The Influence of Solar Radiation, Temperature, Humidity and Water-Vapor

Sorption on Microbial Degradation of Leaf Litter in the Sonoran Desert

by

Alexander Richard Tomes

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Graduate Supervisory Committee:

Thomas Day, Chair
Ferran Garcia-Pichel
Becky Ball
Sharon Hall
Robert Roberson

ARIZONA STATE UNIVERSITY

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ABSTRACT

Decay of plant litter represents an enormous pathway for carbon (C) into the atmosphere but our understanding of the mechanisms driving this process is particularly limited in drylands. While microbes are a dominant driver of litter decay in most ecosystems, their significance in drylands is not well understood and abiotic drivers such as photodegradation are commonly perceived to be more important. I assessed the significance of microbes to the decay of plant litter in the Sonoran Desert. I found that the variation in decay among 16 leaf litter types was correlated with microbial respiration rates (i.e. CO_2 emission) from litter, and rates were strongly correlated with water-vapor sorption rates of litter. Water-vapor sorption during high-humidity periods activates microbes and subsequent respiration appears to be a significant decay mechanism. I also found that exposure to sunlight accelerated litter decay (i.e. photodegradation) and enhanced subsequent respiration rates of litter. The abundance of bacteria (but not fungi) on the surface of litter exposed to sunlight was strongly correlated with respiration rates, as well as litter decay, implying that exposure to sunlight facilitated activity of surface bacteria which were responsible for faster decay. I also assessed the response of respiration to temperature and moisture content (MC) of litter, as well as the relationship between relative humidity and MC. There was a peak in respiration rates between 35-40°C, and, unexpectedly, rates increased from 55 to 70°C with the highest peak at 70°C, suggesting the presence of thermophilic microbes or heat-tolerant enzymes. Respiration rates increased exponentially with MC, and MC was strongly correlated with relative humidity. I used these relationships, along with litter microclimate and C loss data to estimate the contribution of this pathway to litter C loss over 34 months. Respiration was

responsible for 24% of the total C lost from litter – this represents a substantial pathway

for C loss, over twice as large as the combination of thermal and photochemical abiotic

emission. My findings elucidate two mechanisms that explain why microbial drivers were

more significant than commonly assumed: activation of microbes via water-vapor

sorption and high respiration rates at high temperatures.

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1. DISSERTATION INTRODUCTION

Litter Decay in Drylands

Drylands cover over 45% of the world's land surface and contain an estimated 15-27% of the world's total soil organic carbon (C: Lal 2004; Schimel 2010). Furthermore, drylands are expected to expand (Huang et al. 2016), increase in average annual temperature by 1-3°C, and decrease in overall soil moisture and average relative humidity (RH) within the coming decades (Seager et al. 2007; Stocker et al. 2013). Therefore, understanding the processes that contribute to C cycling in drylands is essential in a changing climate.

The decay of plant litter and soil organic matter contributes more C to the atmosphere annually than fossil fuel combustion (Gholz et al. 2000; Schlesinger and Andrews 2000), making it a significant pathway in the global C cycle (Raich and Schlesinger 1992). Thus, identifying the mechanisms that influence litter decay are necessary to accurately model the global C cycle. Litter decay rates in mesic systems are well predicted by empirical models that use climatic factors and litter chemistry (Meentemeyer 1978; Parton et al. 2007; Wieder et al. 2009). However, these models consistently underpredict rates of decomposition in drylands (Whitford 1981; Moorhead and Reynolds 1989; Austin and Vivanco 2006; Adair et al. 2008; Bonan et al. 2013). These models primarily focus on factors that drive microbial degradation of litter to predict decay, thus, the mechanisms driving litter decay in drylands are not well

understood, limiting our ability to model this component of the C cycle (Parton et al. 2007; Adair et al. 2008).

The idea of sunlight accelerating or driving litter decay was first proposed by Pauli (1964) over 50 years ago but received relatively little attention in drylands the next 40 years (Moorhead and Reynolds 1989; MacKay et al. 1994). It was not until the early 2000s that the effects of sunlight on the decay of plant litter became a major focus (Austin and Vivanco 2006; Gallo et al. 2006; Day et al. 2007). The decay of litter caused by exposure to sunlight is termed photodegradation; this includes both direct abiotic decay by photomineralization as well as the subsequent accelerated decay of this litter by microbes. The latter mechanism, termed photofacilitation (Austin et al. 2016), is brought about by the photopriming (Foereid et al. 2010, 2018; Barnes et al. 2015) of litter by sunlight. Both processes, abiotic photomineralization and photofacilitation of microbial degradation of litter, can be significant mechanisms of decay (Austin and Vivanco 2006; Day et al. 2007, 2015, 2018; Austin and Ballaré 2010; Brandt et al. 2010; Rutledge et al. 2010; King et al. 2012; Austin et al. 2016). For example, Day and Bliss (2020) found that the photochemical emission (i.e. abiotic photomineralization) is responsible for 10% of the C lost from litter over a 34-month decay experiment.

Early experiments into photodegradation found that the (UV)-B waveband (280-320 nm) was at least partly responsible for the decay of plant litter (Austin and Vivanco 2006; Day et al. 2007). More recently, many studies have found that UV-A (320-400 nm) and blue solar radiation (≈400-550 nm) are also large drivers of litter decay (Brandt et al. 2009; Austin and Ballaré 2010; Austin et al. 2016; Day et al. 2018; Pieristè et al. 2019). For example, Day and Bliss (2019) found that UV-B, UV-A and blue solar radiation were

responsible for 9, 61 and 30%, respectively, of the abiotic photodegradation of litter (i.e. photochemical emission of CO_2). Thus, both the solar UV and blue radiation spectrum accelerate the decay of plant litter.

Effects of Sunlight Exposure on Microbial Activity and Abundance

The effects of sunlight on microbial activity in litter are poorly understood in drylands (Barnes et al. 2015). In some studies, sunlight or UV radiation has been found to accelerate microbial activity in litter (Gallo et al. 2009; Foereid et al. 2010; Wang et al. 2015a; Baker et al. 2015; Gliksman et al. 2017; Day et al. 2018). Exposure to sunlight can breakdown recalcitrant compounds such as lignin (Gehrke et al. 1995; Gallo et al. 2006, 2009; Day et al. 2007; Austin and Ballaré 2010) or cellulose and hemicellulose (Brandt et al. 2010; Lin and King 2014; Baker et al. 2015; Lin et al. 2015; Day et al. 2018; Esch et al. 2019). Exposure to UV radiation or sunlight can also lead to higher concentrations of sugars (Austin et al. 2016) and water-soluble DOC (dissolved or water-soluble organic C: Gallo et al. 2006; Feng et al. 2011; Wang et al. 2015; Day et al. 2018), providing more labile C for microbes. Day et al. (2018) found that microbial activity (i.e. respiration) in sunlit litter was strongly correlated with concentrations of water-soluble organic compounds. This suggests that exposure to sunlight promotes microbial activity, via providing more labile compounds, but little is known about the microbial groups involved.

Exposure to sunlight can also have direct detrimental effects on microbes. Ultraviolet radiation, specifically UV-B radiation, can negatively affect the growth and survival of bacteria and fungi as well as the production and germination of spores

(Caldwell et al. 2007; Barnes et al. 2015; Erdenebileg et al. 2018). Bacterial and fungal

species can vary in their sensitivity to UV radiation (Moody et al. 1999; Kadivar and

Stapleton 2003) and as a result the microbial community can shift in response to UV

radiation (Johnson 2003; Pancotto et al. 2003; Zepp et al. 2007).

The results vary in studies examining the effect of UV radiation on microbial

abundance in litter. For example, some have found lower abundances of bacteria and

fungi in litter exposed to UV radiation in the laboratory (Brandt et al. 2009), while others

found no effects on the abundance of either group (Wang et al. 2015a). In the field,

Pancotto et al. (2003) found that exposure to solar UV radiation reduced the abundance

of some fungal species but had no effect on the bacterial species, while Austin and

Vivanco (2006) found that exposure to sunlight decreased the abundance of both bacteria

and fungi. Also in the field, Baker and Allison (2015) found that exposure to solar UV

radiation had no effect on bacterial abundance but lead to higher fungal abundance.

Hence, no consistent patterns have emerged concerning the influence of sunlight on

bacterial or fungal abundance in litter. Furthermore, to my knowledge, no studies have

assessed how sunlight exposure influences microbial abundance in conjunction with

microbial activity (e.g. respiration) and litter mass loss.

Microbial Activity in Drylands

The microbial decay of plant litter is a major process influencing terrestrial CO_2

fluxes and ecosystem C storage (Couˆteaux et al. 1995; Aerts 1997; Fierer et al. 2005;

Schlesinger and Bernhardt 2013). Drylands represent one of the most underrepresented

ecosystems in terms of microbial respiration studies (Cable et al. 2011). Because of

limited water availability, extreme temperatures and high UV irradiance, microbes have often been perceived to play a small role in litter decay in drylands. However, microbial activity (i.e. microbial respiration of litter) is strongly correlated with the mass loss of litter in the Sonoran Desert (Day et al. 2018), suggesting that microbes can be a significant driver of litter decay, but the factors that control microbial activity in drylands are poorly understood.

High RH (i.e. > 75%) in the absence of rainfall, can accelerate microbial activity, measured as CO_2 respiration, in standing litter of marshes and wetlands (Newell et al. 1985; Kuehn et al. 2004), promote fungal growth on litter (Jacobson et al. 2015) and elicit litter mass loss in drylands (Dirks et al. 2010; Gliksman et al. 2017, 2018; Wang et al. 2017b; Day et al. 2018; Evans et al. 2019). For example, Dirks et al. (2010) found that microbial decay in the absence of rainfall and photodegradation was responsible for 18% of litter mass loss which constituted 50% of the annual mass loss and they attributed this to periods of high RH. Furthermore, at three sites in Mediterranean drylands, Gliksman et al. (2017) found that high RH during the night resulted in increased litter moisture content that lead to significant microbial activity and faster litter decay.

High RH conditions may be more common in drylands than previously thought. For example, Day et al. (2018) found that RH of air around ground surface litter exceeded 90% for over 11% of the time over three years in the Sonoran Desert. This suggests that microbial activity in litter may occur more often than expected (Day et al. 2018). However, the contribution of microbial decay to C loss in this system is unknown.

Microbial respiration in soil usually peaks between temperatures of 30-40°C in hot ecosystems (i.e. annual average temperature >18°C: Cable et al. 2011; Tucker and

Reed 2016) and between 22-35°C in cooler systems (Carey et al. 2016). However, some have found soil and litter respiration to increase up to 50°C in both cool and hot systems (Pietikäinen et al. 2005; Richardson et al. 2012; Birgander et al. 2013; Carey et al. 2016). Gonzalez et al. (2015) found that soils from latitudes below 40° N had peaks of extracellular enzyme activity between 55 and 75°C, past the temperature enzymes were thought to become inactive or denature (Koffler et al. 1957; Rainey et al. 2005). Furthermore, Santana and Gonzalez (2015) state that thermophilic bacteria are abundant in warm soils and have peak growth rates between 50 to 70°C. The majority of research on the temperature response of microbial respiration of soils and litter has been conducted in mesic, temperate systems. To my knowledge, the temperature response of microbial respiration in litter in drylands has received little attention - this could be particularly interesting in hot systems such as the Sonoran Desert, where temperatures of litter on the soil surface commonly exceed 50°C, and occasionally 70 or even 80°C (Day et al. 2019).

Traits that correlate with decomposability of litter by microbes in mesic systems (referred to hereafter as "litter quality" traits), such as C:N or lignin:N ratios, (Berg and Staaf 1980; Melillo et al. 1982; Taylor et al. 1989; Tian et al. 1992; Aerts 1997; Aerts and De Caluwe 1997) are usually not correlated with litter decay in drylands (Day et al. 2018). While far less studied than traditional litter quality traits, the rate of water-vapor uptake (i.e. sorption) of litter could conceivably explain differences in litter microbial activity and decay rates of litter in drylands (Dirks et al. 2010; Gliksman et al. 2017; Wang et al. 2017b). For example, Dirks et al. (2010), in Mediterranean drylands, found that 2-hour water-vapor sorption rates of seven litter types (measured in the laboratory)

explained much of the variation in the decay of litter over a subsequent four-month field experiment. Thus, it is likely that the rate of water-vapor sorption, which varies among litter types, can have a large influence on microbial activity and subsequent decay.

Description of Dissertation

My dissertation consists of five chapters. A general introductory chapter followed by three chapters that are structured as stand-alone publishable manuscripts and a general summary chapter.

Chapter 1: Dissertation introduction

This chapter introduces plant litter decay in drylands. It briefly reviews the history of litter decay research in drylands, the effects of sunlight on litter decay and microbes and gaps in knowledge.

Chapter 2: Water-vapor sorption rates help explain the decay of a diverse set of Sonoran Desert leaf litter

The litter traits that influence microbial degradation in drylands are unresolved, but recent research suggests that the uptake of atmospheric water-vapor by litter could explain some of the variation among litter types. I examined the decay of a diverse set of 16 leaf litter types over 22 months on the soil surface of the Sonoran Desert, USA, and measured water-vapor sorption rates of litter before and after decay to see if this trait explained differences in decay or microbial respiration among litter types.

Research questions: I investigated (1) if water-vapor sorption rates have a large influence on respiration rates, and as such, I assessed whether they explained differences in respiration rates among litter types, (2) if other litter traits were correlated with sorption rates and (3) I assessed how respiration and water-vapor sorption rates changed with litter age.

Chapter 3: Ultraviolet and blue solar radiation accelerate the bacterial decay of Sonoran Desert leaf litter

Little research has assessed what microbial groups are involved in dryland litter decay, especially in the context of photodegradation and photofacilitation. In this study, I monitored the mass loss and microbial respiration of five litter types under three contrasting solar radiation treatments over 22 months in the Sonoran Desert. I also measured the abundance of bacteria and fungi in whole litter samples, as well as on the surface of litter, to assess their relative abundance in litter, and whether exposure to UV and blue sunlight influenced their abundance in litter.

Research questions: I investigated (1) if litter would decay faster in full sunlight than litter filtered from UV or UV and blue sunlight (i.e. photodegradation), (2) if fungi would be generally more abundant in litter and (3) if exposure to sunlight would shift the relative abundance in favor of bacteria because it would provide higher quality, photoprimed litter.

Chapter 4: Response of microbial respiration of Sonoran Desert leaf litter to temperature and vapor-induced moisture content and its significance to C loss

The response of litter microbial respiration to temperature and vapor-induced MC is not well characterized in drylands. I examined the response of microbial respiration from 16 leaf litter types to 14 temperatures ranging from 5 to 70°C. I selected four of these litter types and examined the response of microbial respiration to MC. I also monitored the RH and MC of one litter type continuously over 30 days and the RH and MC of four types over four contrasting months of the year to characterize the relationship between RH and MC of surface litter in the field. I used these findings to estimate the contribution of microbial respiration of the same four litter types to C loss from litter in a previous litter decay experiment (Day et al. 2018).

Research questions: I investigated (1) if the response of microbial respiration to MC would be similar to other ecosystems, (2) if the high temperatures of this system would promote respiration at higher temperatures than cooler systems, (3) the relationship between litter MC and RH in the field and (4) if water-vapor driven microbial respiration from litter would contribute more to litter C loss than thermal abiotic and photochemical emission from litter.

Chapter 5: Dissertation summary

This chapter summarizes the main findings revealed in each of the chapters that comprise my dissertation. It emphasizes the contributions of my research to our current knowledge of dryland litter decay and how the work impacts the direction of future research on the topic.

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2. WATER-VAPOR SORPTION RATES HELP EXPLAIN THE DECAY OF A DIVERSE SET OF SONORAN DESERT LEAF LITTER

Abstract

Photodegradation can be a significant driver of plant litter decay in drylands, and there is growing evidence that microbial degradation, both in conjunction with photodegradation or alone, can also be a significant driver. The litter traits that influence microbial degradation in drylands are unresolved, but recent research suggests that the uptake of atmospheric water vapor by litter could explain some of the variation among litter types. We examined the decay of a diverse set of 16 leaf litter types over 22 months on the soil surface of the Sonoran Desert, USA, and measured water-vapor sorption rates of litter before and after decay to see if this trait explained differences in decay or microbial respiration among litter types. Decay constants varied considerably among the litter types ranging from 0.16 to 0.85 y^{-1} after 22 months in full sunlight. Traditional indices of litter quality (e.g. C:N or lignin:N ratios) failed to predict differences in decay constants. Water-vapor sorption rates of initial litter over 2 h explained 34 and 26% of the variation in decay of litter in full sunlight and filtered from UV and blue solar radiation, respectively. The 2-h sorption rate also explained 32% of the variation in microbial respiration rates of initial litter. Sorption rates over 2 h were correlated with the specific leaf area and water-soluble fractions of litter, but not cell wall chemistry such as lignin or cellulose concentrations. Unexpectedly, sorption rates were not correlated with litter wax concentrations. The 2-h sorption rate of decayed litter was faster than initial litter in 14 of the 16 litter types. Fragmenting litter into pieces accelerated sorption rates of litter, but this alone did not explain the faster sorption rates of decayed litter. Water-soluble fractions of initial litter were also correlated with decay and explained 36 and 27% of the variation in decay of litter in full sunlight and filtered from UV and blue radiation,

respectively. The litter traits that appear to explain decay and microbial respiration in drylands differ from those in more mesic systems. Water-vapor sorption rates of litter were useful in explaining some of the variation in decay and microbial respiration of litter.

Introduction

The decay of plant litter and soil organic matter contributes more carbon (C) to the atmosphere annually than fossil fuel combustion (Gholz et al. 2000; Schlesinger and Andrews 2000). Drylands cover over 45% of the world's land surface and contain an estimated 15-27% of the world's total soil organic C (Lal 2004; Schimel 2010). Litter decay rates in mesic systems are well predicted by empirical models that use climatic factors and litter chemistry (Parton et al. 2007; Wieder et al. 2009). However, these models consistently underpredict rates of decomposition in drylands (Whitford 1981; Moorhead and Reynolds 1989; Austin and Vivanco 2006; Adair et al. 2008; Bonan et al. 2013). These models primarily focus on factors that drive microbial degradation of litter to predict decay. Photodegradation of plant litter, defined here as the abiotic and biotic effects resulting from exposure to solar radiation, is also a significant driver of litter decay in drylands (Austin and Vivanco 2006; Gallo et al. 2006; Day et al. 2007, 2015; Rutledge et al. 2010). Photodegradation not only contributes directly to litter decay, but likely often makes litter more labile for microbes via photopriming (Gallo et al. 2009; Austin and Ballaré 2010; Foereid et al. 2010; Barnes et al. 2015; Austin et al. 2016; Day et al. 2018; Lin et al. 2018).

A common perception is that because liquid water is uncommon in drylands, microbial activity is limited, and microbes are not a large driver of litter decay. However, microbial activity can strongly influence litter decay in drylands (Dirks et al. 2010; Gliksman et al. 2017, 2018; Day et al. 2018), although the factors that control microbial activity in drylands are poorly understood. Traits that correlate with decomposability of litter by microbes in mesic systems (referred to hereafter as "litter quality" traits), such as

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C:N or lignin:N ratios (Berg and Staaf 1980; Melillo et al. 1982; Taylor et al. 1989; Tian et al. 1992; Aerts 1997; Aerts and De Caluwe 1997), are usually not correlated in drylands (Day et al. 2018).

While far less studied than litter quality traits, the rate of water-vapor uptake (i.e. sorption) of litter could conceivably explain differences in litter microbial activity and decay rates of litter in drylands (Dirks et al. 2010; Gliksman et al. 2017; Wang et al. 2017c). At high relative humidity (RH), litter decay is significant (Daubenmire and Prusso 1963), and high RH conditions may be more common in drylands than previously thought. For example, Day et al. (2018) found that RH of air around ground surface litter exceeded 90% for over 11% of the time over three years in the Sonoran Desert of central Arizona, USA. High RH, in the absence of rainfall, can accelerate microbial activity, measured as CO_2 respiration, in standing litter of marshes and wetlands (Newell et al. 1985; Kuehn et al. 2004), as well as fungal growth on litter (Jacobson et al. 2015) and litter mass loss in drylands (Dirks et al. 2010; Gliksman et al. 2017, 2018; Wang et al. 2017b). For example, at three sites in Mediterranean drylands, Gliksman et al. (2017) found that nighttime water-vapor sorption resulted in increased litter moisture content that lead to significant microbial activity and faster litter decay. Additionally, Dirks et al. (2010), also in Mediterranean drylands, found that 2-hour water-vapor sorption rates of seven litter types (measured in the laboratory) explained much of the variation in the decay of litter over a subsequent four-month field experiment. Thus, it is likely that the rate of water-vapor sorption, which varies among litter types, can have a large influence on microbial activity and subsequent decay.

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Much of our understanding of how plant litter anatomy and chemistry influences litter water-vapor sorption comes from the textile and biocomposite industry through their attempts to use more environmentally friendly bio-based materials (Célino et al. 2014). Lignin is a hydrophobic compound that can act as a barrier to water-vapor sorption (Muzilla et al. 1989; Thakur et al. 2014). Cellulose, on the other hand, is a hydrophilic polymer that absorbs water-vapor quickly and can hold relatively large amounts of water (Kohler et al. 2003; Olsson and Salmén 2004; Pinkert et al. 2009; Persson et al. 2013). Hence, we would expect litter with lower concentrations of lignin or higher concentrations of cellulose to have faster water-vapor sorption rates. While some have found negative correlations between lignin concentration and water-vapor sorption rates of litter (Dirks et al. 2010; Talhelm and Smith 2018) others have not found correlations with either lignin or cellulose concentrations (Iqbal et al. 2013). Another likely predictor of vapor sorption rates is the litter surface area to dry mass ratio (specific leaf area, SLA); indeed, Talhelm and Smith (2018) found a strong correlation between SLA and water-vapor sorption rate of litter. Surprisingly, none of these researchers examined the relationship between litter wax concentrations and water-vapor sorption. Waxes limit the diffusion of water-vapor across membranes in live leaves (Holloway 1969, 1970; Koch and Ensikat 2008), and we suspect that there may be strong correlations between litter wax concentrations and vapor sorption rates.

In this study we examined the decay of a diverse set of 16 leaf litter types, representing four different growth forms, over 22 months on the soil surface of the Sonoran Desert. We measured several chemical and anatomical traits of initial litter to determine if these were useful predictors of decay. We hypothesized that water-vapor

sorption rates may have a large influence on respiration rates, and as such, we also examined whether they explained differences in respiration rates among litter types, as well as if other litter traits were correlated with sorption rates. Lastly, we assessed how respiration and water-vapor sorption rates changed as litter decayed.

Methods

Field experiments

We assessed the influence of sunlight exposure on the mass loss of 16 leaf litter types in the Sonoran Desert in Phoenix, AZ, USA following Day et al. (2018). The 16 litter types consisted of four species of four different growth forms: woody dicots, suffrutescent dicots, grasses and annuals (Table 1). The woody dicots, suffrutescent dicots and grasses were collected from May through July 2013 in central Arizona. Because of drought, annual litter wasn't available over this period and was collected in March and April the following year (2014). Additional *Larrea tridentata* litter was collected at the same time as the annuals to be included in that experiment (described below). All litter was collected as naturally senesced leaves (i.e. lacking photosynthetic pigments) that were attached to standing branches/stems from several individuals of each species. Litter was air-dried (22°C at 10-20% RH) at least 30 d and sorted to remove non-leaf parts.

Litter was placed in envelopes (10 x 10 cm) whose tops were constructed of filter material that either (1) transmitted all solar wavebands (i.e. transmitted >80% of solar UV and visible radiation), using Aclar Type 22A filters (Proplastics, Linden, NJ, USA) which we refer to as the "Full Sun" treatment or (2) absorbed most solar UV and low-wavelength visible radiation through the blue waveband (i.e. having a sharp cutoff with 50% transmittance at 545 nm, using Amber UV filters (UVPS, Chicago, IL, USA) which we refer to as the "No UV/blue" treatment. Envelope bottoms were 153-μm mesh screening (Nitex cloth, Wildlife Supply, Buffalo, NY, USA). Each envelope received 0.88-2.39 g (± 0.05 g) of air-dried litter, depending on litter type, which corresponded to

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a total litter surface area of ≈80% of the surface area of the envelope. Envelopes of the litter types collected in 2013 (woody dicots, suffrutescent dicots, grasses) were deployed in a randomized block design involving 12 litter types x 2 radiation treatments x 6 collection times x 8 replicates in unshaded level areas void of shrubs ≥1 m from plot edges, in a conservation area at the Desert Botanical Garden, Phoenix, AZ, USA. We refer to this as Experiment 1. Experiment 1 is part of a longer litter decay experiment reported by Day et al. (2018); here we used only six of the litter envelope collection times and two of the radiation treatments of that experiment to allow us to have a more robust assessment with further analyses in this study. Envelopes were anchored firmly to the soil surface with nails inserted through the corners. Envelopes were placed in the field on 16 December 2013 and collected after 67, 135, 196, 327, 492 and 634 d (11 September 2015). Envelopes of the litter types collected in 2014 (annuals) along with litter of *L. tridentata* were added to plots of Experiment 1 on 11 December 2014. We refer to this as Experiment 2. In Experiment 2 we added 4 replicates of each litter type/radiation treatment combination to each plot of the 8 plots in Experiment 1. Eight replicate envelopes of each litter type/treatment combination (1 from each of the 8 plots) were collected after 132, 274, 496 and 683 d (24 October 2016) in Experiment 2. Our rationale for including *L. tridentata* in Experiment 2 was to include a common litter type to both Experiments – if decay rates of this litter were similar over the two experiments, it would support our objective of combining results from these experiments for further analyses. Following collection, litter envelope contents were gently poured onto white paper, and extraneous material was removed. The remaining litter sample contained litter along with any soil/microbial film that adhered to its surface. The sample was oven dried (OD, 24 h

at 60°C), and a subsample was ashed (6 h at 550°C), and decay constants were calculated on an oven-dry, ash-free basis.

Litter microclimate

We monitored litter air temperatures over the field experiments in five extra envelopes of the Full Sun and the No UV/blue treatment containing *Simmondsia chinensis* litter placed on the ground surface adjacent to our main plots. A hygrochron temperature/humidity logger (DS1923, iButtonLink, Whitewater, WI, USA) was inserted underneath the litter inside each envelope so that it was shaded and to further minimize absorbance of solar radiation we wrapped the top and side of each hygrochron with white Teflon tape. Hygrochrons recorded litter air temperature every hour over the field experiments. Litter temperatures were summarized by examining both diel and diurnal periods and we defined the latter as hours in which the visible irradiance averaged ≥ 2 μmol m^{-2} s^{-1}. Visible irradiance was measured 1.5 m above the ground with a quantum sensor (LI-190SA, Li-COR, Lincoln, NE, USA) every minute and summarized as hourly means over the experiment with a datalogger (CR23X, Campbell Scientific, Logan, UT, USA).

Litter traits

Several traits of initial litter of each of the 16 litter types were measured following Day et al. (2018). In brief, 20 subsamples of initial litter of each type were oven dried at 60°C (48 h) and ashed at 550°C in a muffle furnace (6 h) to determine OD ash-free (organic) mass. The one-sided silhouette surface area of 20 intact pieces of initial litter of

of each type was measured with a digital scanner and the software ImageJ (Rasband 2016) and oven dried, allowing us to calculate SLA of litter (cm^2 OD g^{-1}). Carbon (C) and nitrogen (N) concentrations of initial litter were measured on 5 subsamples of each litter type with a flash combustion elemental analyzer (model PE2400, PerkinElmer, Waltham, MA), while five additional subsamples were analyzed for C fractions (lignin, cellulose, hemicellulose and neutral detergent (ND) solubles) using sequential digestion with a fiber analyzer (model 200 Fiber Analyzer, ANKOM Technology, Macdeon, NY). We also assessed the water-soluble fraction of initial litter, which we define as the component removed during heating/stirring in water for 1 h. Five subsamples (0.05 ± 0.01 g air-dried) were over dried, weighed and placed in 5 ml of nanopure water in 25-ml Erlenmeyer flasks, heated and gently stirred at 50°C on a hotplate/stirrer. After 1 h, flask contents were filtered through 10-µm polyethylene mesh and litter material recovered from the mesh was oven dried and ashed. The water-soluble fraction that was extracted was expressed as a percentage of the original OD organic mass.

Litter surface wax concentration of both initial and decayed litter were measured generally following McWhorter et al. (1990). The "decayed litter" used in all following analyses are from 634 d Experiment 1 and 683 d Experiment 2 Full Sun treatment samples. Four subsamples of each litter type, containing 24 ± 10 cm^2 one-sided silhouette surface area, were oven dried, weighed and gently stirred for 30 s in 10 ml of chloroform (CAS: 67-66-3, VWR, Radnor, PA, USA) in a 50-ml Erlenmeyer flask. Contents were poured through chloroform washed filter paper (Cat. No: 09-801C, Fisherbrand, Hampton, NH) into preweighed 20-ml scintillation vials. To insure all wax was removed from flasks, they were rinsed with an additional 5 ml of chloroform which was also

filtered into vials. Vial contents were dried under a stream of air at room temperature for 24 h and reweighed. Concentrations were expressed on a mass basis (% OD litter mass).

