) fiberglass bags. Bags were placed in the field during winter (both species) and spring (creosotebush only) in an effort to approximate timing of seasonal leaf abscission of tarbush and seasonal and drought induced leaf abscission of creosotebush (Burk, 1970). Bags were in place from February 3–May 3 (winter tarbush), January 31–April 30 (winter creosotebush), and April 13–July 12 (spring creosotebush), 1999.

For each of the three series, 144 plants were selected. The criterion for plant selection was a minimum distance of 1 and 0.5 m in any direction from the plant crown for creosotebush and tarbush, respectively. Half of the shrubs were randomly assigned to each position (surface or buried). Surface litter bags were pinned in duplicate to the soil surface on the south side of the plant with the nearest edge approximately 10 cm from the shrub base. Duplicate buried bags were located in the same position but at a depth of 5 cm. Bags were collected at 0, 1, 3, 5, 7, 11, 15, 22, 30, 45, 60, and 90 days (six replicates of duplicate bags per time for each treatment in each series), placed immediately on ice, transported to the laboratory, and stored at −120 °C. Prior to analysis, bags were equilibrated at room temperature, weighed, dried in a forced-air oven at 40 °C for 24 h, and contents were ground through a 1-mm screen (Cyclotec sample mill, Model 1093, Tecator Inc., Herndon, VA). Dry matter and ash were determined by standard procedures (Association of Analytical Chemists, 1990). Mass loss was expressed on an OM basis to minimize the influence of soil infiltration into the mesh bags.

TP concentration was measured using the Folin–Denis procedure (tannic acid as standard) described by the Association of Analytical Chemists (1990). Condensed tannin (CT) concentration was analysed using the vanillin–HCl procedure (catechin as standard) described by Burns (1971) and modified by Price et al. (1978). Creosotebush was also analysed for NDGA using high performance liquid chromatography (HPLC). Samples (0.25 g) were extracted in 5 ml of methanol for 20 min, filtered through 0.2 μm polytetrafluoroethylene syringe filters (Millex-FG, Millipore Corp., Bedford, MA), and diluted ten-fold in methanol. A Waters 2695 separations module coupled to a Waters 486 UV detector (283 nm) equipped with a Symmetry C-18 column (2.1 × 50 mm, 3.5 μm particle diameter; Waters Corp., Millford, MA) was used to analyse NDGA (10 μl injection size, isocratic 65% water/35% HPLC grade acetonitrile mobile phase, a flow rate of 0.3 ml/min). Concentrations were quantified with an external standard curve, and either a blank or an NDGA (Sigma Chemical Co., St. Louis, MO) standard was injected after every ten samples.

Precipitation and soil temperature (at the soil surface and 10 cm below the surface) were recorded on-site with a weather station (Campbell Scientific Inc., Logan, UT) equipped with a tipping bucket rain gauge (Model TE525), a temperature probe (Model CS500), and a soil thermocouple probe (Model TCAV).

Analysis of variance (GLM procedure of SAS, 1999) was conducted with species/season and time as the two factors to test for a species/season $x$ time interaction for OM, TP, CT, and NDGA loss. Least-squares means and standard errors were estimated using LSMEANS from the GLM procedure of SAS (1999). Orthogonal polynomials were used to test for linear and quadratic effects across time within each species/season/position combination. Contrasts between day 0 and days 45, 60, and 90 values were performed for each variable in all species/season/position combinations with significant linear and/or quadratic effects.

## 3. Results

Concentrations of TP, CT, and NDGA in creosotebush litter were 46.3, 13.7, and 30.1 mg/g of OM, respectively. TPs and CT in tarbush litter were 20.2 and 2.4 mg/g of OM, respectively.

Litter OM loss (Fig. 1) during the winter sampling period was very low for both shrubs (5.2%, 1.8%, 3.1%, and 1.7% after 90 days for buried creosotebush, surface creosotebush, buried tarbush, and surface tarbush, respectively). OM losses after 90 days for creosotebush litter during the spring were 75.1% and 33.5% for buried and surface samples, respectively (Fig. 1). Loss of OM from creosotebush during spring differed across days ($p < 0.0001$) for both surface and buried litter (Table 1). Spring OM loss differed from day 0 after 45 days ($p = 0.0003$) for buried creosotebush litter and after 60 days ($p = 0.0008$) for surface creosotebush litter.

