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Soil moisture and soil-litter mixing effects on surface litter decomposition: A controlled environment assessment

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ABSTRACT

Recent studies suggest the long-standing discrepancy between measured and modeled leaf litter decomposition in drylands is, in part, the result of a unique combination of abiotic drivers that include high soil surface temperature and radiant energy levels and soil-litter mixing. Temperature and radiant energy effects on litter decomposition have been widely documented. However, under field conditions in drylands where soil-litter mixing occurs and accelerates decomposition, the mechanisms involved with soil-litter mixing effects are ambiguous. Potential mechanisms may include some combination of enhanced microbial colonization of litter, physical abrasion of litter surfaces, and buffering of litter and its associated decomposers from high temperatures and low moisture conditions. Here, we tested how soil-litter mixing and soil moisture interact to influence rates of litter decomposition in a controlled environment. Foliar litter of two plant species (a grass [*Eragrostis lehmanniana*] and a shrub [*Prosopis velutina*]) was incubated for 32 weeks in a factorial combination of soil-litter mixing (none, light, and complete) and soil water content (2, 4, 12% water-filled porosity) treatments. Phospholipid fatty acids (PLFAs) were quantified one week into the experiment to evaluate initial microbial colonization. A complementary incubation experiment with simulated rainfall pulses tested the buffering effects of soil-litter mixing on decomposition.

Under the laboratory conditions of our experiments, the influence of soil-litter mixing was minimal and primarily confined to changes in PLFAs during the initial stages of decomposition in the constant soil moisture experiment and the oscillating soil moisture conditions of the rainfall pulse experiment. Soil-litter mixing effects on CO_2 production, total phospholipid concentrations, and bacterial to total PLFA ratios were observed within the first week, but responses were fairly weak and varied with litter type and soil moisture treatment. Across the entire 32-week incubation experiment, soil moisture had a significant positive effect on mass loss, but soil-litter mixing did not. The lack of strong soil-litter mixing effects on decomposition under the moderate and relatively constant environmental conditions of this study is in contrast to results from field studies and suggests the importance of soil-litter mixing may be magnified when the fluctuations and extremes in temperature, radiant energy and moisture regimes common dryland field settings are in play.

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1. Introduction

Globally, arid and semiarid ecosystems (hereafter 'drylands') account for approximately 40% of land area (Bailey, 1996), 30% of net primary production (Field et al., 1998), and 20% of the soil organic C pool (Lal, 2004). Drylands are thus an important component of global biogeochemical cycles. Despite their significance, controls over biogeochemical processes in drylands are poorly understood relative to mesic systems (Throop and Archer,

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2009; Austin, 2011). This key knowledge gap is increasingly critical given the widespread anthropogenic changes occurring in drylands (MEA, 2005; Peters et al., 2012). In particular, drylands are experiencing widespread land cover change as woody plants encroach into formerly grass-dominated areas (Eldridge et al., 2011; Naito and Cairns, 2011) and climate models suggest that drylands will likely experience increases in drought severity and frequency (IPCC, 2007). An improved understanding of the controls over biogeochemical processes in drylands and how these will respond to future environmental conditions are therefore critical for accurately predicting changes in global biogeochemical cycles.

1.1. Controls over decomposition in drylands

Decomposition is an essential regulator of ecosystem C and nutrient cycling. In most biomes, plant litter decomposition rates can be fairly accurately predicted with simple climate-based models (Meentemeyer, 1978; Aerts, 1997; Parton et al., 2007), with local-scale variation typically accounted for with litter chemistry parameters such as lignin and nitrogen content (Hobbie, 1992; Parton et al., 2007). However, these conventional decomposition models consistently under predict dryland decomposition rates (Whitford et al., 1981; Vanderbilt et al., 2008; Throop and Archer, 2009). The discrepancy between measured and modeled rates in drylands characterized by limited soil moisture availability, high surface temperature, heterogeneous plant canopy cover, and high rates of sediment movement may lie with a failure to adequately account for drivers unique to drylands: soil-litter mixing, high solar radiation loads, and rainfall pulses (Huxman et al., 2004; Throop and Archer, 2009; Austin, 2011; King et al., 2012). Mixing of surface soils with detached litter ('soil-litter mixing') is a common process in drylands where vegetative cover is low and soil surface erosion is high. Soil-litter mixing can positively influence litter decomposition, ostensibly by enhancing microbial decomposition (Throop and Archer, 2007; Barnes et al., 2012; Hewins et al., 2013). High levels of solar radiation can also influence dryland C cycling through photo- and thermal degradation of litter and soil organic matter (Austin and Vivanco, 2006; Rutledge et al., 2010; Austin, 2011; King et al., 2012; Lee et al., 2012). High instantaneous solar radiation and surface temperatures may break down complex compounds such as lignin to release C-based greenhouse gases (King et al., 2012; Lee et al., 2012). However, photodegradation effects may be negated when soil mixes with litter and blocks solar radiation (Barnes et al., 2012).

The role of precipitation in controlling dryland decomposition remains poorly understood. Precipitation is a key driver of biological processes across a wide range of climate zones; but in drylands, precipitation pulse size and the duration of dry periods between pulses are a more important determinant of soil respiration than precipitation totals (Austin et al., 2004; Cable et al., 2008). Although the effects of rainfall pulse size and frequency on dryland litter decomposition are unknown, they are likely important via their combined influence on microbial activity, photodegradation (Brandt et al., 2007; Smith et al., 2010), and soil-litter mixing. The importance of these unique drivers' role on litter decomposition may increase in drylands given the projected decline in precipitation and increase in the frequency and duration of drought with climate change (Milly et al., 2005; Seager et al., 2007; Fawcett et al., 2011; Munson et al., 2012).

While soil-litter mixing has been shown to affect decomposition rates, the mechanistic basis for this relationship is unclear. It has been suggested that soil-litter mixing could enhance litter decomposition via several mechanisms, including 1) acting as a vector for microbial colonization of litter surfaces, 2) buffering litter from temperature or moisture extremes, thereby extending the temporal window of opportunity for microbially-mediated decomposition, or 3) causing physical abrasion and thus increasing the surface area available for microbial colonization and leaching (Throop and Archer, 2007, 2009). The interplay between these possible mechanisms may be complex, particularly in conjunction with the spatial and temporal heterogeneity of soil moisture in drylands and the possibility that soil-litter mixing buffers litter from moisture oscillations following rainfall pulses. Assessing the mechanisms of soil-litter mixing in the context of soil moisture is an important step in improving understanding of biogeochemical dynamics in drylands now and under future vegetation and climate change scenarios. In this study, we sought to ascertain if soil-litter mixing would (*i*) enhance initial microbial colonization of litter and (*ii*) differentially influence decomposition under varying moisture conditions (e.g., constant vs. fluctuating regimes).

