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Soil–litter mixing and microbial activity mediate decomposition and soil aggregate formation in a sandy shrub-invaded Chihuahuan Desert grassland

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Abstract Drylands account globally for 30% of terrestrial net primary production and 20% of soil organic carbon. Present ecosystem models under predict litter decay in drylands, limiting assessments of biogeochemical cycling at multiple scales. Overlooked decomposition drivers, such as soil–litter mixing (SLM), may account for part of this model-measurement disconnect. We documented SLM and decomposition in relation to the formation of soil-microbial films and microbial extracellular enzyme activity (EEA) in the North American Chihuahuan Desert by placing mesh bags containing shrub (*Prosopis glandulosa*) foliar litter on the soil surface within contrasting vegetation microsites. Mass loss (in terms of *k,* the decay constant) was best described by the degree of SLM and soil-microbial film cover. EEA was greatest during periods of rapid litter decomposition and associated SLM. Soil-microbial film cover on litter surfaces increased over time and was greater in bare ground microsites (50% litter surface area covered) compared to shrub and grass microsites (37 and 33% covered, respectively). Soil aggregates that formed in association with decomposing leaf material had organic C and N concentrations 1.5–2× that of local surface soils. Micrographs of soil aggregates revealed a strong biotic component in their structure, suggesting that microbial decomposition facilitates aggregate formation and their C and N content. Decomposition drivers in arid lands fall into two major categories, abiotic and biotic, and it is challenging to ascertain their relative importance. The temporal synchrony between surface litter mass loss, EEA, biotic film development, and aggregate formation observed in this study supports the hypothesis that SLM enhances decomposition on detached litter by promoting conditions favorable for microbial processes. Inclusion of interactions between SLM and biological drivers will improve the ability of ecosystem models to predict decomposition rates and dynamics in drylands.

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Introduction

Leaf litter decomposition is a principal driver of carbon (C) and nutrient cycling in terrestrial ecosystems. Decomposition plays a key regulatory role in soil fertility and ecosystem productivity by modulating soil organic matter content, which influences soil moisture holding capacity and nutrient balance (i.e., cation exchange) (Schlesinger and Bernhardt 2013). Litter inputs are small relative to soil organic matter stores, but may have an outsized effect on C-limited decomposers in ecosystems such as drylands (semi-arid and arid) where soil C and nutrient pools are relatively small (Saetre and Stark 2005; Austin and Vivanco 2006).

Drylands cover an estimated 40% of the terrestrial land area (Hulme 1996), contributing approximately 30% of global primary productivity (Field et al. 1998) and storing approximately 20% of global soil organic carbon (Lal 2004). There is strong evidence that the global expansion of drylands is imminent, owing to the combined influences of climate change and intensification of human land use (Adeel et al. 2005). Given the geographic extent and projected expansion of drylands, a mechanistic understanding of their biogeochemistry is important for the development of management strategies and policy in response to global change.

Decomposition rates in dryland ecosystems are often greater than predicted by models that emphasize climate variables (Whitford et al. 1981; Parton et al. 2007; Austin 2011). This discrepancy has been attributed to the unaccounted abiotic mechanisms including soil–litter mixing (SLM; reviewed in Throop and Archer 2009; Barnes et al. 2015), photodegradation (UV-B; reviewed in King et al. 2012; Song et al. 2013), and thermal degradation (Lee et al. 2012). The relative importance of these factors is likely spatially and temporally heterogeneous due to variation in wind and water erosion, precipitation and its redistribution, and land cover. The latter has changed dramatically in drylands in the past century, with woody plants encroaching into formerly grass-dominated systems (Whitford 2002; Eldridge et al. 2011; Archer et al. 2017). In the Chihuahuan Desert, shrub encroachment occurs at the expense of perennial grass cover (Hennessy et al. 1983; Gibbens et al. 2005), which in turn affects the quality, quantity, and distribution of litter inputs. Furthermore, the reduction in grass ground cover exposes litter to soil redistributed by wind and water (Schlesinger et al. 1996). Field studies from the Chihuahuan and Sonoran Deserts demonstrate that these redistributed soils mix with surface litter to promote litter mass loss (Throop and Archer 2007; Hewins et al. 2013) and the development of soil-microbial films which shield litter from potential photodegradation effects (Barnes et al. 2012; Hewins and Throop 2016). Although this soil–litter mixing (SLM) has been shown to accelerate decomposition, the underlying biological mechanisms of this driver are poorly understood.

SLM purportedly enhances biological activity in the litter layer by mitigating abiotic constraints on microbial activity (Throop and Archer 2009; Barnes et al. 2015). Mechanisms include reduced exposure to thermal and UV stress and greater moisture retention in the litter layer that extends the duration of temporal windows of elevated microbial activity (Lee et al. 2014). Wind- and water-borne soil particles and sediments may also deliver extracellular enzymes that promote litter decomposition (Stursova and Sinsabaugh 2008; Throop and Archer 2009). Electron micrographs from a Chihuahuan Desert study illustrate the development of soil-microbial films on leaf litter surfaces, and qualitatively show enhanced levels of microbial colonization of litter subsequent to its mixing with soil (Barnes et al. 2012). However, direct measurements of biological activity (i.e., quantification of extracellular enzyme activity; EEA) are lacking.

To better resolve the mechanisms underlying SLM-enhanced decomposition, we deployed litterbags in three microsite types (bare ground, perennial grass, or shrub) that represent typical land cover classes in drylands. We tested the hypotheses that (i) SLM and hence decomposition rates would be in a rank order bare patches > shrub patches > grass patches reflecting measured rates of soil flux (Li et al. 2007) and (ii) mass loss will be positively correlated with synergistic interactions among rainfall, SLM, and soil-microbial film cover and their collective facilitation of biological activity. Links between biological decomposition and the extent of SLM were assessed by quantifying EEAs,

which play a principal role in terrestrial biogeochemical cycling (Allison et al. 2007). Accordingly, we hypothesized that (iii) EEA would increase with time as conditions for microbial activity (e.g., microclimate buffering) improved under SLM. During the course of the experiment, we observed the development of three-dimensional aggregates on and around litter material. To assess the influence of litter decomposition on soil aggregates and their properties, we quantified soil aggregate C and N content relative to that of local surface soils to test the hypothesis that (iv) aggregates forming in close proximity to decomposing litter would be enriched in C and N.

Methods

Field site

The field experiment was conducted at the Jornada Experimental Range (JER), near the northern terminus of the Chihuahuan Desert biome and approximately 40 km NE of Las Cruces, New Mexico, USA. Mean annual precipitation is 245 mm (SD ± 85.0 mm; Wainwright 2006) of which approximately 60% falls during intense, spatially heterogeneous late summer monsoons. Mean annual temperature is 14.7 °C (SD ± 0.58 °C; Wainwright 2006). Land cover is a mosaic of native perennial bunch grasses (e.g., *Bouteloua eriopoda* and *Sporobolus flexuosus*), and native shrubs (e.g., *Prosopis glandulosa,* honey mesquite; *Ephedra* spp.; *Gutierrezia sarothrae*; and *Yucca* spp.), heterogeneously distributed within a matrix of bare ground (Gibbens et al. 2005; Li et al. 2007).