Microbial respiration rates were determined by measuring CO_2 emission rates from initial and decayed litter following Day et al. (2018). Initial litter was subjected to an inoculation procedure to reduce potential confounding effects attributable to differing levels of microbial colonization, following Day et al. (2018). We placed 3 g of air-dried litter of each type in coarse white Nylon mesh envelopes (20 x 20 cm) on the unshaded soil surface at the field site (see below). Envelopes were lightly misted with nanopure water from a spray bottle and this was repeated the following morning and evening, and litter was returned to the laboratory the second morning. Respiration was measured over 24 h periods in the dark at 22°C and high air RH (~75%) in 37-ml serum bottles. Evaporation from small culture tubes (50 mm L x 6 mm D) filled with nanopore water were used to increase the RH in the serum bottles. Litter did not contact the liquid water and the only source of water was vapor. Litter was air-dried (22°C and 25% RH) for 30 d, and a subsample (0.25 ± 0.02 g) from five envelopes was placed in serum bottles. Bottles were flushed with ≈400 ppm CO_2 air for 2 min, sealed with a butyl rubber septum and incubated in the dark at 22°C for 24 h. Bottles containing the water filled culture tube without litter inside were used to correct for CO_2 dissolved in water. The final CO_2 concentration in bottles was measured by withdrawing 10 ml of headspace with a gas syringe and injecting into an infrared gas analyzer (LI-6400XT, LICOR Biosciences, Lincoln, NE, USA) modified with a trace gas sampling kit, using a flow rate of 150 µmol/s. Microbial respiration rates were expressed as µg $C-CO_2$ emitted g^{-1} of OD litter h^{-1}.

Water-vapor sorption and desorption

Water-vapor sorption and desorption rates of three subsamples of initial and decayed litter of each litter type were measured with an analytical balance (Mettler Toledo AE 100, Mettler Toldeo, Columbus, OH, USA). A chamber, constructed of PVC pipe (10.5 cm inside D x 4.0 cm H) lined with Teflon tape (FEP Optically Clear Teflon Tape, CS Hyde, Lake Villa, IL, USA), and having a top of Teflon tape, enclosed the litter sample that was on the weighing pan of the balance. Three pieces of steel wire in the chamber supported an aluminum tin (7.0 cm D x 1.0 cm H) filled with either nanopore water to increase the RH in the chamber or with a saturated solution of lithium chloride (LiCl; CAS: 7447-41-8, VWR, Radnor, PA, USA) to decrease the RH. A hygrochron logger on the wire above the weighing pan was used to monitor RH and temperature in the chamber.

Litter subsamples (1.2 g ± 0.6 g OD) were dried in a desiccator for 48 h and placed on the weighing pan to determine initial mass. For initial litter, only whole intact pieces of litter were used, with the exception of grass litter types. Because of their length, grass litter was cut into ≈4-5 cm long pieces and cut ends were dipped in melted wax (covered < 2 mm of the ends) to prevent confounding effects of broken litter pieces. For decayed litter samples, all litter types consisted mostly of broken litter pieces (>75% of each sample). The aluminum tin suspended above the weighing pan was filled with 15 ml of nanopure water and litter mass was recorded every 30 min. Evaporation of water from the aluminum tin increased RH inside the chamber to 75% within 1 h, 90% within 3 h and RH thereafter remained between 91-94%. After 24 h, the water in the aluminum tin

was replaced with 15 ml of a saturated solution of LiCl and the chamber was resealed. Litter mass was recorded again every 30 min for an additional 24 h. After replacing the water with the LiCl solution, RH dropped to 35% within 0.5 h, 20% within 2 h and remained between 17-19% thereafter. Water-vapor sorption and desorption rates were expressed over 2-, 5-, 5 to 24- and 24-h periods on a mass basis (mg H_2O g^{-1} OD litter h^{-1}). Litter moisture content was expressed as a percentage of OD mass.

Because litter pieces fragment or break with decay, we examined the effect of fragmenting litter on sorption and desorption rates, specifically asking if fragmentation might explain the faster sorption of decayed litter. *Simmondsia chinensis* was chosen because (1) the 2-h sorption rates of its initial and decayed litter differed markedly, while (2) wax concentrations of initial and decayed litter were similar, thereby avoiding the potentially confounding influence of waxes on sorption rate. Intact initial litter pieces of *S. chinensis* were mechanically broken into ≈three to five pieces, similar to what was observed in decayed litter samples in the field experiment, by placing the litter between two pieces of plastic film and gently rolling a tube over the litter twice, prior to measuring sorption and desorption rates as described above.

Statistical and data analysis

One-way ANOVAs with post-hoc Tukey's HSD tests were used to compare means among litter traits and decay constants using SigmaPlot 12.5 (Systat Software, San Jose, CA, USA). To examine relationships between litter traits and decay constants, we used correlation analysis to determine significance and quantified their predictive power with linear regressions. Decay constants were calculated using the single exponential

model with the equation $X_t / X_o = e^{-kt}$, where X_o and X_t are the ash-free dry masses

initially and at time t (in year), respectively, and k is the exponential decay constant.

Negative exponential curves were fit on each of the litter/treatment combination

replicates (each plot represented a replicate) using Sigmaplot. A t-test was used to

determine if there was a difference between *L. tridentata* decay constants in Experiment 1

and Experiment 2. To quantify photodegradation, we calculated the response ratios (*RR*)

as the ratio of mass loss in the Full Sun to the No UV/blue treatment litter. Therefore, the

greater the *RR* above 1.0, the more mass loss is attributed to UV and blue radiation.

Results

Comparison of field experiments

Because Experiment 1 and Experiment 2 were conducted over different periods and differed in collection times we compared *L. tridentata* decay constants in the two experiments. The decay constant of *L. tridentata* litter in Experiment 1 (0.32 y^{-1}) was very similar to that in Experiment 2 (0.36 y^{-1}; $p = 0.33$). Average litter air temperatures over the two experiments were also very similar. For example, average diurnal and diel temperatures in a given radiation treatment in the two experiments were within 0.1°C (Table 2). Average daily precipitation, as well as daily integrated fluxes of UV$_{\text{Caldwell,}}$ UV$_{\text{flint}}$ and visible irradiance, were also similar over Experiments 1 and 2 (Table 2). Because of these similarities in *k* and microclimate, we combined the findings of decay rates and traits of initial and decayed litter from Experiment 1 and 2 in our further analyses. All results on *L. tridentata* reported hereafter are from the litter in Experiment 1.

Initial litter traits

There were many differences among litter types in initial traits (Table 1). Among the most notable were the large differences in microbial respiration, which ranged from 0.3 to 5.4 µg C-CO$_2$ g^{-1} h^{-1}. While there were few differences in traits among growth forms, grass litter had the highest concentrations of cellulose, hemicellulose and ND solubles, while suffrutescent dicot and annual litter had the highest water-soluble fractions.

Water-vapor sorption followed a negative exponential pattern with sorption rates declining through time and moisture content approaching a maximum after 24 h (Figure S1). Sorption rates across all litter types averaged 39.9 and 7.9 mg $g^{-1} h^{-1}$ over 2- and 24-h periods, respectively (Figure 1). On average, moisture content after 24 h of sorption was 18.9% (Table S1). Desorption rates across all litter types averaged 49.8 and 6.3 mg $g^{-1} h^{-1}$ over 2- and 24-h periods, respectively (Figure S2). There were few differences in sorption or desorption rates of initial litter among growth forms (Figure S3 and S4).

Decay constants and response ratios

Decay constants varied substantially among litter types. For example, in the Full Sun treatment, *k* ranged from 0.16 y^{-1} *(Simmondsia chinensis)* to 0.85 y^{-1} *(Encelia frutescens*; Figure 2a). On average, *k* was 0.51 y^{-1} in the Full Sun compared to only 0.36 y^{-1} in the No UV/blue treatment, and *k* was greater in the Full Sun than the No UV/blue treatment in 11 of 16 litter types. Decay constants were not significantly different among growth forms within the Full Sun or the No UV/blue treatment (p > 0.05). Response ratios across all litter types averaged 1.4 and ranged from 1.0 to 1.9 (Figure 2b). There were no significant differences in RR among growth forms.

Correlations between initial litter traits and decay and response ratios

The 2-h and 24-h sorption rates of initial litter were both positively correlated with *k* in the Full Sun (r^2 = 0.34 and 0.31, respectively, p ≤ 0.02) and the No/UV blue treatment (r^2 = 0.26 and 0.30, p ≤ 0.04; Table 3). Water-soluble fractions were also positively correlated with *k* in the Full Sun (r^2 = 0.36, p = 0.01) and the No/UV blue

treatment ($r^2 = 0.27$, p = 0.03). Additionally, microbial respiration ($r^2 = 0.27$, p = 0.01) and ash concentrations ($r^2 = 0.43$, p < 0.01) were positively correlated with k in the Full Sun treatment, while C concentrations ($r^2 = 0.29$, p = 0.02) were negatively correlated with k. Traditional indices of litter quality, such as C:N, Lignin:N, or concentrations of lignin or N, were not correlated with k in either treatment (p > 0.05). There were no significant correlations between initial litter traits (on an area basis) and response ratios (Table S2).

Changes in microbial respiration, water-vapor sorption and desorption rates and wax concentrations with decay

On average, respiration rates averaged 8.1 μg C-CO_2 g^{-1} h^{-1} in decayed litter but only 2.1 μg C-CO_2 g^{-1} h^{-1} in initial litter, and respiration rates were higher in decayed than initial litter in 11 of 16 litter types (Figure 3). Microbial respiration rates of decayed annual litter averaged 21.4 μg C-CO_2 g^{-1} h^{-1}, which was significantly higher than other growth forms.

As was the case with initial litter, water-vapor sorption in decayed litter followed a negative exponential pattern with rates slowing through time (Figure S1). Sorption rates across all decayed litter types averaged 66.8 and 8.1 mg H_2O g^{-1} h^{-1} over 2- and 24-h periods (Figure 1). On average, moisture content in decayed litter after 24 h of sorption was 19.4% (Table S1). Desorption rates across all decayed litter types averaged 69.2 and 6.6 mg H_2O g^{-1} h^{-1} over 2- and 24-h periods (Figure S2). There were no differences in sorption (Figure S5) or desorption (Figure S6) rates of decayed litter among growth forms.

Decayed litter had faster 2-h sorption rates than initial litter in 14 of the 16 litter types (Figure 1). There were no consistent differences in 24-h sorption rates between decayed and initial litter; rates were faster after decay in five litter types, slower in five types and similar in six types. Sorption rates of decayed litter were not correlated with rates of initial litter, illustrating that initial sorption rates were not indicative of rates in decayed litter (Table S3). Unlike sorption rates of initial litter, sorption rates of decayed litter were not correlated with decay constants ($p > 0.05$). There was a smaller range in sorption rates in decayed than initial litter. For example, 2-h sorption rates in decayed litter ranged from 54.3 to 79.3 mg H_2O g^{-1} h^{-1} (range = 25.0 mg H_2O g^{-1} h^{-1}) compared to 16.3 to 54.0 mg H_2O g^{-1} h^{-1} (range = 37.2 mg H_2O g^{-1} h^{-1}) in initial litter (Figure 1a).

Because litter pieces fragment or break with decay we examined the effect of fragmenting initial litter on sorption rates. Initial litter that was broken had faster 2-h sorption rates than unbroken initial litter, although rates were not as fast as decayed litter (Figure 4). Hence, while breaking litter pieces accelerated sorption, it alone did not explain the faster sorption rates we observed in decayed litter.

Wax concentrations across all litter types averaged only 0.8% in decayed litter compared to 2.5% in initial litter and were lower in decayed than initial litter in 10 of 16 litter types (Figure 5).

Correlations between sorption rates and other litter traits

Because 2-h sorption rates were a strong predictor of k in both treatments (Figure 6a), we examined which litter traits were correlated with sorption rates. Two-hour sorption rates of initial litter were positively correlated with microbial respiration of

initial litter ($r^2 = 0.32$, p = 0.02; Table 4). In addition, the 2-h sorption rates were positively correlated with SLA ($r^2 = 0.31$, p = 0.02) and water-soluble fractions ($r^2 = 0.29$, p = 0.03) of initial litter. Sorption rates were not correlated with litter traits that some others have found or suggested to be important such as cellulose or lignin concentrations (Table 4).

Rather unexpectedly, the 2-h sorption rates of initial litter were not correlated with initial wax concentrations ($r^2 = 0.02$, p = 0.60). However, the wax concentration of *Ambrosia deltoidea* litter appeared to be an outlier; at 14.5% it was 2.4x higher than the second highest wax concentration and more than three standard deviations higher than the average concentration of all litter types (Figure 5). After removing *A. deltoidea* from the data set, however, there was only a marginally significant negative correlation between 2-h sorption rate and wax concentration in initial litter ($r^2 = 0.20$, p = 0.09; Figure S7). Sorption rates of decayed litter were not correlated with wax concentrations of decayed litter (p > 0.05; Table 5). Hence, wax concentration did not appear to be a dominant factor driving sorption rates.
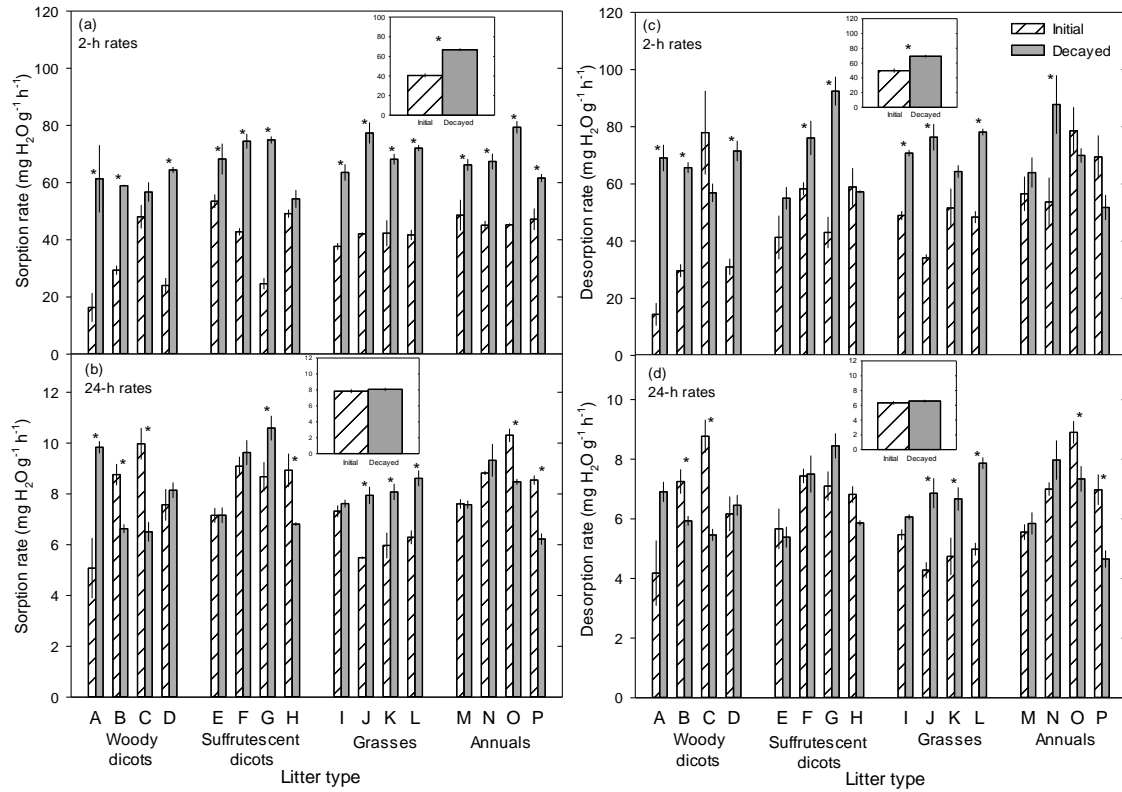
Figure 1. The 2- (a) and 24-h sorption rates (b), and 2- (c) and 24-h desorption rates (d) of initial and decayed litter in the Full Sun treatment. Bars are means (n = 3, ±1 SE). * denotes significant differences (p < 0.05) between initial and decayed litter within a type. See Table 1 for the letters used as litter type codes. The inset of each figure is an average of all litter types for initial and decayed litter (n = 16, ±1 SE).
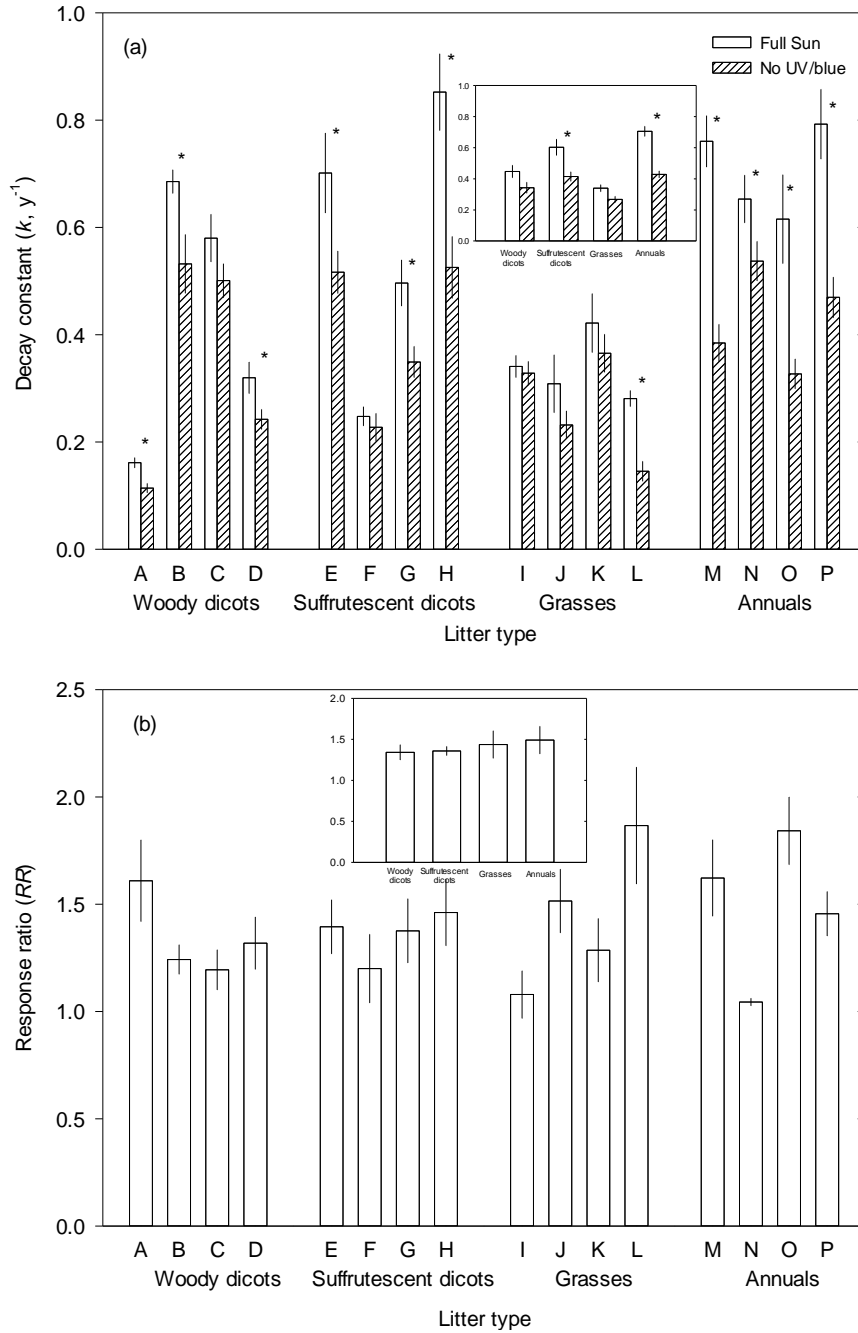
Figure 2. Decay constants (*k*) in the Full Sun and the No UV/blue treatment (a) and
response ratios (*RR*) of mass loss calculated as the ratio of mass loss in Full Sun
treatment litter to mass loss in No UV/Blue treatment litter (b). Values are means (±1 SE;
n = 8). Decay constants within a litter type with a * are significantly different (p ≤ 0.05).
See Table 1 for the letters used as litter type codes. The inset of each figure is an average
of growth forms (n = 4, ±1 SE).
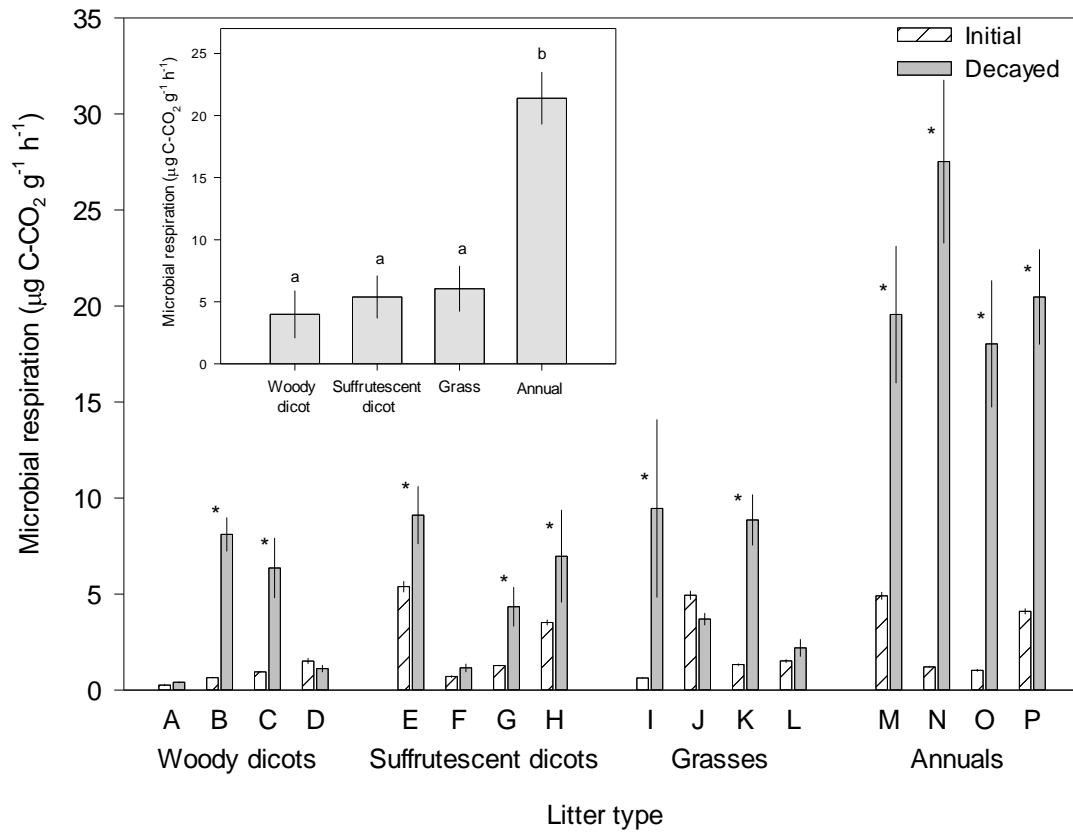
Figure 3. Microbial respiration rates of initial and decayed litter in the Full Sun treatment. Bars are means (n = 4, ±1 SE). A * denotes significantly higher rate in decayed versus initial litter within a litter type (p < 0.05).The inset shows the mean rate of decayed litter of each growth form. Bars with different letters are significantly different (p < 0.05). See Table 1 for the letters used as litter type codes.
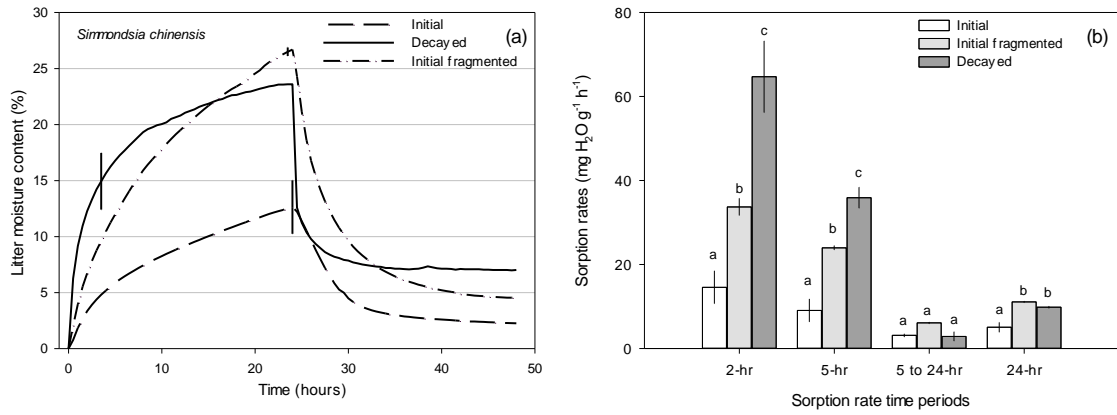
Figure 4. *Simmondsia chinensis* litter moisture content over 24 h of sorption followed by 24 h of desorption for initial litter, decayed litter and initial fragmented litter (a). Lines graphs are means of values taken every 30 minutes with the largest error bar shown (n = 3, ±1 SE). Also included are sorption rates in initial, initial fragmented and decayed litter (b). Bars with different letters within a time period are significantly different (p < 0.05). Bars are means (n = 3, ±1 SE).
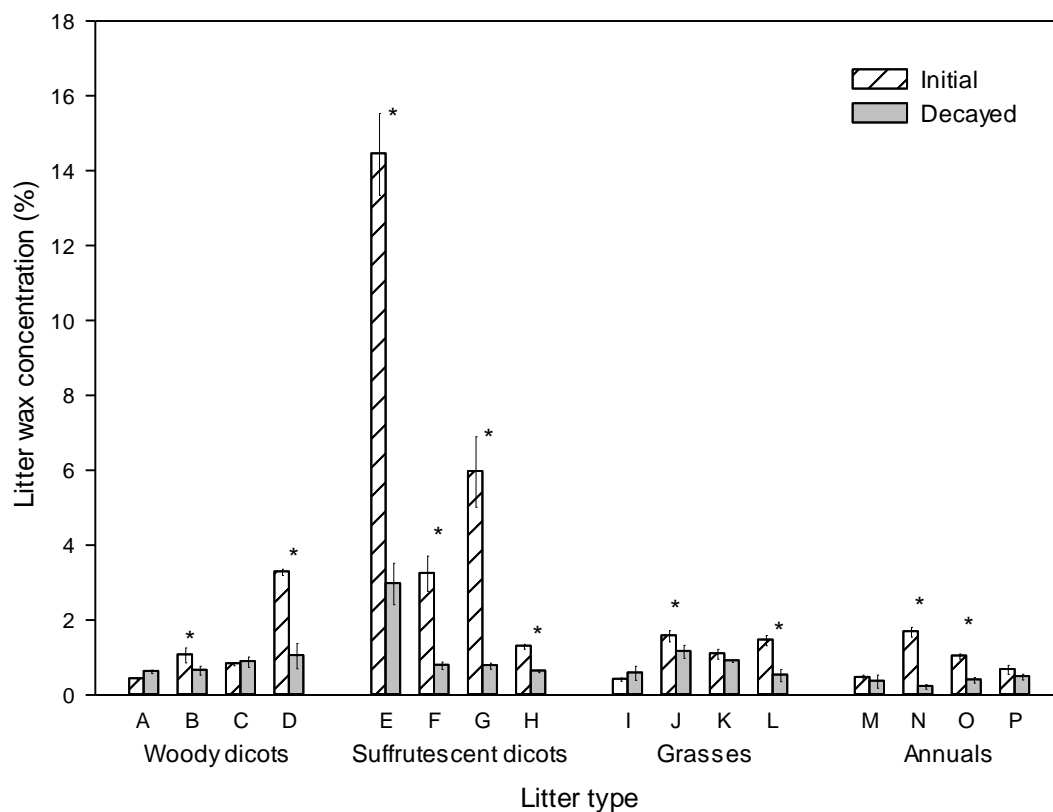
Figure 5. Wax concentrations of initial and decayed litter in the Full Sun treatment. Bars are means (n = 4, ±1 SE). * denotes significant difference between initial and decayed litter within a litter type (p ≤ 0.05). See Table 1 for the letters used as litter type codes.
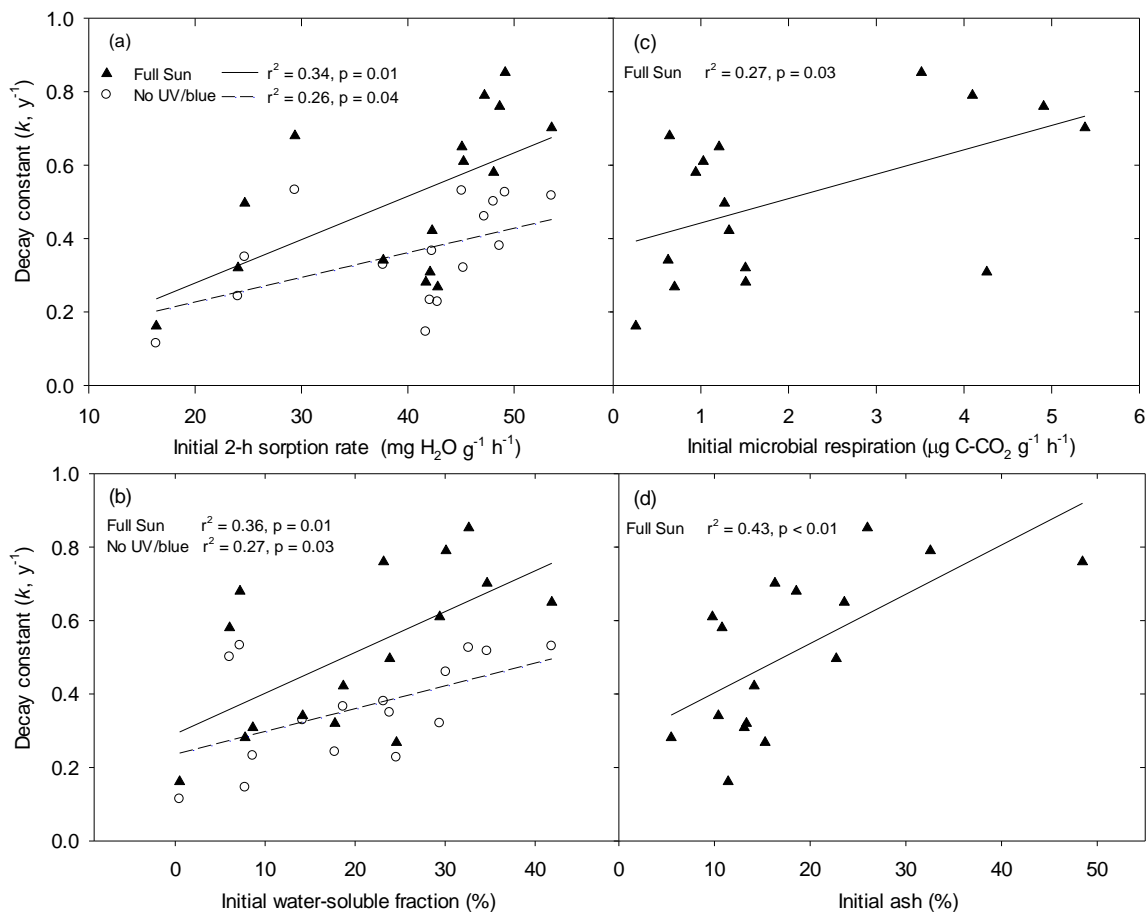
Figure 6. Relationships between the decay constants and 2-h sorption rates of initial litter in the Full Sun and No UV/blue treatment (a), and initial water-soluble fraction (b), decay constants in the Full Sun treatment and initial microbial respiration (c) and decay constants in the Full Sun treatment and initial ash of litter (d). Values are means of each litter type (n = 4 except for decay constants n = 8). Lines are linear regressions with r2 and p-value in legends.