1.2. Study objectives

We report results of two highly controlled laboratory incubation experiments aimed at quantifying how soil-litter mixing and soil moisture interact to affect litter decomposition. These experiments allowed us to assess the relative importance of some of the many environmental factors that might explain field observations of a positive relationship between soil-litter mixing and decomposition. We hypothesized that soil-litter mixing would 1) positively influence the rate of decomposition by enhancing microbial colonization and 2) be most pronounced under variable moisture conditions when soil-litter mixing would enhance microbial activity by buffering litter from moisture extremes. We tested these hypotheses by quantifying the influence of soil-litter mixing on litter decomposition in two separate but complementary laboratory incubations, one using constant soil moisture regimes and the second using simulated rainfall pulses to create fluctuating soil moisture conditions. While there are many possible mechanisms by which soil-litter mixing could affect decomposition, we focused our laboratory incubation experiments on the potential role of soil-litter mixing in influencing litter colonization and in buffering litter from moisture extremes. We recognize that controlled laboratory conditions do not mirror the variability and extremes in temperature, moisture and other environmental conditions that occur under field conditions. Instead, we sought to minimize confounding effects and focus on soil-litter mixing and soil moisture interactions by conducting these experiments under controlled conditions where fine-scale decomposition measurements were possible.

2. Materials and methods

2.1. Litter and soil incubation

Soil and litter were collected at the Santa Rita Experimental Range (SRER), a semiarid savanna 80 km south of Tucson in Pima County, AZ, USA. The soil and litter were chosen to provide a parallel comparison with a field study on the effects of soil-litter mixing in the context of woody plant encroachment (Throop and Archer, 2007). We used two contrasting litter substrates: Lehmann lovegrass (*Eragrostis lehmanniana*; hereafter, "grass"), a C_4 grass native to Africa that now dominates ground cover at the SRER and much of southern Arizona and New Mexico (McClaran, 2003; Schussman et al., 2006); and velvet mesquite (*Prosopis velutina*; hereafter, "shrub"), a N_2-fixing C_3 plant that is the dominant shrub at the SRER (McClaran, 2003) and one of several prominent woody encroachers throughout grasslands of the southwestern United States and southern Great Plains. Leaf litter was collected in autumn 2008. Initial litter chemistry differed dramatically between the two

species, with much greater N content in the shrub than the grass (% N mean ± SE = 2.7 ± 0.001 and 0.7% ± 0.0004, respectively). Senescent mesquite leaves were manually harvested immediately prior to leaf abscission and only leaflets were used for the incubations. Senescent leaves, sheaths, and culms of grass from the current growing season were collected by clipping just above the soil surface. To maximize consistency, only the lowest 10 cm of grass material was used. Grass litter was cut into 1 cm segments to facilitate uniform mixing with soil. Following field collection, litter was 'air dried' at 30 °C to minimize adverse effects on litter chemistry and curtail microbial activity. Subsamples of the litter were also dried at 60 °C to develop wet-dry regressions for estimating initial dry litter mass. Soils (0–5 cm depth) were collected in June 2009 from bare ground patches between mesquite canopies, where organic carbon content is ~0.3% (Throop and Archer, 2008). The soils were Holocene-derived alluvial sandy loam Typic Haplargids in the Continental series (SoilSurveyStaff, 2013). Soils were air dried, passed through a 1 mm sieve, and hand-cleaned to remove visible, non-decomposed organic material to maximize among-replicate uniformity.

2.2. Soil-litter mixing incubation studies

2.2.1. Constant soil moisture experiment

To test the hypothesis that soil-litter mixing would positively influence the rate of litter decomposition by enhancing microbial colonization, we incubated 2 g dry leaf litter and 50 g dry soil in 473 mL glass jars using factorial combinations of three soil-litter mixing treatments and three soil moisture treatments. The three soil-litter mixing treatments reflected a range of possible scenarios (Supplementary Information 1): a '*No Mixing*' treatment (all litter on soil surface), a '*Light Mixing*' treatment (5 g soil mixed into the litter layer and 45 g soil below the litter), and a '*Complete Mixing*' treatment (litter entirely mixed with all 50 g soil). The three soil moisture treatments were 2, 4 and 12% Water-Filled Pore Space (% WFP), representing dry, moderate and wet conditions, respectively. In order to achieve each target moisture level, we added deionized (DI) water to air-dried soil (1.0% WFP), thoroughly homogenized the mixture until no clumps were visible, and let it equilibrate in air-tight plastic bags for 24 h before establishing the soil-litter mixing treatments. All moisture contents were based on volume and converted to WFP. The rainfall equivalent of these treatments is 0.2, 0.4, and 1.2 mm (for 2, 4, and 12% WFP, respectively). Soil moisture treatments bracketed published near-surface (5–15 cm) soil moisture contents from the southwestern United States, where reported values are typically 2–3% volumetric water content (VWC or 4–6% WFP) and range from <1% to 10% VWC (=20% WFP) (Scanlon, 1994; Yoder and Nowak, 1999; Scott et al., 2009). The 2% WFP 'desert dry' soil moisture treatment was used to simulate conditions that typically occur during the dry season and that may arise more frequently with climate change (Milly et al., 2005). Jars were sealed except for periodic flushing, obviating the need to adjust soil moisture during the experiment. The lids were fitted with Luer-Lok stopcocks for headspace gas sampling. The soil and litter were incubated in a controlled environment chamber in the dark at 25 °C, providing an optimum temperature for microbial activity.

Four replicates of each treatment combination were incubated for each harvest period (0, 1, 2, 4, 8, 16, and 32 weeks) and analyzed for litter mass loss ($n = 252$ jars for each of the two litter types). A separate set of six replicates per treatment combination ($n = 54$ jars per litter type) was designated for periodic CO_2 measurements; leaf mass loss was not quantified in these jars. Two additional treatments served as controls for CO_2 measurements (six replicates per treatment): a 'soil only' control consisting of 50 g soil and no litter for each soil moisture treatment and a 'blank' control consisting of empty jars to correct for air leakage.

