



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 CO₂ 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 C₄ 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 N₂-fixing C₃ 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

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