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Soil–Litter Mixing Accelerates Decomposition in a Chihuahuan Desert Grassland

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Abstract

Decomposition models typically under-predict decomposition relative to observed rates in drylands. This discrepancy indicates a significant gap in our mechanistic understanding of carbon and nutrient cycling in these systems. Recent research suggests that certain drivers of decomposition that are often not explicitly incorporated into models (for example, photodegradation and soil–litter mixing; SLM) may be important in drylands, and their exclusion may, in part, be responsible for model under-predictions. To assess the role of SLM, litterbags were deployed in the Chihuahuan Desert and interrelationships between vegetation structure, SLM, and rates of decomposition were quantified. Vegetation structure was manipulated to simulate losses of grass cover from livestock grazing and shrub encroachment. We hypothesized that reductions in grass cover would promote SLM and accelerate mass loss by improving conditions for microbial decomposition. Litter mass decreased exponentially, with the greatest losses occurring in concert with summer monsoons. There were no differences in decay constants among grass cover treatments. A significant, positive relationship between mass loss and SLM was observed, but contrary to expectations SLM was independent of grass cover. This suggests that processes operating at finer spatial scales than those in our grass removal treatments were influencing SLM. Shifts in litter lipid composition suggest increased bacterial contribution to decomposition through time. SLM, which is seldom included as a variable controlling decomposition in statistical or mechanistic models, was a strong driver of decomposition. Results are discussed in the context of other known drivers of decomposition in drylands (for example, UV radiation and climate) and more mesic systems.

Key words: arid; carbon cycle; dryland; dust; erosion; livestock grazing; shrub encroachment; phospholipid fatty acids; *Prosopis*.

Introduction

Decomposition of plant litter is a central process in the cycling of carbon (C) and nutrients in ecosystems (Aerts 1997; Harmon and others 2009). As such, it influences soil fertility, water holding capacity, and primary productivity. The relatively

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low levels of litter input and small nutrient pools in arid and semi-arid ecosystems (hereafter 'drylands') make decomposition a particularly important contributor of plant-available nutrients (Moorhead and Reynolds 1991). Despite its importance, our understanding of the controls over decomposition in drylands lags substantially behind that of mesic systems, where simple models based on climate variables such as actual evapotranspiration predict regional rates relatively accurately (for example, Meentemeyer 1978; Aerts 1997; Parton and others 2007). In drylands, however, these models typically under-predict decomposition relative to field measurements (for example, Whitford and others 1981; Parton and others 2007; Throop and Archer 2009). This disconnect between modeled and measured rates reflects our lack of a mechanistic understanding of decomposition processes in drylands and limits our ability to predict biogeochemical fluxes through space and time. Although productivity in drylands is low, these systems are an important component of global biogeochemical cycles, as they cover 41% of Earth's terrestrial surface (Reynolds and others 2007) and account for 30–35% of terrestrial net primary production (Field and others 1998). In addition, drylands are socioeconomically critical, as they are home to 38% of the world's human population and a large proportion of livestock (Turner and others 1990; Reynolds and others 2007), and their airsheds and watersheds provide numerous ecosystem services (MEA 2005). Understanding biogeochemical processes in these systems is therefore important for global biogeochemical accounting.

A crucial step toward improving our understanding of dryland biogeochemical cycling lies with resolving the differences between modeled and measured decomposition rates. Recent empirical evidence suggests that the discrepancy may be due, at least in part, to the elevated importance of abiotic drivers of decomposition in drylands (reviewed in Throop and Archer 2009). One such driver that accelerates decomposition is soil–litter mixing (SLM), which is characterized by the burial of litter by aeolian and fluvial soils and the subsequent formation of biotic soil films on litter surfaces (hereafter 'soil–litter films') (Throop and Archer 2007; Barnes and others 2012). Although the mechanisms by which SLM enhances decomposition remain unresolved, possibilities include physical abrasion that increases litter surface area for decomposer activity or leaching; soil acting as a transport vector and enhancing microbial colonization of litter; or soil and/or soil–litter films buffering the litter microclimate and increasing the temporal window in which temperature and moisture conditions are suitable for decomposers. A second potentially strong driver of dryland decomposition is solar radiation, particularly UV-B, which can enhance decomposition via direct abiotic degradation of organic compounds and indirect 'photopriming', a change in chemical composition from UV that facilitates later microbial decomposition (reviewed in King and others 2012). However, the role of UV radiation in dryland decomposition is perplexing, with studies showing no UV effect (for example, Kirschbaum and others 2011), minimal UV effects relative to strong microclimate effects (Uselman and others 2011), and detrimental effects of UV radiation on decomposer organisms (Zepp and others 1998; Paul and Gwynn-Jones 2003). SLM and UV photodegradation may affect decomposition individually, but they may also interact: photodegradation could be the predominant initial driver until soil covers litter or forms soil–litter films, shielding it from UV photodegradation and subsequently enhancing microbial decomposition (Barnes and others 2012). The importance of these drivers and their interactions are likely contingent on vegetative cover via its influence on both radiant energy regimes and the movement of soils by wind and water. Although both SLM and UV photodegradation may play a role in decomposition in mesic as well as dryland ecosystems, the typically low and discontinuous vegetation cover and high bare ground cover of drylands make soil transport processes (Field and others 2009a) and solar radiation exposure (King and others 2012) particularly high in these systems. The importance of these processes may also be subject to more dynamic shifts in drylands, as changes in the relative abundance of functional groups (for example, annual plants, perennial grasses, and shrubs) and the pattern and extent of bare ground cover can occur rapidly in these systems in response to disturbance (for example, livestock grazing, fire) and high annual/interannual variability in precipitation.

Vegetation Change and Decomposition

Extensive losses of grass cover have occurred in many of the world's drylands, often as a result of the expansion or intensification of livestock grazing in concert with altered fire regimes, shrub encroachment, and long-term changes in climate (for example, Buffington and Herbel 1965; Milchunas and Lauenroth 1993; Asner and Archer 2010). In the southwestern United States, extensive loss of grasses corresponds to intensive grazing

combined with a series of severe droughts prior to the Taylor Grazing Act of 1934 (Bahre and Shelton 1996; Fredrickson and others 1998). Losses of grasses have often continued following relaxation of grazing, however. For example, at the Jornada Experimental Range in the northern Chihuahuan Desert, cover of *Bouteloua eriopoda,* the former dominant grass, declined from 19% in 1915 to 1.2% in 1998 (Gibbens and others 2005). In addition to grazing alone, declining grasslands in this area could be a function of long-term shifts in climate (for example, greater aridity) and differences in ecophysiological adaptations of grasses and shrubs to current climate conditions (Neilson 1986; Barron-Gafford and others 2011; Throop and others 2012).