Experimental design

We worked in replicate ($n = 3$) 2.25 ha livestock exclosures (hereafter 'blocks') established in 2004 (Li et al. 2007). The center point for these blocks was located at 32.563°, −106.760° (lat./long.), and the three blocks were spaced approximately 1 km apart. Within each block we established replicate ($n = 3$) plots (50 × 30 m) separated by ≥25 m. Within each plot, we randomly designated a grass, a shrub, and a bare ground patch (hereafter 'microsites') for litterbag placement. Microsites were ≥10 m apart and ≥3 m downwind of any large shrubs (>0.5 m tall) to avoid wake effects (Okin 2008). Grass microsites were shrub-free and dominated by *B. eriopoda* or *S. flexuosus*. Shrub microsites consisted of a single mature *P. glandulosa* plant with no or minimal sub-canopy vegetation. Bare ground microsites consisted of exposed soil lacking vegetation. Microsites encompassed a minimum of 3 m^2, with exact size dependent on vegetation structure. Our field sites were located on the 'sand sheet' geomorphic surface at the JER. Surface soil texture in each block was classified as very sandy (>95% sand and <5% silt and clay; Li et al. 2007). Daily precipitation was obtained from the JER headquarters rain gage (approximately 8 km distant), which records climate information at hourly intervals. Daily precipitation totals were used to compute mean daily precipitation (mm day^{-1}) between litterbag collection dates.

Litterbag methods

Decomposition was quantified for leaflets of *P. glandulosa,* a native, deciduous N_2-fixing shrub that now dominates former grasslands in the Chihuahuan Desert and southern Great Plains of North America. Foliage of *P glandulosa* decomposes readily over a 12–30-month time span (Hewins et al. 2013; Hewins and Throop 2016), thus making it amenable for use in standard litterbag studies (Harmon et al. 1999). Black fiberglass mesh (1 × 1 mm openings; New York Wire Co., Hanover, PA) litterbags (10 × 10 cm) transmitted approximately 51% of ambient UV-B radiation and 50% of photosynthetically active radiation (PAR) (SKU 430 broadband UV-B sensor, Skye Instruments Ltd, Wales, UK for UV measurements; LI-190 Quantum sensor for PAR, LI-COR Inc., Lincoln, NE, USA). Leaflets were collected prior to abscission on 19–20 November 2009 and immediately 'air dried' at 30 °C for 5 days. Litterbags were filled with 2 g of leaflets. This mass minimized litter overlap within bags and maximized exposure to solar radiation, precipitation, and soil. Empty mesh bags served as a control in each microsite to assess aggregate formation in the absence of litter. Litterbags were deployed on 19 April 2010 and retrieved after 0, 1, 6, 12, 24, and 30 months. This collection timing was designed to capture expected patterns of rapid mass loss during the initial months of decay (Olson 1963), and to facilitate comparisons with other decomposition studies at this (Hewins et al. 2013; Hewins and Throop 2016) and

other (e.g., Throop and Archer 2007; Levi 2017) arid land sites.

Litterbags were arrayed along transects oriented perpendicular to the prevailing erosive winds (originating from the southwesterly direction 79% of the time; Li et al. 2007). Litterbags in grass and shrub microsites were placed below canopies, where litter typically accumulates. Litterbags were affixed to the soil surface with steel sod staples and spaced at least 30 cm apart to minimize effects of neighboring bags on surface soil movement. We deployed 162 *P. glandulosa* litterbags ($N = 3$ blocks $\times$ 3 plots/block $\times$ 3 microsites/plot x 6 collection dates/microsite) and 54 empty litterbags ($N = 3$ blocks $\times$ 1 plot/block $\times$ 3 microsites/plot $\times$ 6 collection dates/microsite).

Litterbags were stored at −20 °C immediately following retrieval from the field. Within 24 h of collection, litterbag contents were gently passed through a 1 mm sieve so as to not disrupt soil aggregates. Material that did not pass through the sieve was separated into two categories: litter and soil aggregates. Litter was gently dusted with soft bristle cosmetic brushes to remove loose soil. Litter and aggregate samples were stored at −80 °C for ≥48 h and then freeze-dried under vacuum for 24 h (Freezone −58 °C, Labconco Corporation, Kansas City, MO, USA). Dried litter samples were weighed to determine mass remaining.

Subsets of three leaflets were selected at random from each litter sample for microscopy. Random selection was achieved by placing all leaflets in coin envelopes and selecting leaflets individually with forceps. The remaining leaflets were pulverized (Mixer Mill 8000D ball mill, Spex CertiPrep, Metuchen, NJ, USA). Subsamples of pulverized material were analyzed for ash content (550 °C for 6 h in a muffle furnace) and C and nitrogen (N) concentrations ([C] and [N]; % by mass) (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA). Ash content was used as an index of soil accumulation on litter surfaces (Throop and Archer 2007), and was used to express litter mass remaining (%), and C and N (% and mass) on an ash-free basis.

Extracellular enzyme activity

Extracellular enzyme activity (EEA) assays on 0-, 1-, 6-, and 12-month old litter were conducted at the University of New Mexico, following published microplate protocols (Saiya-Cork et al. 2002; Sinsabaugh et al. 2002). Milled litter (0.5 g) was suspended in 125 ml sodium acetate buffer (50 mM, pH 5). Suspensions were assayed for the potential activities of β-1,4-glucosidase, β-1,4-xylosidase, β-1,4-*N*-acetylglucosaminidase, leucine aminopeptidase, and acid phosphatase (hereafter BG, XYLO, NAG, LAP, and PHOS, respectively), using fluorogenic substrates linked to methylumbelliferyl or coumarin residues. Microplates were incubated at 20 °C. Fluorescence at pH 5 was measured hourly for the first 4 h, then again at 6 and 8 h. Plate readings were taken at excitation wavelengths of 365 nm and emission wavelengths of 450 nm (FMax, Molecular Devices Corp., Sunnyvale, CA, USA). Activities were expressed as nmol h^{-1} g^{-1} ash-free litter. In addition, activities were integrated over time to calculate cumulative values. The ratio of cumulative EEA (moles) to litter C mass loss (moles) to cumulative EEA (moles) is an apparent enzymatic efficiency. Its inverse, an apparent turnover activity, can be used to make comparisons across treatments and studies analogous to the way that decay constants (k values) are compared in litter decomposition studies (Gallo et al. 2009).

Soil-microbial films

Soils and associated microbes combined to form distinct films on the surface of leaf litter (hereafter 'soil-microbial films'). The cover of these films was quantified on 3 randomly selected leaflets per litterbag using a stereo fluorescence microscope (M165 FC, Leica Microsystems, Wetzlar, Germany). Micrographs were recorded at ×0.63 magnification across a range of zoom magnifications to capture images of entire leaflet surfaces (DFC 310 FX digital camera, Leica Microsystems, Wetzlar, Germany). Soil-microbial films were defined by soil that was bound to leaf surfaces; film percent cover was analyzed using ImageJ v. 1.44 (National Institutes of Health, Washington, DC, USA). Scanning electron microscopy (Hitachi S-3400, Hitachi LTD., Tokyo, Japan) was used to characterize the structure (e.g., soil particles, hyphae, and extracellular mucilage) of soil-microbial films in finer detail.

