

Leaf litter decomposition is rapidly enhanced by the co-occurrence of monsoon rainfall and soil-litter mixing across a gradient of coppice dune development in the Chihuahuan Desert



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ABSTRACT

Shrub encroachment, a common occurrence in drylands over the past 150 years, has the potential to alter the redistribution of soil and soil resources by wind and water. This may affect decomposition via soil-litter mixing (SLM). SLM can accelerate decomposition, but its contributions and relationship with abiotic controls, particularly in the context of shrub encroachment, are unknown. To better understand the spatiotemporal relationships between decomposition and shrub encroachment, we conducted a 24 month decomposition study aimed at understanding how placement of litter on either up or downwind sides of dunes in association dune volume affected litter decomposition. There was little decomposition in the first six months of the experiment, with 97.2% of mass remaining despite high exposure to solar radiation. Decay occurred in synchrony with monsoons and SLM, suggesting precipitation during the monsoon season plays an important role in facilitating both SLM and decomposition. Litter placements across a gradient of shrub volumes had no effect on decomposition rates and SLM, but litter placement on the downwind side of dunes had a positive influence on soil-microbial film development. Ultimately, monsoons rainfall and SLM promoted decomposition across a gradient of shrub encroachment in this dryland ecosystem.

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1. Introduction

Woody plant encroachment, an increase in the cover of trees and shrubs in savannas and grasslands, has been a major global land-cover change in the past century (Archer et al. 1995; Van Auken, 2000; Naito and Cairns, 2011). The consequences of woody encroachment include changes in plant community composition (e.g. loss of native grass cover), increased spatial heterogeneity of soil resources, and dramatic changes in local topography via the formation of vegetated coppice dunes (Schlesinger et al. 1990; Whitford, 1997; Schlesinger and Pilmanis, 1998; Gibbens et al. 2005). Despite the broad geographic extent of woody encroachment, relatively little is known about the direct and indirect influence of woody encroachment on biogeochemical

processes such as litter decomposition.

Litter decomposition is a central driver of carbon (C) and nutrient cycling, releasing energy and nutrients stored in litter biomass to microbes and plants (e.g., Aerts, 1997; Berg et al. 2005). Despite the importance of decomposition in biogeochemical cycling, understanding of the mechanisms controlling dryland decomposition is limited, particularly in relation to changing land cover. Our lack of a clear mechanistic understanding of decomposition is evident in the under-prediction of dryland decomposition rates by current ecosystem models (Parton et al. 2007; Adair et al. 2008; Throop and Archer, 2009). Recent work suggests photodegradation and soil-litter mixing (SLM) are potentially important drivers of decomposition in drylands that may explain, at least in part, the discrepancy between models and measurements (photodegradation reviewed in King et al. 2012; SLM reviewed in Barnes et al. 2015). SLM by wind and water may promote microbial colonization and buffer litter from extremes in moisture or temperature, thereby extending windows of opportunity for decomposition.

Dune morphology (e.g. height and diameter) in drylands can strongly influence aeolian and fluvial soil transport patterns

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(Gibbens et al. 1983; Langford, 2000; Gillette and Pitchford, 2004), suggesting a mechanism where dune morphology may influence SLM and subsequent decomposition. Similarly, SLM and decomposition could differ among spatial positions on dunes (e.g. upwind vs. downwind sides of dunes). Soil erosion losses occur primarily on the upwind side of dunes, while soil deposition occurs primarily on the downwind side (Langford, 2000).

In order to explore how coppice dune morphology (via its influence on soil movement) affects decomposition, we deployed a two-year decomposition experiment at sites spanning a gradient of coppice dune volume in the Chihuahuan Desert. We hypothesized that 1) decomposition would be more rapid on the downwind sides of dunes because of greater soil accumulation in downwind than upwind sides, and 2) decomposition rates would be positively correlated with coppice dune volume due to increasing SLM with dune volume.

2. Methods

2.1. Study area

Field studies took place at the Jornada Experimental Range (JER) near the northern terminus of the Chihuahuan Desert, approximately 40 km NE of Las Cruces, NM, USA. The long-term (1915–1995) mean annual precipitation at this arid site is 245 mm (SD \pm 85.0 mm; Wainwright, 2006). Approximately 60% of total precipitation falls during intense, spatially heterogeneous late summer monsoons (Wainwright, 2006). The long-term (1915–1993) mean annual temperature is 14.7 °C (SD \pm 0.58°C; Wainwright, 2006). Temperatures are lowest in January with a mean monthly temperature of 3.78 °C and highest in July with a mean monthly temperature of 26.03 °C (Wainwright, 2006).

Our study took place along an 8 km east-to-west gradient of honey mesquite (*Prosopis glandulosa*) coppice dune development. Dunes range from non-existent around shrubs at the western end of the gradient to large coppice dunes in the eastern end of the gradient that are typical of mesquite-encroached rangelands in the northern Chihuahuan Desert (Huenneke and Schlesinger, 2006). We worked in three long-term (>30 y) livestock enclosures (32° 37' 8" N 106° 47' 16" W, 32° 36' 41" N 106° 47' 46" W, and 32° 36' 22" N 106° 51' 2" W) that are all at a similar elevation (1325 \pm 4 m). We selected these enclosures because of prior land surface and aeolian studies at these sites that quantified interactions between shrub encroachment and soil redistribution (Gibbens et al. 1983; Gillette and Pitchford, 2004).