Changes in vegetation structure associated with losses of grass cover in drylands may mediate decomposition via changes in litter quality and quantity, but also via influences on soil movement and subsequent SLM. For example, SLM and subsequent changes in decomposition in the Sonoran Desert were ostensibly a function of grass cover influences on soil transport patterns (Throop and Archer 2007). In this system, decomposition rates were lowest under shrub canopies with dense grass cover and in grass patches that persisted following shrub removal. In contrast, decomposition rates were highest in microhabitats where shrubs were absent, grass cover was low, and SLM was high. In the northern Chihuahuan Desert, encroachment by shrubs occurs in synchrony with reduced cover and density of intercanopy grasses (Gibbens and others 2005), leading to decreased surface soil stability (Li and others 2007) and high rates of soil erosion (Okin 2005, 2008). We propose that under these conditions, SLM and hence rates of litter decomposition will increase.

The effect of vegetation structure on SLM and decomposition was explicitly tested in a litterbag experiment on a Chihuahuan Desert grassland site where vegetation cover was manipulated to simulate the progressive loss of grass cover accompanying livestock grazing and woody plant encroachment. We hypothesized that (i) reductions in grass cover would destabilize soils and promote SLM, and (ii) that SLM would enhance microbial abundance and alter microbial community composition in ways that accelerate decomposition. To test our hypotheses, we quantified mass loss, chemistry, and phospholipid fatty acid (PLFA) profiles of litter incubated on sites with experimental reductions in grass cover (0–100% removals) over a 12-month period.

Methods

Study Site

The study was conducted at the Jornada Basin Long Term Ecological Research site (JRN; 32.5°N, 106.8°W), 35 km northeast of Las Cruces, NM, near the northern boundary of the Chihuahuan Desert. Mean annual temperature is 14.7°C, with annual mean maxima and minima in June (36°C) and January (3.8°C), respectively (Wainright 2006). Mean annual precipitation (MAP; 1915–1995) is 245 mm, 61% of which occurs as late summer (July–September) monsoons (Gibbens and others 2005; Wainwright 2006). Erosive winds at the JRN prevail from a southwesterly direction 79% of the time and occur predominately from March through May (Helm and Breed 1999; Li and others 2007).

Experimental Design

The study was conducted within plots established in 2004 to evaluate the impact of vegetation structure on wind erosion and soil flux (see complete description in Li and others 2007). The initial vegetation was desert grassland dominated by native perennial dropseeds (*Sporobolus* spp.), threeawns (*Aristida* spp.), and black grama (*B. eriopoda).* Cover of scattered shrubs (primarily *Prosopis glandulosa*, *Ephedra torreyana*, and *Yucca elata*) was 11–19%. The site was situated in the ''sand sheet'' geomorphic surface (95% of surface soil particles 0.5–1.0 mm) (Monger 2006). Three experimental blocks were designated. Each block contained four plots (25 m wide × 100 m long; $n = 12$) composed of a 50 × 25 m upwind grass removal subplot and a 50 × 25 m downwind response subplot (hereafter 'removal' and 'response', respectively) (Figure 1). The rectangular plots were oriented lengthwise, parallel to prevailing winds and separated by 25 m buffer strips of unmanipulated vegetation. Vegetation cover in removal subplots was manipulated to simulate the range of herbaceous (grass and forb) cover losses known to accompany livestock grazing and shrub encroachment; grass cover in the downwind response plots was left intact. Canopy cover of herbaceous vegetation was removed (hereafter 'grass removal') in March 2004 at one of four levels: 100, 75, 50, and 0%. Regenerating grasses were removed annually to maintain the treatments. Shrub cover was not manipulated.

Litterbags (10 × 10 cm) were constructed using UV-resistant fiberglass window screen (0.8 × 1.0 mm openings; New York Wire Company, Mount Wolf, PA, USA) to ensure litterbag longevity under field conditions. Naturally senescing honey mesquite

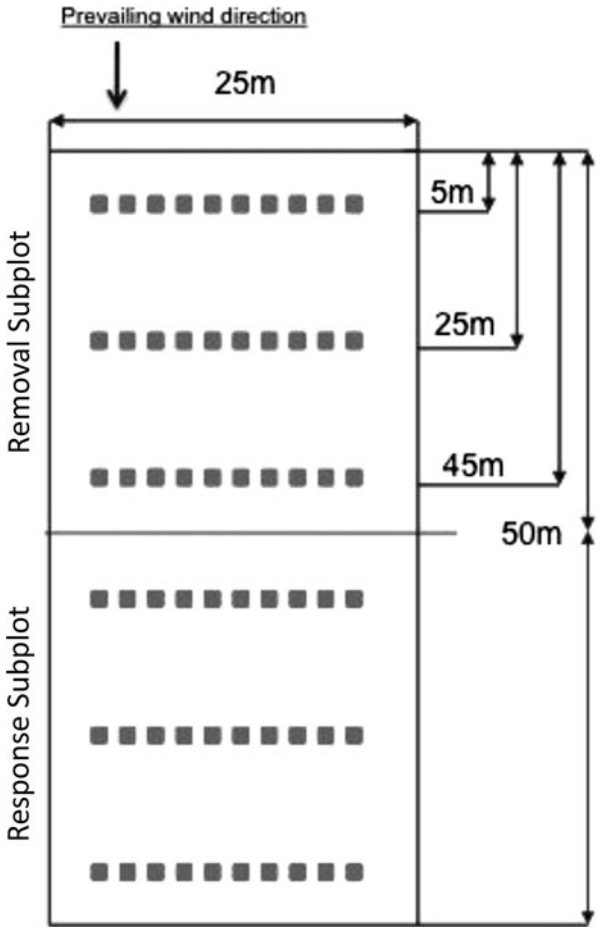

Figure 1. Schematic layout of an experimental plot (25 × 100 m) with grass removal subplots (0–50 m) positioned upwind of response subplots (50–100 m). Each subplot had litterbags (*squares*) placed along transects located 5, 25, 45, 55, 75 and 95 m (fetch lengths) downwind of the upwind plot border. Plots were oriented parallel to the prevailing wind direction. The study consisted of four of these experimental plots (0, 50, 75, and 100% grass removal) in each of three blocks.