Tables

Table 1. Initial litter traits. Values are means (SE; n = 5). Also shown are the means of each growth form (n = 4). Litter type or growth form with different letters in a column are significantly different (p ≤ 0.05). Litter type codes are below each type.

Litter type	Initial litter traits												
	C (%)	N (%)	C:N	Lignin (%)	Cellulose (%)	Hemicellulose (%)	ND soluble (%)	Lignin:N	Water-soluble fraction (%)	Ash (%)	SLA (cm² g⁻¹)	Respiration (μg CO₂ g⁻¹ h⁻¹)	Wax (%)
Simmondsia chinensis (A)	43.9 (0.2)^{de}	1.7 (0.1)^{de}	26.3 (1.7)^{cd}	9.0 (0.4)^{b}	6.4 (0.3)^{i}	10.6 (0.3)^{fgh}	74.4 (0.5)^{c}	5.4 (0.5)^{b}	0.4 (0.1)^{h}	11.4 (1.4)^{ef}	29.3 (2.5)^{f}	0.3 (0.1)^{e}	0.4 (0.0)^{d}
Olneya tesota (B)	42.7 (0.2)^{ef}	3.2 (0.1)^{b}	13.6 (0.4)^{d}	8.9 (0.1)^{b}	9.6 (0.2)^{h}	7.0 (0.3)^{i}	74.8 (0.5)^{c}	2.8 (0.1)^{cde}	7.1 (1.1)^{gh}	18.6 (0.4)^{cde}	91.0 (3.0)^{bc}	0.6 (0.1)^{de}	1.1 (0.2)^{d}
Prosopis velutina (C)	46.9 (0.1)^{ab}	3.7 (0.1)^{a}	12.9 (0.4)^{d}	13.5 (0.2)^{a}	13.8 (0.1)^{f}	9.7 (0.5)^{gh}	63.2 (0.4)^{f}	3.7 (0.1)^{bcd}	6.1 (1.2)^{gh}	10.8 (0.2)^{ef}	113.2 (3.7)^{a}	0.9 (<0.1)^{c}	0.8 (<0.1)^{d}
Larrea tridentata (D)	47.9 (0.2)^{a}	2.3 (0.1)^{c}	21.2 (1.0)^{cd}	4.4 (0.2)^{cd}	6.7 (0.2)^{i}	3.2 (0.1)^{j}	85.9 (0.2)^{a}	2.0 (0.2)^{d}	17.7 (1.1)^{ef}	13.3 (1.0)^{de}	59.5 (2.3)^{d}	1.5 (0.1)^{c}	3.3 (0.1)^{c}
Woody dicots	45.4 (1.2)^{a}	2.7 (0.4)^{a}	18.4 (3.1)^{a}	8.9 (1.9)^{a}	9.1 (1.7)^{a}	7.6 (1.7)^{b}	74.6 (4.6)^{a}	3.4 (0.7)^{a}	7.8 (3.6)^{b}	13.5 (1.8)^{a}	73.2 (18.3)^{a}	0.8 (0.3)^{a}	1.4 (0.6)^{a}
Ambrosia deltoideia (E)	45.9 (0.1)^{c}	2.4 (0.1)^{c}	18.9 (0.4)^{cd}	4.9 (0.5)^{c}	10.7 (0.3)^{gh}	4.9 (0.1)^{j}	79.8 (0.4)^{b}	2.0 (0.2)^{de}	34.6 (2.8)^{ab}	16.3 (1.4)^{c}	65.5 (4.3)^{de}	5.4 (0.4)^{a}	14.5 (0.9)^{a}
Baileya multiradiata (F)	40.8 (0.2)^{g}	1.4 (0.1)^{ef}	29.5 (1.8)^{bcd}	2.8 (0.3)^{e}	22.2 (0.6)^{c}	7.4 (0.5)^{i}	67.8 (0.7)^{e}	2.1 (0.3)^{de}	24.6 (3.9)^{de}	15.3 (1.2)^{de}	46.8 (1.9)^{ef}	0.7 (0.1)^{de}	3.3 (0.4)^{c}
Encelia farinosa (G)	38.8 (0.1)^{h}	2.4 (0.1)^{c}	16.2 (0.4)^{cd}	5.0 (0.3)^{c}	11.0 (0.4)^{g}	12.5 (0.5)^{e}	71.7 (0.4)^{d}	2.1 (0.2)^{de}	23.8 (0.9)^{de}	22.7 (1.1)^{cd}	50.5 (3.0)^{d}	1.3 (0.1)^{cd}	6.0 (0.8)^{b}
Encelia frutescens (H)	36.0 (0.7)^{i}	2.1 (0.1)^{c}	17.0 (0.8)^{cd}	2.8 (0.2)^{ef}	10.6 (0.2)^{gh}	8.6 (0.5)^{hi}	78.3 (0.7)^{b}	1.3 (0.2)^{e}	32.6 (1.9)^{bc}	26.0 (1.3)^{bc}	68.8 (2.8)^{cd}	3.5 (0.1)^{b}	1.3 (0.1)^{c}
Suffrutescent dicots	40.4 (2.1)^{ab}	2.1 (0.2)^{ab}	20.2 (3.0)^{a}	3.9 (0.6)^{ab}	13.6 (2.9)^{b}	8.4 (1.6)^{b}	74.4 (2.8)^{a}	1.9 (0.2)^{a}	28.9 (2.8)^{a}	20.1 (2.6)^{a}	57.9 (5.4)^{a}	2.7 (1.1)^{a}	6.3 (2.9)^{a}
Aristida purpurea (I)	41.5 (0.1)^{fg}	1.9 (<0.1)^{d}	22.4 (0.1)^{cd}	1.3 (0.1)^{g}	37.4 (0.4)^{a}	31.0 (0.2)^{c}	30.2 (0.4)^{i}	0.7 (<0.1)^{e}	14.2 (0.5)^{fg}	10.4 (0.7)^{ef}	64.2 (3.1)^{d}	0.6 (<0.1)^{de}	0.4 (0.08)^{d}
Bromus rubens (J)	41.7 (0.2)^{fg}	0.6 (0.1)^{g}	72.1 (11.0)^{a}	2.0 (0.1)^{f}	36.6 (0.4)^{a}	26.1 (0.2)^{d}	35.2 (0.4)^{h}	3.4 (0.5)^{cde}	8.6 (0.8)^{gh}	13.1 (0.4)^{de}	106.7 (7.7)^{ab}	4.9 (0.2)^{a}	1.6 (0.1)^{c}
Cynodon dactylon (K)	41.8 (0.1)^{fg}	1.4 (0.1)^{ef}	30.8 (1.6)^{bc}	2.4 (0.2)^{ef}	32.6 (0.3)^{b}	35.6 (0.3)^{b}	29.3 (0.5)^{i}	1.8 (0.1)^{e}	18.7 (0.4)^{ef}	14.1 (1.0)^{d}	114.2 (4.5)^{a}	1.3 (<0.1)^{c}	1.1 (0.1)^{d}
Eragrostis curvula (L)	45.3 (0.1)^{cd}	1.0 (0.1)^{efg}	43.7 (1.0)^{b}	2.0 (0.1)^{f}	36.1 (0.2)^{a}	39.6 (0.8)^{a}	22.2 (0.7)^{j}	1.9 (0.1)^{de}	7.8 (0.3)^{gh}	5.5 (0.8)^{f}	51.9 (2.5)^{d}	1.5 (0.1)^{c}	1.5 (0.1)^{c}
Grasses	42.6 (0.9)^{ab}	1.2 (0.3)^{b}	40.5 (9.4)^{a}	1.9 (0.2)^{b}	35.7 (1.1)^{a}	33.1 (2.9)^{a}	29.2 (2.7)^{b}	1.9 (0.5)^{a}	12.3 (2.2)^{b}	10.8 (1.9)^{a}	84.3 (15.4)^{a}	2.1 (1.0)^{a}	1.2 (0.3)^{a}
Amsinckia menziesii (M)	28.5 (0.7)^{k}	1.31 (0.1)^{ef}	22.2 (1.7)^{cd}	4.3 (0.2)^{c}	15.8 (0.6)^{e}	13.2 (0.5)^{e}	66.6 (0.5)^{e}	3.4 (0.4)^{cde}	23.2 (1.5)^{de}	48.4 (1.4)^{a}	78.4 (9.4)^{cd}	4.9 (0.2)^{a}	0.5 (0.1)^{d}
Lupinus sparsiflorus (N)	38.4 (0.2)^{h}	2.05 (0.1)^{cd}	18.8 (0.8)^{cd}	2.5 (0.2)^{ef}	13.3 (0.2)^{f}	10.6 (0.3)^{fg}	73.5 (0.4)^{cd}	1.2 (0.1)^{e}	41.8 (2.7)^{a}	23.6 (1.2)^{c}	113.8 (15.9)^{c}	1.2 (0.1)^{cd}	1.7 (0.1)^{c}
Plantago patagonica (O)	43.1 (0.2)^{ef}	0.7 (0.3)^{g}	61.1 (3.6)^{a}	8.8 (0.2)^{b}	20.2 (0.3)^{d}	12.1 (0.2)^{ef}	58.8 (0.2)^{g}	12.6 (1.0)^{a}	29.4 (1.5)^{bcd}	9.7 (0.4)^{f}	116.9 (6.8)^{ab}	1.0 (0.1)^{c}	1.0 (0.1)^{d}
Cryptantha angustifolia (P)	32.3 (0.6)^{j}	0.8 (0.1)^{fg}	38.5 (4.6)^{b}	3.3 (0.1)^{de}	16.3 (0.2)^{e}	8.8 (0.3)^{hi}	71.5 (0.4)^{d}	4.0 (0.5)^{bc}	30.1 (1.7)^{bcd}	32.6 (0.4)^{b}	110.0 (12.7)^{c}	4.1 (0.2)^{a}	0.7 (0.1)^{d}
Annuals	35.5 (3.2)^{b}	1.2 (0.3)^{b}	35.2 (9.6)^{a}	4.7 (1.4)^{ab}	16.4 (1.4)^{b}	11.1 (1.0)^{b}	67.6 (3.3)^{a}	5.1 (2.5)^{a}	31.1 (3.4)^{a}	28.5 (8.1)^{a}	104.7 (8.9)^{a}	2.8 (1.0)^{a}	1.0 (0.3)^{a}

Table 2. Microclimate comparisons between Experiment 1 and 2. Diurnal and diel temperature means under litter are shown for radiation-treatment envelopes (i.e. Full Sun and No/UV blue, n = 5). Precipitation daily average taken from Sky Harbor International Airport, 6 km from the field site. Daily integrated ultraviolet irradiance, expressed as $UV_{Caldwell}$ and UV_{Flint}, and visible irradiance above litter (n = 1 sensor).

Parameter	Experiment 1 (16 Dec 2013 – 11 Sept 2015)	Experiment 2 (11 Dec 2014 – 24 Oct 2016)
Diurnal Full Sun (^{o}C)	41.0	41.1
Diurnal No/UV blue (^{o}C)	39.5	39.6
Diel Full Sun (^{o}C)	31.4	31.4
Diel No/UV blue (^{o}C)	30.3	30.4
Precipitation (mm d^{-1})	0.55	0.47
$UV_{Caldwell}$ (kJ m^{-2} d^{-1})	3.2	3.1
UV_{Flint} (kJ m^{-2} d^{-1})	24.1	23.6
Visible irradiance (mol m^{-2} d^{-1})	48.6	49.1

Table 3. Correlations between initial litter traits and decay constants (k) in the two radiation treatments. Values are coefficients of determination (r^2) of linear regressions (and p-values in parentheses; n=16 litter types) of mean k and mean initial litter traits. Positive or negative correlations are denoted by + or - in front of r^2, while bold denotes p ≤ 0.05.

Initial trait	Correlation with k (r^2 (p))	
	Full Sun	**No UV/blue**
C (%)	**-0.29 (0.02)**	-0.07 (0.29)
N (%)	+0.05 (0.46)	+0.18 (0.09)
C:N	-0.07 (0.29)	-0.22 (0.06)
Cellulose (%)	-0.16 (0.12)	-0.13 (0.15)
Hemicellulose (%)	-0.18 (0.09)	-0.16 (0.12)
Lignin (%)	+0.01 (0.64)	-0.03 (0.52)
Lignin:N	0.00 (0.81)	-0.02 (0.54)
Cellulose:Lignin	-0.19 (0.08)	-0.12 (0.18)
ND solubles (%)	+0.19 (0.09)	+0.15 (0.13)
Water-soluble fraction (%)	**+0.36 (0.01)**	**+0.27 (0.03)**
Ash (%)	**+0.43 (<0.01)**	+0.17 (0.10)
SLA (cm^2 g^{-1})	+0.12 (0.18)	+0.09 (0.24)
Wax (%)	+0.01 (0.65)	+0.04 (0.45)
Respiration (µg C-CO$_2$ g^{-1} h^{-1})	**+0.27 (0.03)**	+0.08 (0.27)
2-h sorption (mg H$_2$O g^{-1} h^{-1})	**+0.34 (0.01)**	**+0.26 (0.04)**
24-h sorption (mg H$_2$O g^{-1} h^{-1})	**+0.31 (0.02)**	**+0.30 (0.02)**
2-h desorption (mg H$_2$O g^{-1} h^{-1})	**+0.24 (0.05)**	+0.15 (0.13)
24-h desorption (mg H$_2$O g^{-1} h^{-1})	+0.22 (0.06)	**+0.24 (0.05)**

Table 4. Correlations between 2- and 24-h sorption and desorption rates and traits of initial litter. Values are coefficients of determination (r^2) of linear regressions (and p-values in parentheses; n=16 litter types) of mean sorption rate and mean litter trait. Positive or negative correlations are denoted by + or - in front of r^2, while bold denotes p ≤ 0.05.

Initial litter trait	Initial litter rates			
	2-h sorption (mg H_2O g^{-1} h^{-1})	24-h sorption (mg H_2O g^{-1} h^{-1})	2-h desorption (mg H_2O g^{-1} h^{-1})	24-h desorption (mg H_2O g^{-1} h^{-1})
C (%)	-0.05 (0.46)	+0.01 (0.64)	0.00 (0.86)	0.00 (0.81)
N (%)	-0.09 (0.24)	+0.12 (0.18)	0.00 (0.84)	0.00 (0.79)
C:N	+0.05 (0.47)	+0.05 (0.46)	+0.02 (0.54)	+0.05 (0.46)
Cellulose (%)	+0.07 (0.29)	-0.13 (0.15)	+0.02 (0.54)	-0.14 (0.14)
Hemicellulose (%)	0.00 (0.81)	+0.14 (0.14)	0.00 (0.81)	**-0.28 (0.03)**
Lignin (%)	-0.03 (0.52)	+0.14 (0.14)	-0.01 (0.65)	**+0.25 (0.04)**
Cellulose:lignin	+0.01 (0.64)	-0.19 (0.09)	0.00 (0.81)	**-0.23 (0.05)**
SLA (cm^2 g^{-1})	**+0.31 (0.02)**	+0.07 (0.29)	**+0.34 (0.01)**	+0.10 (0.23)
Ash (%)	+0.07 (0.30)	+0.03 (0.52)	0.00 (0.86)	+0.01 (0.65)
ND solubles (%)	+0.02 (0.55)	+0.18 (0.10)	0.00 (0.88)	+0.13 (0.15)
Respiration (µg C-CO_2 g^{-1} h^{-1})	**+0.32 (0.02)**	+0.03 (0.52)	+0.04 (0.49)	+0.02 (0.55)
Water-soluble fraction (%)	**+0.29 (0.03)**	+0.20 (0.09)	+0.13 (0.15)	+0.12 (0.18)
Wax (%)	+0.02 (0.60)	0.00 (0.86)	-0.12 (0.19)	0.00 (0.90)
Wax (%) (outlier removed)	-0.20 (0.09)	+0.03 (0.53)	-0.10 (0.23)	0.00 (0.81)

Table 5. Correlations between 2- and 24-h sorption rates and traits of decayed litter in the Full Sun treatment. Values are coefficients of determination (r^2) of linear regressions (and p-values in parentheses; n=16 litter types) of mean sorption rate and mean litter trait. Positive or negative correlations are denoted by + or - in front of r^2, while bold denotes p $\leq$ 0.05.

Decayed litter trait	Decayed litter rates	
	2-h sorption (mg H_2O g^{-1} h^{-1})	24-h sorption (mg H_2O g^{-1} h^{-1})
Respiration (µg C-CO_2 g^{-1} h^{-1})	0.00 (0.83)	+0.03 (0.52)
Ash (%)	-0.21 (0.07)	**-0.35 (<0.01)**
Wax (%)	0.00 (0.84)	0.00 (0.98)

Discussion

Decay rates varied greatly among litter types, ranging from 0.16 to 0.85 y^{-1} in the Full Sun treatment, corresponding to a range in mass loss of 28.1 to 81.9% over ≈22 months. This is consistent with the growing realization that litter traits have a larger than previously appreciated influence on decay, even across contrasting climates and biomes (Cornwell et al. 2008; Hu et al. 2018). However, decay rates were not correlated with traditional traits of litter quality, consistent with past work in our system (Day et al. 2018), as well as in other drylands (Schaefer et al. 1985; Cepeda-Pizarro and Whitford 1990; Vanderbilt et al. 2008; Liu et al. 2018).

Rather, decay rates were strongly correlated with water-vapor sorption rates; 2-h sorption rates explained 34 and 26% of the variation in decay of litter in the Full Sun and the No UV/blue treatment, respectively. Dirks et al. (2010) found 2-h water-vapor sorption rates and 24-h moisture content (both at 85% RH) of litter explained over 90% of the variation in mass loss of seven litter types over four months. Since the sorption rate dictates how quickly a given litter type can reach moisture contents capable of supporting microbial respiration, the high correlation Dirks et al. (2010) found supports the idea that their litter was primarily degraded by microbes. Similarly, Gliksman et al. (2017) found that the increase in overnight moisture content appeared to explain the microbial degradation of three litter types.

Initial water-soluble fractions explained 36 and 27% of the variation in decay of litter in both the Full Sun and the No UV/blue treatment, respectively. Our water-soluble fractions are likely good indicators of the readily available pool available for microbes and general decomposability (Landgraf et al. 2006). We previously found that microbial

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respiration of initial litter is the best predictor of litter decay over 34 months in both the Full Sun and the No UV/blue treatment, and that microbial respiration was strongly correlated with water-soluble fractions (Day et al. 2018). This may explain why we did not find sorption rates to explain as much of the variation in decay among our litter types as Dirks et al. (2010) - other litter traits such as water-soluble fractions may also play a large role in decay. It may be that sorption rates dictate the potential for microbial activity in litter, but that water-soluble fractions subsequently control microbial activity once favorable moisture contents have been achieved.

Decay of litter in the Full Sun treatment was also negatively correlated with concentrations of C and positively correlated with concentrations of ash and microbial respiration of litter. Concentrations of C may have been negatively correlated with decay because they can be indicative of higher concentrations of less amenable substrates for microbial degradation (Hobbie 1996). Concentrations of ash in litter explained 43% of the variation in decay in the Full Sun treatment, and we previously found that ash explained between 27-43% of the variation in decay of litter (Day et al. 2018). It could be that ash provides nutrients for microbial activity. Indeed, we found microbial respiration of initial litter explained 27% of the variation in decay of the Full Sun treatment litter.

The minimum moisture content of litter required to support microbial activity and lead to decay is assumed to be between 10-15% (Nagy and Macauley 1982; Newell et al. 1985; Gliksman et al. 2017). Moisture contents of initial litter were not above 10% after two hours of sorption (range 3.4-9.8%), although after five hours moisture contents of many litter types were over 10% (range 5.9-15.2%). In contrast, moisture contents of decayed litter ranged from 10.9-15.9% after only two hours of sorption in high RH (Table

S1). Therefore, decayed litter could have supported microbial activity faster than initial litter. In addition, we examined the litter microclimate data over both Experiment 1 and Experiment 2, and RH in the Full Sun treatment was $\geq$ 70, 80 and 90% for at least two consecutive hours 16.9, 13.5 and 10.2% of the time and for at least five consecutive hours 16.5, 13.3 and 10.0% of the time, respectively. Taken together, this suggests significant microbial decay occurred even though rainfall is limited in our system.

Water-vapor sorption rates were correlated with several traits of initial litter. Litter SLA explained 31% of the variation in 2-h sorption rates and Talhelm and Smith (2018) found SLA to be the best predictor of sorption rates among 17 litter types. Litter chemistry also appears to play a role as water-soluble fractions explained 29% of the variation in 2-h sorption rates. Some have found concentrations of lignin or lignin:N ratios explained some of the variation in sorption rates (Dirks et al. 2010; Talhelm and Smith 2018), but, consistent with Iqbal et al. (2013), we did not find these correlations. Surprisingly, wax concentrations were not correlated with sorption rates of litter, even though waxes are well known to limit the diffusion of water-vapor across membranes in live leaves (Holloway 1969, 1970; Koch and Ensikat 2008). It may be that the barrier imposed to water diffusion by waxes is physically broken as leaves senescence and dehydrate, such that wax concentrations have relatively little influence on vapor diffusion in litter.

The faster 2-h sorption and desorption rates found in decayed litter can be partially attributed to litter fragmenting. The majority of decayed litter was not in whole pieces, but fragmented likely due to natural field conditions such as wet-dry cycles and the impact of rainfall (Taylor and Parkinson 1988; Dirks et al. 2010). We found the 2-h

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sorption rates to be faster than initial rates but not as fast as decayed rates in our litter fragmenting experiment. It is thus likely that there is an additional physical or chemical trait in decayed litter responsible for the increased sorption rates. Iqbal et al. (2013) incubated eleven crop residues in soil in the laboratory and assessed moisture content at three stages of decay (0, 49 and 105 d) and found moisture content increased with decay, which they attributed to increased porosity. In addition, since we did not measure chemistry traits of decayed litter, it could be that changes in litter chemistry also drive the increase in sorption rates.

Our research provides further evidence that exposure to UV and blue radiation accelerates litter decay. Litter decay constants were greater in the Full Sun than the No UV/blue treatment in 11 of our 16 litter types. On average, mass loss of litter in the Full Sun was 1.4 times that of mass loss of litter in the No UV/blue treatment. Previously, we found mass loss of litter in the Full Sun treatment was 1.5 times that of mass loss of litter in the No UV/blue treatment after 34 months of decay (Day et al. 2018). Additionally, King et al. (2012) found mass loss to average 32% higher in litter exposed to full sunlight compared to shade in a meta-analysis of 50 experiments.

Conclusion

The decay rates of litter varied substantially among litter types and were not predicted by traditional indices of litter quality. Rather, decay was predicted well by the 2-h sorption rates and water-soluble fractions of initial litter. The 2-h sorption rates of litter also helped explain initial microbial respiration, and sorption rates were most strongly correlated with SLA and water-soluble fractions of litter. Decayed litter generally had faster sorption rates, and some, but not all, of this was due to litter fragmenting. Further studies are required to understand the litter traits that correlate with sorption rates as litter decays and how sorption rates and water-soluble fractions of litter may interact to influence microbial respiration.