TPs loss from litter during the winter sampling period was relatively low for both shrubs (1.6%, 4.8%, 21.6%, and 13.5% for buried creosotebush, surface creosotebush, buried tarbush, and surface tarbush, respectively; Fig. 2). Losses of TP from

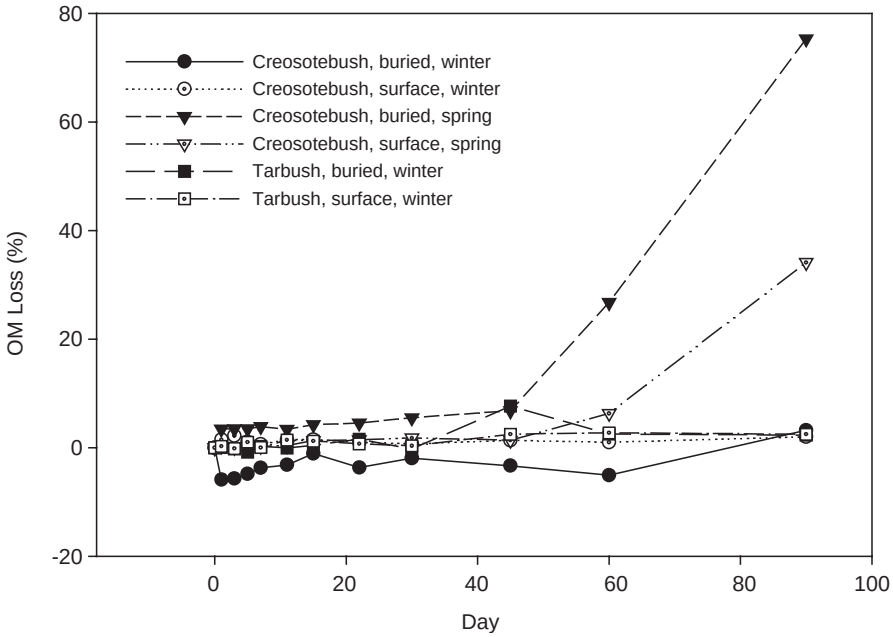


Fig. 1. Percent loss of OM from creosotebush and tarbush leaf litter (surface and buried) during winter and spring: $n = 6$ and S.E. = 1.33.

creosotebush litter during the spring were 87.1% and 43.5% for buried and surface samples, respectively (Fig. 2). Tarbush TP loss differed across days for both buried and surface litter ($p < 0.027$; Table 1). TPs loss differed from day 0 after 45 days ($p < 0.0001$) for buried winter tarbush and after 60 days ($p = 0.0005$) for surface winter tarbush litter. Loss of TP from creosotebush litter during the spring differed across days for buried and surface samples ($p = 0.0005$; Table 1). TPs loss differed from day 0 after 45 days ($p = 0.031$) for buried spring creosotebush and after 90 days ($p < 0.0001$) for surface spring creosotebush litter.

CT losses from litter during the winter sampling period were 45.8%, 56.1%, −34.0%, and –41.8% for buried creosotebush, surface creosotebush, buried tarbush, and surface tarbush, respectively (Fig. 3). Losses of CT from creosotebush litter during the spring were 91.1% and 67.4% for buried and surface samples, respectively (Fig. 3). CT loss from creosotebush litter during the spring differed across days for buried samples ($p = 0.0035$; Table 1), and differed from day 0 after 60 days ($p = 0.034$).

NDGA loss from creosotebush litter was 25.4% and 18.3% during the winter for buried and surface samples, respectively, and 95.2% and 66.7% during the spring for buried and surface samples, respectively (Fig. 4). Loss of NDGA from creosotebush litter during the spring (Table 1) differed across days for buried ($p = 0.0014$) and surface ($p = 0.0003$) samples, with loss from both buried and surface spring creosotebush litter differing from day 0 after 60 days ($p < 0.0001$).