The dominant woody vegetation across this gradient is honey mesquite and herbaceous vegetation is a mix of native perennial grasses including three-awns (*Aristida* spp.) and dropseeds (*Sporobolus* spp.). Less dominant woody plants, including *Yucca* spp. and *Gutierrezia sarothrae*, are also present. Soil conditions across the gradient, like much of the northern Chihuahuan Desert, are inherently complex and variable. Surface soil horizons at the western end of the gradient, where dunes do not occur, are shallow (ca. 10 cm) above an indurated calcium carbonate layer. The soils are fine sandy loams (Typic Haplocambids, Pajarito series) and are the least erodible of the three sites (Gillette and Pitchford, 2004). At the gradient midpoint, dunes are well developed and there is no sign of erosion on upwind faces (i.e. exposed mesquite roots). The topography across this span is hilly due to the rolling dune features (Gillette and Pitchford, 2004). The eastern end of the gradient has the largest dunes and the greatest topographic variation due to the prominence of large dunes and shallow, heavily eroded interspaces where large adventitious roots may at times be visible. The soils from the midpoint to the eastern end of the gradient are a mix of fine sand and fine loamy sands (Typic Haplargid Pintura and Typic

Torripsamment Onite soils), which erode more readily than the western end (Gillette and Pitchford, 2004). We randomly selected 36 focal mesquite coppice dunes from within three LTER net primary productivity livestock enclosures (N = 12 dunes per enclosure) along a gradient of coppice dune development.

2.2. Litter cages

Litter decomposition experiments typically measure mass remaining in mesh litterbags, but this technique can be problematic in systems with high rates of soil erosion and deposition, where litterbags act as traps for surface soils (Hewins et al. 2013). To circumvent this problem, we designed cylindrical 'litter cages' to allow greater soil movement (Fig. 1). The three dimensional nature of litter cages allows soil to enter the cages, mix with litter, and exit. Although we did not directly measure the difference, soil capture in litter cages was lower than in previous studies where we used litterbags at the same study site (DBH, pers. obs.). Litter cages also transmit more radiative energy than litterbags [e.g. 78.5% vs. 38.7% ambient biologically effective UV-B (UVBBE) transmission for litter cages and litterbags, respectively; SKU 430 broadband UV-B sensor, Skye Instruments Ltd, Wales, UK].

Litter cages were constructed of 1 \times 1 mm mesh aluminum window screen (New York Wire Co., Mount Wolf, PA). The cylindrical litter cages (15.25 cm height, 15.25 cm diameter) were assembled using corrosion-resistant Monel staples (Gaylord Brothers, Syracuse, NY) and silicone caulk (Silicone II Window and Door Caulk, General Electric Co., Fairfield, CT). Honey mesquite leaflets were used to assess decomposition. Leaflets were collected prior to abscission at the JER on 19–20 November 2009 and 'air dried' at 30 °C for 5 days. Litter cages were filled with 2 g of mesquite leaflets, forming a monolayer of litter in each cage.

Litter cages were placed immediately beyond the outer edge of the plant canopies, with 6 cages on the upwind side and 6 on the downwind side of each dune (hereafter referred to as upwind and downwind 'placements'). The location beyond the canopy edge was selected to maximize soil and litter deposition while minimizing shading by shrub canopy cover. Litter cages were spaced at least 20 cm apart and were fixed to the soil surface with 15.25 cm steel sod staples. We deployed litter cages on 19 November 2010 and collected one cage per dune on both upwind and downwind sides after 0, 1, 3, 6, 12, and 24 months field exposure. There were 504 litter cages total (N = 6 collections \times 2 placements \times 12 focal shrubs \times 3 enclosures = 504).

2.3. Litter processing

Following litter cage collection, litter was separated from accumulated soil using a 1 mm mesh sieve. Litter was then manually dusted using small brushes to remove soil that was not bound to the litter surface. Litter was frozen at -80 °C for 48 h, lyophilized for 48 h, weighed, and ground to a fine powder using a ball mill (8000D Mixer/Mill, Spex Certiprep, Metuchen, NJ). After being deployed, collected, and processed (i.e. sieved and lyophilized), time 0 litter mass remaining was used to correct for transport losses (Harmon et al. 1999). Litter subsamples were combusted at 550 °C for 6 h to determine the inorganic matter content (% ash), providing an index for soil bound to leaf material (i.e. soil-litter mixing). This conservative estimate of SLM is relevant when considering the influence of soil on microclimate buffering at the litter surface (Throop and Archer, 2007; Hewins et al. 2013). Litter %C and % nitrogen (N) by mass were quantified for two replicates of each litter cage sample by dry combustion (ECS 4010 Elemental Analyzer; Costech Analytical Technologies Inc., Valencia, CA). All mass-dependent measures were expressed as ash-free mass dry mass