(*P. glandulosa*) litter was collected on 19 October 2007 at the JRN and 'air dried' at 30°C for 48 h. Drying at this temperature should not affect litter chemistry, as leaves experienced greater temperatures during the growing season. Litterbags were filled with 2 g of leaflets; this mass filled litterbags with minimal leaflet overlap. For every 10 litterbags filled, a 2 g sample was dried at 60°C to establish a wet–dry mass relationship.

Litterbags were deployed on 19 and 20 April 2008, a time corresponding to the annual peak in mean monthly wind speed (Wainwright 2006). Litterbags were placed along transect lines at locations of 5, 25, and 45 m downwind from the upwind edge (hereafter 'fetch length') of removal subplot borders. Transects at fetch lengths of 55, 75 and 95 m were established in response subplots (Figure 1). Litterbags were spaced at distances approximating the average interplant gap distance (range = 92–892 mm, depending on the subplot) and were fixed to the soil surface with 10 cm long steel staples. To avoid wake effects on soil transport (Okin 2008), litterbag placements were adjusted as needed to ensure that no bags were within 5 m of an upwind shrub. One litterbag from each fetch length in each subplot was randomly designated for collection at 0, 1, 3, 6, and 12 months post-deployment.

Laboratory Processing and Analyses

Litterbag contents (litter + accumulated soil) were separated using a 1-mm mesh sieve. Litter was then manually dusted using small brushes to remove additional soil from leaflets. The brushed litter was frozen at −80°C for 48 h, lyophilized for 48 h, weighed, and then ground to a fine powder using a ball mill (8000D Mixer/Mill, Spex Certiprep, Metuchen, NJ, USA). Subsamples of litter were combusted at 550°C for 6 h to determine the inorganic matter content (% ash). Mass loss and litter C and N content (elemental analyzer; ECS 4010, Costech Analytical Technologies, Valencia, CA, USA) are expressed on an ash-free basis. The % ash was also used as a conservative index of soil accumulation that accounts only for soil adhering to litter surfaces after sieving and brushing (see Throop and Archer 2007). A large proportion of soil that infiltrates litterbags covers or mixes with litter, but does not adhere to litter surface. The mass of these 'bulk' soils entering or exiting litterbags is responsive to wind and water transport processes and is thus likely highly dynamic relative to that of the soil–litter films that form on litter surfaces. Quantifying the magnitude and dynamics of this 'bulk' component of the soil–litter matrix was beyond the scope of this study.

Phospholipid Fatty Acid (PLFA) Analysis

To determine if SLM altered litter lipid profiles, we analyzed PLFA in samples collected in the 0, 50, and 100% grass removal subplots at the 3-, 6-, and 12- month collection dates, at fetch lengths of 5 and 45 m in removal subplots and of 55 and 95 m in response subplots. Lyophilized, ground litter material (250 mg sub-sample) was extracted for total lipids using a single-phase extraction [Bligh and Dyer (1956) with modifications by White and others (1979) and Wilkinson and others (2002)]. Litter was extracted by twice vortexing and heating

(37°C) for 0.5 h with potassium phosphate buffer, methanol, and dichloromethane solution (0.8:2:1 ratio). The phospholipid fraction in the supernatant was isolated using a silicic acid solid phase extraction and then converted to fatty acid methyl esters (FAMEs), which were then purified with octadecyl (C18) resin as described in Dobbs and Findlay (1993) and Findlay and Dobbs (1993). Purified FAMEs were analyzed with a gas chromatograph (Shimadzu 2014, Shimadzu Corp., Japan) equipped with a flame ionization detector (FID) using a non-polar Rtx-1 column (30 m × 0.32 mm × 0.25 mm; Restek Corp., Bellefonte, PA). FAMEs were identified and quantified using known standards (Supelco 37-component FAME mix, Sigma-Aldrich Co., St. Louis, MO) every four samples. Problems with co-elution of compound peaks in the C18 isomer region on the Rtx-1 column that occurred due to high concentrations of some FAMEs were resolved using a very polar Select FAME capillary column (50 m × 0.25 mm × 0.25 mm; Agilent Tech., Santa Clara, CA) attached to a Varian 3900 gas chromatograph with a FID (Agilent Tech., Santa Clara, CA). FAMEs are described based on standard nomenclature.

Total extractable PLFAs are the sum of all identified FAMEs and are presented as a concentration (nmol g^{-1} litter) and as the total amount of PLFA contained in each litterbag (nmol $litterbag^{-1}$, where the concentration was multiplied by the litter mass at the collection time). Although there is some overlap between plants and microbes in the types of FAMEs they can produce (for example, most can produce the saturated FAMEs 16:0, 18:0 and so on; Harwood and Russel 1984), some FAMEs are thought to be relatively unique and are therefore considered biomarkers for certain taxonomic groups. We attributed the following FAMEs to these organismal taxonomic groups: gram-positive bacteria (i15, a15, i16, i17, a17); gram-negative bacteria (cy17, cy19, 18:1n7c, 16:1n5c; 16:1n7c); other bacteria (15:1n5c, 15:1n6c); and diatoms (16:1n3t) (Vestal and White 1989; Sasser 1990; White and others 1996). Although 18:2n6 and 18:1n9 are often used as fungal biomarkers, these can also be produced by plants (Vestal and White 1989). We were therefore unable to distinguish between plant and fungal lipid markers in our samples.