Acknowledgements

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Supplemental Tables and Figures

Figure S1. Litter moisture content during 24 h of sorption followed by 24 h of desorption. Lines are means taken every 30 minutes, vertical bars are the largest SE (n = 3).
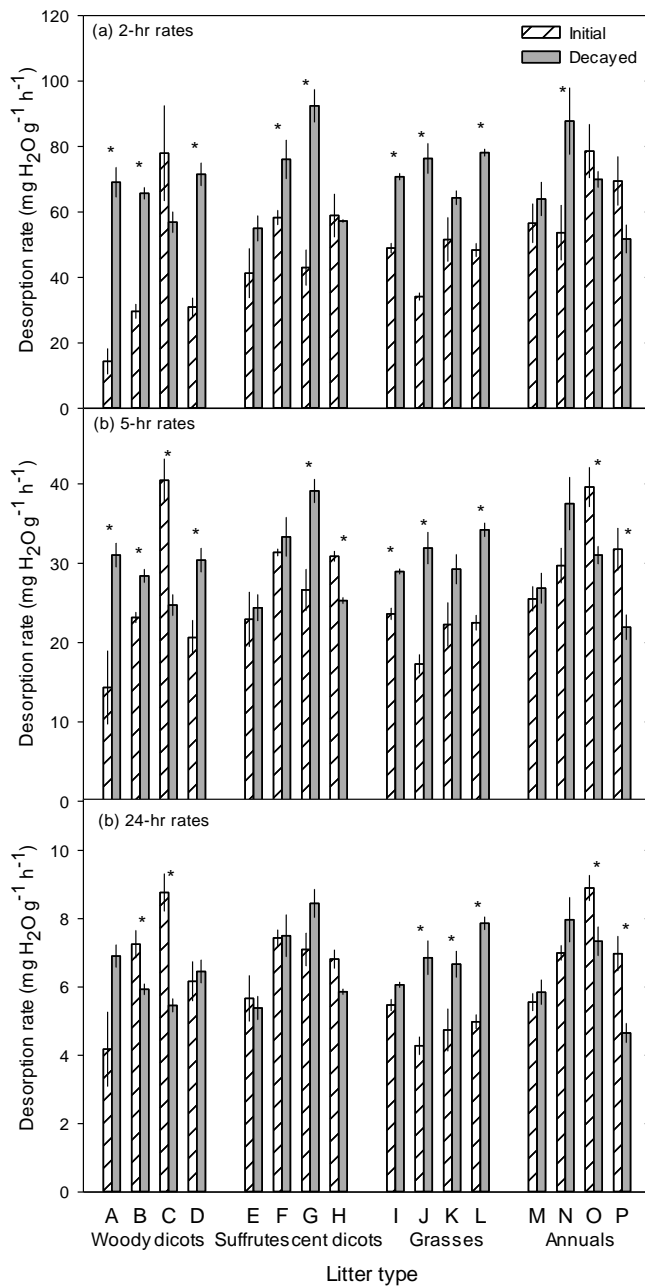
Figure S2. The 2- (a), 5- (b) and 24-h (c) desorption rates of initial and decayed Full Sun treatment litter. Bars are means (n = 3, ±1 SE). * denotes significant differences (p < 0.05) between initial and decayed litter within a type. See Table 1 for the letters used as litter type codes.
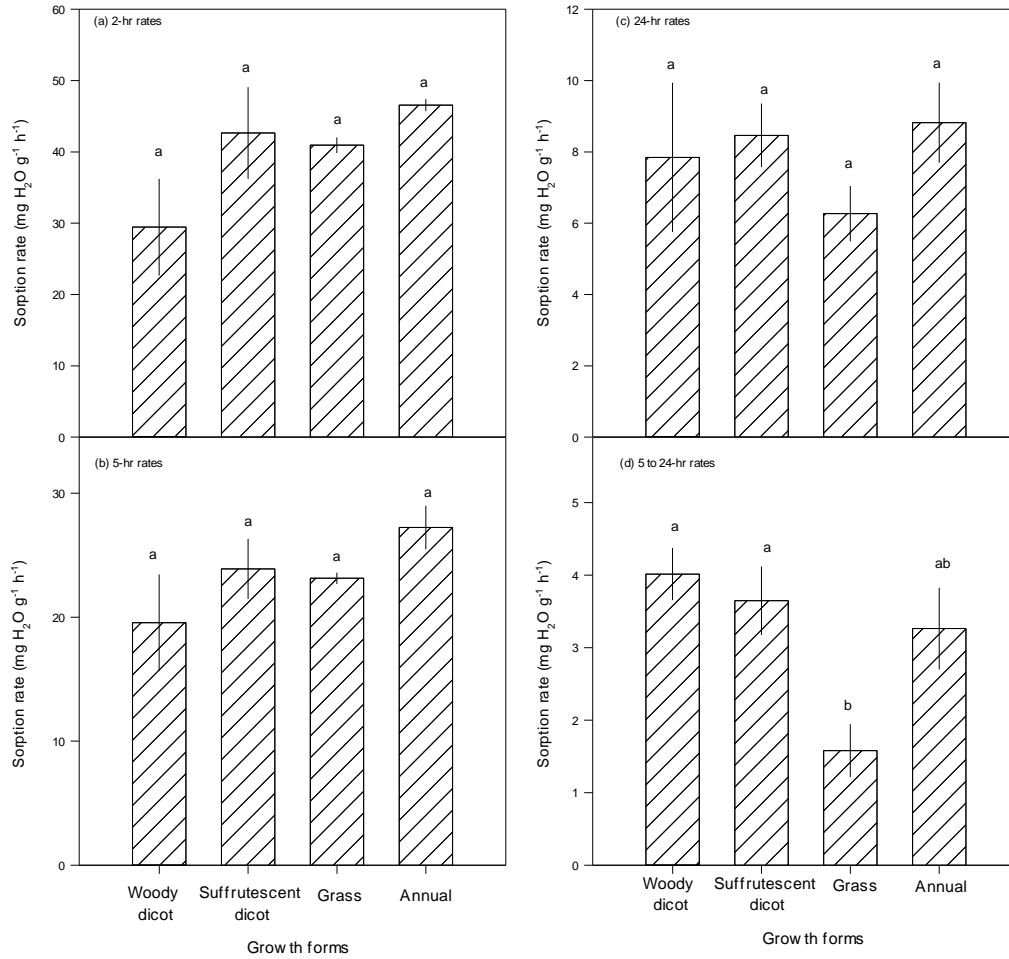
Figure S3. The 2- (a), 5- (b), 24- (c) and 5 to 24-h (d) growth form sorption rates of initial litter. Bars are means (n = 4, ±1 SE). Different letters above a bar are significantly different (p < 0.05).
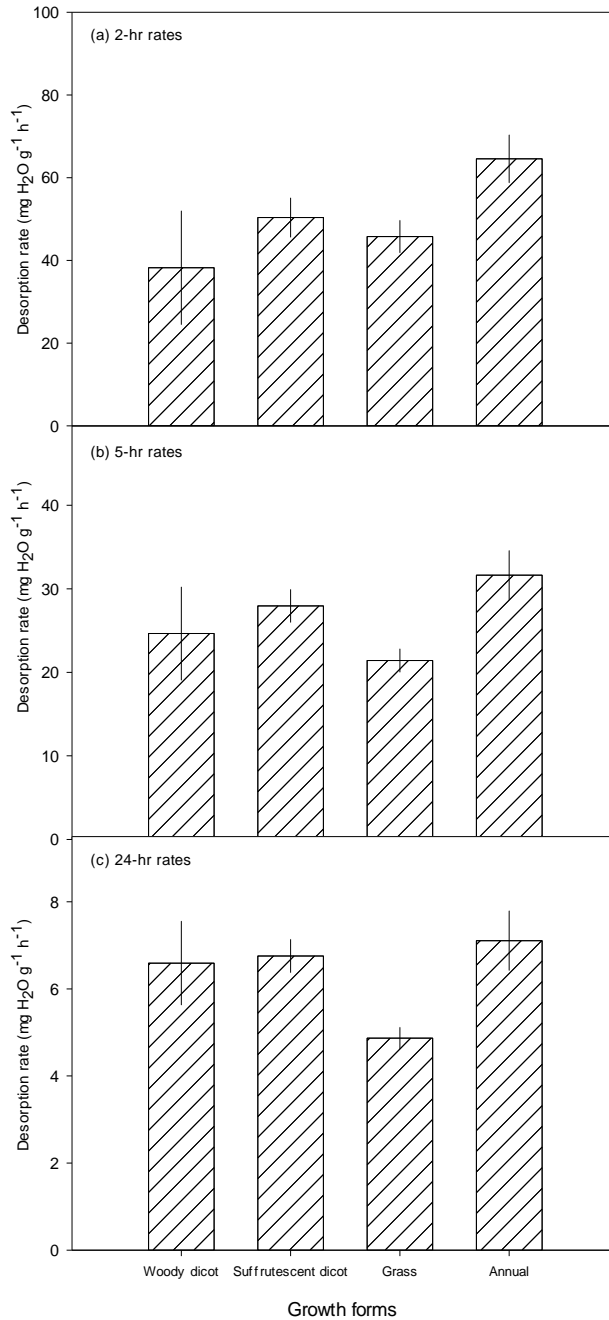
Figure S4. The 2- (a), 5- (b) and 24-h (c) growth form desorption rates of initial litter. Bars are means (n = 4, ±1 SE). There were no significant differences between growth forms (p > 0.05).
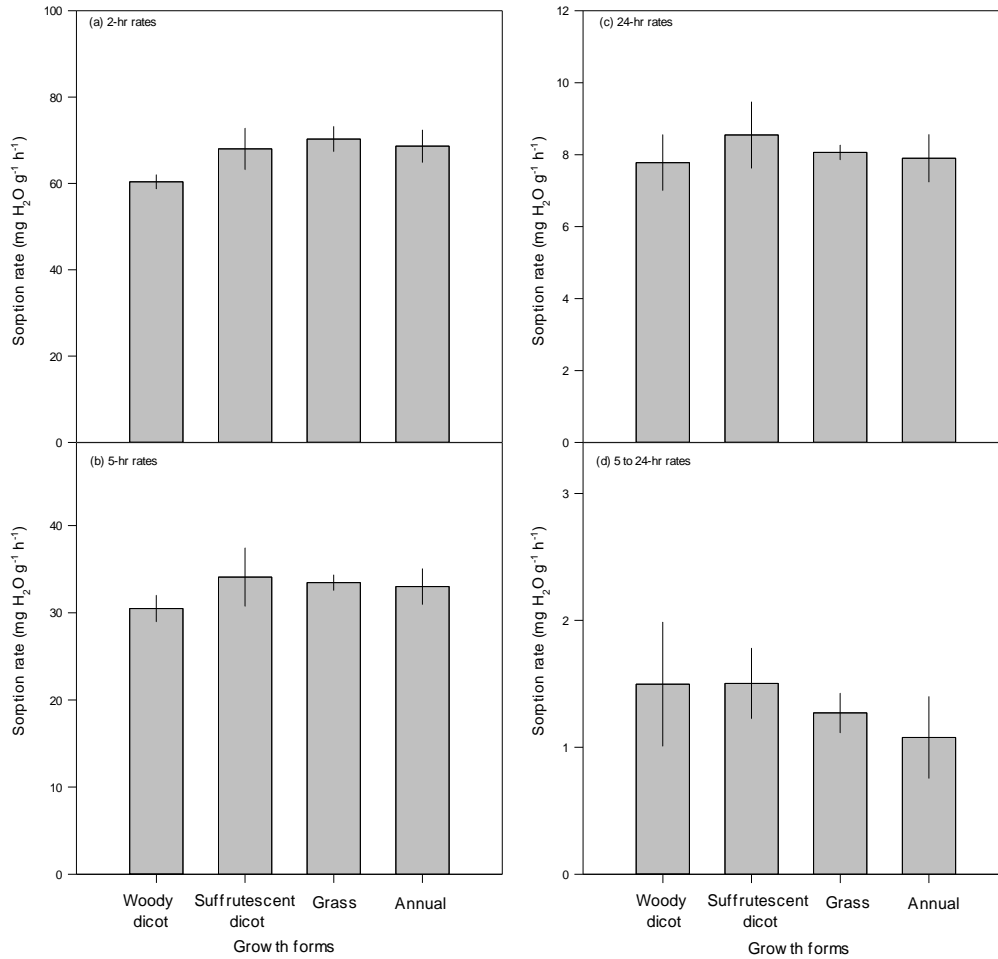
Figure S5. The 2- (a), 5- (b), 24- (c) and 5 to 24-h (d) growth form sorption rates of decayed Full Sun treatment litter. Bars are means (n = 4, ±1 SE). There were no significant differences between growth forms (p > 0.05).
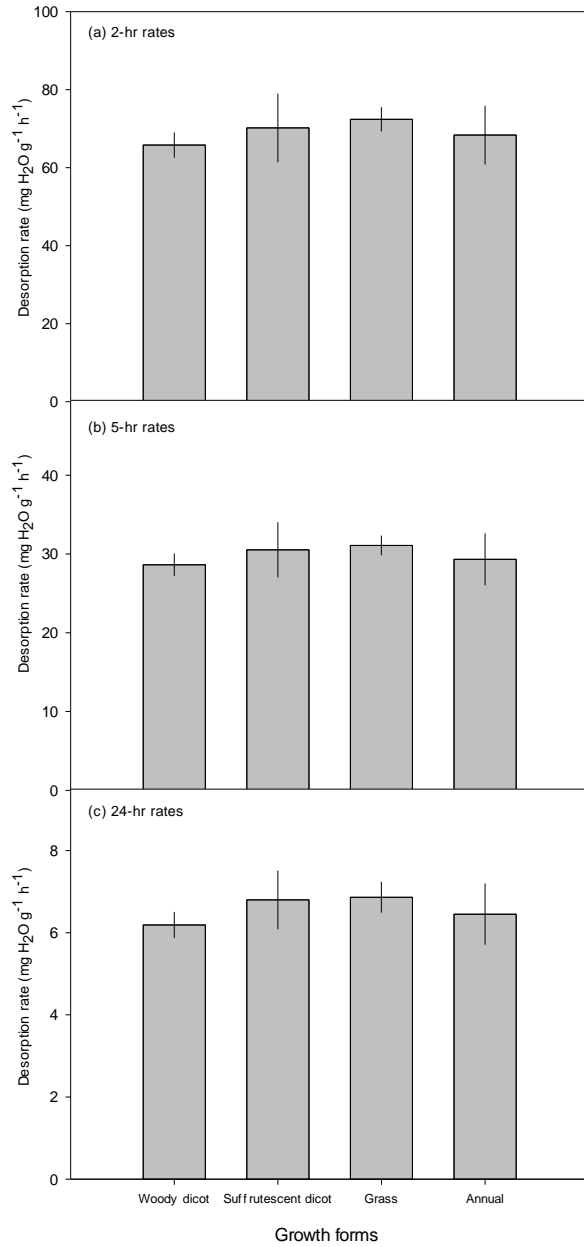
Figure S6. The 2- (a), 5- (b) and 24-h (c) growth form desorption rates of decayed Full Sun treatment litter. Bars are means (n = 4, ±1 SE). There were no significant differences between growth forms (p > 0.05).
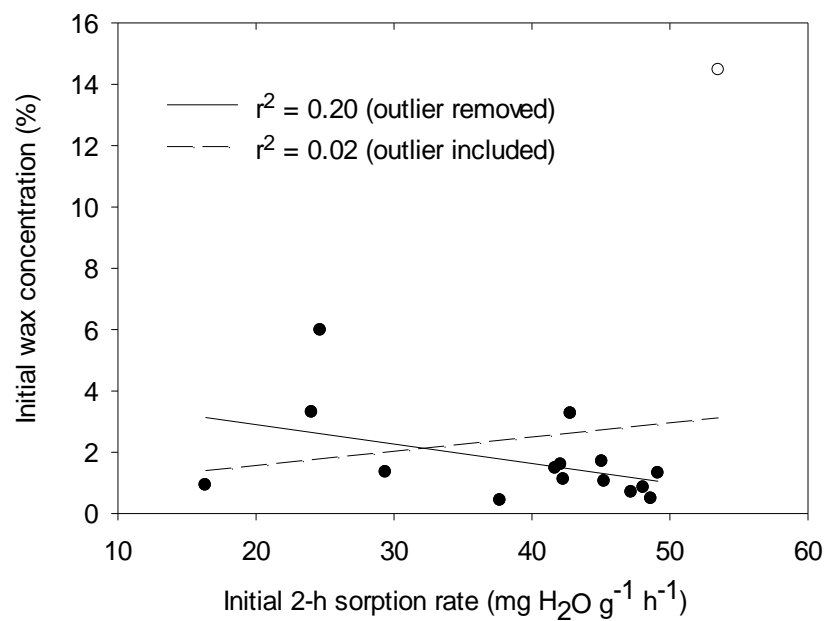
Figure S7. Relationships between 2-h sorption rate of initial litter and wax concentration in initial litter. The empty circle is the outlier. Values are means of each litter type (n = 4). Lines are linear regressions, with outlier removed p = 0.09, with outlier p = 0.53.

Table S1. Litter moisture content (MC, %) of initial and Full Sun treatment decayed litter. Values are means with SE in parentheses (n = 3). Also shown are the means of each growth from (n = 4).

Litter type	Initial litter		Decayed litter	
	2-h MC	24-h MC	2-h MC	24-h MC
Simmondsia chinensis	3.4 (0.7)	12.6 (1.9)	12.3 (1.9)	23.6 (0.5)
Olneya tesota	5.9 (0.3)	21.0 (0.8)	11.8 (0.1)	15.9 (0.3)
Prosopis velutina	9.6 (0.7)	23.9 (1.2)	11.3 (0.5)	15.6 (0.7)
Larrea tridentata	4.8 (0.4)	18.2 (1.2)	12.9 (0.2)	19.5 (0.6)
Woody dicots average	5.9 (1.3)	18.9 (2.4)	12.1 (0.3)	18.7 (1.9)
Ambrosia deltoideia	9.7 (0.9)	18.3 (0.4)	13.7 (0.9)	17.2 (0.6)
Baileya multiradiata	8.6 (0.2)	21.8 (0.7)	14.9 (0.4)	23.1 (1.0)
Encelia farinosa	4.9 (0.3)	20.8 (1.1)	15.0 (0.2)	25.4 (0.9)
Encelia frutescens	9.8 (0.2)	21.4 (1.3)	10.9 (0.5)	16.3 (0.1)
Suffrutescent dicots average	8.3 (1.1)	20.6 (0.8)	13.6 (1.0)	20.5 (2.2)
Aristida purpurea	7.5 (0.2)	17.6 (0.5)	12.7 (0.5)	18.3 (0.3)
Bromus rubens	8.4 (0.1)	13.2 (0.1)	15.5 (0.6)	19.1 (0.7)
Cynodon dactylon	8.5 (0.7)	14.3 (1.0)	13.6 (0.3)	20.1 (0.4)
Eragrostis curvula	8.3 (0.3)	15.1 (0.5)	14.4 (0.2)	21.0 (0.4)
Grasses average	8.2 (0.2)	15.0 (0.9)	14.1 (0.6)	19.6 (0.6)
Amsinckia menziesii	9.8 (0.8)	18.2 (0.4)	13.2 (0.3)	18.2 (0.3)
Lupinus sparsiflorus	6.4 (0.7)	21.2 (0.1)	13.5 (0.4)	22.4 (1.3)
Plantago patagonica	9.0 (0.1)	24.7 (0.5)	15.9 (0.3)	20.3 (0.2)
Cryptantha angustifolia	9.4 (0.6)	20.5 (0.3)	12.3 (0.2)	14.9 (0.4)
Annuals average	8.7 (0.8)	21.1 (1.4)	13.7 (0.8)	19.0 (1.6)
All litter types average	7.8 (0.3)	18.9 (0.6)	13.4 (0.3)	19.4 (0.5)

Table S2. Correlations between initial litter traits on an area basis and Response Ratios (*RR*). Values are coefficients of determination (r^2) of linear regressions (and p-values in parentheses; n=16 litter types) of mean *RR* and mean initial litter traits. Positive or negative correlations are denoted by + or - in front of r^2, while bold denotes p $\leq$ 0.05.

Initial trait	Correlation with *RR* (r^2 (*p*))
C (mg cm^{-2})	+0.03 (0.50)
N (mg cm^{-2})	+0.04 (0.43)
Cellulose (mg cm^{-2})	+0.02 (0.53)
Hemicellulose (mg cm^{-2})	+0.11 (0.19)
Lignin (mg cm^{-2})	+0.02 (0.52)
Water-soluble fraction (mg cm^{-2})	+0.03 (0.51)
Ash (mg cm^{-2})	+0.00 (0.93)
Wax (mg cm^{-2})	-0.04 (0.40)
2-h sorption (mg H$_2$O cm^{-2} h^{-1})	-0.03 (0.51)
24-h sorption (mg H$_2$O cm^{-2} h^{-1})	-0.05 (0.38)

Table S3. Correlations between initial litter sorption/desorption rates and decayed litter sorption/desorption rates (mg H_2O g^{-1} h^{-1}). Values are coefficients of determination (r^2) of linear regressions (and p-values in parentheses; n=16 litter types) of mean initial and decayed litter rates. Positive or negative correlations are denoted by + or - in front of r^2, while bold denotes $p \leq 0.05$.

		Initial litter rates						
		2-h sorption	5-h sorption	5 to 24-h sorption	24-h sorption	2-h desorption	5-h desorption	24-h desorption
Decayed litter rates	2-h sorption	0.00 (0.90)	0.00 (0.98)	-0.02 (0.54)	0.00 (0.83)	0.00 (0.81)	0.00 (0.91)	0.00 (0.85)
	5-h sorption	-0.10 (0.23)	-0.07 (0.30)	+0.02 (0.55)	0.00 (0.90)	-0.01 (0.63)	-0.01 (0.68)	0.00 (0.84)
	5 to 24-h sorption	**-0.26 (0.04)**	-0.22 (0.06)	+0.04 (0.49)	-0.03 (0.52)	-0.10 (0.24)	-0.08 (0.28)	-0.02 (0.54)
	24-h sorption	-0.19 (0.09)	-0.13 (0.15)	+0.06 (0.43)	0.00 (0.79)	-0.07 (0.29)	-0.04 (0.49)	0.00 (0.81)
	2-h desorption	-0.19 (0.09)	-0.15 (0.13)	+0.06 (0.43)	0.00 (0.91)	-0.07 (0.31)	-0.03 (0.54)	0.00 (0.91)
	5-h desorption	-0.13 (0.15)	-0.08 (0.27)	+0.03 (0.52)	0.00 (0.79)	-0.03 (0.53)	0.00 (0.80)	0.00 (0.79)
	24-h desorption	**-0.36 (<0.01)**	**-0.35 (<0.01)**	+0.02 (0.54)	-0.10 (0.23)	-0.21 (0.07)	-0.13 (0.15)	-0.09 (0.24)

Table S4. Correlations with initial litter sorption/desorption rates and initial litter sorption/desorption rates and correlations with decayed litter sorption/desorption rates and decayed litter sorption/desorption rates (mg H_2O g^{-1} h^{-1}). Values are coefficients of determination (r^2) of linear regressions (and p-values in parentheses; n=16 litter types) of mean initial and decayed litter rates. Positive or negative correlations are denoted by + or - in front of r^2, while bold denotes $p \leq 0.05$.

		Initial litter rates						
		2-h sorption	5-h sorption	5 to 24-h sorption	24-h sorption	2-h desorption	5-h desorption	24-h desorption
Initial litter rates	2-h sorption	**1.00**						
	5-h sorption	**+0.64 (<0.01)**	**1.00**					
	5 to 24-h sorption	-0.13 (0.15)	-0.02 (0.53)	**1.00**				
	24-h sorption	**+0.23 (0.05)**	**+0.37 (<0.01)**	**+0.44 (<0.01)**	**1.00**			
	2-h desorption	**+0.51 (<0.01)**	**+0.84 (<0.01)**	0.00 (0.82)	**+0.49 (<0.01)**	**1.00**		
	5-h desorption	**+0.28 (0.03)**	**+0.84 (<0.01)**	+0.13 (0.15)	**+0.81 (<0.01)**	**+0.81 (<0.01)**	**1.00**	
	24-h desorption	+0.05 (0.46)	**+0.30 (0.03)**	**+0.48 (<0.01)**	**+0.95 (<0.01)**	**+0.46 (<0.01)**	**+0.81 (<0.01)**	**1.00**
		Decayed litter rates						
		2-h sorption	5-h sorption	5 to 24-h sorption	24-h sorption	2-h desorption	5-h desorption	24-h desorption
Decayed litter rates	2-h sorption	**1.00**						
	5-h sorption	**+0.65 (<0.01)**	**1.00**					
	5 to 24-h sorption	0.00 (0.80)	**+0.39 (<0.01)**	**1.00**				
	24-h sorption	**+0.29 (0.03)**	**+0.82 P<0.01**	**+0.64 (<0.01)**	**1.00**			
	2-h desorption	**+0.26 (0.04)**	**+0.67 (<0.01)**	**+0.32 (0.02)**	**+0.68 (<0.01)**	**1.00**		
	5-h desorption	**+0.23 (0.05)**	**+0.74 (<0.01)**	**+0.39 (<0.01)**	**+0.77 (<0.01)**	**+0.96 (<0.01)**	**1.00**	
	24-h desorption	**+0.33 (0.01)**	**+0.78 (<0.01)**	**+0.40 (<0.01)**	**+0.81 (<0.01)**	**+0.85 (<0.01)**	**+0.94 (<0.01)**	**1.00**

3. ULTRAVIOLET AND BLUE SOLAR RADIATION ACCELERATE THE BACTERIAL DECAY OF SONORAN DESERT LEAF LITTER

Abstract

There is growing evidence that the faster decay of litter in sunlight (i.e.
photodegradation) may be predominantly caused by the accelerated microbial
degradation of this photoprimed litter (termed photofacilitation), rather than direct abiotic
breakdown by sunlight. Along with this, microbial degradation of litter in drylands
appears more significant than previously thought with recent research illustrating that
microbes in drylands can be activated by high humidity, in the absence of precipitation.
However, little research has assessed what microbial groups are involved in dryland litter
decay, especially in the context of photodegradation and photofacilitation. We examined
the effects of sunlight on the mass loss, bacterial and fungal abundance, and microbial
respiration of five leaf litter types on the soil surface of the Sonoran Desert over 22
months. Litter in full sunlight lost on average 1.3 and 1.6 times more mass than litter
filtered from UV or UV and blue wavebands of sunlight, respectively. Microbial
respiration rates from litter in full sunlight averaged 1.9 times higher than litter filtered
from UV and blue sunlight and were positively correlated ($r^2 = 0.75$, $p = 0.05$) with the
mass loss of this litter. Taken together, this strongly suggests that photofacilitation played
a role in the faster decay of this litter. The abundance of both bacteria and fungi on the
surface of litter was much lower in litter in full sunlight than litter filtered from UV and
blue sunlight. This effect was much greater for fungi than bacteria, suggesting some
bacteria may be more tolerant of sunlight. Exposure to sunlight had no consistent effects
on the total abundance (i.e. surface plus interior) of either bacteria or fungi in litter. The
abundance of bacteria on the surface of litter in full sunlight was strongly correlated with
respiration rates from litter ($r^2 = 0.83$, $p = 0.03$) and the mass loss of that litter ($r^2 = 0.92$,

p = 0.01), implying that exposure to sunlight facilitated activity of surface bacteria which in turn was responsible for accelerated litter decay. Surprisingly, the abundance of fungi was not correlated with respiration rates or mass loss of litter. Collectively, our results suggest that photodegradation by UV and blue sunlight photoprimed litter, enhancing the activity of surface bacteria and accelerating litter decay.

Introduction

The decay of plant litter is a significant pathway in the global carbon (C) cycle (Raich and Schlesinger 1992), and identifying the mechanisms that influence it are necessary to accurately model the global C cycle. Unlike many terrestrial systems, the mechanisms driving litter decay in drylands are not well understood, limiting our ability to model this component of the C cycle (Parton et al. 2007; Adair et al. 2008). One driver of decay that may be particularly significant in drylands is photodegradation, which we define herein as the decay of litter caused by exposure to solar radiation; this includes both direct abiotic decay by photomineralization as well as the subsequent accelerated decay of this litter by microbes. The latter mechanism, termed photofacilitation (Austin et al. 2016), is brought about by the photopriming (Barnes et al. 2015) of litter by sunlight. Both processes, abiotic photomineralization and photofacilitation of microbial degradation of litter, can be significant mechanisms of decay (Austin and Vivanco 2006; Day et al. 2007; Brandt et al. 2010; King et al. 2012; Austin et al. 2016). Regarding photofacilitation, little is known about the microbes involved.

Because of limited water availability, extreme temperatures and high ultraviolet (UV) irradiance, microbes have often been perceived to play a small role in litter decay in drylands. However, microbial activity (i.e. microbial respiration of litter) is strongly correlated with the mass loss of litter in drylands such as the Sonoran Desert, suggesting that microbes can be a significant driver of litter decay (Day et al. 2018). Moreover, there is growing evidence that water-vapor sorption by litter at higher relative humidity can elicit microbial activity and litter degradation and that this may be a significant driver of litter decay in drylands (Dirks et al. 2010; Gliksman et al. 2017; Day et al. 2018).

Nevertheless, the effects of sunlight on microbial activity in litter are poorly understood in drylands (Barnes et al. 2015). In some studies, sunlight or UV radiation has been found to accelerate microbial activity in litter (Gallo et al. 2009; Foereid et al. 2010; Wang et al. 2015; Baker et al. 2015; Gliksman et al. 2017; Day et al. 2018). Exposure to sunlight has been found to breakdown compounds such as lignin (Gehrke et al. 1995; Gallo et al. 2006, 2009; Day et al. 2007; Austin and Ballaré 2010) or cellulose and hemicellulose (Brandt et al. 2010; Lin and King 2014; Baker et al. 2015; Lin et al. 2015; Day et al. 2018; Esch et al. 2019). Exposure to UV radiation or sunlight can also lead to higher concentrations of sugars (Austin et al. 2016) and water-soluble DOC (dissolved or water-soluble organic C: Gallo et al. 2006; Feng et al. 2011; Wang et al. 2015; Day et al. 2018), providing more labile C for microbes. Day et al. (2018) found that microbial activity (i.e. respiration) in sunlit litter was strongly correlated with concentrations of water-soluble organic compounds. This suggests that exposure to sunlight promotes microbial activity, via providing more labile compounds.

Alternately, exposure to sunlight can have direct detrimental effects on microbes. Ultraviolet radiation, specifically UV-B radiation (280-320 nm), can negatively affect the growth and survival of bacteria and fungi as well as the production and germination of spores (Caldwell et al. 2007; Barnes et al. 2015; Erdenebileg et al. 2018). These detrimental effects are generally thought to stem from direct damage to DNA or reactive oxygen species and free radicals from other compounds that subsequently damage DNA or proteins (Hughes et al. 2003; Johnson 2003). Bacterial and fungal species can vary in their sensitivity to UV radiation (Moody et al. 1999; Kadivar and Stapleton 2003) and as a result the microbial community can shift in response to UV radiation (Johnson 2003;

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Pancotto et al. 2003; Zepp et al. 2007). Microbes have evolved several mechanisms to cope with UV radiation, such as replacing damaged genetic components using DNA repair systems (Castenholz and Garcia-Pichel 2013), synthesizing UV-screening compounds (Cockell and Knowland 1999; Gao and Garcia-Pichel 2011), or moving deeper into the soil (Bebout and Garcia-Pichel 1996). The latter suggests that, in the case of litter, microbes may preferentially use the interior of sunlit litter. On the other hand, photopriming would be greatest on the surface of litter, which may favor preferential use of the surface of sunlit litter by microbes.