2.2.2. Rainfall pulse experiment

A second laboratory incubation experiment was established to test the hypothesis that soil-litter mixing would be most pronounced under variable moisture conditions when soil-litter mixing would enhance microbial activity by buffering litter from moisture extremes. We used the same three soil-litter mixing treatments as the constant soil moisture experiment, but manipulated soil moisture as rainfall pulses of different sizes. Dryland precipitation events are classified as small events (<5 mm) and large events (≥5 mm; Huxman et al., 2004). We used this classification to create two water delivery treatments that differed in pulse size and frequency ($n = 5$ replicates per moisture × soil-litter mixing combination). The small-frequent pulse treatment received a 2 mm rainfall equivalent (7.8 mL distributed across the 30 cm^2 surface area) of DI water on days 1, 8, 15, 21, and 29 of the incubation. The large-infrequent moisture pulse treatment received 5 mm rainfall equivalent (19.2 mL) of DI water on days 1 and 16 of the incubation. Thus, the two treatments received the same total water (10 mm) throughout the experimental period. Water pulses were added by carefully pouring the allotted water across the soil surface so that soil and litter distribution was not disturbed. Jars were sealed for 24 h after each water pulse treatment. To eliminate measurement of CO_2 flushing from the pore spaces, headspace gas CO_2 concentrations were measured twice in the 6–12 h interval immediately following the 24 h post wet-up period to estimate the rate of CO_2 production. Lids were removed after CO_2 concentrations were measured and samples were allowed to dry down until the next water pulse. These snapshot measurements of CO_2 production the day after water pulses provided an index of microbial activity in response to rainfall. Two additional treatments served as controls for CO_2 measurements: a 'soil only' control consisting of 50 g soil and no litter for each water pulse treatment and a 'blank' control consisting of empty jars to correct for air leakage.

2.3. Litter decomposition

We assessed the rate of litter decomposition for the constant soil moisture experiment by measuring changes in litter mass through time. Upon harvesting, we manually partitioned litter and soil by passing material through a 1 mm sieve and then brushed leaves individually to dislodge lightly adhering soil particles. Harvested litter and soil were frozen at −80 °C, lyophilized, weighed, and ground using a ball mill. Subsamples of ground litter were ashed in a muffle furnace at 550 °C for 8 h so that mass loss data could be expressed on an ash-free basis. Decomposition rates were estimated using a single exponential decay model ($M_t = M_0\ e^{-kt}$), where M_t is the litter mass at time t, M_0 is the initial litter mass, and k is the decay constant (Olson, 1963). We estimated k by fitting negative exponential decay curves rather than linear fits of log-transformed data to avoid potential error generated from data transformation (Adair et al., 2010).

2.4. CO_2 production

The rate of CO_2 production was quantified as a proxy for microbial activity for both the constant soil moisture experiment and the rainfall pulse experiment. Total CO_2 production included microbial decomposition of soil organic matter and litter. An infrared gas analyzer (LiCor 820, LiCor-Biosciences, Lincoln, NE, USA) was used as an open path system with a 6-port gas injection valve and a 5 mL loop (Valco Instrumental Company Inc., Houston, TX, USA). An airtight syringe was used to collect 10 mL of headspace gas that

accumulated over a known time period (typically 6–12 h interval). A standard curve was created using certified CO_2-in-air standards (301, 1000, and 25,000 ppm) to quantify headspace CO_2 concentrations. The rate of CO_2 production was calculated as the change in CO_2 concentration divided by the time between sampling periods and is expressed as μg CO_2–C gdw^{-1} h^{-1} (e.g. Fig. 5). When expressed as cumulative CO_2 production (e.g. Fig. 2), mg CO_2–C gdw^{-1} was used, where gdw represents per g ash-free dry mass of litter present on a given harvest date. Jars were flushed with ambient air (~400 ppm CO_2) before headspace CO_2 reached 20,000 ppm. All CO_2 concentration and production rate data were corrected by mean CO_2 concentrations of 'blank' controls (see Section 2.2). We calculated cumulative CO_2 production per g of litter over the course of the incubation by integrating the rate of CO_2 production between successive measurement periods (Zibilske, 1994).

2.5. Phospholipid fatty acid (PLFA) analysis

We used PLFA analysis to monitor microbial colonization of the litter material. Owing to logistical constraints, we only analyzed PLFAs on litter samples harvested in week one of the constant soil moisture experiment. We opted to focus on the first week as we expected this would be when soil-litter effects would be most evident. The PLFAs were analyzed from three replicate litter samples for each litter type, moisture, and soil mixing treatment combination ($n = 54$ samples).

Total phospholipids of litter samples were extracted from 250 mg of lyophilized ground litter using a single-phase extraction (Bligh and Dyer, 1959; White et al., 1979). Litter was extracted with potassium phosphate buffer, methanol, and dichloromethane (0.8:2:1), vortexed for 30 s, and heated at 37 °C for 0.5 h with vortexing at 10 min intervals (Wilkinson et al., 2002). Isolation of the phospholipid fraction through silicic acid solid phase extraction, conversion to fatty acid methyl esters (FAMEs), and purification of FAMEs with octadecyl (C18) resin (J.T. Baker, Inc., Phillipsburg, NJ, USA) was performed (Dobbs and Findlay, 1993; Findlay and Dobbs, 1993). The silica-based solid phase extraction step was modified to use a MeOH to silica ratio of 20:1 (Mills and Goldhaber, 2010).

Purified FAMEs were analyzed with a gas chromatograph (Shimadzu 2014; Shimadzu Corp., Japan) equipped with a flame ionization detector (FID; Agilent Tech., Santa Clara, CA, USA) using a non-polar Rtx-1 column (30 m × 0.32 mm × 0.25 μm; Restek Corp., Bellefonte, PA, USA). FAMEs were identified and quantified by running a known standard (Supelco 37-component FAME mix, Sigma–Aldrich Co., St. Louis, MO, USA) every fourth sample. Further peak identification was based on retention times and chromatographs generated from other labs using microbial identification software (Sherlock Microbial Identification System; MIDI Inc., Newark, DE, USA). Problems with co-elution of compound peaks in the C18 isomer region on the Rtx-1 column, which occur with high concentrations of some FAMEs, were resolved using a very polar Select FAME capillary column (50 m × 0.25 mm × 0.25 μm; Agilent Tech., Santa Clara, CA, USA) attached to a Varian 3900 gas chromatograph with a FID. We classified the following FAMEs as bacterial based on previously published data (Vestal and White, 1989; Zelles, 1997) and on their relative abundance being < 1% in initial