Statistical Analysis

Our statistical design incorporated the three replicate blocks with four plots per block. Blocks were treated as a random effect, whereas grass cover reductions were treated as a fixed effect. Multiple regression was used to model decomposition (ash-free mass remaining at a given collection time) as a function of up to three possible variables: degree of SLM (as indicated by % ash), grass cover reduction, and fetch distance. The goodness of fit of all possible models was compared using Akaike Information Criterion (AIC; Akaike 1974). Goodness of fit statistics were generated by using Proc Autoreg in SAS v. 9.2 (SAS Institute, Cary, NC). Decay constants (k) were estimated using a single pool exponential decay model to provide cross-compatibility with other decomposition studies

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

M_t is mass at a given time t, M_0 is the initial mass, and e is the exponential constant (Olson 1963). A double-pool model was also assessed, but model fit was not substantially improved with this approach. To minimize estimation errors, data were not log transformed before fitting to exponential decay curves (Adair and others 2010). Decay constants were estimated for grass cover reduction and fetch lengths separately to determine their independent influence on decomposition rates. In addition, k values were estimated for all possible combinations of grass reductions and fetch lengths. Curve fitting was performed with Sigma Plot v. 11 (Systat Software Inc., San Jose, CA).

The effects of soil accumulation (as indicated by % ash) on decomposition were analyzed at each collection date on data pooled across all blocks, plots, and fetch lengths using Proc Reg in SAS v 9.2 (SAS Institute, Cary, NC). Least square means F tests were used to test for treatment differences in C and N content and total extractable PLFA using the SAS Proc GLM. Some samples were lost during FAME extractions, so we could not run a full factorial analysis on the PLFA data on some dates. Therefore, we pooled fetch lengths within subplots for this analysis (leaving collection date, grass cover reduction, subplot, and their interactions in the analysis).

To evaluate how litter lipid profiles changed over time and in response to grass cover reductions, a community analysis of the relative abundance of FAMEs contributing at least 1% of the total (n = 23 FAMEs; total of 90 FAMEs identified) was performed utilizing a Non-metric Multidimensional Scaling (NMS) ordination technique (PC-ORD v. 4.0; MjM Software, Gleneden Beach, OR) and Sorensen distance measure (Bray-Curtis). Differences between grass cover treatments and collection dates in the ordination were evaluated using

pairwise comparisons performed with a multi-response permutation procedure (MRPP). MRPP generates a test statistic (p) describing the likelihood that observed differences between groups of samples are due to chance and a chance-corrected within group agreement statistic (A) which describes homogeneity within groups (when $A = 1$, all points are identical within a group). To assess the effect of litter C and N content and SLM on lipid profiles, we created a bi-plot overlay on the ordination utilizing the following environmental variables: litter mass remaining, C and N mass at harvest, C and N concentration at time of harvest, and % ash.

Results

Litter Mass Loss

Ash-free litter mass decreased exponentially over the course of the experiment, with the greatest losses occurring in the first 6 months (Figure 2A). There were no differences in decay constants (k) based on grass cover treatments ($F_{3,15} = 1.60$, $P > 0.05$) or fetch length ($F_{5,15} = 2.43$, $P = 0.08$). The single exponential decay model (equation 1) fit the mass loss data well (R^2 range = 0.81–0.86; Table 1). Decomposition progressed in concert with the monsoon rains (Figure 2B) that follow the windy season at our field site.

Litter mass remaining was inversely related to soil accumulation on leaves (% ash). This relationship developed over time, becoming strongest at 6 and 12 months (Figure 3), by which time litterbags were often completely buried by soil. Contrary to expectations, there was no clear effect of grass cover treatment ($F_{3,304} = 1.90$, $P > 0.05$) or fetch length ($F_{5,304} = 0.48$, $P > 0.05$) on mass loss.

Litter mass remaining was best predicted with a single variable model that included only % ash (Table 2). Inclusion of additional variables (grass removal and transect fetch length) did not improve model fit, and models that did not include % ash fit the data poorly. Iterations of the regression procedure were conducted on grass removal subplots and response subplots separately, but results did not differ from the pooled model.

Litter Carbon and Nitrogen

Ash-free litter C concentration by mass ([C]) increased slightly, but significantly, with time ($F_{4,296} = 7.54$, $P < 0.001$; mean ± SE = 52.7% ± 0.12 and 56.5% ± 1.55 for 0- and 12-month litter, respectively; Figure 4A). Litter [C] decreased slightly after one month in all grass cover treatments, and

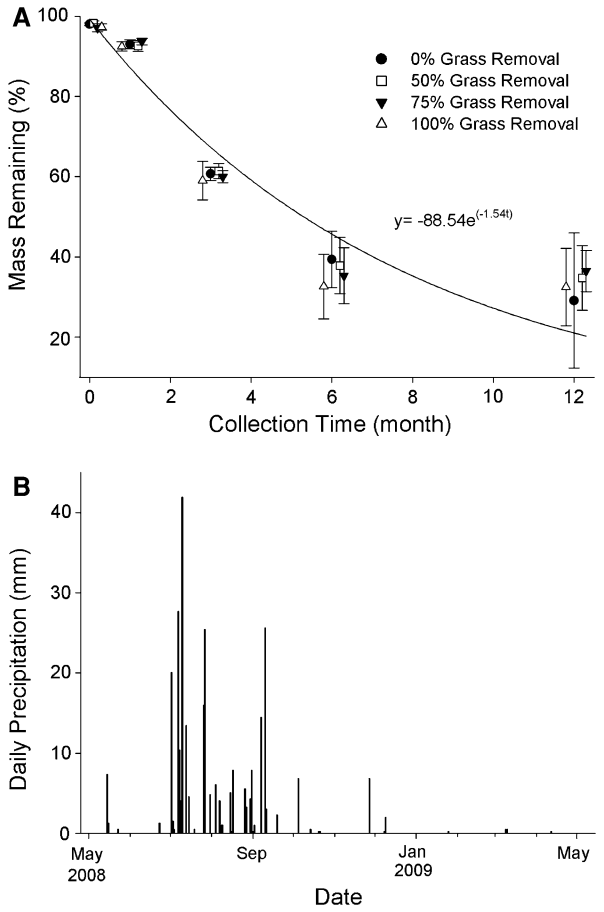

Figure 2. **A** Ash-free dry mass remaining (%) at 0, 1, 3, 6, and 12-month retrievals. Grass removal treatments are represented by different symbols. Fetch length was not significant, so these data were pooled within grass removal plots. Values on the x-axis were adjusted slightly to reduce symbol overlap. A negative exponential decay function for mass loss (equation 1) was fitted to the data (*solid line*; see also Table 1). **B** Daily precipitation (mm) during the experiment (May = collection time 0).