The results from studies examining the effect of UV radiation on microbial abundance in litter are variable. For example, Brandt et al. (2009) found lower abundance of bacteria and fungi in litter exposed to UV radiation for three weeks in the laboratory. In contrast, Wang et al. (2015) found no effects on the abundance of either bacteria or fungi after 195 days of exposure to UV radiation in the laboratory. In a field study in Argentina, Pancotto et al. (2003) found that exposure to solar UV radiation reduced the abundance of some fungal species but had no effect on the bacterial species they assessed. Also in Argentina, Austin and Vivanco (2006) found that exposure to solar radiation decreased the abundance of both bacteria and fungi. In a field study in California, USA, Baker and Allison (2015) found that exposure to solar UV radiation had no effect on bacterial abundance but lead to higher fungal abundance. Recently, Ball et al. (2019) found that the bacterial biomass response to UV depends on the environment in which the litter originates. Hence, no consistent patterns have emerged concerning the influence of sunlight on bacterial or fungal abundance in litter. Furthermore, to our

knowledge, no studies have assessed how sunlight exposure influences microbial abundance in conjunction with microbial activity (e.g. respiration) and litter mass loss.

Fungi can make up a larger percentage of the microbial biomass than bacteria in leaf litter (Joergensen and Wichern 2008) and play key roles in nutrient storage and cycling in drylands (Collins et al. 2008). Additionally, fungi are generally more drought tolerant (Parr et al. 1981; Lennon et al. 2012) and can metabolize at higher temperatures and lower water potentials than bacteria (Allen 2007). Hence, we hypothesized that fungi would be generally more abundant than bacteria in litter at our dryland site.

Fungi are typically more abundant than bacteria in litter in early stages of decay because of their lower nutrient requirements, which enhances their ability to colonize lower quality litter (Bardgett et al. 1996; De Boer et al. 2005; Van Der Wal et al. 2006; Güsewell and Gessner 2009; Santonja et al. 2018). Consequently, bacteria tend to outcompete fungi when there is greater access to more labile and water-soluble nutrients (De Boer et al. 2005; Romaní et al. 2006). At the same site as the current study, we previously found exposure to sunlight lead to higher concentrations of water-soluble organic compounds and microbial respiration rates in litter (Day et al. 2018). Therefore, we hypothesized that exposure to sunlight would favor bacteria over fungi in litter because of the higher quality of this photoprimed litter.

In this study, we monitored the mass loss and microbial respiration of five litter types under three contrasting solar radiation treatments over 22 months in the Sonoran Desert. We also measured the abundance of bacteria and fungi in whole litter samples, as well as on the surface of litter, to assess their relative abundance in litter, and whether exposure to UV and blue sunlight influenced their abundance in litter. We hypothesized

that: (1) litter would decay faster in full sunlight than litter filtered from UV or UV and blue sunlight (i.e. photodegradation), (2) that fungi would be generally more abundant in litter and (3) exposure to sunlight would shift the relative abundance in favor of bacteria because it would provide higher quality, photoprimed litter.

Methods

Field experiment

We assessed the influence of sunlight exposure on the mass loss of five leaf litter types in the Sonoran Desert in Phoenix, AZ, USA, generally following the approach of Day et al. (2018). The five litter types consisted of four annual litter types (*Amsinckia menziesii, Lupinus sparsiflorus, Plantago patagonica, Cryptantha angustifolia*) and one woody dicot (*Larrea tridentata*). All litter was collected as naturally senesced leaves (i.e. lacking photosynthetic pigments) that were attached to standing branches/stems from several individuals of each species. Litter was air-dried (22°C at 10-20% relative humidity (RH)) at least 30 d and sorted to remove non-leaf parts. Twenty subsamples of each five litter types were oven-dried at 60°C (48 h) and ashed at 550°C in a muffle furnace (6 h) to determine initial oven-dry (OD) ash-free (organic) mass.

Litter was placed in envelopes (10 x 10 cm) whose tops were constructed of filter material that either (1) transmitted all solar wavebands (i.e. transmitted >80% of solar UV and visible radiation), using Aclar Type 22A filters, (Proplastics, Linden, NJ, USA) which were refer to as the "Full Sun" treatment, (2) absorbed most solar UV radiation (i.e. having a sharp cutoff with 50% transmittance at 387nm) using Clear UV Filter, (UVPS, Chicago, IL, USA) which we refer to as the "No UV" treatment or (3) absorbed most solar UV and low-wavelength visible radiation through the blue waveband (i.e. having a sharp cutoff with 50% transmittance at 545 nm), using Amber UV filters (UVPS) which we refer to as the "No UV/blue" treatment. Envelope bottoms were 153-μm mesh screening (Nitex cloth, Wildlife Supply, Buffalo, NY, USA). Each envelope received 0.88-1.48 g (± 0.05 g) of air-dried litter, depending on litter type, which

corresponded to a total litter surface area of ≈80% of the surface area of the envelope.

Envelopes of the litter types were deployed in a randomized block design involving five

litter types x three radiation treatments x four collection times x eight replicates in

unshaded level areas void of shrubs ≥1 m from plot edges, in a conservation area at the

Desert Botanical Garden, Phoenix, AZ, USA. Envelopes were anchored firmly to the soil

surface with nails inserted through the corners. Envelopes were placed in the field on 11

December 2014. Eight replicate envelopes of each litter type/treatment combination (1

from each of the 8 plots) were collected after 132, 274, 496 and 683 d (24 October 2016).

Following collection, litter envelope contents were gently poured onto white paper, and

extraneous material was removed. The remaining litter sample contained litter along with

any soil/microbial film that adhered to its surface. The sample was oven-dried (OD, 24 h

at 60°C), and a subsample was ashed (6 h at 550°C), and mass loss was calculated on an

oven-dry, ash-free (organic) basis.

Litter microclimate

We monitored litter air temperatures over the field experiment in five extra

envelopes of the three radiation treatments containing *Simmondsia chinensis* litter placed

on the ground surface adjacent to our main plots. A hygrochron temperature/humidity

logger (DS1923, iButtonLink, Whitewater, WI, USA) was inserted underneath the litter

inside each envelope so that it was shaded and to further minimize absorbance of solar

radiation we wrapped the top and side of each hygrochron with white Teflon tape.

Hygrochrons recorded litter air temperature every hour over the field experiment. Litter

temperatures were summarized by examining both diel, nocturnal and diurnal periods and

we defined the latter as hours in which the visible irradiance averaged $> 2\ \mu mol\ m^{-2}\ s^{-1}$.

Visible irradiance was measured 1.5 m above the ground with a quantum sensor (LI-190SA, Li-COR, Lincoln, NE, USA) every minute and summarized as hourly means over the experiment with a datalogger (CR23X, Campbell Scientific, Logan, UT, USA).

Microbial respiration

Microbial respiration rates were determined by measuring CO_2 emission rates from litter at all collection times following Day et al. (2018). Litter was first subjected to an inoculation procedure to reduce potential confounding effects attributable to differing levels of microbial colonization, following Day et al. (2018). In brief, respiration was measured over 24 h incubations in the dark at 22°C and high air RH (~75%) in 37-ml serum bottles. Evaporation from a small culture tube (50 mm L x 6 mm D) in each serum bottle filled with nanopore water were used to increase the RH in the serum bottles. Litter did not contact the liquid water and the only source of water was vapor. Litter was air-dried (22°C and 25% RH) for 30 d, and a subsample (0.25 ± 0.02 g) of each litter type and radiation treatment combination was placed in serum bottles. Bottles were flushed with ≈400 ppm CO_2 air for 2 min, sealed with a butyl rubber septum and incubated in the dark at 22°C for 24 h. Bottles containing the water-filled culture tube without litter were used to correct for CO_2 dissolved in water. The final CO_2 concentration in bottles was measured by withdrawing 10 ml of headspace with a gas syringe and injecting into an infrared gas analyzer (LI-6400XT, LICOR Biosciences, Lincoln, NE, USA) modified with a trace gas sampling kit, using a flow rate of 150 μmol/s. The CO_2 concentration of the injected sample was determined using a calibration equation developed before each

run, using three CO_2 primary standards (200-1500 ppm) and CO_2-free air. All linear-regression calibration equations had a $r^2 > 0.995$. Microbial respiration rates were expressed as μg C-CO_2 emitted g^{-1} of OD litter h^{-1}.

Bacterial and fungal abundance

We measured the bacterial and fungal abundance in ground litter and on the surface of litter with epifluorescence and scanning electron microscopy. We assumed ground litter provided an estimate of the total (surface and litter interior) microbial abundance. We measured microbial abundance after the third harvest (16 months), rather than the final harvest (22 months), because final harvest litter did not have enough unbroken or intact litter pieces to provide sufficient surface area for measurements. We assessed litter from the Full Sun treatment and the No UV/blue treatment because differences in mass loss and microbial respiration were greatest between these two treatments. Microbial abundances were expressed on a surface area basis. One-sided silhouette surface areas were measured for each litter subsample using a digital scanner and the software ImageJ (Rasband 2016) prior to determining bacterial or fungal abundance.

Total fungal hyphal volumes were determined using a modified procedure of Allison et al. (2013). Litter subsamples (0.05 g $\pm$ 0.01, n = 5) of each litter type and radiation treatment combination were air-dried (22°C at 10-20% RH for at least 10 d), ground to 1-2 mm size pieces with a mortar and pestle, suspended in 10 ml sodium hexametaphosphate solution (0.395% mass/volume; CAS# 10124-56-8) and gently swirled for 1 min. A 1.5 ml subsample was stained for 1 min with a 0.1% solution

(mass/volume) of Calcofluor-White (CAS# 4404-43-7, Sigma Aldrich, St Louis, MO, USA) and vacuum-filtered through a 0.2 µm polycarbonate filter (Poretics, Spectrum Chemical Mfg. Corp., New Brunswick, NJ, USA). The filter was mounted on a slide and five random fields were examined under 200x magnification and violet excitation (400-440 nm) with an epifluorescence microscope (Olympus BX50, Olympus Scientific Solutions, Waltham, MA, USA). Total hyphal length was determined using a grid-count method (Olson 1950) and volume was determined following Daniel et al. (1995). Total hyphal volume was expressed per surface area of litter ($\mu m^3\ mm^{-2}$).

Fungal hyphal volume on the surface of litter was determined using a scanning electron microscope (JSM6300, JEOL, Peabody, MA, USA). Litter subsamples (0.05 g $\pm$ 0.01, n = 5) of each litter type and radiation treatment combination were mounted on aluminum pegs and sputter-coated with a 2-3 nm layer of gold palladium and observed under 200x magnification. Five random images were taken of the litter sample. Hyphal volume was determined as described above with the grid-count method and expressed per surface area of litter ($\mu m^3\ mm^{-2}$).

Total bacterial volumes of litter were determined using a modified procedure of Ball et al. (2009). Litter subsamples (0.05 g $\pm$ 0.01, n = 5) of each litter type and radiation treatment combination were air-dried (22°C at 10-20% RH for at least 10 d), ground to 1-2 mm size pieces with a mortar and pestle and suspended in 10 ml of 3.7% formaldehyde solution (CAS# 50-00-0) and 0.5 ml of 0.1 mol L^{-1} tetrasodium pyrophosphate solution (CAS# 7722-88-5). Solutions were sonicated in ice water for 15 min to dislodge bacteria. A 1 ml subsample was stained for 10 min with 1 ml of 10 $\mu g\ ml^{-1}$ DAPI (4'6-diamidino-2-phenylindole; CAS# 28718-90-3) and vacuum-filtered through a 0.2 µm polycarbonate

filter (Poretics). The filter was mounted on a slide and ten random fields were examined under 1000x magnification and UV radiation excitation (330-385 nm) with an epifluorescence microscope. Cells were counted and noted as to shape (coccoid or rod) and size class (small and large). Bacterial volume was determined using equations for geometric shapes (Wetzel et al. 1991) and expressed as volume per surface area of litter ($\mu m^3\ mm^{-2}$).

Bacterial volume on the surface of litter was determined with the same method used for total bacterial volume except the whole pieces of litter were not ground prior to suspension in solution. We assumed that the bacteria in solution came from the surface of litter.

Statistical and data analyses

We used a three-way ANOVA to assess time, litter type and radiation treatment effects on mass remaining using SigmaPlot 12.5 (Systat Software, San Jose, CA, USA). All mean comparisons (e.g., final mass remaining, respiration, fungal and bacterial volume) were tested with Tukey's HSD test. To examine relationships between bacterial and fungal volumes, and respiration and mass loss, we used correlation analysis to determine significance and quantified their predictive power with linear regressions. To quantify photodegradation, we calculated the response ratios (RR) as the ratio of mass loss of litter in the Full Sun to that of litter in the No UV (RR_{UV}) or the No UV/blue treatment ($RR_{UV/blue}$).

Results

Mass loss and magnitude of photodegradation

Litter type, radiation treatment and time all had significant effects on mass loss, and all interactions, except the three-way, were significant (Table S1). Mass loss varied substantially among the litter types. For example, after 22 months, mass loss in the Full Sun treatment ranged from 78% (*C. angustifolia*) to 50% (*L. tridentata*) (Figure 7). After 22 months, litter lost more mass in the Full Sun than the No UV/blue treatment in four litter types (Figure 7), demonstrating that UV/blue sunlight accelerated decay in most litter types. Litter also lost more mass in the Full Sun treatment than in the No UV treatment in two litter types and lost more mass in the No UV treatment than in the No UV/blue treatment in three litter types, demonstrating that both UV and violet-blue sunlight were effective in driving mass loss. After 22 months, $RR_{UV/Blue}$ averaged 1.6 across all litter types (range 1.0-1.9) and RR_{UV} was 1.3 (range 1.0-1.6; Figure 8).

Microbial respiration

Microbial respiration rates of litter generally increased with decay and were higher in final (22-month) than initial litter within all types and treatments ($p < 0.05$; Figure 9). Final respiration of litter was higher in the Full Sun treatment than the No UV/blue treatment in four of five litter types. Final respiration of litter was also higher in the Full Sun treatment than the No UV treatment in two litter types. Final respiration rates averaged 1.6 and 1.9 times higher in the Full Sun treatment than the No UV and the No UV/blue treatments, respectively, across all litter types.

Microbial respiration of initial litter was positively correlated with final (22-month) mass loss of litter in the Full Sun treatment ($r^2 = 0.75$, p = 0.05) but not in the No UV or No UV/blue treatments ($r^2 = 0.58$, p = 0.13; $r^2 = 0.36$, p = 0.28, respectively; Figure 10a). In addition, final microbial respiration of litter tended to be correlated with final mass loss in all radiation treatments ($r^2 = 0.67$–0.70, p = 0.06-0.08; Figure 10b). Hence, litter types that lost the most mass had higher respiration rates within a given radiation treatment.

Microbial abundance

The abundance of microbes on the surface of litter was lower in litter exposed to full sunlight. For example, after 16 months fungal abundance (i.e. volume) on the surface of litter was lower in the Full Sun treatment than the No UV/blue treatment in all litter types (p < 0.05; Figure 11a) and bacterial abundance on the surface was lower in the Full Sun treatment than the No UV/blue treatment in three litter types (p < 0.05; Figure 11b). The negative effect of full sunlight on surface microbes appeared greater for fungi than bacteria. For example, fungal abundances were significantly lower in the Full Sun treatment in all litter types and the magnitude of this effect was greater in fungi: fungal abundances in the Full Sun treatment averaged 8.0 times lower than in the No UV/blue treatment, but bacterial abundance was only 3.2 times lower in the Full Sun treatment. Radiation treatment effects were less evident on total (ground) abundance of fungi and bacteria, although litter had lower fungal abundance in one litter type in the Full Sun treatment, and lower bacterial abundance in two litter types. In summary, microbial

abundance on the surface of litter was lower in full sunlight, and this reduction was more pronounced in fungi than bacteria.

Fungi were more abundant than bacteria in all litter types within the same treatment in both surface and total measurements (Figure 11). For example, averaged across all litter types, the ratio of surface fungal to bacterial abundance on a volume basis was 32:1 and the ratio of total fungal to bacterial abundance was 125:1 in the Full Sun treatment.

Bacterial abundance on the surface of litter was strongly correlated with microbial respiration of litter in the Full Sun treatment ($r^2 = 0.83$, p = 0.03; Figure 12b). In contrast, bacterial abundance on the surface of litter was not correlated with respiration of litter in the No UV/blue treatment ($r^2 = 0.13$, p = 0.54; Figure 12b). Additionally, neither total bacterial abundance ($r^2 = 0.23$–0.28, p = 0.35–0.40; Figure 12d), or surface or total fungal abundance ($r^2 = 0.05$–0.36, p = 0.70–0.28; Table S2) were correlated with respiration of litter in either radiation treatment. This suggests the bacteria on the surface of litter were responsible for the higher respiration rates of litter in full sunlight.

Bacterial abundance on the surface of litter was strongly correlated with mass loss of litter in the Full Sun treatment ($r^2 = 0.92$, p = 0.01; Figure 12a). In contrast, bacterial abundance (total or surface) was not correlated with mass loss in the No UV/blue treatment ($r^2 = 0.49$, p = 0.18; $r^2 = 0.20$, p = 0.44, respectively; Figure 12). Furthermore, fungal abundance (total or surface) was not correlated with mass loss of litter in either radiation treatment ($r^2 = 0.06$–0.45, p = 0.68–0.21; Table S2). Collectively, this suggests that bacteria on the surface of litter in sunlight were responsible for enhanced respiration which played a role in accelerating the decay of that litter.

Weather and litter microclimate

The average air temperature over the experiment at Sky Harbor International Airport (< 6 km from field site) was 25.1 °C, which was slightly higher than the 20-year historical average of 24.4 °C over the same time period. Total precipitation over the experiment was 322 mm which was lower than the historical average of 356 mm, due to a relatively dry period from February through June 2016. Averaged daily integrated fluxes at the field site were 3.1 and 23.6 kJ m^{-2} d^{-1} of UV$_{Caldwell}$ and UV$_{Flint,}$ respectively, and visible irradiance was 49.1 mol m^{-2} d^{-1}. Litter air temperatures were highest in the Full Sun treatment and lowest in the No UV/blue treatment (Table S3). When averaged across the entire field experiment, temperatures for diurnal, nocturnal and diel periods were 1.5, 0.9 and 1.3 °C higher, respectively, in the Full Sun treatment than the No UV/blue treatment, with temperatures in the No UV treatment intermediate. Average relative humidity over these periods was lower in the Full Sun than the No UV/blue treatment. When averaged across the entire field experiment, relative humidity for diurnal, nocturnal and diel periods were 0.1, 2.3 and 0.4% lower, respectively, in the Full Sun treatment than the No UV/blue treatment, with relative humidity 0.1% lower, 0.7% higher and 0.5% lower, respectively, in the No UV treatment than the Full Sun treatment.

Figures
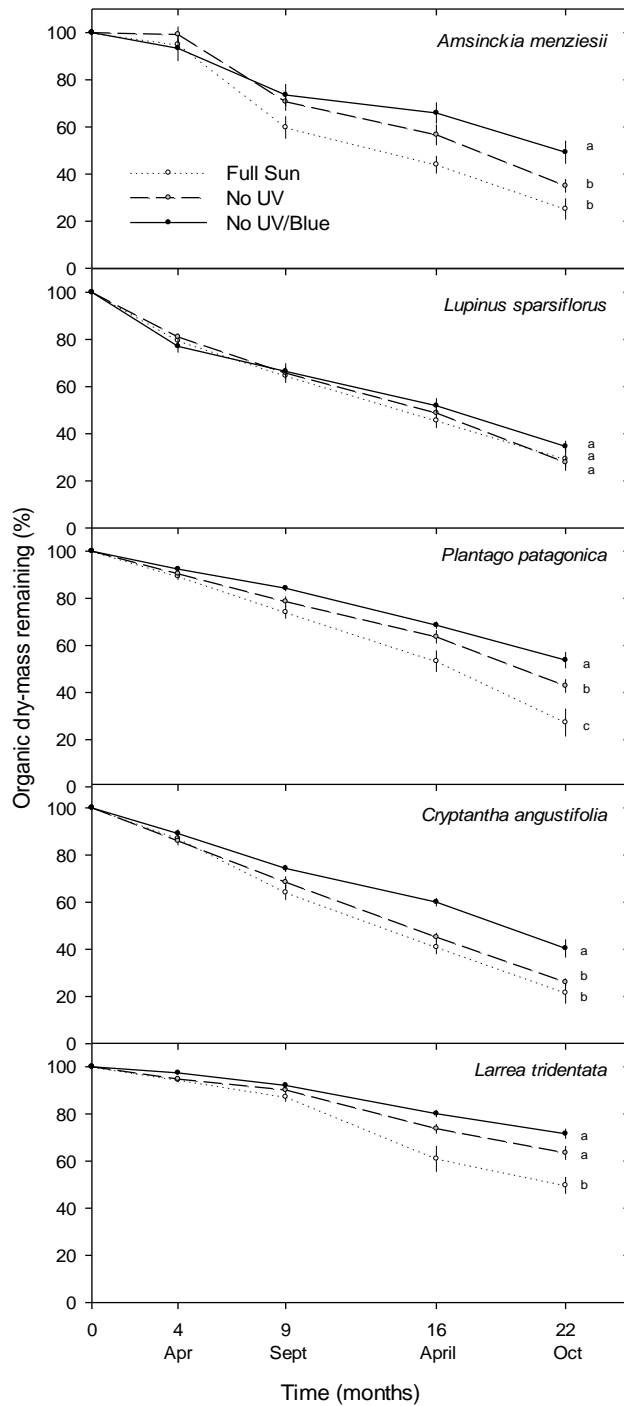
Figure 7. Organic dry-mass remaining of the five litter types in the three radiation treatments (Full Sun, No UV, No UV/blue) over 22 months. Values are means (±SE, n = 8). Final mass remaining with different letters within a litter type are significantly different (p ≤ 0.05).