Soil aggregates

Aggregate mass, quantity, composition, and stability were assessed for litterbags containing aggregates. To

minimize handling of individual aggregates, a composite mass of all aggregates per litterbag was obtained. Three randomly selected aggregates from each litterbag were weighed to estimate mean aggregate mass. Aggregate selection was achieved by placing all aggregates from a given sample into a single weigh boat and haphazardly selecting three for analysis. Aggregate quantity per litterbag was estimated as aggregate mass divided by mean aggregate mass. Another subsample of aggregates (approximately 3–5 per litterbag) was ground with a mortar and pestle, fumigated with HCl to remove carbonates (Harris et al. 2001), and analyzed for [C] and [N] (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA). Stability of the remaining aggregates was measured by wet sieving (Herrick et al. 2001). Aggregates were slowly wetted with water vapor for 1.5 h in a vented chamber to prevent immediate slaking upon immersion. Sieves (1 mm^2 mesh) containing wetted aggregates were then submerged in deionized water for 60 s before being vertically oscillated 25 times in 1 min to a depth of 10 mm. Percent of soil mass remaining following sieving was used as an index of aggregate stability.

Surface soil analyses

Surface soils (0–2.5 cm depth) were collected 10 cm upwind, 10 cm downwind, and beneath litterbags at the time of the 12-month litterbag retrieval ($N = 3$ sampling locations per litterbag $\times$ 27 litterbags $= 81$ soil samples). Soils were passed through a 2 mm sieve and all remaining visible litter (e.g., roots and leaves) was removed by hand. Samples were frozen at -80 °C for at least 48 h, freeze-dried for 24 h, pulverized on a ball mill, acid fumigated (Harris et al. 2001), and analyzed for [C] and [N] content (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA).

Data analysis

First-order decay constants (k values) were estimated by fitting single-pool exponential decay functions (Olson 1963) to percent litter mass remaining over time (Eq. 1).

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

In this model, M_t is the mass of litter at time t, M_0 is the initial litter mass, e is the exponential constant, and k is the decay constant. Estimates of decay constants were derived by regressing the natural logarithm of the mass remaining (%) over time in fractional years to fit a single negative exponential decay model using the dynamic fit tool in Sigma Plot v. 10 (Systat Software Inc., Chicago, IL, USA). Data were not manipulated prior to model fitting (Adair et al. 2010). The use of a single-pool model extends the utility of our results by allowing comparisons to existing studies, while a two-pool model did not improve overall model fit when comparing paired R^2 values from the identical litter bags.

To explore patterns of decomposition we used mixed model ANOVAs and Tukey's HSD. We tested the hypothesis that litter decomposition would be greater in more exposed microsites, by testing the effect of microsite on decay constants (Eq. 1), and on ash-free litter mass remaining (%; hereafter 'mass remaining') at each discrete litter bag collection date. In both cases microsite was considered a fixed effect while block was considered a random effect. Follow-up analyses to test the response of mass remaining to SLM (% ash), soil-microbial film cover (% of leaf area), and precipitation (mm day^{-1}) were performed using step-wise regression, where a cutoff of $\propto = 0.05$ was used to determine if a variable should be retained in a model.

To explore patterns of change in litter [C] and [N], microbial activity (EEA activity and turnover), soil-microbial film cover, and soil aggregate characteristics, we used mixed-model ANOVAs and Tukey's HSD with microsite and collection month as fixed effects and block as a random effect. Pearson's correlation tests were used to assess relationships between soil-microbial film development, decomposition, and precipitation. Pearson's χ^2 test was used to test the likelihood of aggregate development in litterbags relative to time and microsite. Statistical analyses were performed using the Corr, Freq, Mixed and Reg procedures in SAS v. 9.2 (SAS Institute, Inc., Cary, NC, USA). All percentage data were log transformed prior to statistical analysis to improve normality and reduce heteroscedasticity of variance except in the case of model fitting. All figures present non-transformed data for ease of interpretation.

Results

Decomposition

Leaf litter mass declined through time in a negative exponential manner in all three vegetation microsites (Fig. 1a). After 6 months, mean litter mass remaining among all three microsites was 47.7%. Mass loss stalled between the 6- and 12-month collections, during a period of low precipitation cooler autumn and winter temperatures (Fig. 1b). At 24 months, mean mass remaining declined to 18.9%, then slowed during the last 6 months, culminating at 14.4% on the last (30 months) collection date (Fig. 1a). Decomposition did not differ between bare ground, grass, or shrub microsite placements. This result was corroborated by analysis of both decay constants ($F_{2,22} = 1.6$, $P = 0.22$) and mean mass remaining at each litter collection date (Fig. 1a).

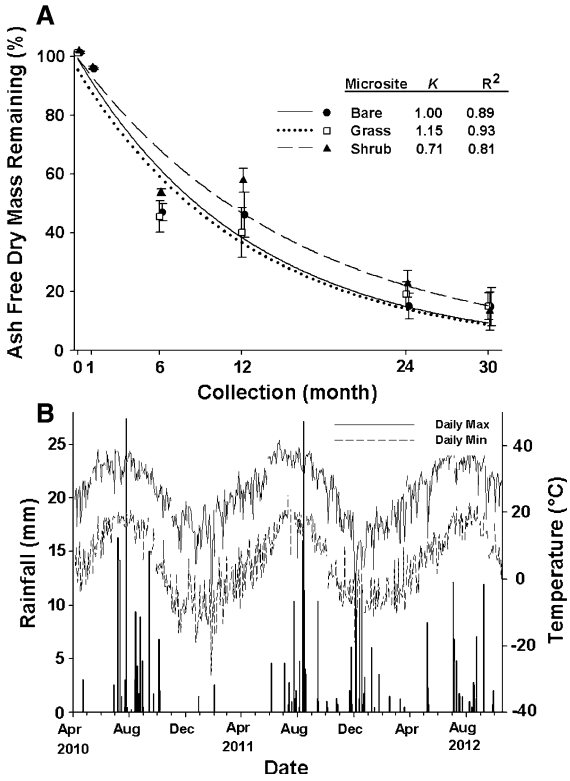

Fig. 1 **a** Mean (±SE) ash-free dry mass remaining (%) for *Prosopis glandulosa* leaflets in litterbags placed in bare ground, grass, and shrub microsites. *Decay curves* were fitted for each microsite with a single-pool negative exponential decay function (Eq. 1). Decay constants did not differ significantly between microsites. **b** Daily precipitation (*bars*, mm), and minimum and maximum temperatures (*lines*, °C) during the field experiment. *X*-axes are on the same scale for ease of interpretation, and data points are slightly jiggered on the *x*-axis for ease of interpretation

Litter decomposition over the course of the experiment (all dates) was positively related to both soil-microbial film coverage (% leaflet litter surface area) and the amount of SLM (% ash). Step-wise regression identified these variables as the combination that best explained the variance in mass loss ($R^2 = 0.37$, $P < 0.001$). Daily precipitation during the periods between collection dates was non-significant and removed from the regression model ($R^2 = 0.007$; $P = 0.29$).

