Enhanced Microbial Respiration of Photodegraded Leaf Litter at High Relative Humidity is Explained by Relative Water Content Rather Than Vapor Uptake Rate or Carbon Quality

by

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ABSTRACT

There is a growing consensus that photodegradation accelerates litter decomposition in drylands, but the mechanisms are not well understood. In a previous field study examining how exposure to solar radiation affects decomposition of 12 leaf litter types over 34 months in the Sonoran Desert, litter exposed to UV/blue wavebands of solar radiation decayed faster. The concentration of water-soluble compounds was higher in decayed litter than in new (recently senesced) litter, and higher in decayed litter exposed to solar radiation than other decayed litter. Microbial respiration of litter incubated in high relative humidity for 1 day was greater in decayed litter than new litter and greatest in decayed litter exposed to solar radiation. Respiration rates were strongly correlated with decay rates and water-soluble concentrations of litter. The objective of the current study was to determine why respiration rates were higher in decayed litter and why this effect was magnified in litter exposed to solar radiation. First, I evaluated whether photodegradation enhanced the quantity of dissolved organic carbon (DOC) in litter by comparing DOC concentrations of photodegraded litter to new litter. Second, I evaluated whether photodegradation increased the quality of DOC for microbial utilization by measuring respiration of leachates with equal DOC concentrations after applying them to a soil inoculum. I hypothesized that water vapor sorption may explain differences in respiration among litter age or sunlight exposure treatments. Therefore, I assessed water vapor sorption of litter over an 8-day incubation in high relative humidity. Water vapor sorption rates over 1 and 8 days were slower in decayed than new litter and not faster in photodegraded than other decayed litter. However, I found that 49-78% of the variation in respiration could be explained by the relative amount of water litter

absorbed over 1 day compared to 8 days, a measure referred to as relative water content. Decayed and photodegraded litter had higher relative water content after 1 day because it had a lower water-holding capacity. Higher respiration rates of decayed and photodegraded litter were attributed to faster microbial activation due to greater relative water content of that litter.

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INTRODUCTION

Plant litter decomposition is a predominant pathway for the release of terrestrial C into the atmosphere, emitting more CO_2 annually than the combustion of fossil fuels (Gholz et al., 2000). In most terrestrial ecosystems, decay rates are well predicted by litter quality indices such as C:N or lignin:N ratios (Meentemeyer, 1978; Melillo et al., 1982; Cornwell et al., 2008). However, models that incorporate these indices and climactic factors frequently underestimate decay rates in drylands (Whitford et al., 1981; Parton et al., 2007).

These failings have led researchers to explore additional drivers of decay in drylands. There is a growing consensus that the acceleration of litter decomposition due to exposure to sunlight (photodegradation) is one such driver (Austin and Vivanco, 2006; Day et al., 2007; King et al., 2012; Huang et al., 2017). We define photodegradation as decay caused by the direct abiotic photochemical breakdown of compounds in litter along with the indirect effects that this can have on subsequent decay, such as through leaching or microbial decomposition. King et al. 2012, in a meta-analysis, found that photodegradation is a significant accelerator of mass loss and can account for the higher than estimated decay rates seen in drylands. Indeed, when photodegradation was included in decomposition models it greatly improved their predictions of mass and C loss (Chen et al., 2016; Adair et al., 2017). Photodegradation, through exposure to UV and lower visible wavebands of solar radiation, can accelerate mass loss of litter via primary and secondary mechanisms. Primary mechanisms of photodegradation include photochemical mineralization of organic compounds into trace gases (Brandt et al., 2009; Lee et al., 2012), which generally accounts for modest amounts of mass loss (Barnes et al., 2012;

Lin et al., 2018). Secondary mechanisms of photodegradation involve the transformations of compounds as a result of solar radiation-induced formation of reactive oxygen species. These abiotic mechanisms can further affect litter decomposition by altering litter chemistry in a process called photopriming. Photopriming, which we define as the change in litter chemistry elicited by exposure to solar radiation, can facilitate microbial decomposition (Foereid et al., 2010; Fellman et al., 2013; Baker and Allison, 2015; Day et al., 2018) and leaching losses (Day et al., 2018; Feng et al., 2011; Gallo et al., 2006; Lin et al., 2018) through the breakdown of recalcitrant compounds to more labile constituents. We refer to this process as photofacilitation.