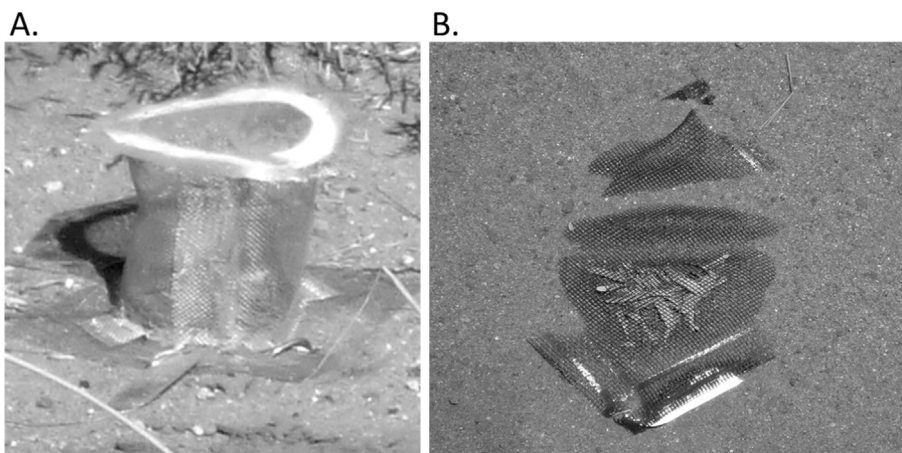


Fig. 1. (A) Photo of litter cages that were used in this experiment. Litter cages have a vertical component that reduces artificial litter burial by soil accumulation. (B) Photo of a typical litter bag used for decomposition experiments. This bag has been deployed for six months and shows significant burial of litter by soil. A small proportion of litter is exposed. Litterbags are shown here for visual comparison but were not used in this experiment.

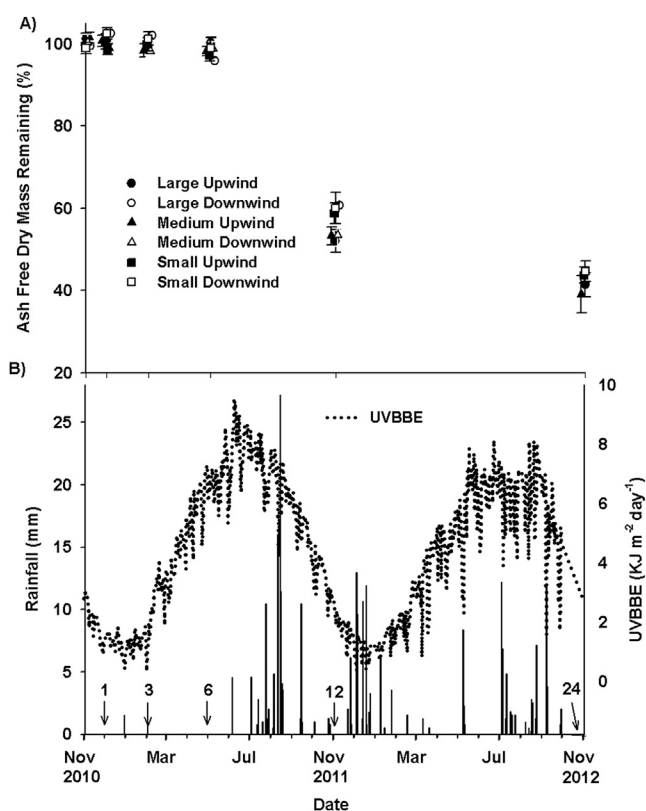


Fig. 2. (A) Mean litter mass remaining for each placement (upwind or downwind of shrubs) at each of the six collection times; data are grouped by volume for ease of interpretation. (B) Daily rainfall (bars) and daily UVBBE during the litter decomposition experiment. Litter collection times are indicated with arrows along the x-axis.

to correct for adhering soil mass.

2.3.1. Soil-microbial films

Soil-microbial film composition (Barnes et al. 2012) was observed qualitatively with a fluorescent stereomicroscope system (2.00× lens with 2.5× zoom with 16.5:1 zoom optics and dynamic magnification, Leica M165 FC) connected to a camera (DFC 310 FX, Leica Microsystems, Wetzlar, Germany). Soil-microbial film coverage of leaflets was quantified from micrographs taken using

the same microscope, but with a 0.63× lens. Leaflet area in micrographs was visually classified as leaf surface or soil-microbial film and measured with ImageJ v1.44 (National Institute of Health, Washington, DC). Soil-microbial film coverage was quantified for three randomly selected leaflets from each litter cage at each collection time. High-resolution micrographs were captured using a Hitachi S-3400N Type II scanning electron microscope (Hitachi High-Technologies Corp., Pleasanton, CA) to characterize soil-microbial film composition (e.g. microbial structures, mucilage coating soil, and leaf surfaces).

2.4. Environmental variables

Precipitation and temperature data were obtained from rain gauges local to the LTER NPP Sites used in this study. Solar radiation was collected from a nearby meteorological station located at the JER headquarters and operated jointly by the JER, the Jornada Basin LTER, and the USDA Natural Resource Ecology Lab UVB Monitoring and Research Program. The meteorological station was within 8 km of all three sites. Data were compiled to obtain values for total daily precipitation, mean daily temperature, and total daily incident biologically effective UV-B radiation (hereafter ‘UVBBE’; Caldwell biologically effective UV [280–320 nm]).