generally increased after that, more so in the 75 and 100% grass removals than in the 0 and 50% grass removals ($F_{3,296} = 7.10$, $P < 0.001$). [C] in the former peaked at 6 months, then declined to levels statistically comparable to those in the other grass removal treatments. Patterns of litter nitrogen concentration ([N]) closely mirrored [C], wherein [N] increased with time ($F_{4,296} = 69.83$, $P < 0.001$; mean ± SE = 2.91% ± 0.28 and 3.88% ± 0.91 for 0 and 12 months, respectively; Figure 4B). As with [C] there was a significant difference between grass cover treatments at the 6-month collection where litter in the 0 and 50% grass cover had lower [N] than litter in the 75 and 100% grass removals ($F_{3,296} = 8.08$, $P < 0.0001$). There were tight, linear relationships between % litter mass remaining and

Table 1. Decay Constants (k, equation 1), Standard Errors (SE), and Explained Variance (R^2) for Litter Mass Loss in Grass Removal Treatments (Upper) and Transects (Fetch Length, m; Lower)

	k (y^{-1})	SE	R^2
Grass removal treatment (%)			
0	1.60	0.110	0.85
50	1.45	0.081	0.86
75	1.27	0.086	0.83
100	1.54	0.105	0.82
Transect fetch (m)			
5	1.36	0.101	0.85
25	1.41	0.108	0.86
45	1.69	0.141	0.84
55	1.56	0.124	0.86
75	1.39	0.113	0.83
95	1.40	0.120	0.81

Data were grouped by transect when estimating k for grass removal treatments (Figure 2), and were pooled across grass removal treatments when estimating k for transect fetch lengths. Standard errors (SE) shown are from pooled data.

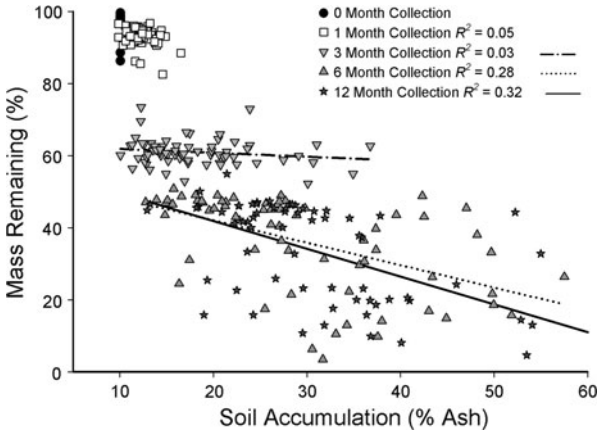

Figure 3. The relationship between litter mass remaining (% ash-free dry mass) after 0, 1, 3, 6 and 12 months and soil accumulation (as indicated by % ash). Grass removal and fetch length effects were not significant, so these data were pooled.

% C mass remaining (R^2 = 0.96, y = 4.45 + 0.97x; Figure 5A) and % N mass remaining (R^2 = 0.92, y = 17.47 + 0.84x; Figure 5B). Although the relationship between % C mass remaining and % mass remaining was nearly 1:1, % N mass remaining showed a clear tendency to be elevated relative to % mass remaining, especially at low values of mass remaining.

Litter Phospholipid Profiles

Total extractable PLFA concentrations (nmol g^{-1} litter) fluctuated through time; concentrations were similar at the 3- and 12-month collections, but were significantly lower (by ~40%) at the 6-month collection (Figure 6A; $P < 0.0001$). Total PLFA per litterbag (nmol) also fluctuated, reflecting trade-offs between PLFA concentrations and the amount of plant material present at a given point in time (Figure 6B; $P < 0.0001$). As with mass loss data, neither PLFA concentration nor total PLFA were significantly influenced by grass cover manipulations (P = 0.27 and 0.20, respectively) or transect fetch length (P = 0.74 and 0.96, respectively).

Changes in PLFA with time were also reflected in the FAME ordination (Figure 7A). Axes 1 (88.2%) and 2 (9.5%) explained 97.7% of the variation in the FAME NMS ordination and reached an acceptable final stress value of 7.6 after 58 iterations. Scores along Axis 1 appear to generally represent changes with time. MRPP analysis indicated that PLFA profiles differed significantly on each of the three collection dates ($P < 0.0001$ for all pairwise comparisons). However, MRPP failed to detect differences in PLFA profiles of litter incubated in the different grass removal treatments ($P > 0.50$ for all pairwise comparisons). This is consistent with the lack of grass cover effects on soil accumulation (% ash). The NMS bi-plot of the environmental variables indicated that the % mass, C, and N remaining were significantly and positively correlated to both axis 1 and 2, the region of the ordination containing the 3-month samples (Figure 7A). This same area of ordination space contained samples with high relative abundance of general, nonspecific FAME biomarkers (for example, 16:0, 18:0, 20:0), a diatom marker (16:1n3t), and a marker that can be produced by either plants or fungi (18:2n6). Percent ash, the proxy for soil accumulation on leaves, and [N] were both

Table 2. Model Fit (R^2) for All Possible Regression Models Predicting Ash-free Mass Remaining (%)

Variables in model	R^2	AIC	ΔAIC
% Ash	0.32	1813	0
Grass removal	0.002	1914	101
Transect fetch	0.00	1915	102
Transect × % ash	0.32	1815	2
Grass Removal × % ash	0.32	1815	2
Grass Removal × transect	0.002	1916	103
Grass Removal × % ash × transect	0.32	1817	4

AIC analysis indicates that the soil accumulation index (% ash) alone was the best predictor of mass loss (AIC values that differ by AIC units of 1 to 2 suggest that models fit the data well; a difference of 4 to 7 is a weakly supported model; and AIC values differing by greater than 10 from the lowest value suggest that a model does not explain data). Differences in AIC value between the best-fit model and all other models are indicated in the ΔAIC column.