Photodegradation can promote the loss of various compounds in litter including cellulose, hemicellulose, and lignin (Day et al., 2007; Gallo et al., 2009; Lin and King, 2014; Austin et al., 2016), but can either promote the loss or accumulation of water-extractable dissolved organic C (DOC; Gallo et al., 2006; Wang et al., 2017a; Day et al., 2018). Day et al. (2018) found that the DOC concentration of recently senesced litter was positively correlated with microbial respiration of said litter, and respiration of litter generally increased with decay. Thus, we were interested in examining whether the DOC concentration of litter also increased with decay and if that would explain the higher respiration measured in decayed litter. UV radiation can break larger organic molecules into smaller subunits, and thereby increase the concentration of DOC in litter (Liu et al. 2014). DOC can also be leached during decay in precipitation events or be utilized by microbes. Wang et al. (2017a) found that DOC concentrations increased during the "intermediate" stage of decay, roughly 100 to 400 days old, but then dropped off during "late stage" decay after 400 days. As such, DOC pools in litter are constantly in flux and

thus it is difficult to assess the impacts of photodegradation upon them. Further complicating the effects of photodegradation, DOC contains many classes of molecules that vary in quality for microbial utilization (Strauss and Lamberti, 2002; Qualls, 2005; Joly et al., 2016) and there is some evidence in aquatic systems that exposure to UV radiation can alter DOC chemistry and make it more easily utilized by microbes (Wetzel et al., 1995; Gareis and Lesack, 2018).

While photodegradation has garnered more acceptance as a major driver of decay in drylands, only recently has photofacilitation been found to be a major mechanism through which photodegradation affects mass loss via subsequent microbial degradation (Foereid et al. 2010; Austin et al., 2016; Day et al. 2018; Lin et al., 2018). Until recently, microbial degradation was perceived as a minor driver of decay in drylands because of lack of precipitation. However, microbes can also be activated with high atmospheric vapor pressure (Bartholomew and Norman, 1950; Nagy and Macauley, 1982; Dirks et al., 2010; Jacobson et al., 2015; Gliksman et al., 2016; Wang et al., 2017a; Day et al., 2018). To our knowledge, no research has been conducted on how photodegradation affects water vapor sorption of litter, although, a good deal of research has been conducted evaluating the water sorption of natural fibers used in industry. Water sorption by plant fibers is largely controlled by their chemical composition and structure (Célino et al., 2014). Major organic macromolecules responsible for water sorption are cellulose, hemicellulose, pectin, and lignin, because they contain polar groups which can establish hydrogen bonds with water molecules (Berthold et al., 1998). Plant fibers can also store water within the voids of the cellular structure, which can swell when moisture is introduced (Dhakal et al., 2007). While photodegradation has been documented to lead to

losses of some of these water-sorbing compounds, including cellulose, hemicellulose, (Brandt et al., 2010; Lin and King, 2014; Baker and Allison, 2015; Lin et al., 2015; Huang et al., 2017) and lignin (Day et al., 2007; Austin and Ballaré, 2010; Austin et al., 2016), we do not know how photodegradation in and of itself affects water vapor sorption of litter.

We recently monitored the decay of leaf litter on the soil surface over 34 months and assessed what traits predicted mass loss and how exposure to different wavebands of sunlight influenced mass loss in the Sonoran Desert (Day et al., 2018). We found that water vapor-induced microbial respiration of litter was the strongest predictor, among traits of new litter (hereafter referred to as 'initial litter'), of mass loss, highlighting the importance of microbial degradation in this system. Concentrations of DOC and water-solubles of initial litter was positively correlated with respiration and with mass loss. Additionally, we found that respiration of litter generally increased through decay and was much greater in 34-month old litter than initial litter, and usually increased more in litter that had been exposed to full sunlight. We also found, somewhat surprisingly, that the water-soluble concentration of litter also increased through decay and was similarly enhanced in litter that had been exposed to full sunlight.

The main objectives of this current study were to determine why microbial respiration was greater in decayed than initial litter, and why exposure to sunlight magnified this effect. Using litter from the previous field experiment described in Day et al. (2018), we first assessed whether DOC concentrations were greater in decayed litter than initial litter. Upon finding that DOC concentrations were not higher in decayed litter, we then examined whether the quality of DOC for microbial consumption was higher in

decayed litter. Upon applying equal concentrations of DOC from different litter types to soil, we found that microbial respiration rates were similar. Hence, neither the quantity nor the quality of DOC in decayed litter, or sunlight-exposed litter, explained higher microbial respiration rates. We hypothesized that another factor, water vapor sorption, might provide an alternative explanation for higher microbial respiration in decayed and sunlight-exposed litter. To this end, we assessed water vapor sorption/water content and microbial respiration of litter over 8-day incubations at high relative humidity.