2.5. Statistical analysis

Decay constants (k values) were estimated by fitting a single pool exponential decay function (Olson, 1963) to ash-free dry litter mass remaining (hereafter ‘mass remaining’) data. Decay functions were fit separately for the two placements (upwind and downwind) at each of the 12 dunes in each of the three livestock enclosures. This generated 1 year k values that can be compared with many published decomposition studies (see Discussion). Model estimated k values were generated by using the dynamic fit tool in Sigma Plot version 10 (Systat Software Inc., Chicago, IL, USA).

$$M_t = M_0 e^{-kt} \quad (1)$$

In these equations, M_t is the mass of litter at a given time t , M_0 is the initial litter mass, e is the exponential constant, k is the decay rate constant over the time t (Eq. (1)).

We analyzed decomposition data in three ways. First, we used a split-plot generalized linear model (GLM) wherein each dune plot is split into upwind and downwind sides to test the hypothesis that

decomposition would vary with placement on either the upwind or downwind side of coppice dunes, while controlling for dune volume. To test this hypothesis, we used an ANCOVA model structure to assess the response of decay constants (k values) to dune placement and the covariate dune volume. Second, we followed up this analysis to test the hypothesis that dune volume was a driver of decomposition. We used simple linear regression to test the relationship between decay constants and dune volumes. Third, to investigate relationships between mass remaining and environmental variables over time, we used step-wise multiple regression and Akaike Information Criterion corrected (AICc) model selection. We explored the response of mass remaining to SLM (% ash), mean daily radiation for each collection period (UVBEE day^{-1}), and mean daily precipitation for each collection period (mm day^{-1}).

We tested the influence of dunes on soil-litter mixing in two ways. We investigated the response of both SLM (% ash) and soil-microbial film cover (%) (dependent variables) to placement (up or downwind) with the covariate dune volume and the duration of time in the field (collection times) using split plot GLM described previously. We followed up this analysis to test the hypothesis that dune volume was a driver of SLM and soil-microbial film cover. We used simple linear regression to test the relationship between SLM and soil-microbial film cover, and varying dune volumes.

We tested the hypothesis that litter C and nitrogen (N) concentrations would vary in response to time in the field (collection times) and placement (up or downwind) with the covariate dune volume. We also assessed the relationship between mass remaining of litter C and N and litter mass remaining using simple linear regression. We fitted a 1:1 line to assess the relative loss of C or N in comparison to total mass loss.

Prior to all analyses, all percentage data were natural log transformed to improve normality. All ANCOVA tests were conducted using PROC Mixed with Tukey HSD *post hoc* mean comparisons, regression was done using PROC Reg, and model selection was carried out using PROC GLMselect in using SAS v. 9.4 (SAS Institute Inc., Cary, NC, USA).

To accurately represent the gradient of dune formation used in our study, the measured coppice dune volume for each dune was used as a continuous variable in all analyses.

However, to ease graphical interpretation, we classified dunes as small, medium or large ($N = 12$ dunes each) based on the volume of dunes at each of three long-term LTER NPP exclosures (Table 1).

3. Results

3.1. Decomposition

We observed no detectable litter mass loss after the first three months of field exposure and a mean mass remaining of 97.2% was measured after six months (Fig. 2A). Mean litter mass remaining decreased to 56.31% ($SE \pm 1.47$) after 12 months and 41.93% (± 1.01) after 24 months. During the first six months of the experiment, litter was exposed to an estimated 4.1 mm of precipitation. Total measured precipitation was 115.3 mm and 265.46 mm in the 6–12

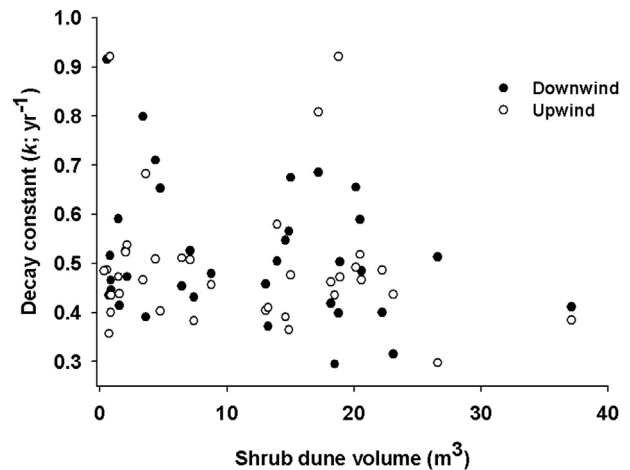


Fig. 3. Relationship between decay constants (k ; yr^{-1}) from single pool exponential decay functions and dune volume. Decay constants were calculated separately for each placement (upwind or downwind) for each shrub ($n = 72$).