Table 1
Linear and quadratic contrasts and separation between day 1 and days 45, 60, and 90 for OM and phenolic compound loss from surface and buried creosotebush and tarbush litter over time in winter and spring

| Variable | Linear | Quadratic | Day 1 vs. | | |
|---|---|---|---|---|---|
| | | | Day 45 | Day 60 | Day 90 |
| *Creosotebush, winter, buried* | | | | | |
| OM | NS | 0.0282 | NS | 0.0086 | NS |
| TPs | NS | NS | — | — | — |
| CTs | NS | NS | — | — | — |
| NDGA | NS | NS | — | — | — |
| *Creosotebush, winter, surface* | | | | | |
| OM | NS | NS | — | — | — |
| TPs | NS | NS | — | — | — |
| CTs | NS | NS | — | — | — |
| NDGA | NS | NS | — | — | — |
| *Creosotebush, spring, buried* | | | | | |
| OM | 0.0001 | 0.0001 | 0.0003 | 0.0001 | 0.0001 |
| TPs | 0.0005 | 0.0001 | 0.0309 | 0.0001 | 0.0001 |
| CTs | NS | 0.0035 | NS | 0.0338 | 0.0001 |
| NDGA | 0.0014 | 0.0001 | NS | 0.0001 | 0.0001 |
| *Creosotebush, spring, surface* | | | | | |
| OM | 0.0001 | 0.0001 | NS | 0.0008 | 0.0001 |
| TPs | NS | 0.0001 | NS | NS | 0.0001 |
| CTs | NS | NS | — | — | — |
| NDGA | NS | 0.0003 | NS | 0.0001 | 0.0001 |
| *Tarbush, winter, buried* | | | | | |
| OM | 0.0038 | 0.0381 | 0.0001 | NS | NS |
| TPs | 0.0161 | NS | 0.0001 | 0.0017 | 0.0001 |
| CTs | NS | NS | — | — | — |
| *Tarbush, winter, surface* | | | | | |
| OM | NS | NS | — | — | — |
| TPs | 0.0270 | NS | NS | 0.0005 | 0.0167 |
| CTs | 0.0267 | NS | NS | 0.0179 | NS |

NDGA: nordihydroguaiaretic acid; NS: non-significant ($p > 0.05$); OM: organic matter; TP: total phenolic; CT: condensed tannin; dash indicates mean separations were not appropriate because no linear or quadratic effects were observed.

A series $x$ position $x$ day interaction was observed for OM ($p < 0.0001$), TP ($p = 0.008$), and NDGA ($p = 0.023$), and a series $x$ day interaction existed for CT ($p < 0.0001$). However, interactions were due to differing rates of loss in time within a series/position combination for a given variable. Thus, results pooled across series and/or position are of interest. When examined across days within a series, OM loss from buried litter was greater than surface litter for winter tarbush ($p < 0.003$) and spring creosotebush ($p < 0.0001$), and less than surface litter for winter creosotebush ($p < 0.001$). TPs loss from buried litter was greater than from surface litter for winter