MATERIALS AND METHODS

Prior field experiment and litter material

We assessed the relationships between DOC concentration, DOC quality for microbial consumption, and water vapor sorption on respiration of litter obtained from the field experiment of Day et al. (2018). In brief, Day et al. (2018) examined what litter traits predicted mass loss of 12 leaf litter types in a 34-month field photodegradation experiment. The 12 species or litter types consisted of 4 species from each of 3 growth forms: woody dicots (*Simmondsia chinensis, Olneya tesota, Prosopis velutina, Larrea tridentata*), suffrutescent dicots (*Ambrosia deltoidea, Baileya multiradiata, Encelia farinosa, Encelia frutescens*), and grasses (*Aristida purpurea, Bromus rubens, Cynodon dactylon, Eragrostis curvula*). Leaf litter was collected as naturally senesced leaves that were attached to standing branches and stems of several plants of each species in spring/summer 2013, and placed in envelopes whose tops were filters that either (1) transmitted all solar wavebands (>80% transmittance of solar UV and visible radiation; Aclar Type 22A filter, Proplastics, Linden, NJ, USA) which we refer to as the “Full sun”

treatment, (2) absorbed most solar UV radiation (having a sharp cutoff with 50% transmittance at 387 nm; 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 (having a sharp cutoff with 50% transmittance at 545 nm; Amber UV filter, UVPS) which we refer to as the "No UV/blue" treatment. Each envelope received 0.88-2.39 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. There were 8 replicate envelopes of each of the 12 litter types. Envelopes were secured firmly to the soil surface in a conservation area at the Desert Botanical Garden, Phoenix, AZ, USA on 16 December 2013 and collected on 24 October 2016, after ≈34 months. In the current study, we assessed "initial" litter (collected but not deployed in the field experiment) and "decayed" litter (collected after 34 months in the field).

Experiment 1: Does DOC quantity explain higher respiration of decayed and photodegraded litter?

To assess how the DOC concentration of litter varied with age and radiation treatment, we quantified the water-soluble and DOC concentration of initial and decayed litter in each treatment. Five samples (0.05 ± 0.005 g air-dried) of each litter type were oven dried (OD) at 60°C for 24 h and weighed. Separate subsamples (n = 8) of each litter type were ashed (550°C for 6 h) to correct for inorganic ash. The former samples were placed in a 25-ml Erlenmeyer flask with 10 ml of nanopure water and gently stirred at 50°C. After 1 h, the contents of each flask were filtered through 10-μm polyethylene mesh, and the remaining litter material was recovered, dried at 60°C for 48 h, weighed,

and corrected for ash. The water-soluble concentration was expressed as the percentage ash-free dry mass loss.

The DOC concentration of the leachate was measured with a TOC/N Analyzer (Shimazdu TOC-V/TN, Columbia, MD, USA). Leachates were filtered through a 0.2-µm polycarbonate mesh, and a 2-ml subsample of each leachate was diluted in nanopure water using a 1:10 ratio. A standard curve was developed with potassium hydrogen phthalate, and concentrations were corrected for dilution and expressed as mg DOC g^{-1} ash-free dry mass of litter. We also measured the specific ultraviolet absorbance ($SUVA_{254}$) and used it as an indicator of aromaticity of DOC (Weishaar et al. 2003). $SUVA_{254}$ was measured with a spectrophotometer (Lambda 2, PerkinElmer, Waltham, MA, USA) using a 1-cm, quartz cuvette and nanopure water as a blank. $SUVA_{254}$ was calculated as the sample absorbance at 254 nm divided by the DOC concentration and multiplied by the cell length (1 cm) and expressed as L mg^{-1} DOC m^{-1}.

We assessed microbial respiration of initial and decayed litter by measuring CO_2 emission rates over a 1-day incubation. Any references to "respiration of litter" refer to this measurement after 1 day, and should be distinguished from other respiration measurements described in Experiment 3 which will be indicated with the day they were measured (i.e. day 8 respiration). Five samples (0.10 ± 0.005 g) of each litter type were oven dried and weighed, placed into pre-weighed 37-ml serum bottles, flushed with 400 ppm CO_2 air for 2 min, and sealed. Evaporation from small glass test tubes filled with nanopure water within each bottle increased the relative humidity in the bottles to 70% in 6 h, and to 80% in 20 h. Samples were placed in a dark area of the lab at 22°C. After 24 h, we determined the CO_2 concentration of each sample by withdrawing 10 ml of

headspace with a gas-tight syringe and injecting it into an infrared gas analyzer (LI-6400XT, LI-COR Biosciences, Lincoln, NE, USA) modified with a trace gas sampling kit, using a flow rate of 150 μmol s^{-1}. The CO_2 concentration of each sample was determined by using a calibration equation developed with 4 CO_2 primary standards (300 - 1500 ppm) and CO_2-free air. All linear regression calibration equations had $r^2 > 0.995$. We measured controls (n = 5), consisting of empty bottles with a tube of water, to correct for the initial concentration of CO_2 in the headspace and for CO_2 dissolving into the water. Headspace CO_2 content was calculated using the ideal gas law and respiration rates were expressed as μg C-CO_2 g^{-1} OD litter h^{-1}.