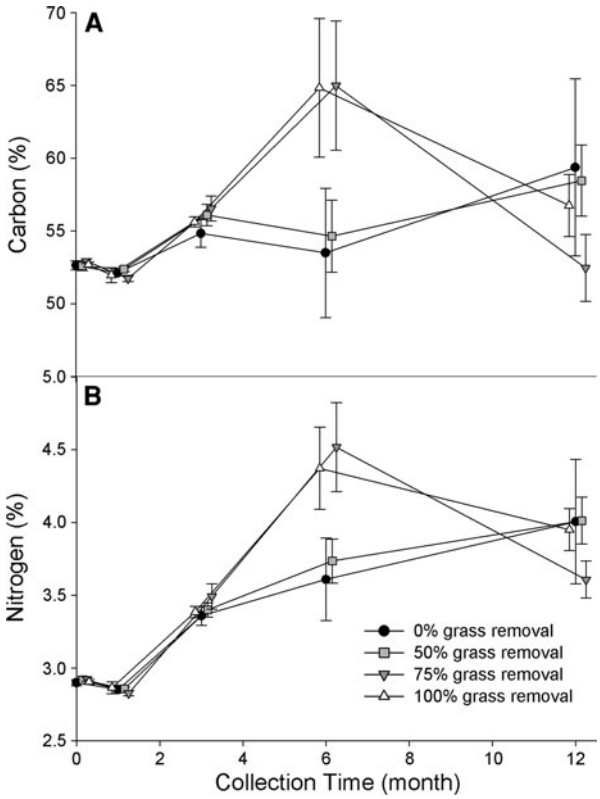

Figure 4. Changes in **A** carbon concentration ([C]) and **B** nitrogen concentration ([N]) of litter (on a percent by mass basis of ash-free litter) over the one-year experiment. Fetch length was not significant, so these data were pooled within grass removal treatments, which are indicated by different symbols. Collection month was significant for both [C] and [N] (ANOVA $F_{4,\ 298} = 7.03$, $P < 0.0001$ and $F_{4,\ 298} = 61.35$, $P < 0.0001$, respectively); and Fisher LSD tests showed that mean C and N in 75 and 100% removal plots differed from 0 and 50% plots ($P < 0.001$ for both C and N). Values on the *x*-axis were adjusted slightly to reduce symbol overlap.

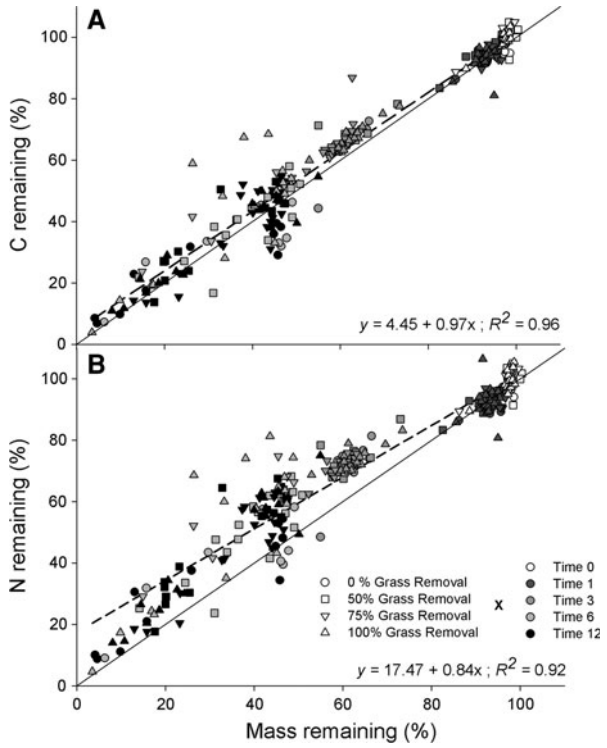

Figure 5. Relationship between percent ash-free litter mass remaining and percent ash-free **A** C mass and **B** N mass remaining. *Symbols* represent grass removal treatments, whereas *shades of gray* represent collection dates. In each figure, regression lines are *dashed*; and the 1:1 line is *solid*.

negatively correlated to axis 1. Samples in this region of the ordination, primarily 6- and 12-month collections, had high relative abundance of FAMEs specific to bacteria (for example, 15:1n5c, 15:1n6c, i15, 16:1n5c, cy19; Figure 7B), suggesting an increase in bacterial abundance as litter decomposed and [N] and SLM increased.

Discussion

Decomposition Rates

Our results show that SLM, as measured by the ash contributions of soil–litter films, accelerates decomposition in this Chihuahuan Desert site. These results are consistent with findings from the Sonoran Desert where % ash was positively correlated with mass loss (Throop and Archer 2007) and a study in a central New Mexico arid grassland that found a positive relationship between bulk soil accumulation and mass loss (Brandt and others 2010). Failure to account for SLM may thus explain some of the under-prediction of decomposition by ecosystem models. However, although our *k* values for *P. glandulosa* litter (1.27–1.60 y^{-1}; Table 1) fell within the range reported by Whitford (2002) for other Chihuahuan Desert plants, they were considerably greater than those reported for *P. velutina* in the Sonoran Desert (0.55 - 0.73 y^{-1}; Throop and Archer 2007). This may be an artifact of differences in the litter surface area exposed to environmental conditions. Throop and Archer (2007) filled the same dimension litterbags (10 × 10 cm) with twice the mass of litter; the monolayer of litter in our bags may have allowed for increased exposure to drivers of decomposition. Timing of rainfall relative to the soil transport process may also be important in driving decomposition in the Chihuahuan Desert, which receives the majority of its precipitation during late summer monsoons when ambient and

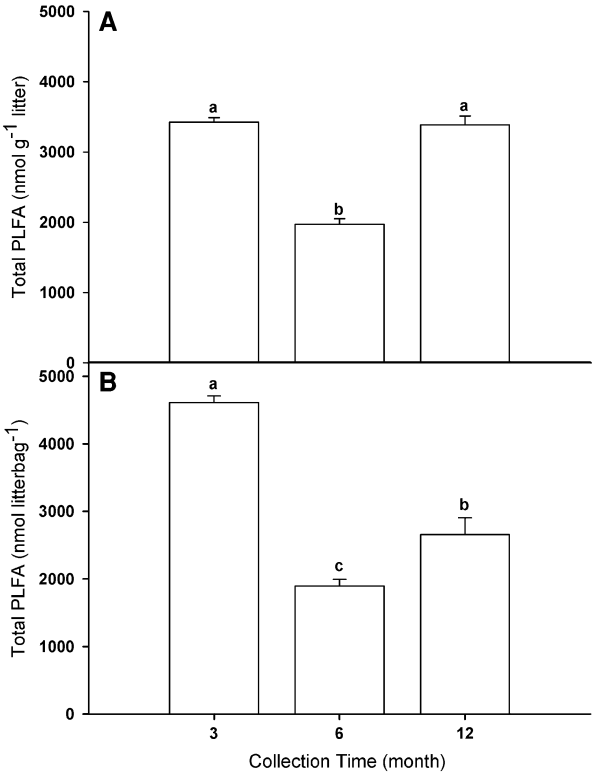

Figure 6. Total phospholipid fatty acids (PLFAs) extracted from litter collected at 3, 6, and 12 months presented as **A** concentration (nmol PLFAs g^{-1} litter) and **B** total PLFAs per litterbag (nmol). *Different letters above bars* indicate significant ($P < 0.05$) differences between means at each collection time. Interactions between grass removal and transect fetch length main effects were not significant ($P > 0.05$).