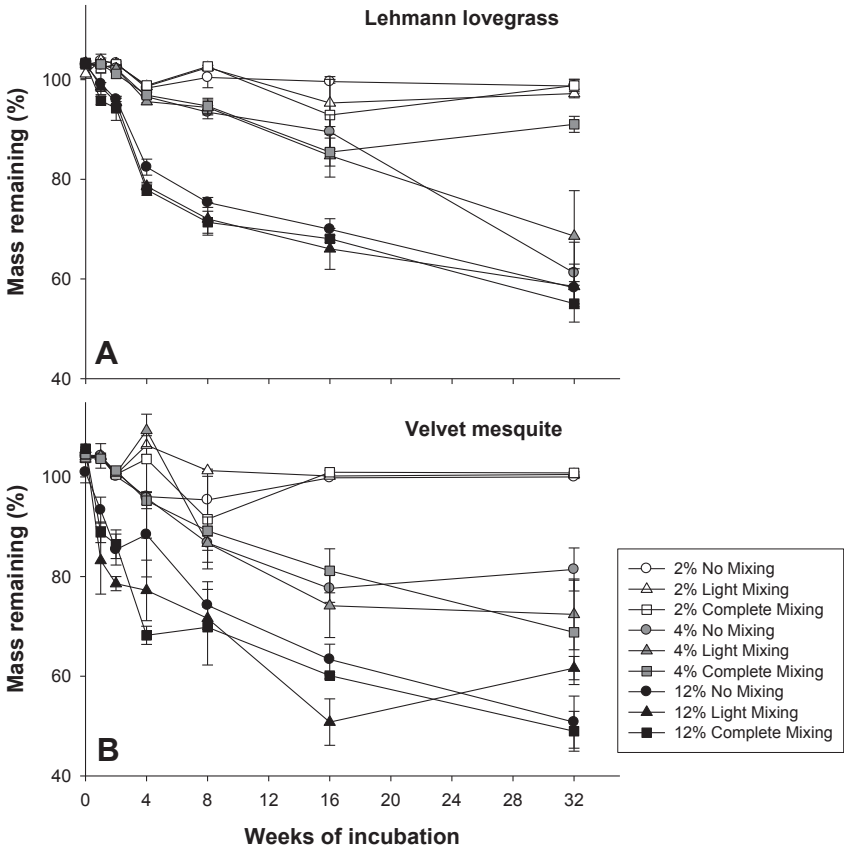

Fig. 1. Mean (standard error, SE; $n = 4$) ash free mass remaining (%) in soil moisture (2%, 4%, or 12% WFP) and soil-litter mixing (No, Light, and Complete Mixing) treatments over 32 weeks estimated by direct harvest for A) grass (*Eragrostis lehmanniana*) and B) shrub (*Prosopis velutina*) litter. The ANOVA table shows *F* and *df* values in a four-way ANOVA, where MO is soil moisture, MX is soil-litter mixing, SP is species, and TM is harvest time. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

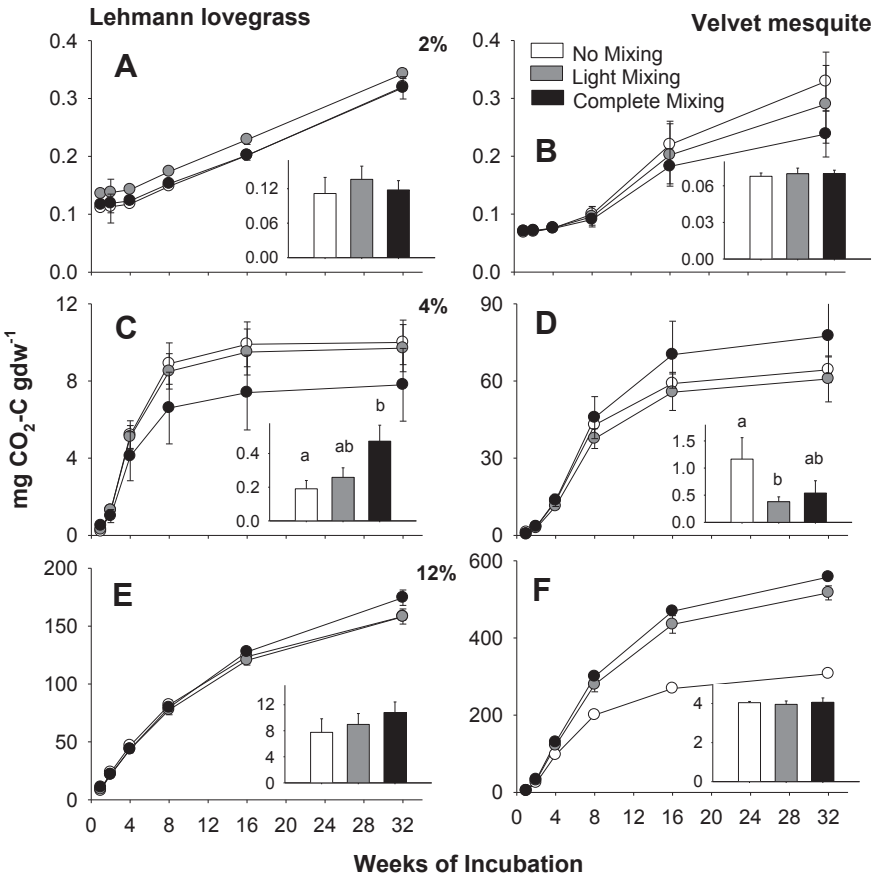

Fig. 2. Cumulative CO_2 production per gram of ash-free dry litter on a given harvest date (mg CO_2–C gdw^{-1}) from a factorial soil moisture (2, 4, and 12% WFP; A and B, C and D, and E and F, respectively) and soil-litter mixing (No, Light, and Complete Mixing) treatments with grass (*Eragrostis lehmanniana*; A, C, and E) and shrub (*Prosopis velutina*; B, D, and F) litter over 32 weeks of incubation. Panel insets show first week cumulative CO_2 production and indicate that differences between soil-litter mixing treatments during this period were significant only for the 4% WFP treatment (different small capital letters in panel insets represent statistical difference [$P < 0.05$] based on Tukey's multiple comparison test). Note differences in *y*-axes scale among panels.

litter samples for these two plant species (data not shown): i14, i15, a15, i16, 16:1n9c, 16:1n7c, 16:1n6c, 16:1n5c, 17:1n9c, 17:1n8c, i17:1n7, 10Me16, i17, a17, cy17, 10Me17, 18:1n6c, 18:1n5c, 10Me18, cy19. The abundance of these bacterial markers was summed, and we calculated the ratio of bacterial:total PLFA extracted from each sample to illustrate how soil moisture and soil-litter mixing affected the bacterial colonization and abundance after one week of incubation. We excluded a few FAMEs known to be produced by gram negative bacteria, such as 18:1n7c, from the bacterial group analysis when they were present at >1% relative abundance in the initial litter samples, suggesting they may also be produced by plants.