Experiment 2: Does DOC quality for microbial consumption explain higher respiration rates in decayed and photodegraded litter?

To assess whether the DOC from litter types or treatments differed in terms of quality for microbial consumption, hereafter called "DOC quality", we equalized DOC concentrations in leachates from each litter type, applied them to a soil substrate, and assessed microbial respiration. Five subsamples of leachates from each litter type were diluted/concentrated to 225 mg L^{-1}. Samples requiring dilution were diluted with nanopure water, and samples requiring concentration were evaporated with a vacuum concentrator equipped with a refrigerated vapor trap (Savant Speed Vac SC110 with RVT4104, Woonsocket, RI, USA).

The soil substrate served as a standard, low-nutrient substrate during incubations, while also serving as an inoculum by providing microbes from our field site. Eight samples of the upper 2 cm of soil were collected from the field site, passed through a 2-

mm sieve and thoroughly homogenized. The C concentration of the soil, measured with a flash combustion elemental analyzer (PE2400, PerkinElmer), was typical of a hyperarid desert (0.32%). However, the N concentration was higher than expected (0.36%), possibly due to runoff from nearby residential areas.

For incubations, 1 g of soil substrate was placed in serum bottles, 0.4 ml of leachate was added, bottles were sealed, and respiration was measured after 1 day. Controls (n = 5), in which nanopure water was added to the soil instead of the leachate, were used to correct for respiration from the soil substrate. The respiration rate averaged 1.0 and 0.6 μg $C\text{-}CO_2$ h^{-1} from samples receiving leachate (initial and decayed litter) and water, respectively. In other words, samples respired ≈1.7 times higher than controls, indicating that leachate addition enhanced microbial activity, thereby affording our protocol with enough sensitivity to assess DOC quality for microbial consumption. Respiration rates, which we hereafter refer to as "leachate respiration", were expressed as μg $C\text{-}CO_2$ emitted mg^{-1} DOC added to soil substrate h^{-1}.

Experiment 3: Does water vapor sorption explain enhanced respiration rates in decayed and photodegraded litter?

Since neither DOC concentration nor DOC quality could explain the enhanced respiration of decayed litter, and we suspected that water vapor sorption rates varied with decay and could influence microbial respiration rates, we monitored respiration and water vapor sorption over an 8-day incubation. We extended the incubation described in Experiment 1, adding additional respiration measurements after 2, 3, 4, and 8 d. We interpolated the respiration rates on days 5-7 for each sample assuming a linear change

between days 4 and 8 and calculated the total $C\text{-}CO_2$ respired over the entire incubation, expressed as mg $C\text{-}CO_2$ respired g^{-1} OD litter. After respiration was measured, we weighed each sample to determine the water content of litter as the percent mass of water per mass of OD litter, and the bottle was resealed and flushed with ≈400 ppm air. After each sample was flushed, the relative humidity in the bottle decreased by 10% on average and recovered to its pre-flush relative humidity within 5 h. Samples were always flushed 24 h before the next respiration measurement, including the day 8 measurement, to avoid any bias that a multi-day incubation might cause.

Water vapor adsorbs to hydrophilic surfaces on litter (Talhelm and Smith 2018), creating thin water films in the porous inner environment. As the water content of litter increases, these water films thicken and become more interconnected between pores. This process is important for microbial activity because it promotes conduction of dissolved nutrients within the litter, as well as providing the necessary water for cellular function (Skopp et al. 1990, Or et al. 2006). Litter water content was still increasing after 8 days of incubation at high relative humidity. However, the rate of increase had slowed substantially, and the water content of many litter types was beginning to plateau. Hence, we used the water content of litter on day 8 as a proxy for the water-holding capacity of litter. To estimate the water-filled pore space on day 1, we divided the water content on day 1 by the water content on day 8 and expressed it as a proportion. We refer to this parameter as relative water content.

Relative Water Content = Day 1 Water Content (%) / Day 8 Water Content (%) * 100 (1)

Statistical and data analyses

We used a series of one-way ANOVAs to assess effects of decay and radiation treatment on the water-soluble and DOC concentrations, leachate respiration, litter respiration, water content, and relative water content. Mean comparisons among decay and radiation treatments were tested with a Tukey's HSD test. Some data sets required transformations to meet the assumptions of normality. To assess relationships between litter traits, respiration, and mass loss we used linear least-squares regressions to determine significance and quantify their predictive power.

RESULTS

Experiment 1: Does DOC quantity explain higher respiration of decayed and photodegraded litter?