Litter C and N remaining (%) both were strongly related to mass loss (%) (Fig. 2; $R^2 = 0.97$ for C and 0.95 for N). When plotted relative to mass remaining, C remaining was nearly 1:1, while N remaining at 6 and 12 months trended greater than 1:1, indicating potential N immobilization in litter material. Both litter C concentration [C] and N concentration [N] fluctuated over time and among microsites (Table 1). Litter [C] was influenced by a collection month × microsite interactions such that the rank order of litter [C] among microsites was inconsistent over time ($F_{10,268} = 4.04$, $P < 0.001$). Overall, litter [C] was greater at grass and shrub than bare ground microsites ($F_{2,268} = 3.17$, $P < 0.001$), and decreased after 12 months ($F_{5,268} = 18.63$, $P < 0.001$). The observed declines in litter [C] after 12 months are in line with the observed losses in litter mass. Litter [N] was significantly influenced by a collection month by microsite interaction, primarily due to fluctuations of litter [N] in grass microsites ($F_{10,268} = 4.06$, $P < 0.001$). Litter [N] generally increased over the first 12 months, then declined to initial concentrations by 30 months (Table 1; $F_{3,\ 268} = 16.14$, $P < 0.001$), paralleling the patterns observed in N mass remaining. Litter in shrub microsites generally had greatest [N] ($F_{2,268} = 13.96$, $P < 0.001$).

Extracellular enzyme activity

The EEA mirrored patterns of early litter decomposition over the first 12 months (Fig. 3). Enzyme activity related to C cycling [i.e., β-glucosidase (BG) and xylosidase (Xylo)] was greatest at the 6- and 12-month collections. Similarly, the activity of NAG, an enzyme that plays a role in both C and N cycling,

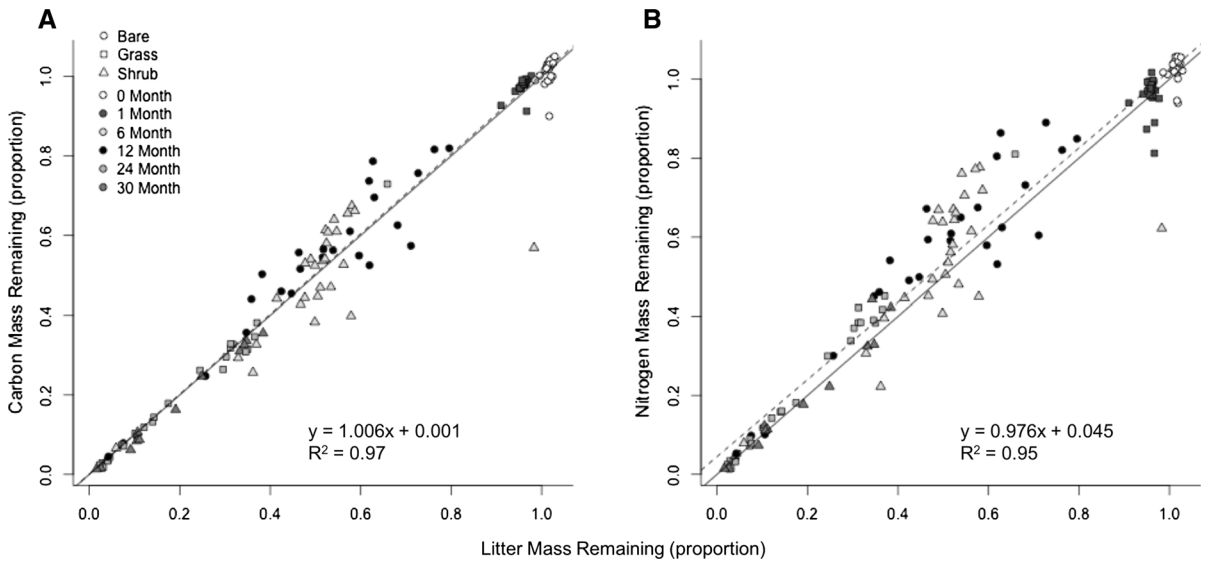

Fig. 2 The relationship between litter mass remaining (ash-free dry mass, %) and ash-free **a** carbon mass remaining and **b** nitrogen mass remaining. Mass remaining values are calculated on a percent basis using initial masses and concentrations. Regression lines (*dashed*) with associated R^2 and linear equations, and 1:1 lines (*solid*) are shown. *Symbol* shapes represent microsite placements; *shades* represent different collection dates

Table 1 Mean (± SE) *Prosopis glandulosa* leaflet litter carbon and nitrogen concentration (% by ash-free mass) in bare ground, grass, and shrub microsites

Litter carbon (%)				Litter nitrogen (%)			
Microsite				Microsite			
Month	Bare	Grass	Shrub	Months	Bare	Grass	Shrub
0^	48.0 (0.19)	48.0 (0.39)	47.9 (0.17)	0*	2.9 (0.01)	3.0 (0.02)	2.9 (0.02)
1^	46.3 (2.70)	48.7 (0.22)	49.0 (0.06)	1^	3.0 (0.02)	2.9 (0.04)	3.0 (0.01)
6^	42.4 (1.95)	48.6 (1.82)	50.9 (1.15)	6^	2.8 (0.13)	3.2 (0.16)	3.7 (0.09)
12^	49.0 (1.67)	51.8 (1.47)	49.9 (0.81)	12^	3.2 (0.13)	3.3 (0.11)	3.5 (0.08)
24^	46.8 (0.83)	45.23 (1.89)	48.2 (0.68)	24^	3.3 (0.05)	3.1 (0.21)	3.5 (0.05)
30*	41.2 (1.80)ab	43.5 (1.6)b	38.3 (2.09)a	30*	3.8 (0.10)a	2.8 (0.13)b	3.0 (0.19)b

Symbols indicate differences among collection months (months), while different letters indicate differences among microsites after 30 months of decomposition

increased at 6 and 12 months. In contrast, changes in acid phosphatase (PHOS) and the N-acquiring enzyme leucine aminopeptidase (LAP) did not change significantly (Fig. 3b, c). At 6 months, BG activity was an order of magnitude greater than the other EEAs. Similar to decomposition, there were no significant microsite effects for the enzymes assayed. EEA turnover activity (moles substrate converted) based on all analyzed collection dates differed among enzymes (PHOS > NAG = BG > LAP > XYLO; $F_{4,\ 96} = 26.83$; $P < 0.0001$), but not among microsites (Table 2).

Soil-microbial films

Soil-microbial films were composed of soil particles that remained on leaf surfaces after gentle brushing (Fig. 4a–c). Scanning electron micrographs revealed microbial structures (e.g., fungal hyphae) and mucilage coating soil particles, filling spaces between