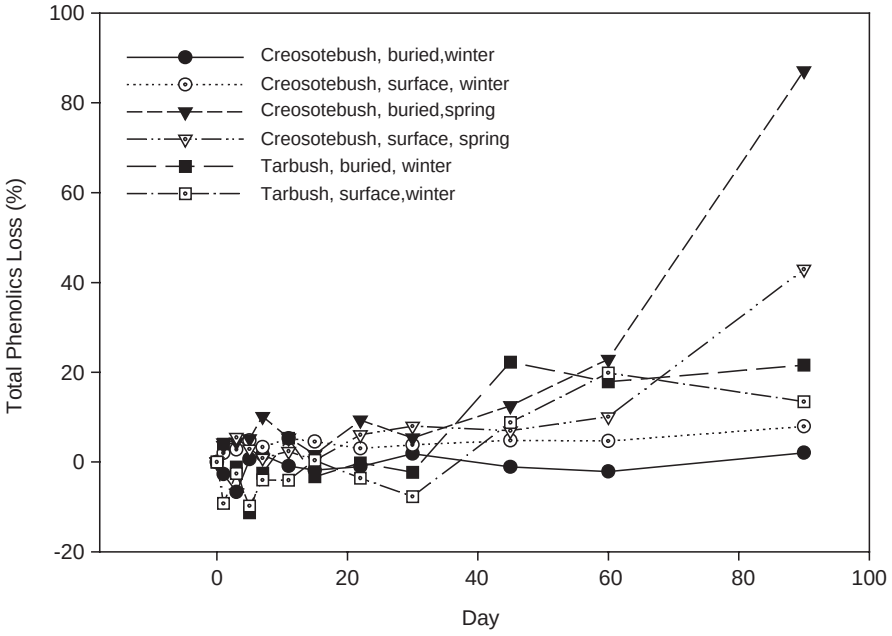


Fig. 2. Percent loss of TPs from creosotebush and tarbush leaf litter (surface and buried) during winter and spring: $n = 6$ and S.E. = 3.98.

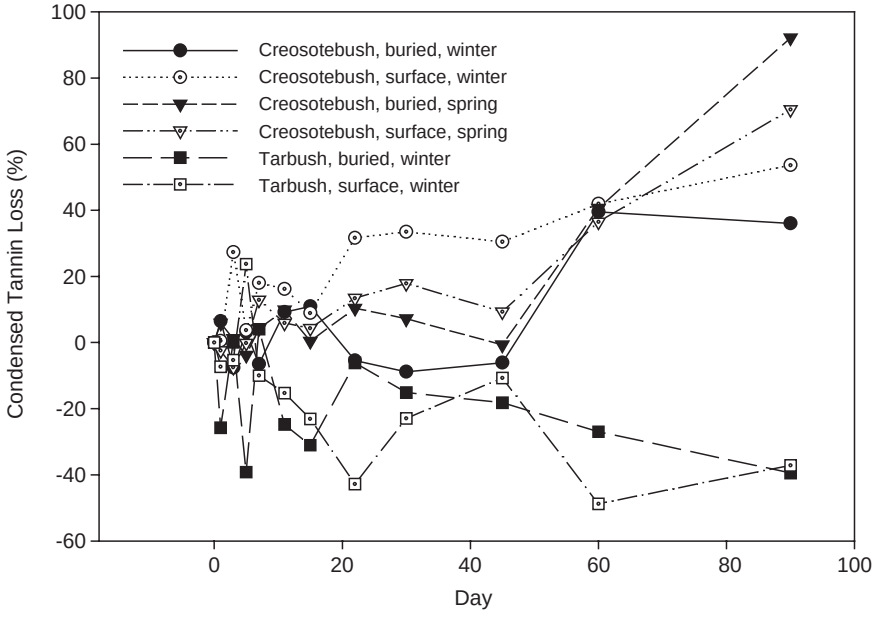


Fig. 3. Percent loss of CTs from creosotebush and tarbush leaf litter (surface and buried) during winter and spring: $n = 6$ and S.E. = 14.91.