The water-soluble concentration was significantly greater in decayed litter than initial litter in all litter types in the Full sun treatment, in 10 litter types in the No UV treatment, and in 6 litter types in the No UV/blue treatment, illustrating that water-soluble concentrations increased with decay in most cases (28 of 36; Fig. 1a) and radiation exposure promoted this trend. The water-soluble concentration of litter in the Full sun treatment was significantly higher than litter in the No UV treatment in 5 litter types and higher than litter in the No UV/blue treatment in 9 litter types (Fig. 1a), indicating that exposure to UV and UV/blue radiation often increased water-soluble concentrations.

In contrast to water-solubles, concentrations of DOC in decayed litter were not significantly different from initial litter in most cases (20 of 36; Fig. 1b). Additionally, in cases in which there were significant differences, there was not a consistent trend

between initial and decayed litter. For example, concentrations of DOC in initial litter were higher than decayed litter in 4 litter types but lower in 3 litter types in the Full sun treatment (Fig. 1b). Further, radiation treatment had few effects on the DOC concentration of decayed litter (Fig. 1b). While DOC concentration was strongly correlated with the water-soluble concentration in initial litter ($r^2 = 0.82$, $p < 0.01$, data not shown), DOC was not correlated with the water-soluble concentration in decayed litter ($r^2 = 0.00\text{-}0.25$, $p \geq 0.10$, data not shown).

$SUVA_{254}$ was significantly higher in leachates from decayed litter than from initial litter in 10, 8, and 8 litter types in the Full sun, No UV, and No UV/blue treatments, respectively (Fig 1c), indicating that the DOC from decayed litter was usually more aromatic than that of initial litter. $SUVA_{254}$ was higher in leachate from litter in the Full sun treatment than in litter from the other radiation treatments in a some litter types (3 and 4 in No UV and No UV/blue respectively; Fig. 1c), indicating that DOC from litter in the Full sun treatment was sometimes more aromatic than litter in the No UV or No UV/blue treatments.

Decayed litter respired more than initial litter in most cases (29 of 36 cases; Fig. 2). Decayed litter in the Full sun treatment respired more than in the No UV and No UV/blue treatments in 4 litter types (Fig. 2). While we did not find enhanced respiration of litter in the Full sun treatment in the majority of litter types, the mean of all litter types within the Full sun treatment respired significantly more than litter in the No UV/blue treatment, with litter in the No UV treatment as an intermediate (Fig. 2 inset).

Respiration rates of initial litter were not significantly correlated with concentrations of water-solubles or DOC (Fig. 3a, b), although there were two outliers

(defined as values that were more than 1.5x the interquartile range from the median) that had much higher respiration rates than other litter types (*Encelia frutescens* and *Bromus rubens*). When removed, respiration rates were strongly correlated with concentrations of water-solubles and DOC ($r^2 = 0.59$, $p < 0.01$, Fig. 3a, b). Respiration rates of decayed litter were positively correlated with water-soluble concentration in the Full sun treatment ($r^2 = 0.91$, $p < 0.01$, Fig. 3d), but not in the No UV or No UV/blue treatments ($r^2 = 0.21$-0.28, $p \geq 0.08$, Fig. 3d). Respiration rates of decayed litter were not correlated with DOC concentration in any radiation treatment (Fig. 3e), illustrating that DOC concentration could not explain the differences of respiration among litter types in decayed litter.

Respiration rates of initial litter were positively correlated with $SUVA_{254}$ ($r^2 = 0.79$, $p < 0.01$, Fig. 3c), but the correlation was contingent on the two outliers. When the outliers were removed there was no significant correlation ($r^2 = 0.22$, $p = 0.17$, Fig. 2c). Respiration rates of decayed litter were positively correlated with $SUVA_{254}$ in the Full sun and No UV treatments ($r^2 = 0.34$-0.57, $p < 0.05$, Fig 3f), and tended to be positively correlated in the No UV/blue treatment ($r^2 = 0.32$, $p = 0.06$, Fig 3f), suggesting that decayed litter with more aromatic DOC respired more. In summary, DOC concentrations did not increase with decay. Hence, they did not explain the higher respiration rates of decayed litter. Furthermore, DOC concentrations in decayed litter were not correlated with respiration rates of that litter.

Experiment 2: Does DOC quality explain higher respiration rates in decayed and photodegraded litter?

Respiration from soil receiving leachate (leachate respiration) from initial litter differed substantially among litter types, ranging from 3.7 to 7.0 μg $C\text{-}CO_2$ mg^{-1} DOC h^{-1}. However, leachate respiration from initial litter was not significantly different from that of decayed litter in most cases (27 of 36), and was even significantly lower in a few cases (Fig. 4a). Hence, DOC quality did not explain the higher respiration rates of decayed litter. Leachate respiration from decayed litter did not vary among radiation treatments, illustrating that exposure to solar radiation did not affect DOC quality.