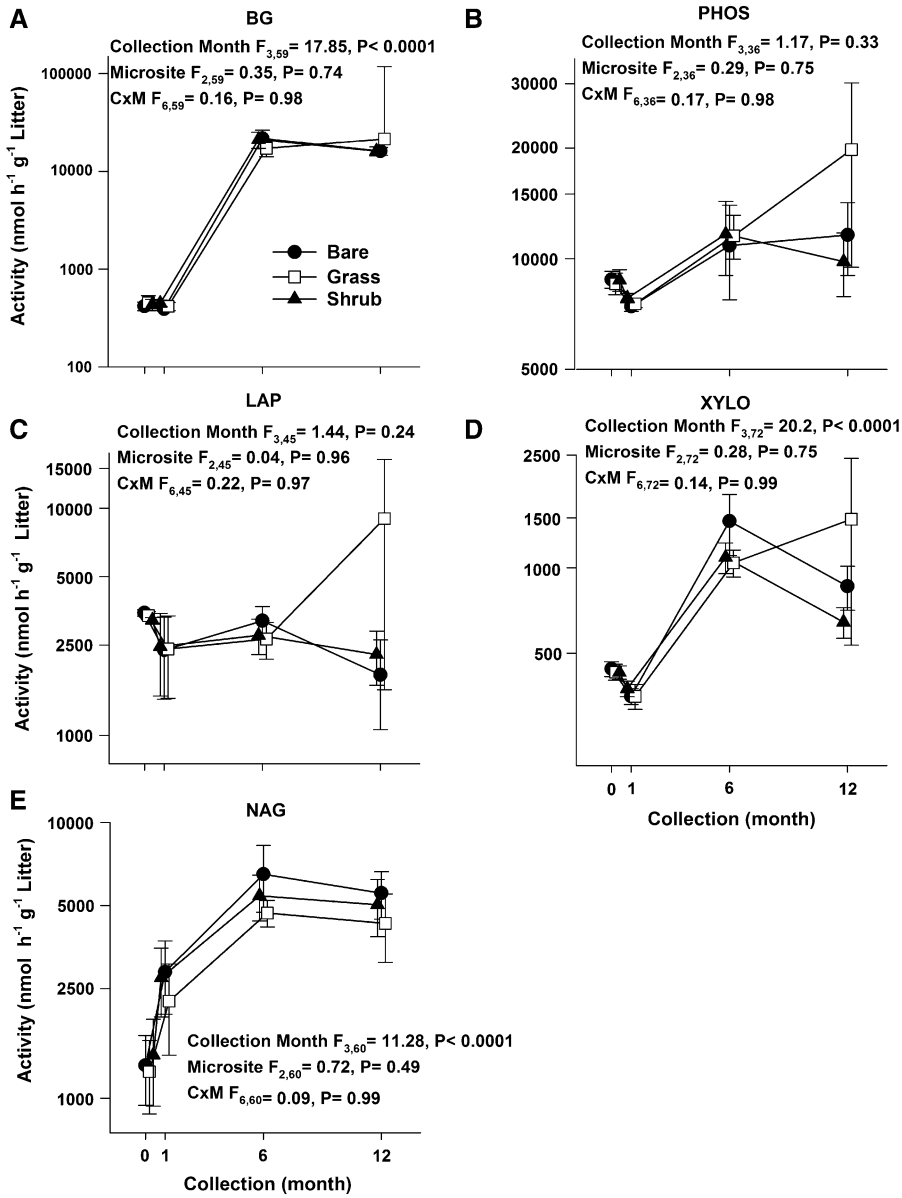

Fig. 3 Activity for **a** β-1,4-glucosidase (BG), **b** acid phosphatase (PHOS), **c** leucine aminopeptidase (LAP), **d** β-1,4-xylosidase (XYLO), and **e** β-*N*-acetylglucosaminidase (NAG) associated with decomposing *P. glandulosa* leaflet litter in bare ground, grass, and shrub microsites. ANOVA results are *inset* in the figures. Positive and negative standard error bars appear to be different lengths due to log scale *y*-axes; *lower error bars* were omitted if the error was small or large

particles and apparently binding soil particles to litter surfaces (Fig. 4c).

Soil-microbial film cover (%) was temporally dynamic; no leaflets had films at the 1-month collection, but all litterbags contained numerous leaflets with soil-microbial films at the 6-month collection following seasonal monsoon rains (July–Sept.). Soil-microbial film cover was positively correlated to average daily rainfall between litterbag collection dates ($r = 0.28$, $P = 0.004$). Mean (±SE; $n = 81$) leaflet surface area covered by soil-microbial films was 48.2% ± 2.5 at 6 months, declined at the 12-month collection (26.9% ± 2.8), and generally increased at the 24- and 30-month collections (39.7% ± 2.7 and 45.3% ± 3.1, respectively; Fig. 4d). Among all collection dates, mean (±SE; $n = 81$) film cover was greater in bare ground (50.1% ± 2.4), than shrub (37.4% ± 2.4) or grass (33.0% ± 2.2) microsites (Fig. 4d). A collection month × microsite interaction was driven by differences in microsite patterns after 12 months: film cover

Table 2 Mean (±SE) EEA substrate turnover activity (moles substrate converted) associated with decomposing *Prosopis glandulosa* leaflet litter in contrasting microsites

Enzyme	Microsite		
	Bare ground	Grass	Shrub
β-1,4-glucosidase (BG)[b]	50.8 (9.55)	29.7 (7.07)	42.1 (4.45)
Leucine aminopeptidase (LAP)[b]	26.4 (6.82)	27.9 (8.77)	35.9 (13.72)
β-*N*-acetylglucosaminidase (NAG)[b]	44.5 (8.42)	42.2 (10.4)	48.2 (12.04)
Acid phosphatase (PHOS)[a]	113.9 (45.80)	97.9 (24.73)	80.4 (23.37)
β-1,4-xylosidase (XYLO)[c]	11.2 (2.78)	7.6 (1.46)	9.1 (1.21)

Differences in turnover among enzymes are indicated by different letters. There was no effect of microsite on EEA turnover