2.6. Statistical analysis

Decomposition responses to the soil-litter mixing and moisture treatments were assessed in several different ways. The effects of soil-litter mixing, soil moisture, litter type, and collection time on litter mass remaining were analyzed using PROC MIXED in SAS 9.2 (SAS Institute Inc., Cary, NC, USA). Soil-litter mixing, soil moisture, and time were considered fixed factors. Estimates of decay constants (k) were conducted by fitting single pool exponential decay functions to percent ash-free mass remaining data for each treatment using the dynamic fit tool in Sigma Plot 10.0 (Systat Software Inc., Chicago, IL, USA). The rate of CO_2 production for soil-litter mixing and soil moisture treatments and rainfall pulse experiments were compared using ANOVA in R 2.11.1 (R Development Core Team). The PLFA data were analyzed two different ways. The effects of soil-litter mixing and soil moisture treatments on total extractable PLFA (nmol g^{-1} dry litter) and bacterial:total PLFA were analyzed using PROC GLM for each species separately. Tukey's multiple comparison tests were used to evaluate statistical differences ($P < 0.05$) in cumulative CO_2 production and PLFA measurements between treatments. Non-metric multidimensional scaling (NMS) ordination based on Bray–Curtis distance measures (PC-ORD ver. 4, MjM Software Design, Gleneden Beach, OR, USA) was used to explore relationships among FAMEs present in >1% relative abundance when averaged across all samples ($n = 15$ FAMEs). FAMEs of questionable bacterial or plant origin, e.g. 18:1n7c, were included in the NMS ordination analysis if they were present in >1% relative abundance when averaged across all samples. Individual FAMEs that strongly correlated ($R^2 > 0.50$) positively or negatively with the two independent axes identified by the ordination as accounting for majority of the variability are reported.

3. Results

3.1. Constant soil moisture experiment

3.1.1. Litter mass response

There was no significant effect of soil-litter mixing on overall decomposition, expressed as ash-free mass loss and the decay

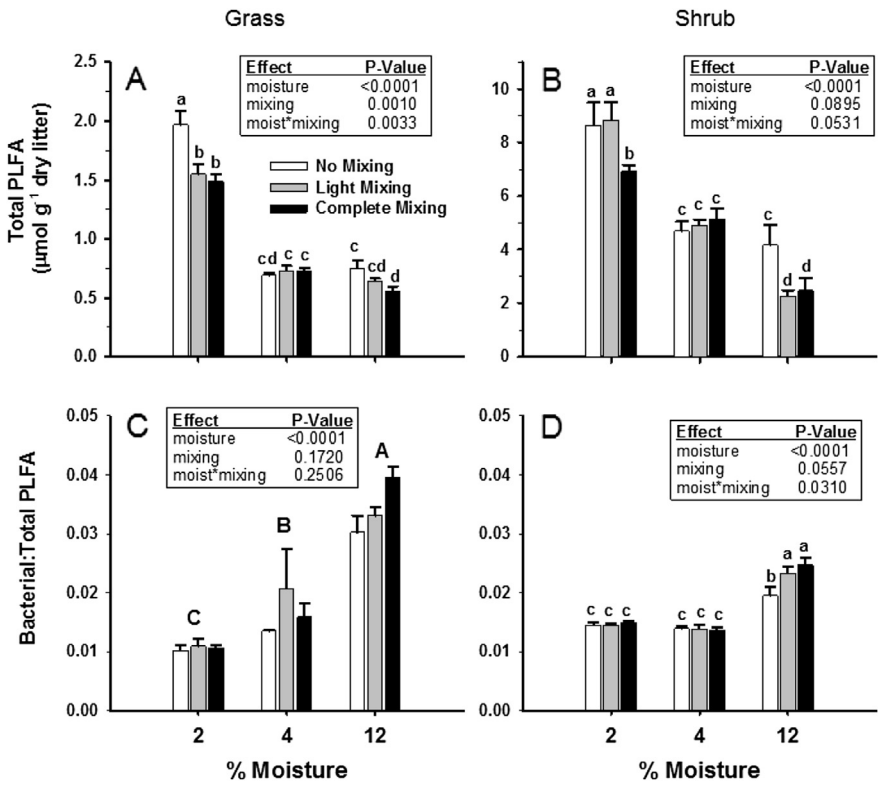

Fig. 3. Mean (±SE; $n = 3$) total (A, B) extractable phospholipid fatty acids (PLFAs) and the ratio of bacterial to total PLFAs (C, D) associated with grass (*Eragrostis lehmanniana*) and shrub (*Prosopis velutina*) litter experiencing different levels of soil moisture treatments (2, 4, and 12% WFP) and soil-litter mixing (No, Light, and Complete Mixing) after one week of incubation. Note the difference in scale between A and B. Bars with different letters represent statistically significant differences (Tukey's multiple comparison test at $P < 0.05$). The capital letters represent same letters for the group. For grass bacterial:total PLFA (C), only differences between moisture treatments are shown with capital letters, as the other main effect and interaction were not significant.

constant (k), for either grass or shrub litter for the duration of the 32-week incubation in the constant soil moisture experiment (Fig. 1, Supplementary Information 2&3). Soil moisture had a significant positive effect on the rate of litter decomposition ($P < 0.001$, Fig. 1). After one week of incubation, mass loss was greatest in the 12% WFP moisture treatment. The mass loss for the 2 and 4% WFP moisture treatments did not differ from each other until week 4 for the grass and week 8 for the shrub. After 32 weeks, neither litter type had lost appreciable mass in the 2% WFP moisture treatment (mean % mass remaining = 99% for the grass and 100% for the shrub). In contrast, the mass remaining (mean ± standard error; SE, $n = 12$) in the 4% and 12% moisture treatments were 74 ± 5 and 57 ± 2% for the grass and 74 ± 4 and 54 ± 3% for the shrub, respectively. The stimulation in mass loss was greater when soil moisture changed from 2 to 4% WFP (~4 to 30% mass loss from 2 to 4% WFP; ~13% mass loss per 1% WFP increase) than from 4 to 12% WFP (~30 to 50% mass loss from 4 to 12%WFP; ~2.5% mass loss per 1% WFP increase) for both litter types. Neither soil-litter mixing and moisture interactions nor soil-litter mixing and species interactions were significant.