and 12–24 month intervals, respectively (Fig. 2B). During the first six months (November–May) of the experiment while decomposition was minimal and litter was largely free of soil (see below), UVBEE radiated was estimated as 511.75 kJ m^{-2} , with a mean monthly dose of $108.65 \text{ kJ m}^{-2} \text{ month}^{-1}$. UVBEE radiation was greater during the summer months (experiment months 6–12, May–October) at 994.36 kJ m^{-2} ($165.73 \text{ kJ m}^{-2} \text{ month}^{-1}$). During the second year (November–November), total UVBEE was $1313.42 \text{ kJ m}^{-2}$ ($109.45 \text{ kJ m}^{-2} \text{ month}^{-1}$; Fig. 2B). Overall, decay constants (Eq. (1); k values), calculated for each dune by placement combination, were not affected by up or downwind placement (Fig. 3; $F_{1,34} = 0.48$; $P = 0.50$), when controlling for dune volume. In addition, dune volume when analyzed alone was not a significant driver of decomposition ($R^2 = 0.03$).

Stepwise regression and AICc model selection techniques elucidated the relationship between decomposition and measured environmental variables: SLM, daily mean UVBEE, and daily mean precipitation. Litter mass remaining was negatively related to SLM and daily precipitation ($R^2 = 0.84$; $\text{AICc} = 2553$), while daily UVBEE was eliminated by stepwise regression. In univariate models, both SLM ($R^2 = 0.74$; $\text{AICc} = 2594$) and daily precipitation ($R^2 = 0.75$; $\text{AICc} = 2586$) were strongly negatively related to mass remaining, while UVBEE was not a strong predictor ($R^2 = 0.07$; $\text{AICc} = 3147$).

3.2. Soil litter mixing and soil-microbial films

Soil litter mixing (% ash) was nearly constant for the first 6 months of the experiment (mean = $9\% \pm 0.17$), but increased following monsoon precipitation events to $45.2\% \pm 1.49$ at 12 months and then decreased slightly to $40.2\% \pm 0.93$ at 24 months (Fig. 4A; $F_{5,403} = 19.4$, $P < 0.0001$). *Post hoc* means separations of SLM grouped 0–6 months together and 12 and 24 months together.

Table 1
Morphological characteristics of dunes used in this study at each of three long-term livestock exclosures. Values are means (\pm standard error) of the 13 focal dunes at each NPP site along the gradient. Dune morphology measurements [height, shrub height, total height (dune + shrub), and dune diameters (north to south and east to west)] were made with a total station and survey pole.

Site	Dune height (m)	Shrub height (m)	Total height (m)	Diameter (m)
Small	0 ± 0	0.87 ± 0.066	0.87 ± 0.066	2.53 ± 0.226
Medium	0.80 ± 0.069	0.64 ± 0.073	1.44 ± 0.080	5.14 ± 0.369
Large	1.13 ± 0.072	0.57 ± 0.047	1.69 ± 0.038	7.10 ± 0.298

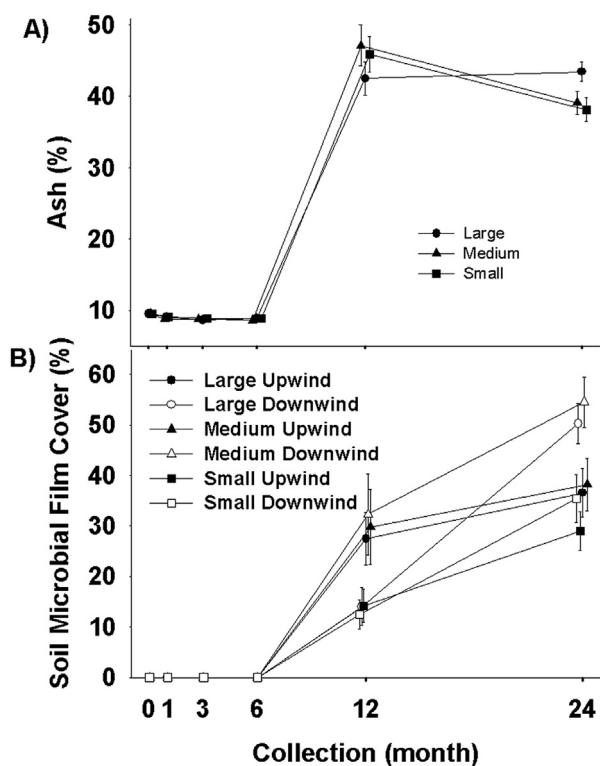


Fig. 4. Changes in soil-litter interactions during the 24 month decomposition experiment grouped by dune volume (small, medium, and large dunes): (A) the ash content of litter and (B) percent litter area covered by soil microbial films, as quantified from light microscopy. Values for response variables are pooled among the two dune placements (upwind and downwind) when there was no difference between placements.

There were no differences in ash content among upwind or downwind placements ($F_{1,403} = 0.44$, $P = 0.51$) when controlling for dune volume. There was no relationship between SLM and dune volume when dune volume was analyzed ($R^2 = 0.002$).

Soil microbial films occurred only after the six month collection (Fig. 4B). Film cover increased from 12 months (25.8%) to 24 months (40.6%) ($F_{1,131} = 7.83$; $P = 0.006$). Cover of soil microbial films was greater on the downwind side of coppice dunes (36.8%) than the upwind side (29.6%; $F_{1,135} = 4.13$; $P = 0.04$) when pooled across all collection months. When analyzed on alone, there was no relationship between soil microbial film cover and dune volume ($R^2 = 0.002$).