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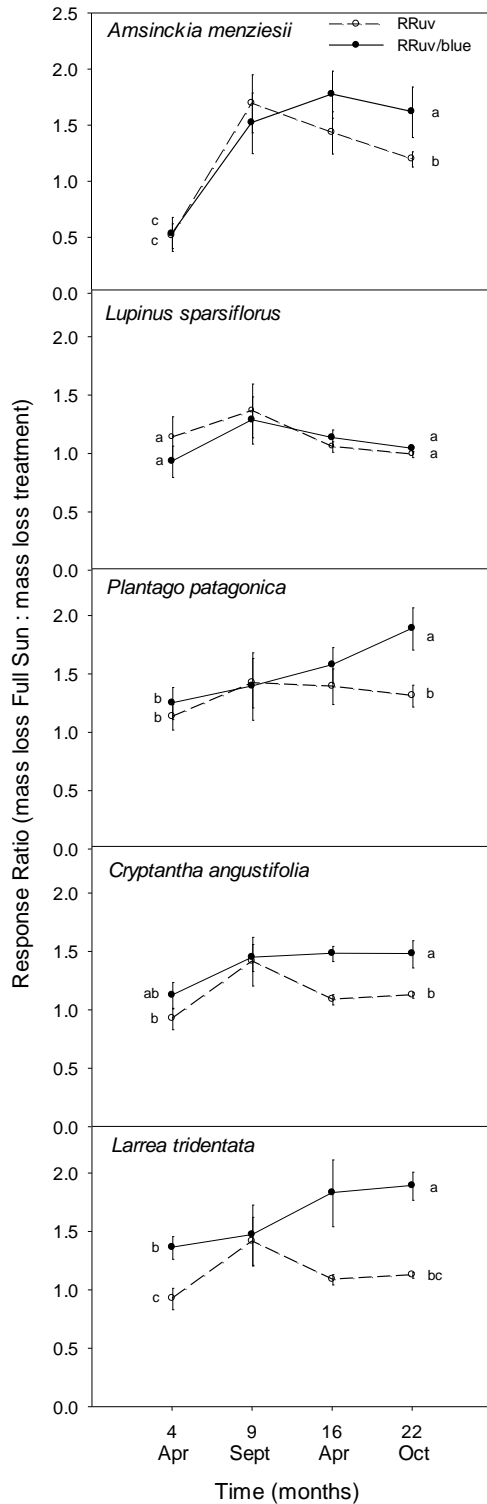
Figure 8. Response ratios of mass loss (RR_{UV} and $RR_{UV/blue}$) of each litter type over the experiment. Values are means ($\pm$ SE, n = 8). Response ratios at 4 or 22 months with different letters within a litter type are significantly different ($p \leq 0.05$).
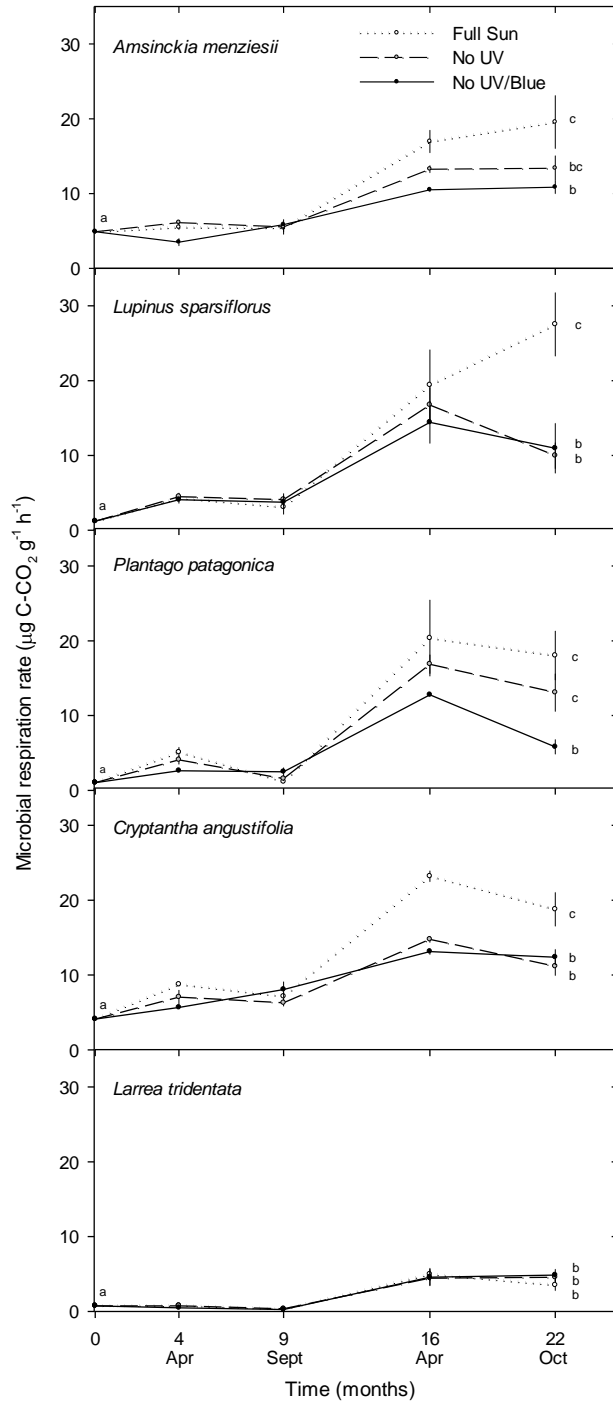
Figure 9. Microbial respiration rates of the five litter types in the three radiation treatments (Full Sun, No UV, No UV/blue) over the 22-month experiment. Values are means (±SE, n = 5). Initial and final respiration rates within a litter type with different letters are significantly different (p < 0.05).
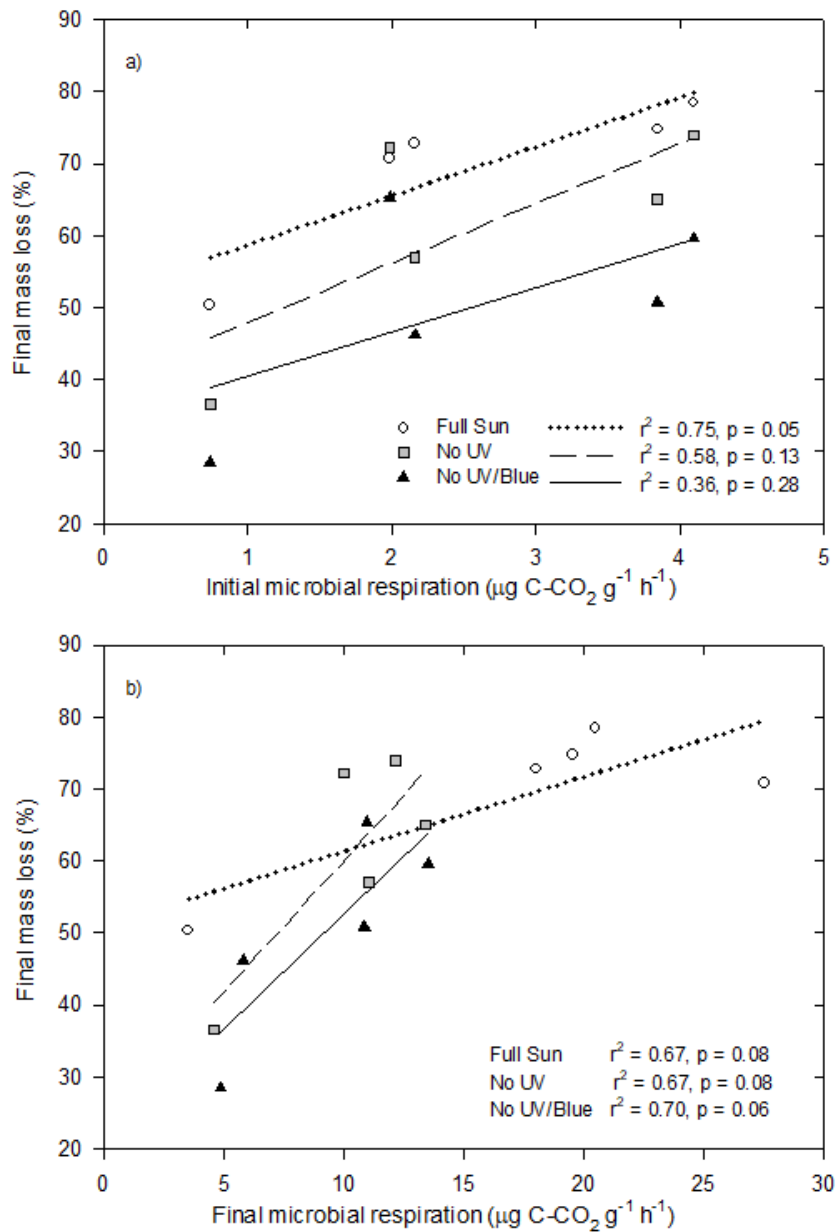
Figure 10. Relationships between initial microbial respiration (a) and final (22-month) microbial respiration (b) with final mass loss (%) in the three radiation treatments (Full Sun, No UV, No UV/blue). Values are means (n = 5 for respiration, n = 8 for mass loss). Lines are linear regressions with r^2 and p shown.
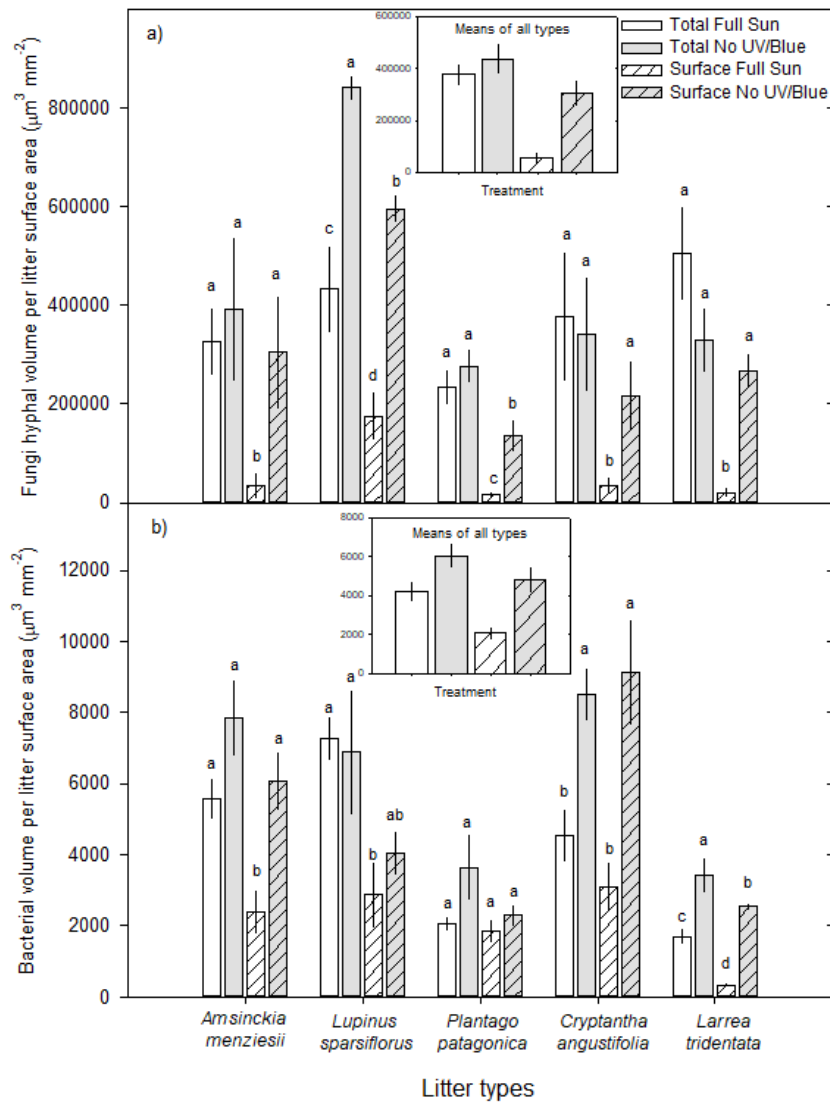
Figure 11. Fungal hyphal abundance (a) and bacterial abundance (b) per litter surface area (μm^3 mm^{-2}) for the Full Sun and the No UV/Blue treatment litter after 16 months in the field. Total and Surface indicate abundance from ground litter or on the surface of litter, respectively. Values are means ($\pm$ SE, n = 5). Different letters within a litter type in each panel are significantly different ($p < 0.05$). Inlaid figures are treatment means ($\pm$ SE) of all litter types.
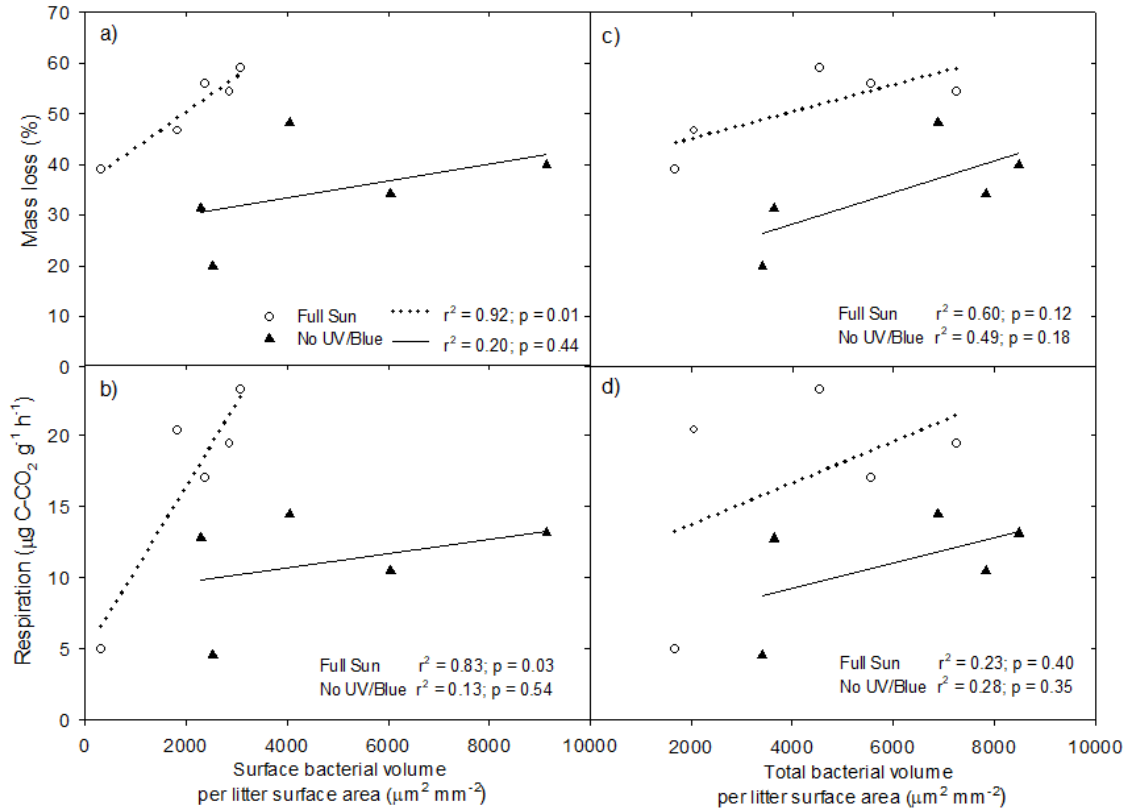
Figure 12. Relationships between bacterial abundance on the surface of litter and mass loss (a) or respiration (b) of that litter and bacterial abundance in ground litter (total) and mass loss (c) or respiration (d) of that litter after 16 months in the field. Values are means of each litter type (n = 5 for respiration, n = 8 for mass loss). Lines are linear regressions with r^2 and p shown.

Discussion

Consistent with our first hypothesis, sunlight accelerated litter decay, with litter in full sunlight losing on average 1.3 and 1.6 times more mass than litter in the No UV and the No UV/blue treatments, respectively. This is in agreement with previous work in our system (Day et al. 2007, 2015, 2018) and with the growing body of evidence that sunlight accelerates litter decay in many systems (King et al. 2012; Wang et al. 2015; Baker et al. 2015; Austin et al. 2016; Adair et al. 2017; Huang et al. 2017).

Faster litter decay in full sunlight was likely not solely an abiotic process, as microbial respiration rates of initial and final litter explained 75 and 67%, respectively, of the variation in final mass loss among litter types in this litter. Additionally, microbial respiration rates of final litter were generally highest in full sunlight. Taken together, this strongly suggests that photofacilitation of microbial degradation of litter was involved in faster decay. This is consistent with our findings in a previous study at the same site, in which mass loss and microbial respiration were strongly correlated and respiration rates were greater in litter in full sunlight (Day et al. 2018). In that study, we also found that water-soluble organic compound fractions and microbial respiration rates were strongly correlated. Thus, the higher concentration of water-soluble DOC in litter after exposure to UV radiation or sunlight (Gallo et al. 2006; Feng et al. 2011; Wang et al. 2015; Day et al. 2018) may help explain the accelerated microbial degradation of litter (Foereid et al. 2010; Frouz et al. 2011; Baker et al. 2015; Austin et al. 2016; Day et al. 2018; Lin et al. 2018).

Final microbial respiration rates explained 67 to 70% of the variation in final mass loss across all radiation treatments (Figure 10b). This strongly suggests that

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microbial degradation was a large driver of litter decay across radiation treatments. Interestingly, initial microbial respiration correlated with final mass loss in full sunlight only. The No UV and No UV/blue treatments likely had different microbial communities from initial litter since initial litter was exposed to full sunlight and the microbial community composition is often different in filtered sunlight conditions (Johnson 2003; Pancotto et al. 2003; Zepp et al. 2007). Thus, initial respiration rates did not explain final mass loss in the No UV and No UV/Blue treatments possibly due to differing microbial communities between initial and final litter. Additionally, it is possible that the lack of photofacilitation in the No UV and No UV/blue treatments resulted in microbial consumption of the soluble or labile fractions in litter. To summarize, microbial degradation played a large role in the decay of litter regardless of radiation treatment, but initial microbial respiration does not predict mass loss in filtered sunlight treatments possibly due to different microbial communities or reduced litter quality.

Consistent with our second hypothesis, fungi were always more abundant than bacteria, which is in agreement with what others have found in litter in drylands (Austin and Vivanco 2006; Bell et al. 2009) and across several biomes (Joergensen and Wichern 2008). In a meta-analysis, Fierer et al. (2009) found bacteria to be more abundant than fungi in dryland soils. Therefore, in agreement with others, conclusions on microbial abundance in soils may not correlate with the same findings in litter in drylands. Some working with litter in drylands found that bacteria were more abundant than fungi (Baker and Allison 2017; Baker et al. 2018), but these authors do conclude that their fine mesh litterbags (0.2 µm) likely inhibited fungi from infiltrating their litterbags and confounding their results.

While both bacteria and fungi were less abundant on the surface of sunlit litter (Figure 11), fungi appeared more sensitive to sunlight than bacteria. For example, on average, fungi were 8.0 times less abundant on the surface of litter in full sunlight than in the No UV/blue treatment, whereas bacteria were only 3.2 times less abundant. Others have also found that solar UV radiation has a greater negative effect on the abundance of fungi than bacteria in litter (Denward et al. 1999; Pancotto et al. 2003; Austin and Vivanco 2006). Furthermore, Rainey et al. (2005) found several genera of Sonoran desert bacteria with efficient DNA repair mechanisms that made them resistant to the detrimental effects of UV radiation. Some in dryland systems have found that solar UV radiation has no negative effects on either the bacterial or fungal abundance of litter (Baker et al. 2015), but these authors use a common method of grinding litter and thus this would include fungi and bacteria inside of litter. While we did that for our total litter analysis, we also attempted to examine microbial abundance directly on the surface of litter, which resulted in different results from the total litter samples. Thus, directly viewing microbes on the surface of litter may be a useful method of determining the influence of sunlight on microbial abundances. In summary, our findings suggest that the bacterial community on the surface of litter was more tolerant to full sunlight than the fungal community.

Consistent with our third hypothesis, exposure to sunlight favored the activity of bacteria, as the abundance of bacteria on the surface of this litter was strongly correlated with the microbial respiration of that litter. Notably, this was not the case with litter in the No UV/blue treatment. This implies that surface bacteria were predominantly responsible for the higher microbial respiration rates of litter in full sunlight. The abundance of

bacteria on the surface of litter was also strongly correlated with the mass loss of that litter in full sunlight, but this was not the case in the No UV/blue treatment. Taken together, this suggests that surface bacteria on sunlit litter were responsible for the faster decay of that litter. This aligns with the idea that photopriming would be most pronounced on the surface of litter where radiation fluxes are greatest. Furthermore, since litter in full sunlight is of higher quality for microbial consumption (Day et al. 2018), bacteria, rather than fungi, appeared to benefit more from this photopriming likely because bacteria have higher nutrient requirements and colonize higher quality litter than fungi (Bardgett et al. 1996; Van Der Wal et al. 2006; Güsewell and Gessner 2009; Santonja et al. 2018). Therefore, exposure to sunlight may favor bacterial, rather than fungal, degradation of litter.

While the abundance of surface bacteria was strongly correlated with the respiration of litter in full sunlight (Figure 12b), surface bacteria were actually more abundant on litter in the No UV/blue treatment than on litter in full sunlight (Figure 11b). This strongly implies that bacterial abundance by itself is not indicative of microbial activity, which agrees with other findings in drylands that suggest that substrate supply, rather than absolute abundance of microbes, largely drives respiration (Wang et al. 2003; Zhao et al. 2016). Therefore, abundance across treatments was not indicative of respiration because of differences in substrate quality across treatments.

Conclusion

Photodegradation was a significant mechanism of litter decay in our system and appears to involve a substantial photofacilitation or microbial component. Our findings

suggest that enhanced microbial degradation of sunlit litter was largely attributable to the greater activity of bacteria on the surface of this litter, and that surface fungi were more sensitive to sunlight than bacteria. It may be that decay in sunlight is largely occurring on the surface of litter, and this is driven by bacteria rather than fungi. Our findings highlight the importance of microbes in the decay of surface litter and further research is needed to understand the spatial and temporal dynamics of microbial degradation in drylands.

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Supplemental Tables and Figures

Table S1. Three-way ANOVA of organic dry-mass loss of litter over the experiment.

Source	df	F	P
Radiation trt	2	71.64	<0.001
Litter type	4	127.17	<0.001
Time	3	810.96	<0.001
Radiation trt x Litter type	8	3.34	<0.001
Radiation trt x Time	6	10.60	<0.001
Litter type x Time	12	8.34	<0.001
Radiation trt x Litter type x Time	24	0.66	0.88

Table S2. Correlations between fungal hyphal abundance and mass loss or respiration after 16 months in the field. Total and Surface indicates abundance from ground litter or on the surface of litter, respectively. Values are coefficients of determination (r^2) of linear regression (and p-values in parentheses; n=5 litter types). Positive or negative slopes are denoted by + or – in front of r^2. Regressions were not significant ($p > 0.05$).

Parameter	Correlation with 16-month fungal abundance (r^2 (p))			
	Total abundance		Surface abundance	
	Full Sun	No UV/Blue	Full Sun	No UV/Blue
Mass loss (%)	+0.06 (0.68)	+0.45 (0.21)	+0.10 (0.58)	+0.38 (0.26)
Respiration (μg C-CO_2 g^{-1} h^{-1})	+0.36 (0.28)	+0.12 (0.56)	+0.05 (0.70)	+0.07 (0.65)

Table S3. Microclimate means over the experiment. Diurnal, nocturnal and diel temperature means under litter are shown for radiation-treatment envelopes (i.e. Full Sun, No UV and No UV/blue, n = 5). Diurnal hours were defined as those having a mean hourly visible irradiance > 2 µmol m^{-2} s^{-1}.

Parameter	Full Sun	No UV	No UV/ Blue
Diurnal temperature (°C)	41.1	39.8	39.6
Nocturnal temperature (°C)	20.3	19.9	19.4
Diel temperature (°C)	31.4	30.4	30.1
Diurnal RH (%)	27.9	27.8	28.0
Nocturnal RH (%)	49.9	50.6	52.2
Diel RH (%)	38.7	38.2	39.1

4. RESPONSE OF MICROBIAL RESPIRATION OF SONORAN DESERT LEAF LITTER TO TEMPERATURE AND VAPOR-INDUCED MOISTURE CONTENT AND ITS SIGNIFICANCE TO C LOSS

Abstract

      Recent research has demonstrated that the microbial respiration of plant litter at high relative humidity (RH) can explain a large amount of the variation in decay rates among litter types in drylands. However, the response of litter microbial respiration to temperature and vapor-induced moisture content (MC) is not well characterized. We examined the response of microbial respiration from 16 leaf litter types to 14 temperatures ranging from 5 to 70°C. We selected four of these litter types and examined the response of microbial respiration to MC. We also monitored the RH and MC of one litter type continuously over 30 days and the RH and MC of four types over four contrasting months of the year to characterize the relationship between RH and MC of surface litter in the field. We used these findings to estimate the contribution of microbial respiration of the same four litter types to C loss from litter in a previous litter decay experiment (Day et al. 2018). Microbial respiration rates increased with temperature from 5 to 35 or 40°C, with an apparent peak in respiration at 35 and 40°C in five and seven litter types, respectively. Unexpectedly, respiration increased from 55 to 70°C in most litter types (12 of 16), and in 10 types respiration rates were highest at 70°C. Hence, respiration in our system peaks beyond the temperature peaks of cooler systems, which suggests thermophilic microbes or heat-tolerant enzymes exist in this leaf litter. Respiration rates increased exponentially with the MC of litter and had a log-linear relationship with the estimated water potential (WP) of litter. The minimum MC and WP required for significant litter respiration averaged 13.5% and -1.2 MPa, respectively, and were similar to those reported by others for litter and soils in more mesic systems. The MC of surface litter was strongly correlated with RH ($r^2 > 0.61$, $p < 0.01$). On average,

the period of July to October accounted for 60% of the total annual respiratory C loss from litter, and a second period of high respiration occurred from December to March in most litter types and accounted for 23% of annual losses. We estimate that respiration was responsible for an average of 23.6% of the total C lost from litter over a 34-month period on the surface of Sonoran Desert. Hence, respiration appears to represent a substantial pathway for litter C loss and was over two-fold greater than the combined losses we have previously found attributable to thermal and photochemical abiotic emission. Our findings strongly suggest that microbial respiration is a substantial driver of litter decay in the Sonoran Desert and are consistent with our past findings that litter respiration rates are strong predictors of litter C loss in our system.

Introduction

　　Drivers of plant litter decay in drylands are not well understood, limiting our ability to model this component of the carbon (C) cycle (Parton et al. 2007; Adair et al. 2008), and models have been unable to account for the unexpectedly high C loss rates from litter in drylands (Whitford 1981; Moorhead and Reynolds 1989; Austin and Vivanco 2006; Bonan et al. 2013). Low available moisture together with high temperatures and solar irradiance in drylands have led to a common perception that degradation of litter by microbes may be a relatively minor pathway for decay and C losses. Photodegradation, which we define here as the decay of litter caused by abiotic photolysis due to exposure to solar radiation, is one possible additional driver that may be significant in drylands (Austin and Vivanco 2006; Day et al. 2007, 2015; Rutledge et al. 2010; King et al. 2012). However, in the Sonoran Desert site where we conducted the current study we estimate that abiotic photodegradation (i.e. photochemical emission of CO_2) was responsible for only 10% of the total C lost from litter over a 34-month study (Day and Bliss 2020). Thermal abiotic emission, defined as the emission of C gases at higher temperatures (generally >50°C) in the absence of solar radiation and microbial activity (Day et al. 2019), is another possible driver. However, at the same site we estimate that thermal abiotic emission was only responsible for 1% of total C losses from litter over the same period (Day et al. 2019). Hence, it may be that degradation of litter by microbes is a larger pathway of C loss in drylands than often perceived.

　　While precipitation (and liquid water) is infrequent in drylands, there is growing evidence that water-vapor sorption during periods of high relative humidity (RH) or dew can elicit appreciable microbial activity and respiration in litter (Dirks et al. 2010;

Gliksman et al. 2017, 2018; Wang et al. 2017b; Evans et al. 2019). For example, Dirks et al. (2010) found that microbial decay, in the absence of solar radiation and rainfall, was responsible for 18% of litter mass loss which in turn constituted 50% of the annual litter mass loss and they attributed this to periods of high RH (i.e. nighttime). Additionally, Evans et al. (2019) found that including non-rainfall moisture (i.e. fog, dew and high RH) into their decomposition models increased estimates of mass loss from six-fold in a mesic Iowa, USA, site to more than 100-fold at an arid Namib Desert site. While these researchers provided estimates of the contribution of microbial decay to C loss, in the absence of rainfall, these studies were relatively short term (four months to one year (Dirks et al. 2010) to ≈11 months (Evans et al. (2019)). Additionally, they did not consider the influence of temperature on microbial respiration in their estimates (Dirks et al. 2010; Evans et al. 2019). In the current study, we assessed the response of microbial respiration in litter to RH and temperature and incorporated these responses to estimate the contribution of microbial respiration to litter C loss over a 34-month in the field.

Microbial respiration of litter increases with litter moisture content (MC; Gliksman et al. 2017; Evans et al. 2019). Respiration is also commonly found to have a log-linear relationship with the water potential (WP) of litter (Moore 1986; Lee et al. 2004; Manzoni et al. 2012). The minimum MC and WP for significant microbial respiration of leaf litter has usually been found between 10 and 20% MC (Bartholomew and Norman 1947; Nagy and Macauley 1982; Newell et al. 1985; Gliksman et al. 2017; Evans et al. 2019), and between -0.1 and -4.0 MPa (Dix 1984; Moore 1986; Thomsen et al. 1999; Chambers et al. 2001; Manzoni et al. 2012). Litter types vary in their rates of water-vapor sorption (Dirks et al. 2010) and therefore usually vary in MC under identical

conditions of air RH (Jacobson et al. 2015; Evans et al. 2019). Interestingly, WP minimums for microbial activity are generally similar across biomes and thus are generally not lower in litter or soils in drylands than more mesic systems (Manzoni et al. 2012).

Microbial respiration in soil usually peaks between temperatures of 30-40°C in hot biomes (i.e. annual average temperature >18°C: Cable et al. 2011; Tucker and Reed 2016) and between 22-35°C in cooler climates (Carey et al. 2016). However, some have found soil and litter respiration to increase up to 50°C in both cool and hot biomes (Pietikäinen et al. 2005; Richardson et al. 2012; Birgander et al. 2013; Carey et al. 2016). Wang et al. (2017a) concluded that the source of CO_2 emission at these high temperatures was unlikely to be solely intracellular respiration by microbes, but rather, could be a combination of emission from extracellular oxidative metabolism (EXOMET) of microbial enzymes, emission from reactive oxidative species (ROS) released by microbes, thermal abiotic emission, photochemical emission or emission from inorganic sources such as carbonates. Therefore, while some of the abiotic sources of emission have microbial origins, we use the term abiotic here to refer to any CO_2 emission source that is not intracellular microbial respiration. Indeed, Kéraval et al. (2018) found that 13 to 50% of the CO_2 emission from a wide range of soils were from these abiotic sources. Furthermore, Gonzalez et al. (2015) found that extracellular enzyme activity in soils from latitudes at or below 40° N peaked at temperatures between 55 and 75°C, well above the temperatures that enzymes were thought to become inactive or denature (Koffler et al. 1957; Rainey et al. 2005). Santana and Gonzalez (2015) state that thermophilic bacteria are abundant in soils from warm biomes (latitude < 40°N) and have peak growth rates

between 50 and 70°C. Therefore, it is probable that "respiration" (CO_2 emission) at high temperatures in soil and litter is a result of both biotic and abiotic activity. To our knowledge, the temperature response of microbial respiration in litter in drylands has received little attention - this could be particularly interesting in hot systems such as the Sonoran Desert, where temperatures of litter on the soil surface commonly exceed 50°C, and occasionally 70 or even 80°C (Day et al. 2019).

In this study, we characterized the temperature and MC responses of microbial "respiration" (CO_2 emission) from a diverse set of 16 leaf litter types from the Sonoran Desert. Respiration responses were assessed over short-term (6 to 24 h) incubations over a large range of temperatures (5 to 70°C) and air RH (48-90%), with the latter providing a large range in litter MC. In a series of field experiments, we also characterized and quantified the relationship between air RH and the MC of litter on the soil surface. We then used the temperature- and MC-response relationships, along with surface litter microclimate and C loss data from a previous experiment (Day et al. 2018), to assess seasonal patterns of microbial respiration and estimate the contribution of this to pathway to total C loss from litter over 34 months. We hypothesized that water-vapor driven microbial "respiration" from litter would contribute more to litter C loss than thermal abiotic and photochemical emission from litter.

Methods

Litter collection

We collected leaf litter from 16 species comprising four species in each of four growth forms: woody dicots, suffrutescent dicots, grasses and annuals (Figure 13). The woody dicots, suffrutescent dicots and grasses were collected from May through July 2013. Because of drought, annual litter was not available over this period and was collected in March through April the following year (2014). Litter was collected as naturally senesced leaves (i.e. lacking photosynthetic pigments) that were still attached to standing branches/stems from several individuals of each species growing at the base or in the foothills of the Sierra Estrella and Superstition Mountains in the Sonoran Desert of central Arizona. Litter was air-dried (22°C at 10-20% RH) for at least 30 d and sorted to remove non-leaf parts.

Response of microbial respiration to temperature

Microbial respiration rates from litter were determined by measuring CO_2 emission generally following Day et al. (2018). In brief, CO_2 emission was measured at high RH ($\approx$75%) over 24 h incubations at 14 different temperatures ranging from 5 to 70°C in 5°C increments. We chose this range because it generally covers the range of temperatures experienced by litter on the soil surface in our system (Day et al. 2019). Litter was subjected to an inoculation procedure to reduce potential confounding effects attributable to differing levels of microbial colonization, following Day et al. (2018). We placed 3 g of air-dried litter of each type in coarse white Nylon mesh envelopes (20 x 20 cm) on the unshaded soil surface at the field site (see below) on an evening in late

January 2018. Envelopes were lightly misted with nanopure water from a spray bottle and this was repeated the following morning and evening, and litter was returned to the laboratory the second morning. Inoculated litter was air dried for 30 d, and four subsamples (0.25 ± 0.02 g) of each type were placed in 37-ml serum bottles and open bottles were placed in a desiccator at 22°C for 24 h. Bottles were flushed with ≈400 ppm CO_2 air for 2 min, sealed with a butyl rubber septum and incubated in the dark for 24 h in a growth chamber (PGR15, Conviron, Winnipeg, MB, Canada) that maintained temperature within ± 0.5°C of the target incubation temperature. Evaporation from a culture tube (50 mm L x 6 mm D) filled with nanopore water increased the RH in each serum bottle to 50% within 2 h, 70% within 8 h and RH remained between 70-80% for the remainder of each incubation. Litter did not contact the liquid water and the only source of water was vapor. Three control bottles containing a water-filled culture tube but lacking litter were used to correct for CO_2 dissolved in water. To monitor and confirm temperature and RH, a hygrochron temperature/humidity logger (DS1923, iButtonLink, Whitewater, WI, USA) was inserted into three additional blank serum bottles. The final CO_2 concentration in bottles was measured by withdrawing 10 ml of headspace with a syringe and injecting into a modified infrared gas analyzer (LI-6400XT, LICOR Biosciences, Lincoln, NE, USA) having a flow rate of 150 μmol/s. The CO_2 concentration of the injected sample was determined using a calibration equation developed before each run, using 3 CO_2 primary standards (200-1500 ppm) and CO_2-free air. All linear-regression calibration equations had $r^2 > 0.995$. Headspace CO_2 content was calculated using the ideal gas law, and total CO_2 emission rates from litter were expressed as μg C-CO_2 emitted g^{-1} of desiccator-dried litter h^{-1}. Emission rates were

corrected for CO_2 dissolved in water in the control bottles. After each respiration measurement, bottles were opened and dried for 24 h in a desiccator, and then incubated at the next (i.e. 5^oC higher) temperature and emission was assessed.