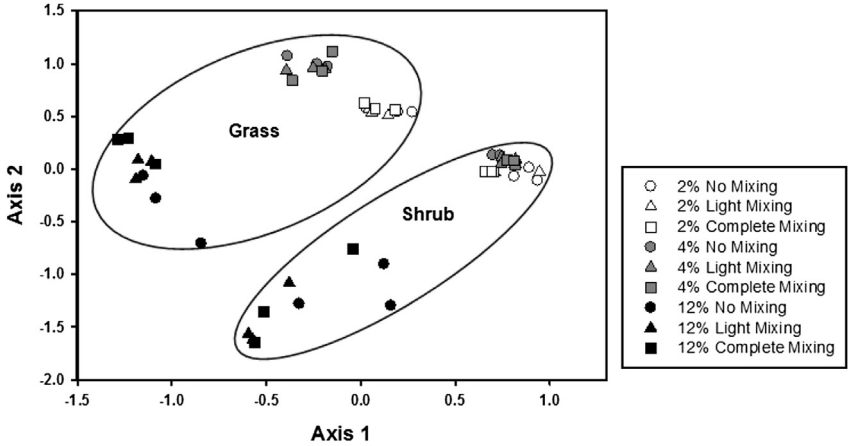

Fig. 4. Ordination of phospholipid fatty acids (PLFAs) extracted per gram litter at harvest after one week of incubation of grass and shrub litter experiencing differing soil moisture and soil-litter mixing treatments. The ordination accounted for 98.6% of the variation (axis 1, $R^2 = 0.402$; axis 2, $R^2 = 0.584$) and had a stress value of 4.49.

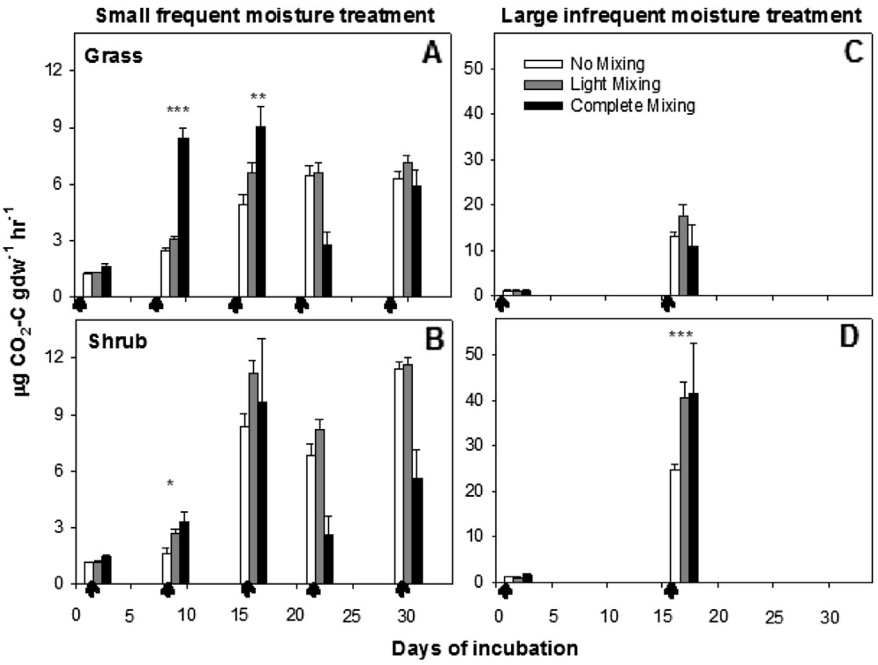

Fig. 5. Mean CO_2 production rate (SE, $n = 5$) observed within 24 h of rainfall treatments in grass (*Eragrostis lehmanniana*; A and C) and shrub (*Prosopis velutina*; B and D) litter with soil-litter mixing (No, Light, and Complete Mixing) treatments. The arrows indicate each pulse treatment. A and B are small-frequent moisture treatments that represent five separate 2 mL rainfall equivalent DI water additions throughout the 35-day incubation whereas C and D are large-infrequent moisture treatments that represents two separate 5 mL rainfall equivalent DI water additions throughout the 35-day incubation period. Note the different scale of *y*-axes for small and large moisture treatments. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$ from one-way ANOVA.

3.1.2. CO_2 production

Temporal patterns of cumulative CO_2 production responses to moisture treatments were generally similar for the grass and shrub litter (e.g., greatest in 12% WFP and least in 2% WFP soil moisture treatments; Fig. 2), but the magnitude of CO_2 production from shrub litter was approximately 4-fold greater than that from grass litter, especially at the 4 and 12% WFP levels. Cumulative CO_2 production at 32 weeks did not differ across the soil-litter mixing treatments, except for the 12% WFP soil moisture treatment for shrub litter. In this case, cumulative CO_2 production for 12% WFP soil moisture and shrub litter was significantly lower in the '*No Mixing*' treatment compared to the '*Light Mixing*' and '*Complete Mixing*' treatments ($F_{2,15} = 160.5$, $P < 0.001$).

In contrast to later stages of the incubation, cumulative CO_2 production during the first week was often greater in grass than shrub litter, and corresponded with visible proliferation of fungal hyphae by the second day of incubation for grass litter and the fourth day for shrub litter (H. Lee pers. obs.). These visible patterns were accompanied by sharp increases in CO_2 production in the 4 and 12% WFP soil moisture treatments (Supplementary Information 4). The degree of soil-litter mixing had no significant effect on cumulative CO_2 production in the 2 and 12% WFP soil moisture treatments during week one (Fig. 2 insets). In contrast, cumulative CO_2 production in the 4% WFP soil moisture treatment increased with soil mixing for grass litter ($P < 0.01$), but decreased with soil mixing for shrub litter ($P < 0.05$).

3.1.3. Microbial responses

Total extractable phospholipids (total PLFAs) present after one week were negatively correlated with soil moisture treatment, with total PLFAs in the 4 and 12% WFP soil moisture treatments being significantly lower than those in the 2% WFP soil moisture treatment (Fig. 3A and B). Total PLFA for both grass and shrub samples were lowest in the 12% WFP samples that experienced soil-mixing: *Light* and *Complete Mixing* treatment values were similar to each other and lower than *No Mixing* treatment samples. Soil mixing effects on PLFA were also evident for the 2% WFP soil moisture treatment for both species; again, soil-litter mixing reduced total PLFA concentrations (Fig. 3A and B).