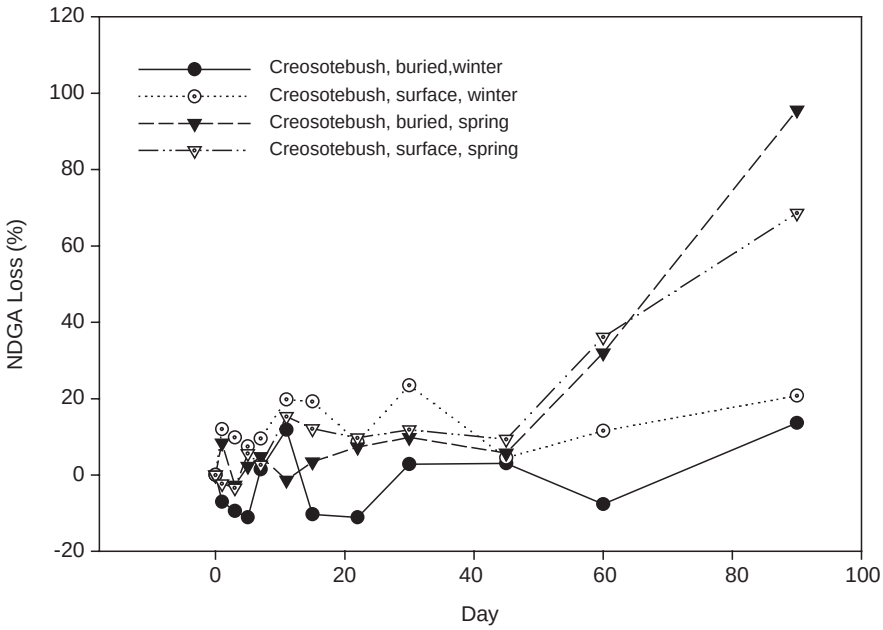


Fig. 4. Percent loss of NDGA from creosotebush leaf litter (surface and buried) during winter and spring: $n = 6$ and S.E. = 4.42.

tarbush ($p < 0.013$) and spring creosotebush ($p < 0.0001$). Neither CT nor NDGA loss differed between surface and buried litter for any series ($p > 0.18$).

When data were examined across days and series, loss of OM and TP from buried litter was greater than from surface litter ($p = 0.0002$). When examined across days and position (buried and surface), a species effect existed (greater loss from winter tarbush than winter creosotebush) for OM, TP, and CT ($p < 0.0001$). A season effect was also observed when examined across days and position (greater loss for spring vs. winter creosotebush) for OM, TP, and CT ($p < 0.0001$).

## 4. Discussion

Concentrations of TP and CT in creosotebush leaf litter were approximately two- and five-fold greater than tarbush, respectively. Concentrations of phenolic compounds in leaf litter in the present study (collected in December) were generally much lower (50–75% lower) than values reported for these species during periods of active growth. Creosotebush harvested between July and October contained approximately 9.9% and 5.8% TP and CT, respectively (OM basis; Holechek et al., 1990). TPs and CT ranged from 6.5% to 8.1% and 0.30% to 0.37%, respectively, in the dry matter of tarbush leaves collected in four growth stages over a 3-yr period (Estell et al., 1996). NDGA typically ranges from 5% to 10% of the dry weight of

creosotebush (Mabry et al., 1977). In contrast, values reported by Hyder et al. (2002) for creosotebush leaves collected in October (TP, CT, and NDGA averaged 3.6%, 0.06%, and 3.8% of the dry matter, respectively) were more in line with values reported in this study. Leaves were collected in December, well after a killing frost, and after processes such as resorption should have already taken place. Chemical data support this assumption, given that levels of all chemicals measured were much lower than previously reported for growing leaves.

OM loss was very low for both shrub species during winter and was relatively extensive during spring (measured only in creosotebush), occurring primarily during the last 30–45 days (Fig. 1). While OM loss from buried litter of both plant species during winter was statistically detectable (Table 1), it was extremely low (3–5% loss after 90 days). Santos et al. (1984) reported creosotebush litter loss in the Chihuahuan Desert during a 2-month interval between mid-March and early June was essentially 0% for surface litter and 23% for buried litter. Whitford et al. (1986) observed that surface creosotebush litter OM loss during a 3-month interval in December–March was about 5%. Schaefer et al. (1985) reported losses of OM between mid-January and mid-March for creosotebush and tarbush litter of approximately 16% and 5% for surface and 19% and 24% for buried litter, respectively, and losses between mid-January and early July of approximately 19%, 15%, 37%, and 50% for surface creosotebush, surface tarbush, buried creosotebush, and buried tarbush litter, respectively. In general, their results showed more activity during winter and lower degradation during late spring/summer than observed in our study.