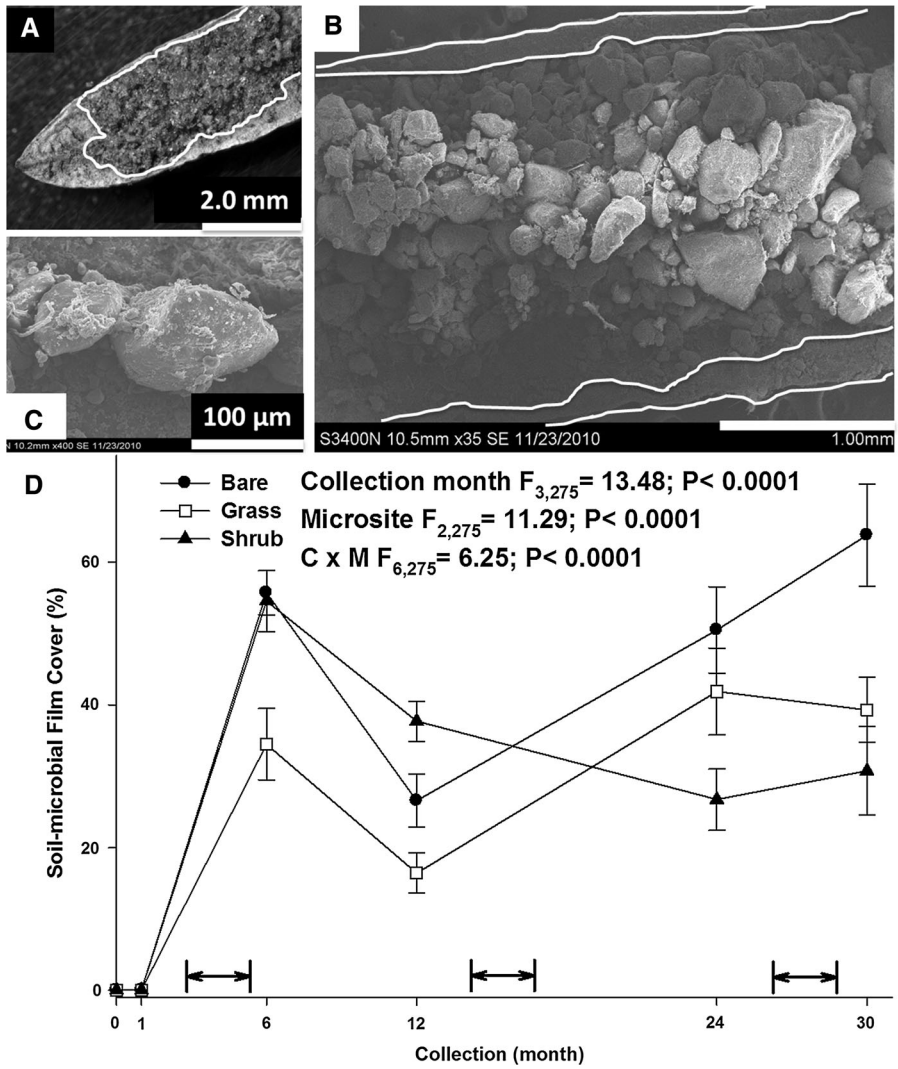

Fig. 4 Soil-microbial films on *P. glandulosa* leaflets at the 6-month collection date. **a** A stereo micrograph showing soil-microbial film coverage on a leaflet. The *white line* delineates the perimeter of the film. **b** An electron micrograph of the surface of a leaflet with a dense coating of soil. The *outer white lines* delineate the leaf margins; *inner lines* delineate the perimeter of the soil film. **c** An electron micrograph showing the binding between individual soil particles and binding of soil particles to leaf surfaces. **d** Mean (±SE; $n = 27$ per collection) percent cover of soil-microbial films on the surface of nearly intact *P. glandulosa* leaflets recovered at random from litterbags placed in bare ground, grass and shrub microsites. *Brackets* along *x*-axis indicate the approximate start and end of each monsoon season

increased linearly in bare ground microsites, generally declined in shrub microsites, and increased, then plateaued in grass microsites.

Soil aggregates

Soil aggregates were observed in leaf-containing litterbags at the 6-month collection date, but were not found in litter-free control bags. These structures enveloped portions of leaflets (Fig. 5a) or formed as discrete structures (Fig. 5b). Individual soil particles were connected to one another and to leaf surfaces by extracellular mucilage Fig. 5c). The frequency of aggregate formation was highest among litterbags in bare ground microsites (74.9% at 6 months and later) and lowest in grass and s*P*hrub microsite placements (both 44.4%; Table 3; $\chi^2 = 4.59$, $= 0.10$). However, the number of aggregates per bag was statistically comparable among microsites (Table 3; $F_{2,45} = 1.06$, $P = 0.36$) and collection date ($F_{3,45} = 0.74$,

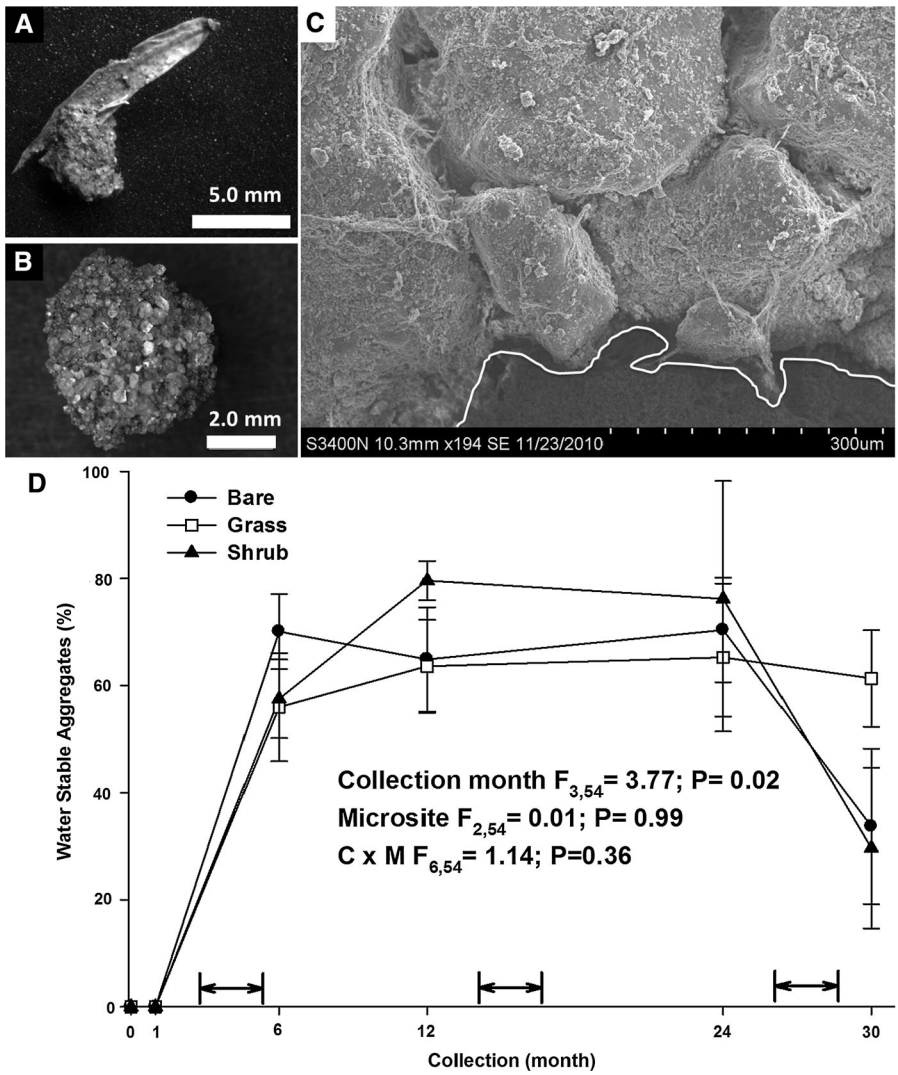

Fig. 5 Micrographs of *P. glandulosa* leaflets at the 6-month collection date showing **a** an aggregate developing at the proximal end of an individual leaflet and **b** an aggregate that formed within a litterbag. **c** A scanning electron micrograph of a soil aggregate showing connections between soil particles on the leaflet surface. The border between the leaflet and soil aggregate is delineated with a *white line*. **d** Mean (+SE) percentage of water-stable aggregates associated with leaflet litter in bare ground, grass, and shrub microsites (based on mass remaining after wet sieving). *Bracket*s along *x*-axis indicate the approximate start and end of each monsoon season

Table 3 Percentage of litterbags containing soil aggregates, the mean (±SE) number of soil aggregates per litterbag when aggregates were present, and the mean (±SE) mass of individual aggregates ($n = 27$ bags for each collection month × microsite combination)

Collection month	Microsite	Bags with aggregates (%)	Individual aggregate mass (mg)
6	Bare	100	18.1 (5.43)g
	Grass	33.3*	31.5 (6.43)f
	Shrub	66.6	3.4 (5.87)h
12	Bare	55.5	9.7 (6.4)c
	Grass	55.5*	14.3 (7.2)c
	Shrub	55.5	6.9 (6.4)c
24	Bare	88.8	19.8 (8.29)a
	Grass	88.8^	32.4 (10.16)a
	Shrub	33.3	#
30	Bare	55.5	32.9 (4.79)a
	Grass	33.3^	12.8 (7.19)b
	Shrub	22.2	29.4 (5.08)a

No aggregates formed in any of the liter-free control bags. Different symbols indicate differences in the grand mean of aggregate mass (mean of microsite means) among collection months. Different letters indicate differences in the mean mass of aggregates among microsites within a distinct collection month

Insufficient number of samples

$P = 0.36$). Dry mass (mg) of individual aggregates was greater at the 24- and 30-month collection dates than at the 6- and 12-month collection dates (Table 3; $F_{3,163} = 3.93$, $P = 0.009$) and was marginally greater in bare ground and grass microsite placements than in shrub microsite placements (Table 3; $F_{2,163} = 2.88$; $P = 0.058$). Aggregate stability was relatively high across the 6- through 24-month evaluation dates and statistically comparable among microsites (Fig. 5d).