The NMS ordination of phospholipid profiles showed distinct patterns. Grass litter profiles clustered separately from those of shrub litter; and samples from the 2 and 4% WFP soil moisture treatments clustered together and separately from those associated in the 12% WFP soil moisture treatment (Fig. 4). Lipid profiles of grass litter showed some separation between the 2 and 4% WFP soil moisture treatments, but this trend was much less evident in the shrub litter. Lipid profiles moved to more negative ordination space with increasing soil moisture, and individual FAMEs associated with this region of the ordination included 14:0 (a general marker), 18:1n9c and 18:2n6c (each known to be produced by plants and fungi), and 18:1n7c (a gram negative bacterial marker but also found in our initial litter samples; Supplementary Information 5; Vestal and White, 1989; Zelles, 1997). All of these markers had greater relative abundance in the 12% WFP moisture treatment compared to the 2 and 4% WFP treatments, except for 18:2n6c for grass, where the relative abundance in the 2 and 12% WFP treatments was similar and higher than in the 4% WFP treatment (data not shown). There was no clear separation among soil mixing treatments at any moisture level for either litter type, which was confirmed by multi-response permutation (MRPP) comparisons. Although there was some visual separation of *No Mixing* vs. *Mixed* treatments in the 12% WFP treatment in both litter types, the MRPP comparisons were not significant for either species using a Bonferroni adjusted $P < 0.017$.

Trends in bacterial:total PLFA abundance differed between the two plant species (Fig. 3C and D). The bacterial:total PLFA ratio increased with increasing soil moisture for both the grass and shrub, but the response was most pronounced in the grass litter.

Soil mixing also increased bacterial:total PLFA ratios, but only in the shrub litter and only in the 12% WFP soil moisture treatment (Fig. 3D).

3.2. Litter decomposition in the moisture pulse experiment

Rates of CO_2 production following small-frequent water pulses were lower on a per event basis (range = 1–12 μg CO_2–C gdw^{-1} h^{-1}) than those receiving the large-infrequent pulse (range = 1–40 μg CO_2–C gdw^{-1} h^{-1}, Fig. 5). For both water pulse treatments, the first pulse had little effect on CO_2 production, and the second pulse showed varying effects depending on pulse size and litter type. CO_2 production in the small-frequent watering treatment was typically greater under the two soil-litter mixing treatments (*Light* and *Complete Mixing* treatments) than in the *No Mixing* treatment. This pattern held within the small pulse treatments for the second and third rainfall pulses for grass litter (second pulse: $F_{2,12} = 82.54$, $P < 0.001$; third pulse: $F_{2,12} = 9.23$, $P = 0.003$) and for the second pulse for shrub litter (second pulse: $F_{2,12} = 4.34$, $P = 0.038$; third pulse: n.s.). By the fourth small water pulse, CO_2 production had increased in the *No Mixing* treatment and there was no consistent soil-litter mixing effect. On the other hand, the rate of CO_2 production in the large-infrequent pulse treatment showed a significant soil-litter mixing effect in the second rainfall pulse treatment for shrub litter ($F_{2,12} = 83.84$, $P < 0.001$). However, the soil-litter mixing effect was not statistically significant for grass litter and the CO_2 production per event was overall much lower for grass litter than shrub litter.

4. Discussion

It has been well established that decomposition rates of buried litter exceed those of litter on the surface and that burial of litter negates many abiotic drivers and enhances the number and diversity of microarthropods involved in litter transformations (Santos et al., 1984; Moorhead and Reynolds, 1989). However, we know little about the rates and processes by which litter becomes buried or how much decomposition might occur during the burial process. When insects or small mammals transport litter belowground, burial may be instantaneous. However, in many cases litter deposited on the soil surface mixes with soils being moved by wind and water to form a litter-soil matrix, a first step in a longer burial process. Several field studies have shown a significant correlation between the extent of soil-litter mixing and the rate of litter decomposition (Throop and Archer, 2007; Hewins et al., 2013), but were unable to identify the mechanisms involved. Our controlled laboratory experiment sought to determine how soil-litter mixing effects on decomposition play out with respect to litter type (grass vs. shrub), patterns and amounts of soil moisture availability, and their combined effects on early microbial colonization. In combination, our results suggest that soil moisture strongly controlled decomposition, and that soil-litter mixing effects 1) were minor in the constant moisture experiment, interacting with moisture availability and plant species in complex ways, 2) are likely to be more important when precipitation events are small and delivered in discrete pulses, and 3) may be magnified by factors not manipulated or accounted for in our experiments. The latter inference is based on comparisons with field studies where there is evidence of long-term soil-litter mixing effects (e.g., Throop and Archer, 2007; Hewins et al., 2013).

4.1. Influences of soil-litter mixing

Our hypothesis that soil-litter mixing positively influences the rate of litter decomposition by enhancing microbial colonization and activity was not strongly supported by our data. Significant, but variable, effects were largely confined to the early stages of decomposition or with fluctuating soil moisture. Although total PLFA after one week of incubation was reduced in *Light* and *Complete Mixing* soil-litter treatments for both 2 and 12% moisture treatments in both litter types, these reductions suggest that *de novo* bacterial lipid production was less responsive than plant lipid degradation (as total PLFA reflects both microbe and plant lipids). In fact, total bacterial PLFA was not significantly affected by soil-litter mixing for either litter type at any water treatment (data not shown). Therefore, although bacterial:total PLFA ratios increased with soil-litter mixing in the 12% WFP shrub litter treatment (Fig. 3D), this effect was primarily driven by the reduction in total PLFA. Unfortunately, we could not clearly ascertain fungal responses to soil-litter mixing owing to the fact that common fungal lipid biomarkers (e.g., 18:2n6c) were present in the initial shrub and grass litter. Hence, the abundance of these lipid biomarkers reflects a balance between the decomposition of plant lipids and the production of new microbial lipids.