Leachate respiration from initial litter was not correlated with respiration rates of initial litter ($r^2 = 0.11$, $p = 0.30$, Fig. 4b), indicating that DOC quality does not explain the differences in respiration rates among litter types. Leachate respiration from decayed litter was positively correlated with respiration of decayed litter in the Full sun treatment ($r^2 = 0.33$, $p = 0.05$, Fig. 4c), but not in the No UV or No UV/blue treatments ($r^2 \leq 0.15$; $p \geq 0.21$, Fig 4c). In summary, DOC quality did not increase with decay and, while it may have affected respiration rates of litter in the Full sun treatment, it did not explain the enhanced respiration rates of decayed litter in general.

Experiment 3: Does water vapor sorption explain enhanced respiration rates in decayed and photodegraded litter?

On day 1, decayed litter had lower water content than initial litter in most cases (22 of 36; Fig. 5a). Hence, enhanced respiration rates of decayed litter were not explained by elevated water content. Additionally, radiation treatment did not affect the water

content of decayed litter on day 1 (Fig. 5a), so elevated water content could not explain enhanced respiration of photodegraded litter. The water content of litter on day 1 was positively correlated with respiration rates in initial litter ($r^2 = 0.47$, $p = 0.01$, Fig. 5b), indicating that water content explained differences in respiration among litter types in initial litter. However, the water content of decayed litter on day 1 was not well correlated with respiration rates in decayed litter in the Full sun and No UV/blue treatments ($r^2 \leq 0.12$, $p \geq 0.28$, Fig. 5c), and was actually negatively correlated in the No UV treatment ($r^2 = 0.53$, $p < 0.01$, Fig. 5c), indicating that elevated water content on day 1 did not explain differences in respiration of decayed litter.

Water content of litter increased asymptotically with incubation time (Fig. 6). Water content on day 8 was higher in initial litter than decayed litter in all litter types, regardless of radiation treatment (Fig. 7a), suggesting that initial litter had a greater water holding capacity than decayed litter. Radiation treatment did not affect the water content of decayed litter on day 8 (Fig. 7a), suggesting that exposure to solar radiation did not affect the water holding capacity of litter. Initial litter had a lower relative water content on day 1 than decayed litter in all but one litter type, regardless of radiation treatment (Fig. 8a). Litter in the Full sun treatment had a higher relative water content on day 1 than litter in the No UV treatment in 5 litter types, and in 6 litter types in the No UV/blue treatment, indicating that litter exposed to Full sun saturates faster than litter in the No UV and No UV/blue treatments.

Overall, relative water content of litter on day 1 was the strongest and most consistent predictor of day 1 respiration rates. It was strongly positively correlated with day 1 respiration, regardless of decay or radiation treatment ($r^2 = 0.49$-0.78, $p \leq 0.01$, Fig.

8b, c), strongly suggesting that the water-filled pore space of litter was an important facilitator of microbes in water vapor-induced respiration. As mentioned, respiration rates of initial litter on day 1 were positively correlated with the water content on day 1. However, respiration rates of decayed litter were not correlated with water content on day 1, but instead, were negatively correlated with water content on day 8 in the No UV and No UV/blue radiation treatments (r^2 = 0.56-0.67, $p < 0.01$, Fig. 7c), and tended to be negatively correlated in the Full sun treatment (r^2 = 0.31, p = 0.06, Fig. 7c), indicating that decayed litter with a lower water-holding capacity respired more.

The relative water content of decayed litter on day 1 was highly positively correlated with mass loss measured by Day et al. (2018) regardless of radiation treatment (r^2 = 0.49-0.94, $p < 0.01$, Fig. 9c). This correlation seems to stem from the strong negative correlation between water content on day 8 and mass loss (r^2 = 0.62-0.78, $p <$ 0.01, Fig 9b) thereby decreasing the time needed for litter to saturate given similar water vapor sorption rates. The water content of initial litter on day 1 and 8 were not correlated with mass loss (data not shown). Similarly, the relative water content of initial litter was not correlated with mass loss (data not shown).

Respiration from initial litter usually increased with incubation time, and was highest on day 8, the last day of the incubation, in all litter types. Respiration rates of initial litter varied greatly among growth forms, with woody dicots respiring relatively slowly (<2 μg $C\text{-}CO_2$ g^{-1} h^{-1}) over the entire incubation compared to suffrutescent dicots and grasses which respired on average 13.2 μg $C\text{-}CO_2$ g^{-1} h^{-1}. Respiration from initial litter sharply increased from day 4 to 8 of the incubation, on average 25x more in suffrutescent dicots and grasses, and 2x more in woody dicots (Fig. 10). In contrast,

respiration of decayed litter usually peaked on day 2 (median: 2, average: 2.8) and tended to peak earliest in litter in the Full sun treatment (average: 2.4 d) and latest in litter in the No UV/blue treatment (average: 3.3 d). This suggests that microbes in decayed litter began respiring more quickly than in initial litter and photodegraded litter tended to respire more quickly than non-photodegraded litter.