Soil aggregate [C] and [N] (Fig. 6) was an order of magnitude lower than that in leaf litter (Table 1). Temporal patterns in soil aggregate [C] and [N] were similar (Fig. 6a, b) and reflected microsite differences in surface soil chemistry, though [C] and [N] of soil aggregates was typically higher than that of bulk surface soils. Aggregate [C] and [N] in shrub microsites was greater than that of aggregates in bare ground and grass microsites. Similarly, [C] and [N] in surface soils were greater in shrub microsites than grass or bare ground microsites ($F_{2,68} = 7.80$, $P < 0.001$ and $F_{2,68} = 7.52$, $P = 0.001$, respectively).

Discussion

Leaf litter decomposition during this Chihuahuan Desert field study showed strong temporal synchrony with soil–litter mixing (SLM), a mechanism that has been identified in several recent studies as a driver of dryland decomposition (Throop and Archer 2007; Hewins et al. 2013; Hewins and Throop 2016). The development of soil-microbial films following seasonal monsoon rains lends support to the notion that SLM enhances conditions (e.g., microclimate, solar radiation) that favor microbial activity (Barnes et al. 2012, 2015). Simultaneously, we measured elevated activity of C-degrading extracellular enzymes during the first year when the most decomposition occurred. This further supports the notion that SLM enhances decomposition by facilitating microbial activity. The significant relationships we observed among mass loss, soil-microbial film development, and SLM indicate that these processes are important drivers of surface litter decomposition. The development of soil aggregates with elevated [C] and [N] relative to bulk soils suggests a plausible link between the chemical residues resulting from organic matter decomposition and the development of soil-nutrient complexes that can stabilize surface soils (Tisdall and Oades 1982; Six et al. 1999, 2000, 2006). Future studies quantifying the C and N content of aggregates associated with litter to that of comparably sized aggregates in the surrounding soil will further our understanding of this soil–litter relationship (Fig. 7).

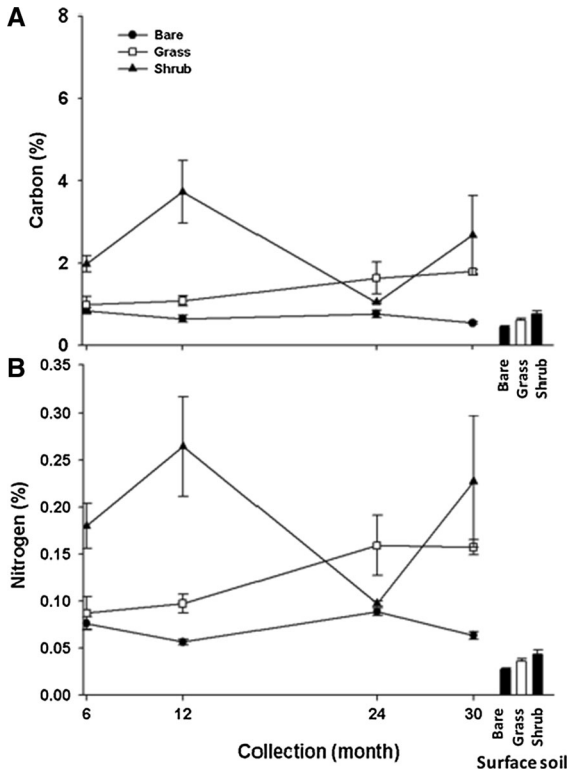

Fig. 6 Mean (+SE) % by mass C (**a**) and N (**b**) content of soil aggregates that formed in litterbags placed on bare ground, grass, and shrub microsites. *Inset bar* graphs show mean (±SE) % C and % N of surface soil (2 cm depth taken at time 0) in the three microsites for comparison. No aggregates had formed at the 0- and 1-month sample collection dates

Temporal dynamics

The pattern of rapid litter decay in response to monsoon rain (July–September) coupled with SLM was identified as a potential mechanism for decomposition in previous studies in the Chihuahuan (Hewins et al. 2013; Hewins and Throop 2016) and Sonoran (Throop and Archer 2007) Deserts. Elevated extracellular enzyme activity occurring in association with SLM and soil-microbial film development highlights the importance of microbial decomposition on surface litter in dryland environments. Limited decomposition between 6 and 12 months ostensibly reflects the cooler and drier conditions occurring in autumn and winter which can limit biotic and enzymatic activity (Schimel et al. 2007) and the predominance of more recalcitrant litter components occurring at this stage in the decomposition process. During this period of low litter mass loss, soil-microbial film cover also declined, regardless of microsite. This suggests dynamic linkages between biological decomposition activity, the availability of C in litter, and the creation and maintenance of soil-microbial films and aggregates.

Litter chemistry

Litter C mass remaining (%) was strongly linearly related to litter mass remaining (%), indicating potential C limitations on soil-microbial abundance, a result that is supported by previous studies in this Chihuahuan Desert system (Hewins et al. 2013; Hewins and Throop 2016) and the Sonoran Desert (Throop and Archer 2007). Litter N mass remaining was also strongly linearly related to litter mass remaining, however, at times, the relationship trended greater than 1:1 with respect to litter mass remaining. This linear pattern deviates from the non-linear dynamics observed by Parton et al. (2007), which may be due to the relatively high [N] of *P. glandulosa* relative to the litter used by Parton et al. (2017). This result is consistent with microbial EEA results, which show high C-degrading EEA at periods of high decomposition, and no clear relationship between decomposition and EEAs is responsible for N cycling (i.e., NAG and LAP).

Litter [C] and [N] fluctuated among vegetation microsites over time. Overall, litter [C] was greatest in grass-dominated microsites, suggesting that the dense canopy structure of grasses may have shaded litter, thus attenuating photodegradation (Austin and Vivanco 2006) or thermal degradation (Lee et al. 2012) by reducing incident solar radiation resulting in a lower surface temperature. Litter [N] also fluctuated among vegetation microsites over time. Similar to N mass remaining, [N] increased through time, and returned to initial concentrations at the last collection date. Litter [N] was greatest in shrub microsites, which may be related to the close proximity of this material to N_2-fixing *P. glandulosa* shrubs and the likelihood that soil N is more available to decomposers in these microsites (Throop and Archer 2008).