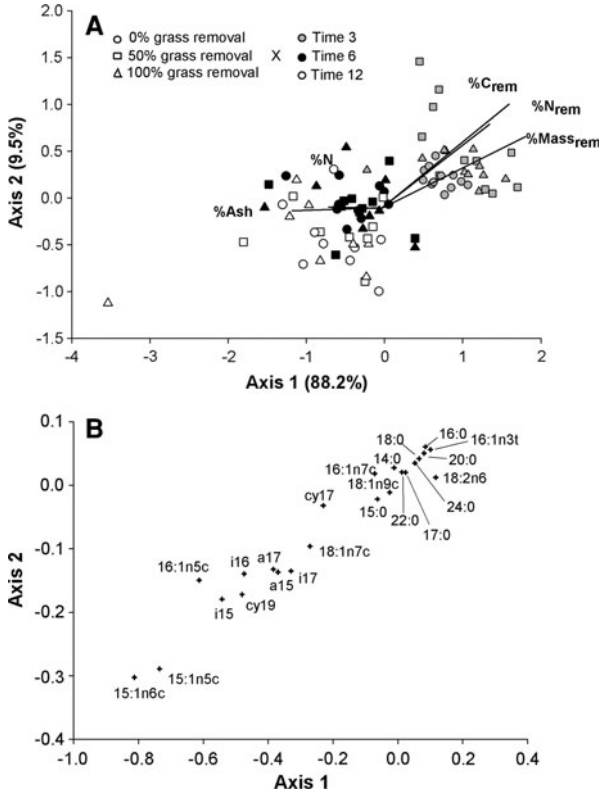

Figure 7. Non-metric Multidimensional Scaling (NMS) ordination of the 23 fatty acid methyl esters (FAMEs) comprising greater than 1% of the total phospholipid extracted from litter samples harvested after 3, 6, and 12 months of field exposure in the 0, 50, and 100% grass removal plots. **A** *Symbols* represent grass removal treatments, whereas *shades of gray* represent collection dates. **B** FAME placement within ordination space based on correlations between the relative abundance of a particular FAME and its axis 1 and 2 scores in **A**. Bi-plot environmental overlay results are shown by vector direction and length in **A**. *X*- and *Y*-axis scaling issues prevented the overlay from being displayed in **B**.

ground surface temperatures are highest. Winds preceding the monsoon season would mix soil and litter, setting the stage for development of soil–litter biofilms with the onset of monsoon rains. In contrast, rainfall in the Sonoran Desert is bimodal, with much of it occurring in the colder winter months. Although MAP is considerably greater at the Sonoran Desert site (370 mm) compared to our Chihuahuan Desert site (240 mm), our 12-month study was carried out during an unusually wet year (366 mm during the study period, 81% of which was during the 1 June to 1 October hot monsoonal period). In contrast, the Sonoran study was carried out during an usually dry year (278 mm during the 12-month study period, 51% of which occurred during the hot monsoonal period). Greater total rainfall, coupled with a greater coincidence of rainfall with temperatures conducive to high rates of decomposition, may account for the faster decomposition rates recorded in our study.

SLM mixing effects were not strongly expressed at the 1- and 3-month collections, relative to the 6- and 12-month collections (Figure 3). Although wind-deposited soil had mixed with litter by the 3-month collection date, there had been minimal precipitation (Figure 2B), which likely limited biological activity and the formation of soil–litter films. Furthermore, fluvial processes may lead to substantial soil redistribution in drylands (Field and others 2009b), and thus may be a driver of SLM. Together, this suggests that SLM effects on decomposition occurred primarily between 3- and 6- month collections, by which time soil had infiltrated litterbags such that monsoon precipitation could facilitate biological activity leading to the formation of soil–litter films.

The C and N concentration of litter typically exerts strong control over decomposition (Hobbie 1996; Aerts 1997; Parton and others 2007). Litter [C] decreased within the first 3 months, ostensibly the result of soluble C leaching or breakdown by UV radiation (Austin and Vivanco 2006; Austin and Ballaré 2010). The increase in [C] at the 3- to 12-month collection dates most likely reflects a combination of C imported to litterbags with soils [likely marginal due to the extremely low soil organic C (0.1–0.3%; Monger 2006) at our site], microbial biomass, microbially derived C (for example, extracellular C), and losses of non-C compounds (Berg and others 2005). When compared to mass remaining, litter [N] can be an indicator of the interplay between abiotic physical fragmentation processes and biotic decomposer activities (Hobbie and others 2000; Aerts and others 2006). A 1:1 relationship between [N] and mass remaining would be expected when mass loss is the result of fragmentation; our data diverged from this 1:1 relationship in a manner suggesting that microbial byproducts and/or the loss of non-N compounds were contributing to the observed increases in litter [N] with time. It is unclear what caused the short-lived separation of [C] and [N] between grass removal treatments at the 6-month collection.