3.3. Litter carbon and nitrogen content

Both litter C (% C) and nitrogen (% N) were significantly affected by time (Fig. 5; $F_{5,835} = 104.13$, $P < 0.0001$ and $F_{5,835} = 38.5$, $P < 0.0001$ for C & N respectively). During the first 3 months of the experiment, litter % C and % N were relatively stable, similar to mass loss. Both % C and % N decreased between the 6 and 12 month collections while they increased between the 12 and 24 month collections (Fig. 5). Neither dune volume nor placements were significant factors in affecting % C and % N.

There were strong linear relationships between mass remaining and % C mass remaining (Fig. 6A; $R^2 = 0.96$, $y = -16.95 + 1.07x$) and % N mass remaining (Fig. 6B; $R^2 = 0.95$, $y = -5.84 + 1.04x$). Both % C and % N mass remaining were linear with respect to % mass remaining, and both were typically near or below 1:1 relative to mass remaining.

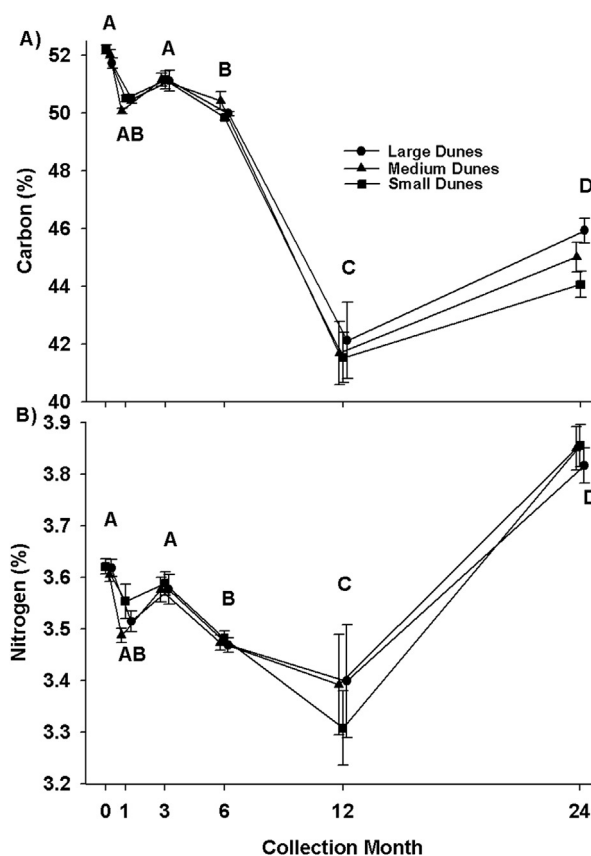


Fig. 5. Changes in litter concentrations by mass of (A) carbon and (B) nitrogen in the 24 month decomposition experiment. Values are presented based on ash-free dry mass. Post hoc tests were used to separate statistically different collection times; mean values at collection times with the same letters are not different. Data points include both the up- and downwind placements due to the lack of statistical difference between these groups. For ease of visualization data were grouped based on their relative dune volume.

4. Discussion

4.1. Soil-litter mixing positively influenced decomposition across a gradient of shrub encroachment

A primary consequence of woody encroachment into many dryland environments is the physical change in surface topography associated with dune formation (Langford, 2000). Coppice dune morphology in the Chihuahuan Desert strongly influences surface soil transport dynamics, leading to soil deposition at the base of shrubs while creating pathways for wind and water erosion from shrub interspaces (Gibbens et al. 1983; Langford, 2000; Gillette and Pitchford, 2004). Although we did not find a positive relationship between factors associated with woody encroachment (litter placement or dune volume) and decomposition rates or SLM, we did observe a positive relationship between SLM and decomposition that is congruent with recent studies from the American Southwest (Throop and Archer, 2007; Hewins et al. 2013). Moreover, the importance of SLM among a range of local vegetation communities, which vary widely in soil cover, highlights the importance of SLM in a variety of dryland environments. This result is compatible with previous work in the Chihuahuan Desert, suggesting that SLM may be a result of localized processes that are not captured by soil flux measurements (Hewins et al. 2013).

Previous studies of soil flux in the Chihuahuan Desert highlight the importance of dune morphology on soil redistribution showing