Extracellular enzyme activity

The activity of C-degrading enzymes increased markedly from 1 to 6 months—coincident with the period of greatest litter mass loss. Between 6 and

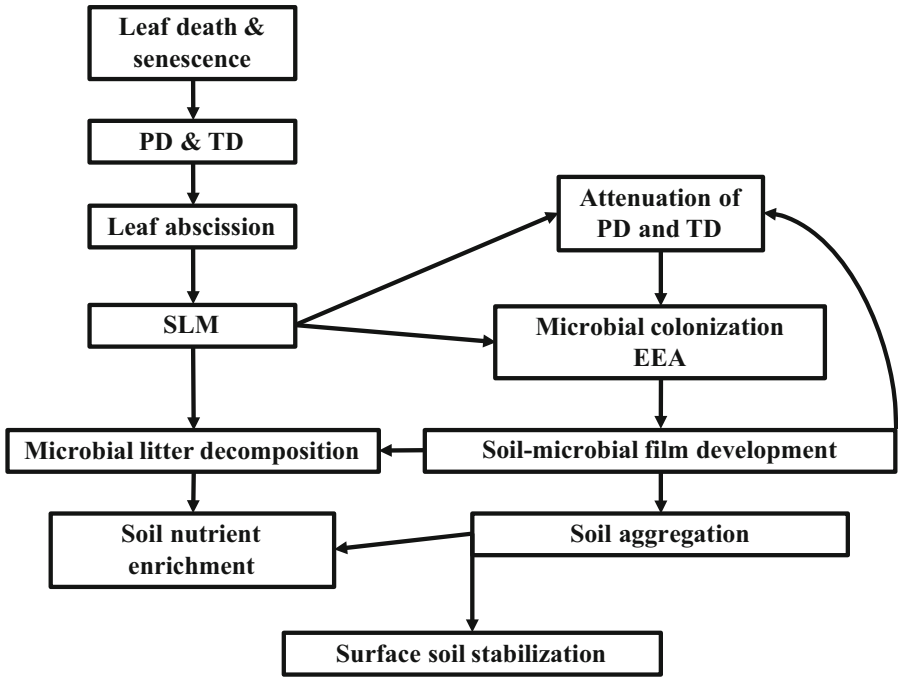

Fig. 7 A conceptual diagram of decomposition in drylands where soil–litter mixing (SLM) occurs. After senescence and prior to SLM, litter material can be photodegraded (PD) by solar radiation and thermal degradation (TD). Following soil mixing, PD and TD are attenuated. Following SLM, microbial decomposers colonize litter, form soil-microbial films, and decompose litter via extracellular enzyme activity (EEA). Some carbon (C) and nutrients are released via decomposition directly into the soil, while some C and nutrients are transformed into extracellular compounds that contribute to the stability, and C and nutrient content of soil aggregates. The soil aggregates that are a result of biological litter decomposition contribute to the development of more stable surface soils

12 months, a period of virtually no litter mass loss, activity stabilized at relatively high levels. These hydrolytic enzymes catalyze the breakdown of soluble organic compounds and sugars (Allison et al. 2007; Sinsabaugh et al. 2008), which would be expected to be present and most abundant in the early stages of litter breakdown. Maintenance of EEA between months 6 and 12, a period of limited litter mass loss, is congruent with the idea that enzymes may persist during microbial dormancy (Schimel et al. 2007; Stursova and Sinsabaugh 2008; Alster et al. 2013), and the possibility that enzymes are degrading dead microbial cells, or root and microbial exudates.

The mean substrate turnover activities observed for BG (50.8 mol) and NAG (44.5 mol) are comparable to those reported by Gallo et al. (2009) for photodegradation of tree (*Pinus edulis*, *Juniperus monosperma,* and *Populus* spp.) surface litter in northern Chihuahuan Desert montane zones (BG: mean = 45 mol, range 23–90; NAG: mean = 23 mol, range 10–53). However, the ratios of LAP and AP, which reflect the availability of and demand for N and P, were greater in this study than Gallo et al. (2009) by factors of >20 and >2, respectively. These greater values are consistent with soil–litter biofilm development, accumulation of litter N (which was not observed by Gallo et al. 2009), and the three to fourfold greater mass loss rates in our study than the photodegradation study.

Soil-microbial film and aggregate development, stability and chemistry

Our data support the notion that SLM and soil-microbial film development are inter-related processes that link abiotic and biotic drivers of litter decomposition. Soil-microbial films developed regardless of local vegetation cover in this study, suggesting that they are likely common in the Chihuahuan Desert and other deserts such as the Sonoran Desert where similar litter types (e.g., *Prosopis velutina*) occur in conjunction with similar soils (Levi 2017). However, the degree of soil-microbial film development varied both

temporally and spatially. Between 1 and 6 months of this study, soil-microbial film development on leaf surfaces was greater in the bare ground and shrub patches where soil surface herbaceous ground cover is lower than grass-dominated sites. However, by month 12, soil-microbial film cover was comparably high among all three microsites. There was potential for photodegradation early in the study, despite solar radiation being blocked by fiberglass mesh (Hewins and Throop 2016). However, in ecosystems where SLM rates are high, solar radiation is likely attenuated rapidly when soils cover litter (Barnes et al. 2012). Micrographs of soil-microbial films and aggregates show putative binding agents that may be byproducts of biotic activity associated with decomposition. A variety of studies have identified organic substrates (Six 2006) and biomineralized carbonate (Monger et al. 1991; Bird et al. 2002; Cacchio et al. 2003; Ercole et al. 2007) as agents of soil aggregation. Our work links the transformation of detrital material to binding agents that may be stabilized in resulting soil aggregates. The soil-microbial films and aggregates formed during surface litter decomposition in this study have similar structural composition to that reported for soil aggregates that form belowground (Tisdall and Oades 1982; Oades 1993; Six et al. 1999, 2000). We hypothesize that the presence of microbes in soil-microbial films and aggregates is tied to the availability of energy (e.g., C) and nutrients (e.g., N) from litter material, which intrinsically enables the development and maintenance of soil aggregates (Six 2006).

Temporal patterns of soil-microbial film cover suggest strong relationships with increased SLM and associated decomposition, where the extent and continuity of film cover may be influenced by changes in the quantity and quality of litter as it decomposes. Soil-microbial films developed rapidly during the period of high biotic decomposition between months 1 and 6. When decomposition slowed in the drier, cooler period from months 6–12, soil-microbial film cover decreased. Soil-microbial film cover stabilized toward the end of the experiment except in bare ground patches. These similar temporal dynamics suggest that SLM and soil-microbial film development occur under similar environmental control (e.g., moisture, temperature), or suggest the possibility that soil-microbial films form as a direct result of microbial decomposition.

Soil aggregates formed during surface litter decomposition have the potential to mitigate winnowing and saltation erosion forces, while stabilizing and storing C and nutrients (i.e., N). In this study, [C] and [N] concentrations in soil aggregates were higher than surface soils sampled within the same microsites. This likely reflects occlusion of C- and N-rich microbial residues that bind soil aggregates. The enhanced stability of soil aggregates in shrub (*P. glandulosa*) microsites compared to grass microsites that we observed has also been noted in another study conducted at the JRN Chihuahuan Desert site (Bird et al. 2002) and may reflect the higher [C] and [N] concentrations and pools in soils associated with *P. glandulosa* plants (Throop and Archer 2008).

The link between litter [C] and aggregate stability suggests a mechanism for the marked reductions in aggregate stability observed in the last 6 months of our study, a period receiving considerable rainfall. This decline in aggregate stability at bare ground and shrub microsites corresponded with marked reductions in litter [C]. We suggest that this represents a threshold where the microbial production of substrates needed to stabilize aggregates was being adversely affected.

Conclusions

This study highlights the importance of novel relationships between SLM, soil-microbial film development, and biological drivers of decomposition (i.e., EEA), while providing the basis for a mechanistic representation of SLM in the decomposition process (Fig. 7). Adoption of this perspective will improve conceptual and quantitative models of dryland decomposition.

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