We observed virtually no OM loss during the first month in any series. Other studies have observed more rapid early loss. Fowler and Whitford (1980) reported OM loss from creosotebush surface litter during the fall (September–November) ranged from approximately 15–35% in 1 month and 35–40% in 2 months. Whitford et al. (1982) reported a 35–50% loss of surface creosotebush litter in a single month during May–September and a 10–30% monthly loss of OM during October–February. However, it is impossible to directly compare our results to other studies because of variable environmental conditions from year to year and differences in methodology among studies (e.g. litter characteristics, season, sampling interval).

Across days, OM loss was greater for buried vs. surface litter for spring creosotebush and winter tarbush litter. In contrast, winter creosotebush litter loss was more rapid from surface vs. buried litter. Santos et al. (1984) observed a greater loss from buried vs. surface creosotebush litter between mid-March and early June. Schaefer et al. (1985) reported litter loss between mid-January and mid-March was similar for surface and buried creosotebush litter (16% vs. 19%, respectively) and was approximately five-fold greater for buried vs. surface tarbush litter (24% vs. 5%, respectively). Between mid-January and early July, they observed losses of approximately 19%, 15%, 37%, and 50% for surface creosotebush, surface tarbush, buried creosotebush, and buried tarbush litter, respectively. Schaefer et al. (1985) also reported that loss of OM from buried litter of the two species between mid-January and early July differed (37% vs. 50% for creosotebush and tarbush, respectively). In our study, both species exhibited very low decomposition during

winter (<5%; Fig. 1), and while statistically different, the biological significance is questionable.

Loss of phenolics (TP, CT, and NDGA) from litter revealed some consistent patterns. Generally, phenolic losses during the winter period were low for both shrub species (Figs. 2–4). However, loss of CT from creosotebush during winter was relatively high (although not statistically significant) for both positions (46% and 56% for buried and surface litter, respectively). In contrast, loss of CT from tarbush litter was negative (−34% and –42% for buried and surface samples, respectively), but only surface litter differed statistically. Losses of TP, CT, and NDGA from both surface and buried creosotebush litter during the spring were large (and statistically significant in all cases except for CT loss from surface litter). With the exception of CT in tarbush litter, loss of phenolic compounds typically followed the same pattern as OM loss. This pattern was particularly evident for creosotebush during the spring, with substantial losses of OM and phenolics occurring during the last 30–45 days (Figs. 1–4).

As was the case with OM, we observed a general tendency for phenolic losses to be greater for buried than surface samples, particularly during spring. Buried litter decays faster than surface litter, is controlled biologically by microflora and microfauna, and is affected by soil temperature and moisture (Santos and Whitford, 1981; Moorhead and Reynolds, 1989; Whitford, 2002). In contrast, surface losses are more influenced by physical processes such as leaching, fragmentation by wind and water, termite activity, and photooxidation and volatilization due to UV radiation and high temperatures (Schaefer et al., 1985; Moorhead and Reynolds, 1989; Whitford, 2002). Below-ground temperature exhibited less diurnal and seasonal temperature variation (Fig. 5) as would be expected in desert soils (Whitford, 2002), which should provide a more stable environment for biotic activity.

Generally, spring litter exhibited OM and chemical losses that were greater in magnitude than winter samples for a given variable, and greater losses were generally coincident with increased soil temperature and precipitation (Fig. 5). These conditions may have promoted greater biotic activity than during the winter period. Whitford et al. (1982) reported that OM loss was related to below-ground soil temperature but not to rainfall or soil surface temperature. However, Weatherly et al. (2003) reported that precipitation was the most important determinant of decomposition of surface leaf litter for arid shrubs (including creosotebush), with much faster decomposition during a wet than dry year. Precipitation during the winter period did not appear to affect loss of OM or phenolics, possibly because it was insufficient in amount or duration or because other conditions (e.g. soil temperature) were suboptimal.