To summarize the entire incubation, initial litter respired less than decayed litter in the beginning of the incubation, but began respiring more than decayed litter in most litter types after day 4 of the incubation, indicating that microbial activity was delayed in initial litter. There was no consistent pattern of decay on the total $C\text{-}CO_2$ respired over the 8-day incubation, where initial litter respired less than decayed litter in 12 of 36 cases, and more than decayed litter in 14 of 36 cases (Fig. 11). Radiation treatment did not affect total respiration of decayed litter.

DISCUSSION

Similar to Day et al. (2018), respiration rates of decayed litter were higher than those of initial litter, and this effect was magnified in photodegraded litter. DOC concentrations in decayed litter were not higher than initial litter and did not explain the higher respiration rates of decayed litter. Additionally, DOC concentrations of photodegraded litter were not higher than other radiation treatments and did not explain the higher respiration rates of photodegraded litter. Similarly, leachate respiration was not higher in decayed litter than initial litter; thus, DOC quality did not explain the higher respiration rates of decayed litter. Further, leachate respiration was not higher in photodegraded litter than other decayed litter. Therefore, DOC quality did not explain the

higher respiration of photodegraded litter. Leachate respiration explained 33% of the variation in respiration among litter types in the Full sun treatment, but it did not correlate with respiration in any other treatment, suggesting that DOC quality may play a role in explaining the enhanced respiration of photodegraded litter. As DOC quantity and quality did not explain the enhanced respiration of decayed/photodegraded litter, we assessed whether differences in water vapor sorption could explain these patterns. Water content of decayed litter after 1 day was lower than initial litter, thus it did not explain the higher respiration of decayed litter. Additionally, water content of photodegraded litter after 1 day was not higher than other decayed litter, therefore it could not explain the enhanced respiration of photodegraded litter. Gliksman et al. (2016) and Wang et al. (2017a) both found microbial respiration of litter increased with water content within a given litter type, and we found similar results in initial litter where litter types with a higher water content tended to respire more. However, decayed litter types with higher water content did not tend to respire more, suggesting this was dictated by factors other than water content by itself. We suspect that the differing water-holding capacity among decayed litter types could influence microbial respiration. Therefore, we calculated the relative water content as the ratio of water content after 1 day to the water content after 8 days. We found that decayed litter had a higher relative water content than initial litter after 1 day, and this effect was magnified in photodegraded litter, providing a possible explanation for the enhanced respiration of decayed and photodegraded litter.

Relative water content was the most consistent predictor of day 1 respiration rates regardless of decay or radiation treatment, explaining 49-78% of the variation in respiration among litter types, suggesting that it is an important driver for microbial

respiration. In drying soils, the relative water content (i.e. water-filled pore space) can have a large influence on microbial activity (Or et al. 2007). As a soil dries, the water-filled pore space decreases leaving thin water films on hydrophilic surfaces (Or et al. 2007). Water sorption of litter at high relative humidity is an analogous process but in reverse. Water vapor diffuses into the porous interior of the litter and sorbs to hydrophilic surfaces, creating water films that thicken with continued diffusion (Talhelm and Smith 2018). As the water films thicken, they provide more liquid pathways that can supply dissolved nutrients to microbes (Skopp et al. 1990). In soils, these water films are rarely thick enough to fully immerse microbes in water (<1 μm) but water is retained in crevices through capillary forces, providing habitats where microbes can be fully immersed (Or et al. 2007). Microbial activity, controlled by the film-dependent nutrient and water availability, increases with water-filled pore space until gaseous diffusion of O_2 from the atmosphere becomes limiting (Or et al. 2007).

Respiration of decayed litter usually peaked on the second day of the incubation, compared to the eighth day for initial litter, suggesting that microbes began respiring more quickly in decayed litter. Furthermore, we found that respiration rates in initial litter on day 8 were an order of magnitude higher than decayed litter in many litter types, suggesting that the potential for respiration in initial litter was much higher. Therefore, the enhanced respiration rates of decayed and photodegraded litter over 1 day could be attributed to faster activation of microbes, and not higher litter quality, in terms of microbial consumability. We concede that the faster activation of microbes could conceivably be attributed to a more established microbiome being present in decayed litter than in initial litter, but we contend that the strong correlations between water

content and respiration rates suggest that vapor sorption is an important factor. The faster activation of microbes in decayed/photodegraded litter could in turn be attributed to the greater relative water content increasing the supply of water and nutrients to microbes. Pores in decayed litter filled more quickly because they did not hold as much water, not because decayed litter absorbed water faster. This might be due to reduced capacity of pores in decayed litter to swell, or because the pores are physically smaller in decayed litter. We also found that the water content of decayed litter on day 8 was highly negatively correlated with mass loss measured in the field experiment, suggesting that litter that lost more mass had a lower water-holding capacity. Taken together, photodegraded litter lost more mass than the other radiation treatments, tended to have a lower water-holding capacity, and thus a higher relative water content after 1 day, in turn explaining its higher respiration rates.