At higher temperatures, particularly $>50^oC$, litter emits CO_2 in the absence of microbial respiration and photochemical emission induced by solar radiation, and this is referred to as thermal abiotic emission (Lee et al. 2012; Day et al. 2019). Hence, some of the CO_2 emission from litter we incubated at higher temperatures was likely thermal abiotic emission. We accounted for this by using the equations in Day et al. (2019) that estimate thermal abiotic emission as a function of temperature for 12 of the litter types used in the current study (Table S1). The 4 annual litter types used in the current study were not assessed by Day et al. (2019). Hence, we measured the thermal abiotic CO_2 emission from the annual litters at each incubation temperature following Day et al. (2019). In brief, litter was incubated in the dark at low RH (15-20%) such that photochemical emission and microbial respiration were negligible, and exponential equations were fit to the temperature response of emission. For each litter type, thermal abiotic emission rate was subtracted from the total CO_2 emission rate at each incubation temperature to estimate microbial respiration rate. Because our dark incubations prevented any photochemical emission and we accounted for thermal abiotic emissions, and the other "abiotic" CO_2 emission at high temperature is likely from microbial extracellular ROS or EXOMET of microbial enzymes (Wang et al. 2017a), we refer to CO_2 emission at high temperature as microbial respiration.

Response of microbial respiration to moisture content

To assess the response of microbial respiration to litter MC ((litter mass during incubation – litter mass after 24 h in a desiccator) / litter mass after 24 h in a desiccator x 100), we chose four litter types from the temperature experiment above (*Simmondsia chinensis, Bromus rubens, Ambrosia deltoidea, Cynodon dactylon*) that provided contrasting microbial respiration rates; the former two litter types had relatively low respiration rates while the latter two had relatively high rates (see Figure 13).

Litter was subjected to an inoculation procedure to reduce potential confounding effects attributable to differing levels of microbial colonization, following Day et al. (2018). We placed 3 g of air-dried litter of each type in coarse white Nylon mesh envelopes (20 x 20 cm) on the unshaded soil surface at the field site (see below) on an evening in late January 2018. Envelopes were lightly misted with nanopure water from a spray bottle and this was repeated the following morning and evening, and litter was returned to the laboratory the second morning.

Litter was kept in a desiccator for 24 h prior to incubation. Four subsamples (0.25 ± 0.02 g) of litter of each of the four types were placed in 37-ml serum bottles with a culture tube filled with either a saturated salt solution or water to provide different air relative humidities over incubations. We used the salts magnesium nitrate (CAS: 13446-18-9, Alfa Aesar, Tewksbury, MA, USA), sodium bromide (CAS: 7647-15-6, Alfa Aesar), sodium chloride (CAS: 7647-14-5, Sigma Aldrich, St. Louis, MO, USA) and ammonium chloride (CAS: 12125-02-9, Alfa Aesar) to provide RH of ≈48, 55, 64 and 74%, respectively. A single culture tube filled with water was used to provide incubations at ≈80% RH, while two culture tubes filled with water were used for incubations at ≈90%

RH. A hygrochron temperature/humidity logger was inserted into three additional bottles of each litter type and recorded RH and temperature every 15 min over incubations. Relative humidity varied slightly ($\pm$ 2%) among litter types in a given saturated salt or water incubation because of differences in vapor sorption rates among types. Bottles were flushed with $\approx$400 ppm CO_2 air for 2 min, sealed with a Teflon PTFE/Silicone septa, and incubated in the dark for 18 h, then reflushed with $\approx$400 ppm CO_2 air for 2 min, and incubated for another 6 h. We chose to reflush after 18 h because preliminary tests found that litter water-vapor sorption was very fast during initial hours of incubations and litter MC increased substantially (Tomes, Chapter 2 of this dissertation). However, vapor sorption slowed considerably by 18 h and consequently the MC of litter varied by less than 1% from 18 to 24 h in a given incubation. Hence, measuring respiration over a 6-h incubation from 18 to 24-h provided litter with relatively stable MC. Three control bottles with culture tubes filled with water or salt solutions, but lacking litter, served as controls to correct for CO_2 dissolved in the solution. Respiration rates over the 6 h incubations were measured and calculated as described in the above experiment. For subsequent data analysis and graphical presentations, we report RH as the average RH over the 6-h incubation (i.e. 18 to 24 h).

We ran these MC-response incubations at 32°C. We chose this temperature because there was a peak in respiration at high RH ($\approx$75%) of most litter types (12 of 16) at 35 or 40°C (see Figure 13), and it was close to the average diel temperature of unshaded surface litter of 29.8^{o}C that we found over a previous 34-month field study in our system (Day et al. 2018). Different subsamples of each litter type were used for incubations at the different relative humidities (i.e. different saturated salt solutions or

water). No corrections were made for thermal abiotic emission as this was negligible at 32℃. After CO_2 sampling at 24 h, litter was weighed, and MC was expressed as a percentage of its desiccator dry mass.

Estimating microbial respiration of litter under field conditions

1) Litter moisture content over 30 days in the field

To characterize how MC of litter changes in the field over short time scales, we monitored the MC of one of our litter types, *A. deltoidea*, for 30 d in a conservation area on the campus of Arizona State University, Tempe, AZ, USA. Litter (0.75 g) was dried in a desiccator for 24 h and weighed to determine initial dry mass. Only whole intact pieces of litter were used, and litter pieces did not overlap on the weighing pan. The sample was placed on the weighing pan of an analytical balance (Mettler Toledo AE 100, Mettler Toldeo, Columbus, OH, USA). For stability, the balance sat on a square piece of plywood (≈30 cm L x W), which was placed on the ground in an area shaded from direct sunlight. The pan and litter were ≈ 15 cm above the ground surface. Two hygrochron temperature/humidity loggers were placed next to the litter and pan on the balance and recorded air RH and temperature every 15 min. After allowing the litter to equilibrate to field conditions for 24 h, we recorded litter mass every 15 min from 12 March to 12 April 2018. We dried the litter in a desiccator again for 24 h to confirm that the dry mass did not change over the experiment (< 0.01 g difference), and MC was expressed as a percentage of initial dry mass.

2) Litter moisture content of four types on the soil surface over four contrasting months

We also investigated how MC of litter changes during months with contrasting climate, as well as provide a more realistic assessment of surface litter by measuring MC of litter that was on the soil surface. We assessed the MC of litter for four months: March, April, June and July of 2018; we chose these months because they represented contrasts in average temperature and RH. We assessed MC with the same four litter types that we assessed the response of microbial respiration to MC in the laboratory. The experiment was in a conservation area at the Desert Botanical Gardens, Phoenix, AZ, USA on the north side of *Olneya tesota* (ironwood) trees that shaded litter subsamples from direct sunlight. The soil surface was free of rocks and any litter on the surface was lightly brushed aside.

Three samples (0.20 ± 0.02 g) of each litter type were dried in a desiccator (24 h) to obtain an initial dry mass and placed in litterbags (4.5 x 4.5 cm) constructed of 153-µm mesh Nitex cloth (Wildlife Supply, Buffalo, NY, USA). Prior to securing bags to the soil surface, a piece of Nitex cloth was placed between the litterbag and the soil to prevent any soil from adhering to the litterbag. Each month, new litter samples were used to avoid any confounding effects of decay. Litter was allowed to equilibrate for 24 h in the field before measurements began. A hygrochron temperature/humidity logger wrapped in white Teflon tape was placed underneath litter in two supplemental bags of each litter type and recorded air temperature and RH every 15 min.

We assessed the mass of each litterbag twice each day: in early morning between 05:00-07:00 h and again in late afternoon between 15:00-17:00 h local time, using a digital balance (Gempro 250, MyWeigh, Erkenlenz, Germany). We chose these times to

attempt to measure litter mass at the highest and lowest RH each day because preliminary tests found litter MC strongly correlated with RH. The mass of each bag and enclosed litter were measured together – preliminary tests found that moisture uptake/loss by empty bags was insignificant. The bag weight was subtracted from the masses recorded in the field and litter MC was expressed as a percentage of initial dry mass.

We stopped measuring litter mass if MC was too low for microbial respiration across all litter types for two consecutive measurements, based on estimates of the minimum MC required for respiration acquired from our experiment on the response of respiration to MC. Measurements resumed when the daily high RH increased or if precipitation was expected. Therefore, the number off sampling times differed with the month. We recorded litter mass and MC a total of 79 times over the four months: 27 times in March, 10 in April, 22 in June and 20 in July.

3) Estimating respiration of four litter types over 34 months in the field

To estimate average microbial respiration rates of litter over all months in a year in the field, we used hourly air temperature and RH data collected on litter in course-mesh bags in full sunlight on the soil surface at the conservation area at the Desert Botanical Gardens over 34 months (December 2013 – October 2016; described in Day et al. (2018)). These data were collected adjacent (≈50 m) from the site where we measured the MC of four litter types over four months discussed above. We estimated the MC of the four litter types from air RH using the linear relationship we developed over the four contrasting months (see Results; Figure 19). We used the exponential relationships we developed between respiration and MC of litter to estimate respiration rates of the four

litter types (Figure 14). We then accounted for temperature effects on respiration by normalizing rates within each litter type to rates at 32°C, because the relationship between respiration and MC was assessed at this temperature. Rates at other temperatures were expressed as a proportion of the rate at 32°C. Linear regressions between each 5°C measurement increment (5-70°C in Figure 13) were used to determine the appropriate proportion or weight used to correct for temperature effects for each litter type. Estimated hourly microbial respiration rates were totaled by month and we averaged the monthly totals for each calendar month of the experiment. Because microbial respiration rates increase with decay, we used respiration rates over the 34-month experiment (Day et al. 2018) to create weighting functions for each litter type (Figure S1). Rates at each hour were then weighted to estimate the contribution of microbial respiration to C loss over the 34-month experiment.

Statistical and data analysis

To examine relationships between RH and litter MC in the field we used correlation analysis to determine significance and quantified their predictive power with linear regressions using SigmaPlot 12.5 (Systat Software, San Jose, CA, USA). The response of microbial respiration to litter MC were fitted with two-parameter exponential functions using SigmaPlot. To determine the minimum temperature necessary for significant microbial respiration we performed a one sample t-test to determine if the respiration rate difference between microbial respiration and zero was significant. We quantified the response of microbial respiration to temperature by calculating the temperature coefficient (Q_{10}), which gives the average increase in respiration rate for an

increase of 10°C. We used the equation $K = (\ln R_2 - \ln R_1) / (T_2-T_1)$ and $Q_{10} = \exp(10 \times K)$ following Wallenstein et al. (2009), where R_2 and R_1 are the respiration rates at temperatures T_2 and T_1, respectively. We calculated Q_{10} values over the ranges 5 to 35°C and 55 to 70°C. We further characterized the response of respiration to temperature by calculating the activation energy (E_a) of respiration over the same two temperature ranges using the Arrhenius equation: $k = A \exp(-Ea/RT)$, where k is the reaction rate constant, A is the preexponential factor, E_a is the activation energy, R is the gas constant and T is the temperature in Kelvins. We tested for significant differences in E_a and Q_{10} between the two temperature ranges with paired t-tests.

Results

Response of microbial respiration to temperature

Microbial respiration rates generally increased with temperature from 5 to 35 or 40°C, with an apparent peak in respiration at 35 and 40°C in five and seven litter types, respectively (Figure 13). Rather unexpectedly, respiration also increased from 55 to 70°C in most litter types (12 of 16), and in 10 types respiration rates were highest at 70°C. While thermal abiotic emission rates were much lower than respiration rates at most temperatures, at higher temperatures thermal abiotic emission was substantial in several types, and at 70°C it was higher than respiration rates in four litter types.

We estimated the minimum temperature required for respiration by determining the temperature at which respiration rates were significantly greater than 0 µg C-CO_2 g^{-1} h^{-1}. The minimum temperature necessary for microbial respiration was 10°C in nine litter types, 15°C in six types and 20°C in one type (Figure 13). In four litter types no significant respiration occurred at or above 60 or 65°C.

Microbial respiration appeared more sensitive to temperature over the lower temperature range of 5 to 35°C than the higher temperature range of 55 to 70°C in nearly all litter types (Table 6). For example, 15 of 16 litter types had a higher Q_{10} over the lower temperature range (5 to 35°C, $p < 0.01$; Table 6), and 14 of 16 types had a higher E_a over the lower temperature range (Table 6).

Response of microbial respiration to moisture content

Microbial respiration of all litter types increased with litter MC, and responses were well described by 2-parameter exponential equations (average $r^2 = 0.93$, range =

0.89 – 0.98; Figure 14). Respiration rates varied substantially among litter types at high MC (>25%). For example, at a litter MC of $\approx$ 27%, respiration of *C. dactylon* averaged 29.5 µg C-CO2 g^{-1} h-1, but only 1.3 µg C-CO2 g^{-1} h^{-1} in *S. chinensis*.

We did not attempt to measure the WP of litter or its relationship with litter MC (i.e. retention curves). However, there have been some attempts to assess the relationship between litter or soil WP and respiration rates. To examine this, we used the retention curve equation presented by Lee et al. (2004) for forest litter to estimate litter WP from MC. Respiration rates were minimal (< 1.0 µg C-CO2 g^{-1} h^{-1}) at WP less than -0.75 MPa (Figure 15a), but increased exponentially at higher WP. Some have found a linear relationship between respiration rate and the log of litter WP (Moore 1986; Manzoni et al. 2012). Generally, this relationship was linear, but this varied by litter type with significant linear relationships in *S. chinensis* ($r^2 = 0.92$, p = 0.002) and *A. deltoidea* ($r^2 = 0.63$, p = 0.05), a marginally significant relationship in *B. rubens* ($r^2 = 0.61$, p = 0.06) and a tendency for significance in *C. dactylon* ($r^2 = 0.51$, p = 0.10; Figure 15b). We used the regression equations in Figure 15b to estimate the minimum WP of litter for microbial respiration (i.e. the WP when the function intercepts the x-axis). The minimum WP of litter for microbial respiration was -1.38, -1.22, -1.09 and -1.10 MPa for *S. chinensis*, *A. deltoidea*, *B. rubens* and *C. dactylon*, respectfully. Converting these values of minimum WP to MC gave minimum MC values for microbial respiration of 9.8, 13.7, 15.6 and 15.0% for *S. chinensis*, *A. deltoidea*, *B. rubens* and *C. dactylon*, respectfully.

Estimating microbial respiration of litter in the field

1) Litter moisture content over 30 days in the field

Litter MC was strongly correlated with air RH over the 30-day continuous monitoring period ($r^2 = 0.73$, $p < 0.001$; Figure 16). This was expected, although the strength of the correlation was somewhat surprising given the expected time lags associated with vapor sorption/desorption by litter. The litter MC (and WP) was relatively buffered from changes in air RH and WP (Figure 16a and 17). To assess this, we expressed both litter and air moisture as WP, calculating air WP from air RH and temperature (Campbell and Norman 1998).The range in litter WP over the 30-day period was only 1.16 MPa (-3.24 to -2.08 MPa) while the range in air WP was 257.32 MPa (-353.52 to -96.20 MPa; Figure 17).

There was hysteresis in the relationship between litter MC and RH, which was partly related to whether litter was in water-vapor sorption or desorption phase (Figure 18). At a given air RH, litter MC was higher during desorption than sorption phases. This may have been caused by faster declines in air RH during desorption periods, which typically occurred in early morning when sunrise and rising temperatures usually led to rapid declines in RH. For example, RH declined on average 7.5% in the two hours after the peak RH and increased 2.7% in the two hours after the minimum RH each day. Whether this hysteresis was wholly attributable to the faster decline in RH associated with desorption or also involved differences in physiochemical mechanisms controlling vapor desorption/sorption is unclear. In any case, one outcome associated with this hysteresis was a delay in the decline in litter MC during morning desorption periods: the median time it took for litter MC to decline after RH began to decline during the morning

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desorption period was 37 min, whereas the median time it took for litter MC to increase

after RH began to increase during evening sorption periods was 15 min.

2) Litter moisture content of four types over four contrasting months

Over the four months that litter MC was monitored, MC averaged the highest in

July in all litter types (Table 7). Moisture content was intermediate in March and lowest

in either April or June. As expected, MC was higher in mornings than afternoons for all

months. Moisture content varied substantially among litter types and were generally

highest in *A. deltoidea,* intermediate in *B. rubens* and *C. dactylon* and lowest in *S.*

chinensis. Consistent with our 30-day monitoring experiment, litter MC was highly

correlated with RH in all types ($r^2 > 0.61$, $p < 0.001$; Figure 19). Relative humidity

averaged higher in the mornings than afternoons in all months and was higher in March

and July than April and June (Table S2).

3) Estimating respiration of four litter types over 34 months in the field

We used hourly data on air temperature and RH of litter on the soil surface

(described in Day et al. 2018) along with the above relationships between litter MC and

air RH (Figure 19), and respiration and MC (Figure 14) and respiration and temperature

(Figure 13), to estimate the respiration rate of four litter types over that 34-month field

experiment. This allowed us to calculate the average respiration C losses from litter over

each month of the year and assess seasonal patterns in respiration. Because total C losses

from litter were assessed over the 34-month experiment of Day et al. (2018), we could

also assess the contribution of respiration to total C loss from litter. For this assessment,

we took into account that respiration increases substantially over the course of decay in our system – Day et al. (2018) found that, on average, respiration rates increased by a factor of 27 times from initial to 34-month old litter. We quantified this effect by fitting exponential functions to the temporal respiration patterns of respiration through decay in Day et al. (2018) for each of the four litter types. Single-parameter exponential functions fit the data well ($r^2 = 0.85 – 0.97$; Figure S1) and allowed us to incorporate this increase in respiration over decay in our estimates of C losses.

There was a period of relatively high respiration in July through October with the highest monthly respiration rates in August in all litter types (Figure 20). On average, the July to October period accounted for 60% of the total annual respiratory C loss from litter. While not as prominent, a second period of high respiration occurred from December to March in three of the litter types (*A. deltoidea, B. rubens* and *C. dactylon*) and accounted for, on average, 23% of the annual respiratory C losses. While those three litter types exhibited very similar seasonal patterns in monthly respiration, respiration from *S. chinensis* was very modest during the winter months, suggesting that litter type could have a strong influence on seasonal patterns of microbial respiration. During December through March the average litter air temperature was 18°C while RH averaged 53%. During July through October the average litter air temperature was 38°C and RH averaged 37%. Hence, while RH and litter MC were highest over the December through March period, temperatures were not high enough to promote large respiratory losses. In contrast, relatively modest RH during the July through October period, often associated with moister monsoonal systems, along with higher temperatures, promoted the highest respiratory losses from litter.

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We estimate that cumulative respiratory C losses over the 34-month field experiment were 37.2, 93.2, 31.8 and 84.3 mg C-CO$_2$ g^{-1} for *S. chinensis, A. deltoidea, B. rubens* and *C. dactylon*, respectfully. This would account for 9.5, 24.3, 8.8 and 23.5% of the original C in each of these litter types over the 34-month experiment, respectively, and would correspond to 22.9, 28.2, 13.2 and 30.1% of the total C lost from these four litter types over the 34-month experiment.

Figures
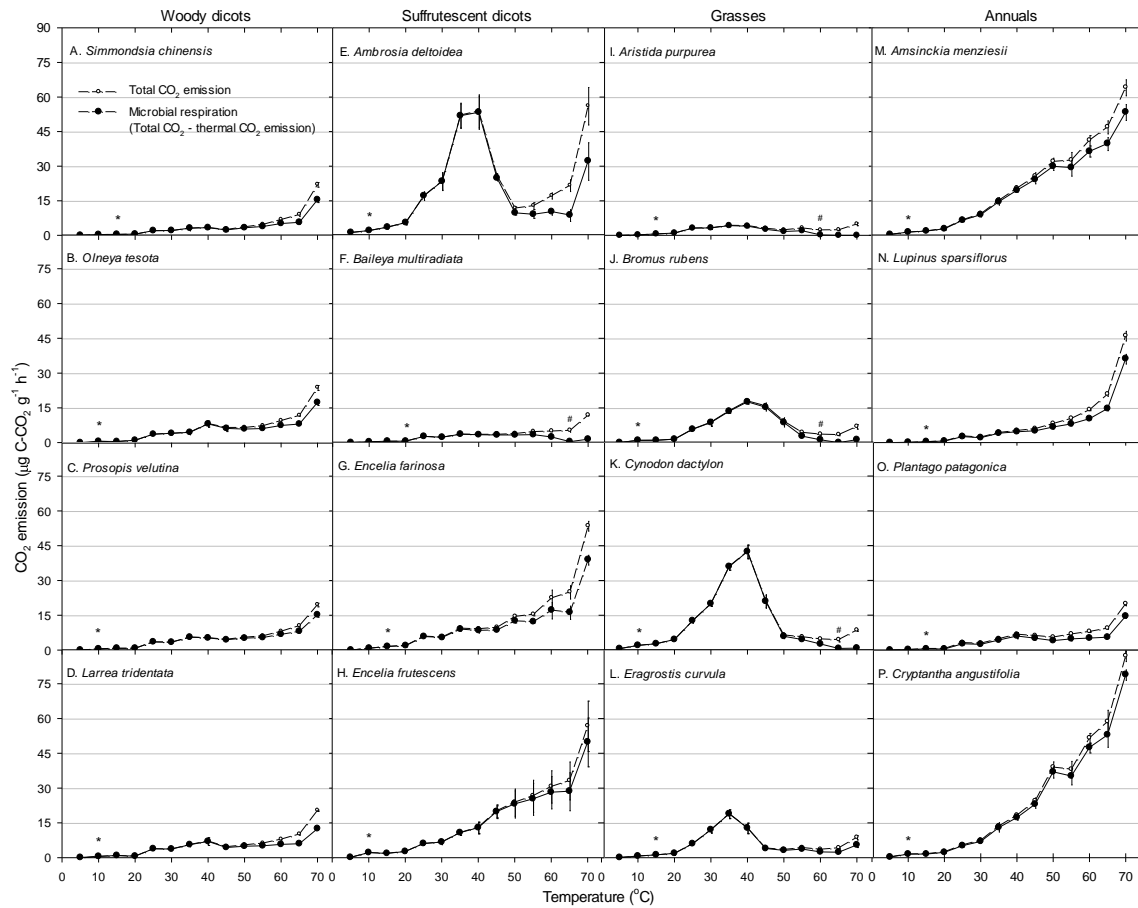
Figure 13. Response of CO_2 emission of litter over a 24-h incubation at ≈75% RH to temperature. Microbial respiration was calculated by subtracting thermal abiotic emission (CO_2 emission measured in the absence of water vapor) from total CO_2 emission (symbols are n = 4 ±SE). The lowest temperature of significant microbial respiration within a litter type is denoted with an * (different from zero, $p < 0.05$). Respiration was not significant within a litter type at and above temperatures with a #.
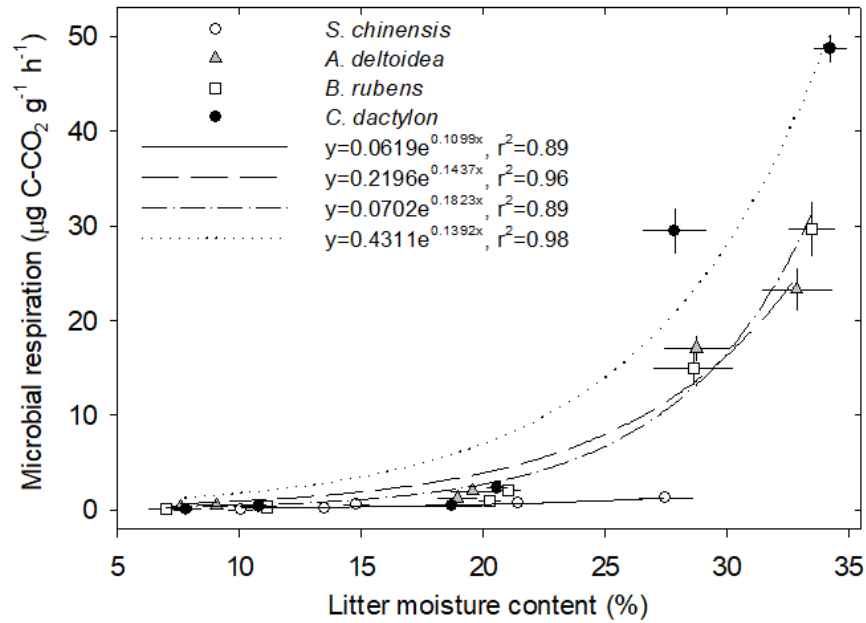
Figure 14. The relationship between microbial respiration and litter MC measured at 32°C. Symbols are means of respiration and MC (n = 4 ±SE). Lines are two-parameter exponential functions with equations and r^2 (n = 6 for each litter type).
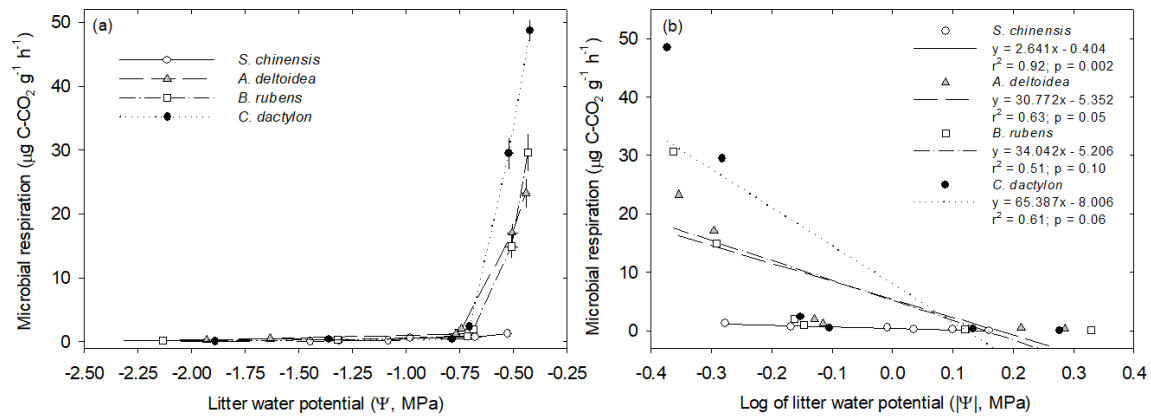
Figure 15. The relationship between microbial respiration and the WP of litter (a) and respiration and the logarithm of the WP of litter (b) within each litter type. Symbols are means of litter types (n = 4) and error bars on (a) are ±SE. Lines in (b) are linear regressions with equations, r^2 and p-value in legends (n = 6 for each litter type).
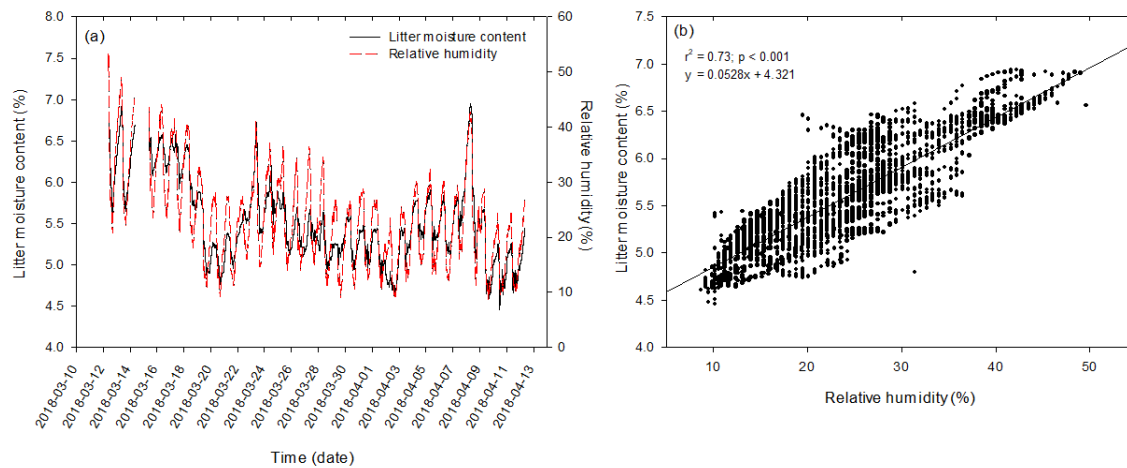
Figure 16. *Ambrosia deltoidea* litter MC and RH over the 30 days in the field (a) and the relationship between litter MC and RH for all 30 days (b). The line on (b) is a linear regression with equation, r^2 and p-value. Measurements of MC and RH were recorded every 15 min (n = 2 RH sensors).
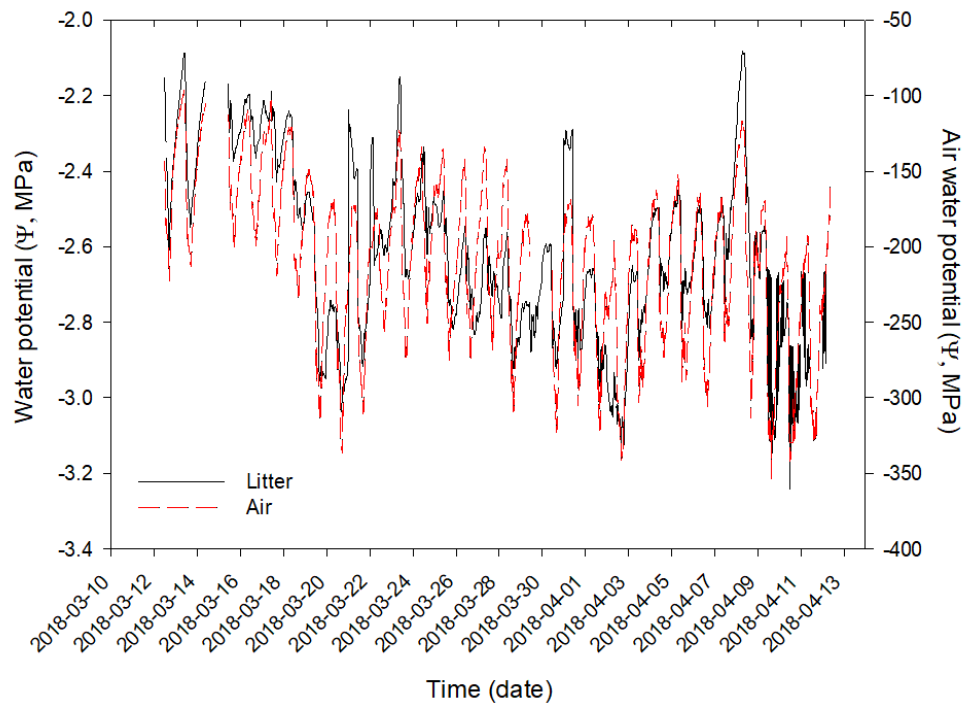
Figure 17. *Ambrosia deltoidea* litter and air WP over the 30 days in the field. Measurements were recorded every 15 min (n = 2 RH sensors).
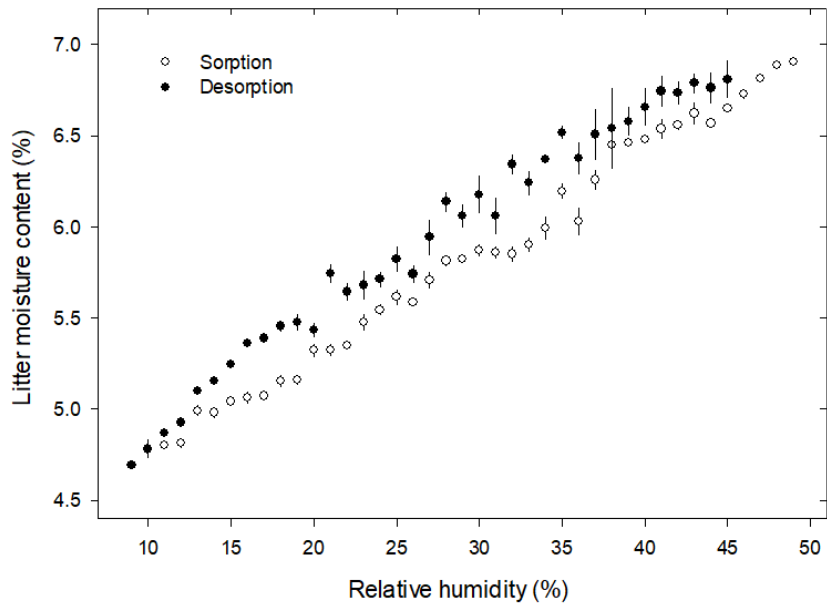
Figure 18. *Ambrosia deltoidea* litter MC during sorption (water uptake) and desorption (water loss) at each percent of RH for all 30 days in the field. Values are mean ± SE.
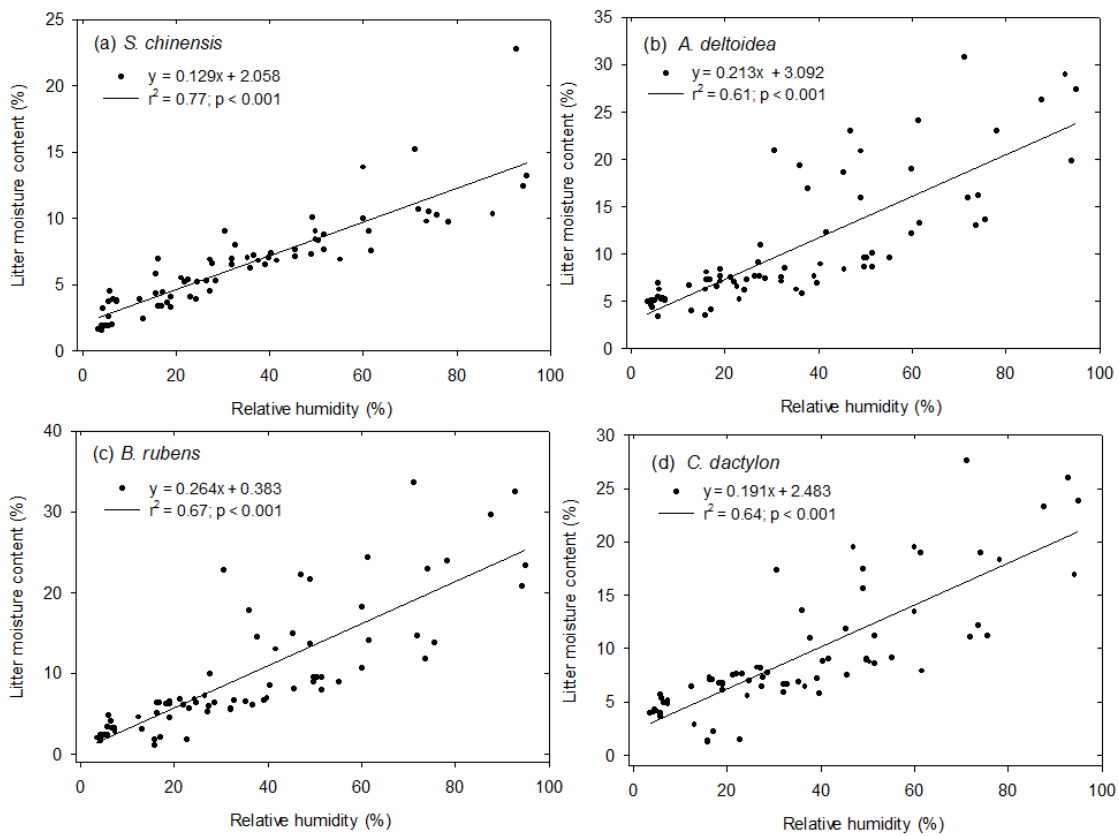
Figure 19. The relationship between litter MC and RH at the Desert Botanical Gardens over all four months for *S. chinensis* (a), *A. deltoidea* (b), *B. rubens* (d) and *C. dactylon* (d). Lines are linear regressions with equations, r^2 and p-values (n = 79 for each litter type). Note: The maximum MC measurement for July is not shown because this one value was at least 50% higher MC than all other measurements but is reported in Table 7 and factored into the linear regressions reported in this figure.
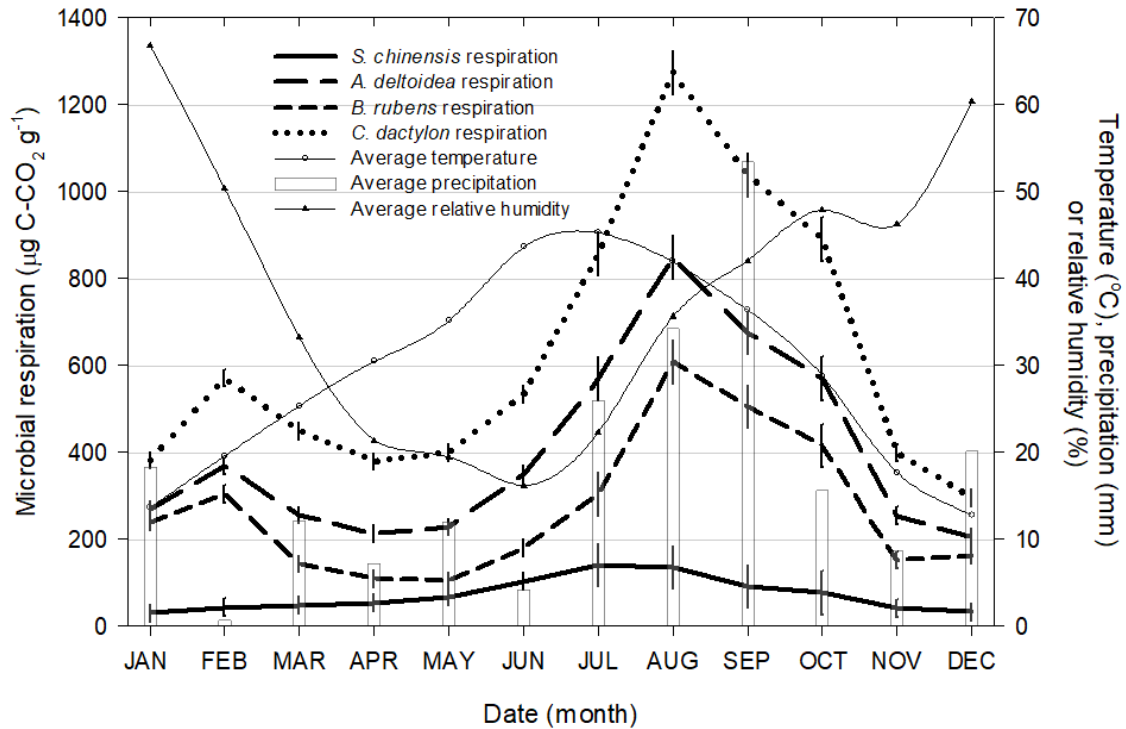
Figure 20. Estimated average microbial respiration each month. Lines for each litter type are averages of monthly estimated microbial respiration using the 34-months of microclimate field data in the Desert Botanical Garden. The vertical line at each type/month combination is ±SE. The solid line and open circles are average temperature and the solid line and closed triangles are average RH for each month. The vertical open bars are average monthly precipitation.