Inconsistencies between the responses of the two litter types to soil-litter mixing at both the early and late stages of decomposition may reflect differences in microbial colonization and subsequent decomposition rates associated with differences in grass and shrub litter quality (e.g., much greater initial N content for the shrub [2.7%] than the grass [0.7%]). Given the observed differences in visible fungal colonization times between the two litter types and the clear separation between grass and shrub lipid profiles after one week of incubation, it is possible that the CO_2 production differences, in both the short- and long-term, reflect temporal offsets in colonization, differences in microbial communities overall, or changes in the degree to which C and N are limiting to microbes during decomposition. For example, in the 4% WFP treatment, CO_2 production in the first week of incubation was greatest in the *Complete Mixing* treatment for grass litter, but was greatest in the *No Mixing* treatment for shrub litter. Interestingly, the lipid data showed no significant soil-mixing effect for either litter type in that moisture treatment at that point in time. The contrasting results of CO_2 production and PLFAs for the two litter types and across the moisture and soil-litter mixing treatments illustrate the complexity of these responses and potential difficulty in inferring the relative importance of co-occurring drivers of early stage decomposition. It is possible that with additional time these different metrics of decomposition for the two litter types would have become more similar.

4.2. Pulse controls

Results from the water pulse experiment support our hypothesis that soil-litter mixing effects would be most pronounced under variable moisture conditions when soil-litter mixing would be most likely to enhance microbial activity by buffering litter from moisture deficits. Under field conditions, even a few millimeters of surface soil can buffer temperature, moisture, and radiation extremes (Garcia-Pichel and Belnap, 1996; Whitford, 2002) and high potential evapotranspiration levels typically lead to rapid losses of moisture at the soil surface (Loik et al., 2004) where litter is concentrated. Litter in the *No Mixing* treatment is therefore likely to have dried more rapidly when incubation jars were opened in the post-pulse period in comparison to the completely mixed treatment where litter was fully covered by soil. Increased CO_2 production after water pulses in both small-frequent and large-infrequent regimes of light and completely mixed soil-litter combinations relative to the *No Mixing* treatment suggest that soil-litter mixing expanded the window of opportunity for microbial activity and that physical effects of repeated wetting-drying may have

increased litter susceptibility to microbial processing. Considerable work in dryland systems indicates that the size and temporal distribution of precipitation pulses are often more important than total precipitation in controlling biological processes (e.g., Austin et al., 2004, 2009; Belnap et al., 2004; Cable et al., 2008; Barron-Gafford et al., 2012). Our study provides evidence that pulses may interact with soil-litter mixing to influence dynamics of surface processes such as decomposition in drylands. However, soil-litter mixing mediation of decomposition responses to rainfall pulses will likely depend on soil properties that influence water holding capacity and availability and the spatial heterogeneity of water resources (e.g., texture, bulk density, organic matter content).

4.3. Soil moisture effects on decomposition

Biological processes such as soil respiration and decomposition are generally assumed to be strongly controlled by moisture availability in drylands. Our results from different soil moisture treatments followed these expectations with positive responses to increasing soil moisture being more dramatic from 2 to 4% WFP than from 4 to 12% WFP in the constant soil moisture experiment. This non-linear response suggests that small increases in water availability under dry conditions will increase decomposition rates more so than larger rainfall events received under moister conditions. Our observation of a non-linear response of litter decomposition to soil moisture adds to a growing body of literature on the topic of controls over C mineralization in soils and litter, which illustrates a wide range of potential moisture response functions: linear (Epron et al., 1999), quadratic (Tang and Baldocchi, 2005), exponential (Davidson et al., 1998), logarithmic (Raich et al., 2002), and hyperbolic (Hanson et al., 1993). Although decomposition rates were linearly correlated with annual precipitation in one field study (Yahdjian et al., 2006), other studies have found no consistent relationship between annual precipitation and decomposition rate (Vanderbilt et al., 2008; Austin, 2011). The latter may reflect the long-term manifestation of the non-linear relationships observed in our study, along with the fact that annual precipitation inputs are greatly modified by canopy interceptions losses, topographic runoff/run-on relationships, and local differences in infiltration/percolation rates. Furthermore, soil moisture controls over decomposition typically act in concert with other factors (e.g., co-controls by UV radiation and precipitation frequency, Smith et al. 2010). In our experiments, the influence of other factors was minimal as environmental conditions (e.g., temperature and radiant energy) were maintained at constant levels.

4.4. Implications for interpreting field results

The relatively limited importance of soil-litter mixing in our controlled studies contrasts with results obtained from field studies and provides important insights into potential mechanisms at play. Field studies have shown an increase in the importance of soil-litter mixing throughout the first year of decomposition (Throop and Archer, 2007; Hewins et al., 2013). We suggest two plausible explanations for these contrasting results from field and lab studies: 1) soil-litter mixing effects are minimized under benign environmental conditions (e.g., stable, near-optimal temperatures for microbial activity and lower evaporative water loss in the laboratory experiments than occur in typical field conditions with extreme day–night temperature fluctuations and radiation regimes and above-optimal surface temperatures) and 2) additional drivers may be at play under field conditions that would influence the importance of soil-litter mixing on litter decomposition (e.g., physical abrasion of litter by soil particles or interactions with UV photodegradation). The former explanation is consistent with the high rate of decomposition measured in the 12% WFP treatment of the constant moisture laboratory study ($K > 1.0\ y^{-1}$ for both species) relative to dryland field studies (e.g., $K = 0.55–0.73\ y^{-1}$ for mesquite litter and $0.28–0.55\ y^{-1}$ for grass litter; Throop and Archer, 2007). The latter explanation is consistent with the notion that radiant energy regimes and erosional processes in drylands, neither of which were at play in our laboratory experiments, interact to influence litter decomposition (Barnes et al., 2012). Microclimatic buffering associated with soil-litter mixing may be more important in governing microbial decomposition under field conditions where UV levels may be high, where daytime soil surface temperatures are substantially higher than ambient air temperature (Rosentreter and Belnap, 2003), and where soil moisture is highly variable and characterized by long dry periods punctuated by rainfall pulses that allow short bursts of biological activity (Moorhead and Reynolds, 1989; Sala et al., 1992; Huxman et al., 2004).

5. Conclusions

Our results suggest that soil-litter mixing effects on litter decomposition processes are minimal under controlled environment conditions, with subtle effects varying with time, soil moisture conditions, and litter type. The influences of soil-litter mixing were more pronounced when moisture was delivered in discrete pulses than under constant moisture conditions. Our lack of strong responses to soil-litter mixing under controlled and benign environment conditions suggests the primary influence of soil-litter mixing under field conditions may be through attenuation of environmental extremes related to temperature, solar radiation, and litter moisture.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2014.01.027.

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