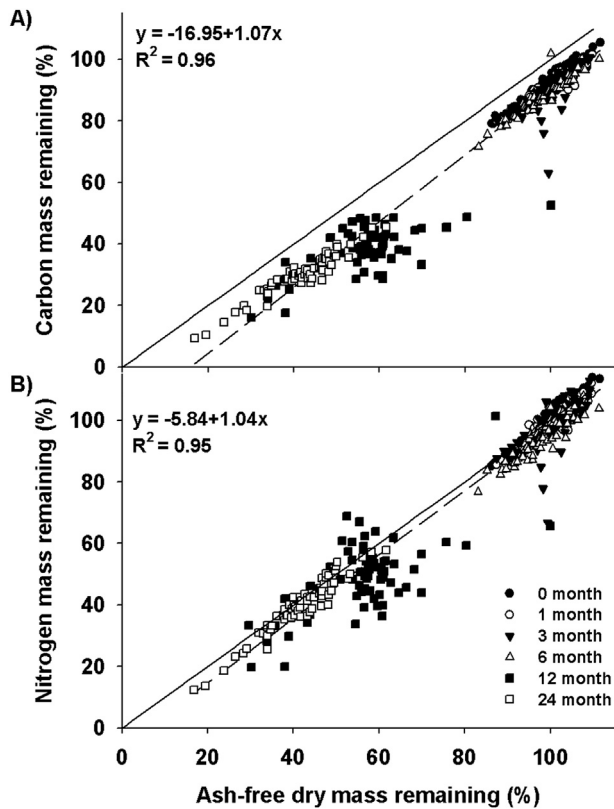


Fig. 6. Relationship between litter ash-free dry mass remaining and ash-free (A) carbon mass remaining and (B) nitrogen mass remaining. Mass remaining values are calculated as percent by mass of the initial value. Symbol and shade combinations represent different collection month. In each figure regression lines are dashed and 1:1 lines are solid.

that soil deposition is typically greater on the downwind side of dunes, while erosion greater on the upwind side (Gibbens et al. 1983; Langford, 2000; Gillette and Pitchford, 2004). Following monsoon rains and the initiation of soil-microbial film development, we observed greater soil-microbial film cover in downwind placements. While this soil-microbial film pattern is consistent with expectations for higher deposition in downwind placements, SLM did not follow the same pattern. The lack of similar pattern for SLM suggests that soil-microbial film cover may not be a function of cumulative deposition and erosion. One possibility is that greater soil-microbial film cover on litter from downwind placements may be due to relatively lower exposure to erosive forces that may impact film development (Gibbens et al. 1983; Langford, 2000; Gillette and Pitchford, 2004).

4.2. The role of precipitation and solar radiation on decomposition

A striking and unexpected finding in our field decomposition experiment was the near absence of measureable mass loss during the first six months of field exposure. The drought during these initial months of the experiment likely suppressed microbial decomposition and contributed to the overall limited decomposition for the duration of the experiment. In contrast to our very slow decay ($k = 0.53, 0.52$ and 0.45 yr^{-1} for the large, medium and small dune NPP sites), other studies have found much greater decomposition of *Prosopis* litter during litterbag studies in the Chihuahuan Desert ($k = 1.27\text{--}1.60 \text{ yr}^{-1}$; Hewins et al. 2013) and slightly greater

values in the Sonoran Desert ($k = 0.55\text{--}0.73 \text{ yr}^{-1}$ for *P. velutina*; Throop and Archer, 2007). Cumulative precipitation was far greater in both Hewins et al. (2013; 272 mm in the first six months and 293 mm in the first year) and more evenly distributed in Throop and Archer (2007; 144 mm in the first six months and 286 mm of precipitation in the first year) compared to this study (4.06 mm in the first six months and 115.3 mm in the first year). Reported decomposition rates during prolonged dry periods in deserts vary and may be affected by site-specific factors. For example, in the Namib Desert the majority of decomposition of buried litter occurred following periods of rainfall, while the limited decomposition that occurred during rainless periods was attributed to macrodetritivores (Jacobson and Jacobson, 1998). In contrast, microbially-mediated decomposition was reported during dry periods in a Mediterranean shrubland, but this decomposition was attributed to moisture inputs from dew (Dirks et al. 2010). Our results provide support for the idea that, in the absence of extenuating circumstances such as dew, moisture from seasonal precipitation plays a strong controlling role over dryland decomposition, similar to many other biological processes in drylands (Noy-Meir, 1973; Freckman, 1986; Whitford, 2002; Collins et al. 2008).

While we did not explicitly manipulate or test the influence of solar radiation in this experiment, the lack of decomposition during the initial six months of the study provides compelling evidence that decomposition in the 6–24 month exposure period was driven predominantly by biological activity. During this time of high decomposition, litter was exposed to relatively high inputs of solar radiation and precipitation. Given the high rates of photodegradation reported by other researchers (e.g., 60% of total decomposition; Austin and Vivanco, 2006) and the high measured solar radiation during the first six months of the experiment, we expected high rates of decomposition from photodegradation despite potential restriction of biotic decomposition due to low precipitation. Although significant photodegradation has been reported by some researchers (e.g., Austin and Vivanco, 2006; Day et al. 2007; Yang et al. 2013), others have reported little or no effect on decomposition rates in drylands (Kirschbaum et al. 2011; Song et al. 2011; Uselman et al. 2011). One challenge when comparing photodegradation results among studies is that many studies provide little or no information about the solar radiation conditions under which the research took place (Barnes et al. 2015). Biologically effective UV radiation in our study (maximum monthly mean of $8.02 \text{ kJ m}^{-2} \text{ day}^{-1}$ UVBBE in July; mean 2.90, 4.64 and $4.34 \text{ kJ m}^{-2} \text{ day}^{-1}$ UVBBE over 6, 12 and 24 months respectively) was higher than reported in other studies where there was substantial photodegradation (maximum monthly average of $5 \text{ kJ m}^{-2} \text{ day}^{-1}$ UVBBE in June, an estimated 2.65 and $2.62 \text{ kJ m}^{-2} \text{ day}^{-1}$ UVBBE over 6 and 12 months respectively and 21% litter mass loss were reported by Brandt et al. 2007). The apparent absence or minimal importance of photodegradation in several previous studies has been attributed to soil covering litter and negating photodegradation (Throop and Archer, 2007; Uselman et al. 2011; Barnes et al. 2012). Our results suggest that solar radiation at the time of litter fall has little positive effect on leaf litter decomposition of the one of the predominant deciduous shrubs in the Chihuahuan Desert. This may be, in part, due the timing of leaf abscission during periods of moderate solar radiation relative to extremes throughout the summer. A possible alternative explanation for the lack of photodegradation could be that *P. glandulosa* litter has a limited sensitivity to photodegradation. However, laboratory studies with *P. velutina*, closely related to *P. glandulosa* used in the present study, demonstrated measurable instantaneous flux rates of H_2 , CO, CO_2 , and CH_4 from both thermal degradation and