Our hypothesis that SLM would increase with decreasing grass cover was not supported. This finding was surprising given a previous study in the same experimental plots indicated that aeolian soil flux, surface soil C, and nutrient losses on the 50, 75, and 100% grass cover reduction plots were elevated relative to control plots (Li and others 2007). There are several possible explanations why decreased grass cover did not translate into increases in SLM. First, the degree of SLM may be regulated by microtopography and fine-scale spatial heterogeneity in vegetation. Our litterbag placement criteria were intended to minimize potentially confounding effects of upwind shrubs, but in retrospect, variation in local-scale aeolian and fluvial transport (Okin and Gillette 2001; Bergametti and Gillette 2010) and local features in the immediate vicinity of litterbags (for example, distance to nearest plant, spatial variation in soil crusts, and so on) may have predominated over plot-scale grass and shrub cover. Many of these local features change seasonally (for example, ephemeral annual plants) and are dependent on factors not measured in this experiment. The wide range of ash contents observed for the 3, 6, and 12-month collections (10 to >40%; Figure 3) are presumably indicative of localized variation in environmental conditions and biological soil-film formation. For example, although increases in plot-level soil aeolian fluxes were shown to accompany reductions in ground cover, these were at heights 1.2 and 2.5 m above the soil surface (Li and others 2007). Fluxes at these heights are likely quite different than those on the soil surface where litterbags were situated. In addition, the above-average precipitation during the period of our experiment may have elevated localized soil inputs into litterbags via raindrop splash or overland flow independent of plot-scale variation in total plant cover.

SLM influenced both lipid profiles and decomposition, but the mechanisms by which SLM enhances decomposition remain elusive. Changes in decomposer composition may accompany changes in the biochemistry of the material being degraded. However, physical changes may also be at play. Based on our results and visual observations of fungal hyphae on soil–litter films in the early stages of decomposition at this site (Barnes and others 2012), we suggest that SLM facilitates the growth of bacterial decomposers by altering the microclimate around litter material. This hypothesis is supported by increases in gram-positive and gram-negative bacterial lipid biomarkers and decreases in the relative importance of the fungal and plant biomarker 18:2n6 (Figure 7A) accompanying the accumulation of soil in 6- and 12-month litter samples. These observations are consistent with conceptual models contending that fungal activity is predominant when water availability imposes restrictions on bacterial activity (Collins and others 2008). In our case, soil deposition occurred during the three dry pre-monsoon months and 18:2n6 predominated on plant litter. The relative abundance of bacterial lipid biomarkers increased as water availability increased with the arrival of monsoonal rains, suggesting that SLM may facilitate bacterial colonization and/or make the litter microclimate more favorable to bacteria. When coupled with precipitation, SLM may favor the growth of bacterial decomposers by creating and maintaining a moister microclimate around litter. The radiant energy regime could also influence microbial communities, but these effects may be confined to the period of time preceding the development of soil–litter films. In this study, the direct effect of UV radiation on lipid profiles of litter incubated for more than 3 months in the field was likely negligible because by this time litterbags were typically covered by surface soils. At 6 months, litterbags remained buried and well-developed soil biofilms had developed on litter surfaces to further attenuate potential photodegradation effects (Barnes and others 2012).

Broader Implications: SLM in Drylands and Beyond

The density and cover of native grass species has decreased dramatically over the last 150 years in the Chihuahuan Desert (Gibbens and others 2005). This decrease in grass cover and subsequent change in vegetation structure contributes to patterns of soil erosion and deposition occurring in a spatially heterogeneous manner as a function of interactions between exposed surface soil, surface hydrology, and local wind patterns (Breshears and others 2003; Gillette and Pitchford 2004; Li and others 2007). Heterogeneous vegetation cover also influences the location of deposition zones of soil and litter transported by wind and water (Shen and others 2011). We predict that interactions between vegetation structure, litter inputs and transport vectors will strengthen as vegetation communities become more heterogeneous at coarse spatial scales; and this will, in turn, strengthen the relationship between SLM and decomposition at finer spatial scales.

Although our results provide insight into decomposition dynamics in drylands, they may also be broadly applicable in other systems. We focused on drylands due to the generally high rates of soil movement inherent to systems with discontinuous and low vegetative and high bare ground cover (Field and others 2009a). However, the general need to correct mass loss estimates in litterbag decomposition studies for soil infiltration (Harmon and others 1999) suggests that SLM is not unique to drylands. It would be interesting to know if taking soil accumulation into account (for example, Figure 3) in litterbag studies conducted in more mesic systems would significantly reduce unexplained variance associated with predictions of mass loss. However, the success of simple decomposition models in mesic systems suggests that processes such as SLM may be less important, or at least less variable, in mesic systems relative to more xeric systems. In particular, microclimate buffering, one of the putative mechanisms for the importance of SLM, would be relatively less important in mesic systems where windows of temperature and moisture well suited for microbial activity are longer than those in pulse-driven drylands. Indeed, working along a grassland aridity gradient, Brandt and others (2010) found that soil transport into litterbags was a significant driver of decomposition at the driest site. SLM was not an important factor in the more mesic sites, but this was due, at least in part, to a lack soil accumulation in litterbags at these sites with greater biomass and ground cover.

In mesic systems, SLM is likely to play the greatest role (i) where surface soils are disturbed and subject to wind and water erosion; or (ii) on sites downwind or downslope of areas where wind and water erosion have been accelerated by disturbance. For example, decomposition models based on actual evapotranspiration, which work well in many mesic systems, under-predict decomposition rates in clear cut forests and tilled agricultural systems (Whitford and others 1981; Aerts 1997). Accounting for SLM effects may improve model performance in such settings. Several studies have assessed surface litter decomposition in disturbed mesic ecosystems where soil movement might be a factor (Blair and Crossley 1988; Neher and others 2003; Xu and others 2004), but changes in rates and patterns of soil movement and the extent of its mixing with litter have not been accounted for nor explicitly considered in assessments of the relative importance of factors driving decomposition. We suggest further exploration of the role of SLM on decomposition in systems where SLM occurs, especially those wherein surface disturbances enhance movement of surface soil and litter.

Conclusions

Our results support the proposition that SLM is an important, often overlooked driver of decomposition. Accounting for the effects of SLM may ultimately improve decomposition models, especially in disturbed and dryland systems where they tend to underestimate rates of mass loss. In addition, the potential for SLM to negate the effects of UV radiation (for example, Barnes and others 2012) suggests that studies that have explored UV impacts on decomposition in isolation from SLM may overestimate the effects of UV photodegradation on decomposition. The work presented here suggests that SLM affects litter decomposition via a combination of biochemical and biophysical effects, but that the drivers of SLM may function at finer scales than those in our removal plots (for example, at the plant patch scale rather than plant community scale). Informed management decisions require a clear understanding of the drivers of C and nutrient fluxes and their controls. These processes are particularly important given current and projected global shifts in land cover and its potential influence on C source-sink dynamics.

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