The fact that the pattern and extent of loss of phenolic compounds were generally similar to that of OM during the spring suggests these compounds were not resistant to degradation, which is somewhat surprising, given that certain classes of phenolics are associated with lignin and cell walls (Hagerman and Butler, 1991), which are typically considered to be resistant to microbial degradation. In forest ecosystems, the ratio of lignin:N was inversely related to OM loss from litter (Melillo et al., 1982) and the proportion of lignin in litter residue increased with time (Berg et al., 1984). In

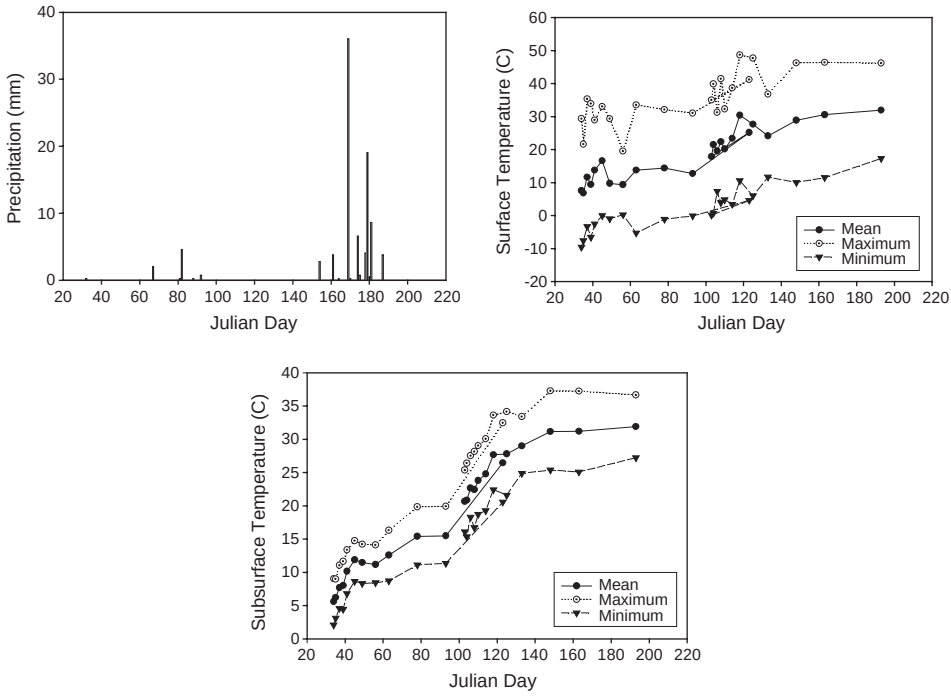


Fig. 5. Precipitation and surface and subsurface (10 cm) soil temperatures during winter and spring sampling periods (spring sampling began on day 103).

arid environments, Schaefer et al. (1985) detected no relationship between lignin concentration and OM loss from leaf litter, although Mun and Whitford (1998) reported that decomposition of grass roots was negatively correlated to lignin content, and that concentration of lignin increased with time. Schofield et al. (1998) reported rapid loss of TP and CT from sandbar willow (*Salix exigua* Nutt.) leaf litter (within 6 weeks). However, this work was conducted in a wet environment and the authors attributed the rapid loss of phenolics to leaching. To our knowledge, no data regarding loss of phenolics from shrub litter in arid environments are available for direct comparison to our data.

As stated earlier, percentage loss of CT at 90 days was negative for tarbush (both surface and buried). Thus, CT in tarbush litter bags appeared to accumulate with time (statistically significant only for surface litter). Ultraviolet light can catalyse breakdown of phenolic compounds (Whitford, 2002). Although this might explain the accumulation of CT in surface litter, the same general pattern occurred with buried tarbush samples. Moreover, the opposite trend (loss of CT over time) occurred for creosotebush litter. Possibly, chemical breakdown and structural alteration of CT in tarbush may increase the number of molecules detected by the vanillin–HCl procedure without a net change in TP as measured by the Folin–Denis method. Colorimetric assays have limitations because they do not measure specific molecules (Reed, 2001).

In summary, this study demonstrated that losses of OM and phenolics from leaf litter of creosotebush and tarbush in the northern Chihuahuan Desert vary depending on season and position above- or below-ground. Further work is warranted to determine the fate of these secondary chemicals.

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