photodegradation (Lee et al. 2012a, 2012b).

4.3. Temporal dynamics of soil-litter mixing and microbial film development

The temporal patterns of SLM in litter cages and soil-microbial film development generally mirrored patterns of decomposition, with all both variables increasing by the 12 month collection. The parallel increase of soil-microbial film cover and decomposition rate suggests that the two are related. However, we are not currently able to determine if: 1) soil-microbial films enhance decomposition, 2) decomposition leads to soil-microbial film development, 3) there are feedbacks between the two, or 4) they simply both occur when requisite conditions are met (e.g. available moisture and SLM). Accelerated decomposition rates were observed in studies of buried litter relative to surface litter in drylands (Schaefer et al. 1985; Jacobson and Jacobson, 1998), suggesting that cover by soil contributes to conditions that enhance decomposition. SLM in a lab incubation experiment enhanced C mineralization under oscillating moisture conditions, ostensibly the result of soil buffering litter from low moisture (Lee et al. 2014). In field conditions, decomposition, SLM, and soil-microbial film development occur rapidly and nearly simultaneously during or following precipitation events. These interrelated processes make it difficult to isolate the potential sensitivity of decomposition to moisture alone in the absence of SLM or soil-microbial film development (Throop and Archer, 2007; Barnes et al. 2012; Hewins et al. 2013).

4.4. Litter chemical changes occurred as a function of decomposition

The C and N concentration of litter is a strong regulator and predictor of decomposition worldwide (Aerts, 1997; Hobbie et al. 2000; Parton et al. 2007). In our study, changes in C and N concentration were largely congruent with litter decomposition. We observed only minor variation in C and N concentration during the first six months of our experiment; this was a similar pattern to mass remaining. Concentrations of both C and N decreased sharply between 6 and 12 months, a trend that mirrored an acute decrease in litter mass remaining. When decomposition slowed between 12 and 24 months, we observed an increase in C and N concentration, suggesting that remaining C and N were concentrated in complex organic compounds (Coûteaux et al. 1995). The increase in the concentration of both C and N at 24 months indicates C and N indicates that most of the material remaining (ca. 40%) is more difficult to decompose relative to litter fall from the current year, and microbial communities are more likely harvesting energy and nutrients from these more recent and labile inputs.

When assessing the relationship between litter mass remaining of C and N over time, we observed trends that shed light on the potential drivers of decomposition in this study. The mass of C remaining was typically well below a 1:1 relationship with total litter mass remaining highlighting 1) that C was lost at a rate greater than total litter mass suggesting that C was in high demand by microbes given their high C requirements (Manzoni et al. 2010), and 2) that soluble C was lost via leaching due to the onset of monsoon rains (Cleveland et al. 2006). Moreover, this suggests that decomposition was not a result of physical fragmentation, which would be a near 1:1 ratio of C-to-litter mass remaining. The mass of N remaining had a relationship that was near or greater than 1:1 with respect to litter mass remaining throughout our experiment, which indicates that N mineralization was tightly coupled with litter decomposition and that litter N was not being mobilized by microbes in most cases.

5. Conclusions

After a two-year litter decomposition study, we found that decomposition was most strongly related to precipitation and SLM. We found evidence of biological activity in the form of soil-microbial films on the surface of leaf material, supporting the premise that microbial activity is a strong component of decomposition in these systems. Solar radiation (i.e. UVBBE) had a minor influence on decomposition even during the first six months of field exposure before much SLM occurred; there was 97.2% mass remaining at this time despite high UVBBE exposure.

In the context of shrub encroachment, we did not observe any clear evidence to support the hypothesis that upwind and downwind litter placements, or shrub morphology (i.e. volume) had an effect on SLM or decomposition. As a result, we conclude that SLM occurs at a scale that is not adequately captured by studies of soil redistribution in coppice dune areas of the Chihuahuan Desert, but SLM is a critical process that enhances decomposition by modulating the soil-litter micro-environment and facilitating biological decomposition.

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