Tables

Table 6. Microbial respiration Q_{10}, and activation energy (E_a) from 5-35°C and 55-70°C. A NA indicates that respiration did not increase over that temperature range. An asterisk denotes that values of Q_{10} or E_a at 5-35°C were significantly higher than those at 55-70°C ($p < 0.05$). Values are means (n = 4 for individual litter types, n = 16 for the average of all types).

Litter type	Q_{10} (5-35°C)	Q_{10} (55-70°C)	E_a, kJ mol^{-1} (5-35°C)	E_a, kJ mol^{-1} (55-70°C)
Simmondsia chinensis	2.4	2.6	69.7	81.6
Olneya tesota	2.2[*]	1.9	73.4[*]	56.2
Prosopsis velutina	2.6[*]	2.0	74.2[*]	60.5
Larrea tridentata	2.5[*]	1.8	72.9[*]	49.5
Ambrosia deltoidea	3.5[*]	2.6	89.7[*]	78.7
Bailyea multiradiata	3.2[*]	NA	77.5[*]	NA
Encelia farinosa	2.4[*]	2.2	67.7[*]	63.6
Encelia frutescens	1.9[*]	1.6	52.4[*]	42.1
Aristida purpurea	2.6[*]	NA	74.4[*]	NA
Bromus rubens	4.4[*]	NA	100.1[*]	NA
Cynodon dactylon	2.8[*]	NA	84.1[*]	NA
Eragrostis curvula	4.0[*]	2.0	109.4[*]	66.0
Amsinckia menziesii	3.8[*]	1.5	86.9[*]	35.1
Lupinus sparsiflorus	3.0[*]	2.7	82.6	90.2
Plantago patagonica	2.9[*]	2.1	89.1[*]	62.2
Cryptantha angustifolia	3.9[*]	1.8	84.9[*]	50.6
Average (SE)	3.0 (0.2) [*]	2.0 (0.1)	80.6 (3.4) [*]	61.4 (4.1)

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Table 7. Moisture content of litter in the field at the Desert Botanical Gardens site over the four contrasting months. Moisture contents of litter are the average in morning (5:00-7:00 h) and afternoon (15:00-17:00 h), and the maximum and minimum each month in 2018 (n = 14, 5, 11 and 10 for the mornings and n = 13, 5, 11 and 10 for the afternoons in March, April, June and July, respectively).

Litter type	Moisture content (%)	Month			
		March	April	June	July
Simmondsia chinensis	Morning	8.7	5.2	5.8	16.9
	Afternoon	7.9	3.9	3.7	6.5
	Maximum	13.2	5.5	13.8	76.7
	Minimum	4.2	3.1	1.5	3.6
Ambrosia deltoidea	Morning	13.0	7.1	7.4	31.7
	Afternoon	7.1	5.2	4.3	12.3
	Maximum	27.4	7.5	19.0	107.5
	Minimum	3.5	4.3	3.2	3.9
Bromus rubens	Morning	11.4	6.1	7.2	29.6
	Afternoon	8.7	3.8	4.0	11.3
	Maximum	23.3	6.8	18.2	113.3
	Minimum	4.3	2.2	1.6	3.1
Cynodon dactylon	Morning	12.8	6.9	7.3	27.1
	Afternoon	5.4	4.9	4.1	10.9
	Maximum	23.9	7.7	19.5	106.6
	Minimum	4.0	4.2	3.5	2.9

Discussion

We estimate that the majority (60%) of annual microbial respiration occurred over a four-month summer-early fall period, from July through October. Litter temperatures averaged 38°C over this period, close to the peak in respiration found at 35-40°C in most litter types (Figure 13). Litter temperatures averaged 39°C from May and June, but lacked the monsoonal rainfall that increased RH, and therefore litter MC during the July through October period. Another period of relatively high respiration occurred over the four-month winter period from December through March, accounting for 23% of annual respiration in three of the litter types. While average RH was higher over this latter period (53%) than during July through October (37%), temperatures were usually suboptimal for respiration (average 18°C), which strongly limited respiration over the winter period.

There was a peak in respiration in the majority of litter types at 35-40°C, consistent with past findings on microbial respiration in drylands (Cable et al. 2011; Tucker and Reed 2016) and many other systems (Moore 1986; Chen et al. 2000); hence, the temperature response of microbes in our hot dryland were similar to those in cooler systems, at least up to ≈50°C in most cases. On the other hand, there was a distinct increase in respiration between 55 and 70°C in most litter types (12 of 16) and emission rates were highest at 70°C in 10 types. This is consistent with findings that extracellular enzyme activity and the growth rate of thermophilic bacteria in soils from warm climates peaks between 50 and 75°C (Gonzalez et al. 2015; Santana and Gonzalez 2015). The E_a of CO_2 emission between 55 and 70°C were relatively high, averaging 61.4 kJ mol^{-1}, and many researchers have taken E_a >50 kJ mol^{-1} as evidence of an abiotic component involved in the process (Lenhart et al. 2015; Liu et al. 2019). This is consistent with

others who concluded soil respiration at higher temperatures can involve a large abiotic component (Kéraval et al. 2018). While our dark incubations prevented any photochemical emission and we accounted for thermal abiotic emissions, Wang et al. (2017a) suggested other abiotic processes such as emission via extracellular ROS or EXOMET may explain the high emissions that we observed at high temperatures. Maire et al. (2013) found some enzymes released from microbes can function and release CO_2 up to 150°C. Additionally, extracellular ROS can be released by both bacteria and fungi (Kersten and Kirk 1987). To summarize, the CO_2 emission measured at high temperature may have biotic and abiotic components, but the abiotic source of emission here is likely the result of extracellular enzymes or molecules released by microbes. Thus, we suggest it is appropriate to refer to CO_2 emission at high temperature as microbial respiration.

Microbial respiration rates of litter increased exponentially with litter MC, in agreement with others who found this relationship with soil respiration in drylands (Wang et al. 2014) and respiration of litter in mesic systems (Moore 1986). Additionally, we found a linear relationship between respiration and the log of WP, consistent with others who found this relationship (Moore 1986; Lee et al. 2004; Manzoni et al. 2012). Furthermore, the average minimum MC of 13.5% for microbial respiration was similar to others in mesic systems (Bartholomew and Norman 1947; Gliksman et al. 2017; Evans et al. 2019) as was the average minimum WP of -1.2 MPa (Moore 1986; Thomsen et al. 1999; Manzoni et al. 2012). The WP minimums we found are in the range where bacterial activity is significantly reduced or ceased (Chapman et al. 1981) and when diffusivity of solutes occurs (Manzoni and Katul 2014). Some have found fungal respiration in litter at more negative WP than our minimums (Chambers et al. 2001), but

because microbial respiration of litter in our system strongly correlates with bacterial abundance (Tomes, Chapter 3 of this dissertation) may be why our values were not as low as some have found. To summarize, the responses of microbial respiration to WP and MC of litter in our dryland system were similar to those found for microbes in more mesic systems, consistent with the conclusion of Manzoni et al. (2012) who found no difference in the minimum WP for significant microbial respiration from soils and litter from xeric systems compared to more mesic systems.

We found that the MC of litter strongly correlated with RH in both our 30-day continuous measuring of the MC of *A. deltoidea* litter and our measurements of the MC of four litter types over four contrasting months. This demonstrates that the MC of litter in the field can be estimated by monitoring RH under litter, in agreement with others who found this relationship in laboratory conditions (Wang et al. 2015). Similar to what others found in drylands (Whitford 1981; Whitford and Wade 2002; Evans et al. 2019), MC of litter peaked in the early morning and dropped dramatically in the afternoon. Interestingly, we also found that *A. deltoidea* litter generally had higher MC during water-vapor desorption than water-vapor sorption when compared at the same RH, demonstrating a hysteresis effect. This hysteresis was at least partly attributable to a delay in the decline of litter MC after air RH rapidly declined during sunrise. This effect may be important in sustaining microbial respiration during morning hours when the litter MC is still relatively high and rising temperatures are becoming more optimal for respiration.

Because air RH is typically continuously changing in the field and can change dramatically over short periods of time, water-vapor sorption and desorption rates of litter are likely to have a large influence on the MC of a given litter type. Sorption rates varied

by a factor of three across the 16 litter types assessed in this chapter (Tomes, Chapter 2 of this dissertation). Consequently, the MC of *S. chinensis* litter was generally lower than the other three types over the four months of measuring MC in the field, and moreover, the slope of the relationship between MC and RH was much lower for this litter type (0.129) than the other three litter types (0.191, 0.213 and 0.264; Figure 19). Slower rates of water-vapor sorption may also explain why, unlike the other three litter types, respiration rates of *S. chinensis* litter did not increase during the four-month winter period mentioned above.

To assess how significant microbial respiration is in terms of pathways of C loss from litter in our system, we compared our estimates of respiratory C losses from litter to C losses via other pathways that we have recently estimated for the same four litter types at the same site and time period used in the current study. Day et al. (2019) estimated that thermal abiotic emission from litter was responsible for an average of 1.4% of the total C lost from the four litter types over 34 months on the soil surface. Day and Bliss (2020) estimated that abiotic photodegradation (i.e. photochemical emission of CO_2) was responsible for an average of 10.9% of the total C lost from the same four litter types. In the current study, we estimate that respiration was responsible for an average of 23.6% of the total C lost from these litter types. Hence, consistent with our hypothesis, respiration appears to represent a substantial pathway for C losses, averaging over two-fold greater than the combined losses attributable to these two abiotic emission pathways. This idea is consistent with findings that microbial respiration rates of initial (as well as decayed) litter are strong predictors of litter C loss in our system (Day et al. 2018), strongly suggesting that respiration is a substantial driver of litter decay.

In regards to what our findings suggest in the context of climate change, drylands in the future are expected to increase in average annual temperature (Stocker et al. 2013), which would increase microbial respiration in most, if not all months in nearly all litter types. On the other hand, precipitation patterns in the Sonoran Desert are predicted to become more extreme, with fewer but heavier rainfall events, which could alter the community and activity of microbes (Nielsen and Ball 2015). Taken together, this suggests average RH would generally decline and consequently litter MC would also. Hence, a warmer, drier climate would present opposing changes to microbial respiration of litter.

Conclusion

The response of microbial respiration to litter MC in the Sonoran Desert was similar to those found in more mesic systems and microbes did not appear to be active at a lower MC or WP than those from other climates. Rather unexpectedly, respiration increased from 55 to 70°C in most litter types. Hence, respiration in our system peaks past the temperature peaks found in cooler systems. It may be that our litter has thermophilic bacteria adapted to high temperature (>50°C) or extracellular ROS or enzymes that can still function at these high temperatures and thus requires further investigation to understand the mechanisms behind high temperature respiration. The seasonal patterns of microbial respiration differed among litter types, indicating the importance of including diverse litter types into future assays and predictions of respiration rates and microbial decay. Collectively, our results strongly suggest that the microbial respiration of litter contributes substantially more than thermal abiotic and

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photochemical emission to the C loss of litter and future research should focus on

building our understanding of microbial respiration in the field.

Acknowledgements

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Supplemental Tables and Figures
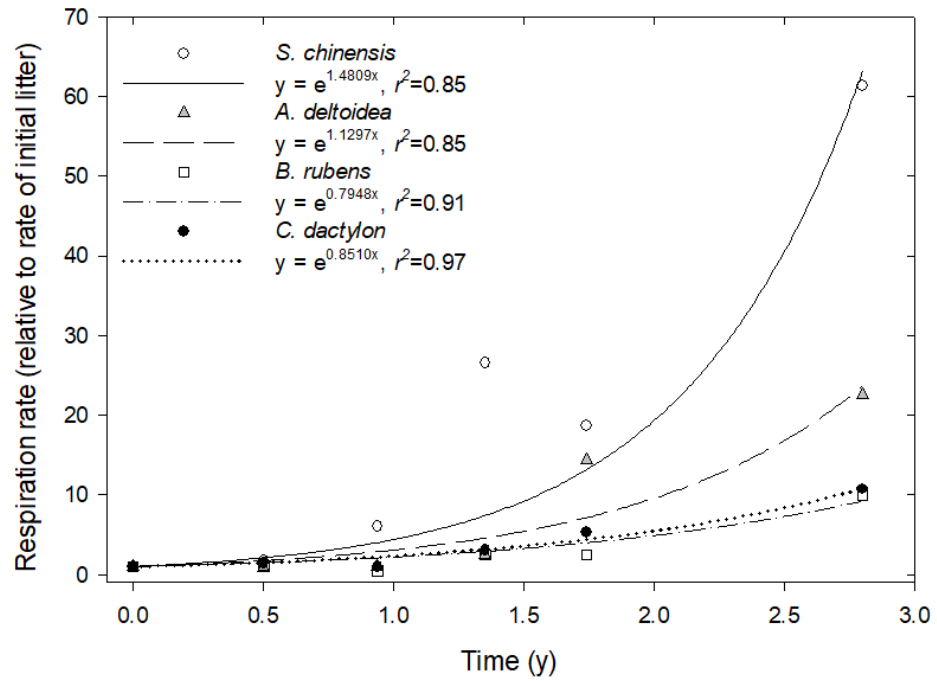

Figure S1. The relationship between the relative respiration rate and time in years. Symbols are means of respiration and time (n = 5, ±SE). Lines are single-parameter exponential functions with equations and r^2 (n = 6 for each litter type). See Day et al. 2018 for actual rates.

Table S1. Thermal abiotic emission equations. Equations for each litter type are fitted exponential regressions of thermal abiotic emission measured at 37, 44, 55 and 70°C. Equations were used to calculate thermal abiotic emission at all temperatures (5 to 70°C). Next to each equation is the r^2 of the regression and all were significant ($p < 0.001$).

Litter growth form	Litter type	CO_2 thermal abiotic emission equations
Woody dicots	*Simmondsia chinensis*	$y = 0.0016e^{0.1188x}$; $r^2 = 1.00$
	Olneya tesota	$y = 0.0020e^{0.1170x}$; $r^2 = 1.00$
	Prosopsis velutina	$y = 0.0014e^{0.1160x}$; $r^2 = 1.00$
	Larrea tridentata	$y = 0.0016e^{0.1223x}$; $r^2 = 1.00$
Suffrutescent dicots	*Ambrosia deltoidea*	$y = 0.0166e^{0.1017x}$; $r^2 = 1.00$
	Bailyea multiradiata	$y = 0.0018e^{0.1230x}$; $r^2 = 1.00$
	Encelia farinosa	$y = 0.0132e^{0.1001x}$; $r^2 = 1.00$
	Encelia frutescens	$y = 0.0071e^{0.0988x}$; $r^2 = 0.99$
Grasses	*Aristida purpurea*	$y = 0.0039e^{0.1066x}$; $r^2 = 1.00$
	Bromus rubens	$y = 0.0041e^{0.1050x}$; $r^2 = 1.00$
	Cynodon dactylon	$y = 0.0103e^{0.0917x}$; $r^2 = 1.00$
	Eragrostis curvula	$y = 0.0021e^{0.1058x}$; $r^2 = 1.00$
Annuals	*Amsinckia menziesii*	$y = 0.0429e^{0.0789x}$; $r^2 = 1.00$
	Lupinus sparsiflorus	$y = 0.0153e^{0.0925x}$; $r^2 = 0.99$
	Plantago patagonica	$y = 0.0686e^{0.0623x}$; $r^2 = 0.99$
	Cryptantha angustifolia	$y = 0.0695e^{0.0680x}$; $r^2 = 1.00$

Table S2. Microclimate of the four months in 2018. Morning (5:00-7:00 h), afternoon (15:00-17:00 h) and diel averages under litter are shown (n = 4 sensors). Measurements of RH and temperature were recorded every 15 min.

Parameter	Month			
	March	April	June	July
Morning RH (%)	55.1	21.4	27.2	64.0
Afternoon RH (%)	33.4	7.2	9.5	28.0
Diel RH (%)	44.1	13.8	17.2	46.2
Morning temperature (^{o}C)	11.4	16.8	24.3	29.1
Afternoon temperature (^{o}C)	23.1	33.5	45.7	43.5
Diel temperature (^{o}C)	17.2	25.6	34.1	36.2
Total precipitation (mm)	6.3	0	0.3	21.1

5. DISSERTATION SUMMARY

The work presented in this dissertation significantly improves our understanding of microbial degradation of leaf litter in drylands. First, in Chapter 2, I showed that the decay rates of 16 leaf litter types were not predicted by traditional indices of litter quality. Rather, decay was predicted well by the 2-h sorption rates and water-soluble fractions of initial litter. The 2-h sorption rates of litter also helped explain initial microbial respiration, and sorption rates were most strongly correlated with SLA and water-soluble fractions of litter. Decayed litter generally had faster sorption rates, and some, but not all, of this was due to litter fragmenting. To summarize, my findings suggest the rate of water-vapor sorption is a litter trait that is useful in helping to explain mechanisms of decay and microbial respiration in drylands and these findings were strengthened by the robust inclusion of many litter types and long length of decay.

Secondly, in Chapter 3, the data revealed that photodegradation was a significant mechanism of litter decay and appears to involve a substantial photofacilitation for the microbial component. My findings suggest that enhanced microbial degradation of sunlit litter was largely attributable to the greater activity of bacteria on the surface of this litter, and that surface fungi were more sensitive to sunlight than bacteria. It may be that decay in sunlight is largely occurring on the surface of litter, and this is driven by bacteria rather than fungi. The microbes involved in the photofacilitation of litter have received little attention until now, and this chapter contributed to our knowledge of solar radiation effects on microbial degradation.

Lastly, in Chapter 4, I characterized the response of microbial respiration to temperature and vapor-induced MC. Rather unexpectedly, respiration increased from 55 to 70°C in most litter types (12 of 16), and in 10 types respiration rates were highest at 70°C, which suggests thermophilic bacteria or heat-tolerant enzymes may exist in this leaf litter. The minimum MC and WP required for significant litter respiration averaged 13.5% and -1.2 MPa, respectively, and were similar to those reported by others for litter and soils in more mesic systems. I estimated that respiration was responsible for an average of 23.6% of the total C lost from litter over a 34-month period on the surface of the Sonoran Desert. Hence, respiration appears to represent a substantial pathway for litter C loss and was over two-fold greater than the combined losses previously found attributable to thermal and photochemical abiotic emission. These findings strongly suggest that microbial respiration is a substantial driver of litter decay in the Sonoran Desert and are consistent with our past findings that litter respiration rates are strong predictors of litter C loss in our system.

While this dissertation advanced our knowledge of the microbial degradation of leaf litter in the Sonoran Desert, the findings also revealed gaps in knowledge and in turn help guide the direction of future dryland litter decay research. Further studies are required to better understand the litter traits that dictate water-vapor sorption rates, and how these traits change with decay, and how sorption rates and water-soluble fractions of litter may interact to influence microbial respiration. Sorption rates, water-soluble fractions and microbial respiration rates all appear to be useful in explaining litter decay rates, thus explaining their interactions will be beneficial to understanding how mechanisms may change with litter age. Furthermore, these findings highlight the

importance of microbes, especially bacteria, in the decay of surface litter and further research is needed to understand the spatial and temporal dynamics of microbial degradation in drylands. I found surface bacteria correlate well with decay, but it is unknown if this trend changes with litter age or season. Lastly, these findings demonstrated the sensitivity of microbial respiration to RH and temperature fluctuations in the field. This suggests that climate change may have dramatic effects on C emissions from this dryland system and thus warrants further investigation. It was my hope to further our understanding of the microbial degradation of leaf litter in the Sonoran Desert with this dissertation, and I believe the coupling of field and lab experiments to elucidate underlying mechanisms of decay produced meaningful contributions to our knowledge of this important process.

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