Little research has examined the process and impact of humidity-induced respiration in drylands. Gliksman et al. (2017) demonstrated that microbes were activated in the absence of precipitation through the absorption of water vapor by litter in the field, and that most of the CO_2 efflux from litter during the dry season could be attributed to water vapor induced microbial activity. They also found that the microbial respiration rate within a given litter type was largely explained by litter moisture content. Similarly, Dirks et al. (2010) found that a significant portion of litter mass loss (15-50%) occurred during a rainless period in Mediterranean shrublands, and this mass loss was attributable to humidity-induced respiration. Wang et al. (2017a) found that greater litter moisture content of standing-dead litter stimulated greater microbial activity compared to litter on the soil surface. We found that litter water content was well correlated with the

respiration of initial litter but not in decayed litter, suggesting that water content of litter is a good predictor of respiration when examining recently senesced litter or litter with similar water-holding capacities. However, we found that respiration of decayed litter was positively correlated with relative water content and negatively correlated with the water content on day 8, suggesting that dynamics in water-holding capacity during decay should be considered when assessing humidity-induced respiration.

The water-soluble concentration of litter was consistently greater in decayed and photodegraded litter but the DOC concentration was not. The water-soluble concentration may have included fine particulates between 0.2 and 10 μm in size (due to mesh sizes chosen in the methodology) that were not included in the DOC measurement. These particulates, while not water-soluble per se, would be effectively leached during a precipitation event. They were apparently more abundant in decayed litter and could explain why the water-soluble concentrations were greater in decayed litter. These particulates could also explain the higher $SUVA_{254}$ found in water extracts from decayed litter. There was no effect of decay or photodegradation on leachate respiration indicating that decay and exposure to sunlight had no effect on the quality of DOC for microbial utilization. $SUVA_{254}$, however, was significantly higher in decayed than initial litter, indicating higher aromatic content. This increase is probably due to the preferential loss of non-aromatic DOC either through leaching or microbial metabolization, leaving behind less labile aromatic compounds. Litter with more aromatic DOC is typically considered to be less amenable to microbial consumption (Don and Kalbitz, 2005; Wang et al., 2017a). This further illustrates that the higher respiration rates in decayed litter were not due to better DOC quality of decayed litter.

Concentrations of DOC in decayed litter were usually lower or not significantly different than initial litter. Our results add to the inconsistent findings other authors have published regarding how DOC concentration varies with decay and radiation exposure. Feng et al. (2011) found that exposure to UV increased the water-extracted organic C in only one of their two litter types. Wang et al. (2017b) found that concentrations of DOC in litter increased after ~400 days in the field and exposure to UV radiation facilitated this increase. They also found that concentrations of DOC began to decrease after 400 days in what they call "late stage" decomposition. Brandt et al. (2009) did not find any effect of UV exposure on DOC concentration. We found that concentrations of DOC explained 59% of the variation in respiration among litter types in initial litter but did not explain respiration in decayed litter, suggesting that DOC concentration becomes a less important driver of water vapor induced respiration as litter decays.

CONCLUSION

The greater respiration of decayed and photodegraded litter was best explained by the higher relative water content of that litter. Decayed litter respired more than initial litter over 1 day because microbes began respiring more quickly due the higher relative water content, which was a result of the lower water-holding capacity of decayed litter. Furthermore, initial litter had a much higher potential for microbial respiration than decayed litter, but it took much longer for microbes to begin respiring. Water-vapor driven respiration seems to be an important driver of litter decay in drylands and would mostly occur in transient periods of high relative humidity lasting less than one day. Our results suggest that more decayed litter would respire more in these circumstances.

Neither the quantity nor the quality of DOC were higher in decayed litter and they were not higher in decayed litter exposed to full sunlight. Hence, these traits did not explain the higher respiration rates of decayed litter or litter exposed to full sunlight. Concentrations of DOC and water-solubles explained variation in respiration among initial litter types but could not explain respiration in decayed litter. Overall, decayed litter respired more over 1 day because there was more available water for microbes, and not because it provided a better substrate for microbial utilization. Our findings that the relative water content of litter was strongly correlated with both water-vapor driven respiration and mass loss of litter corroborate the contentions recently put forth by others that microbial decomposition is a more important driver of litter decay in deserts than previously recognized and water-vapor driven respiration is a significant part of this process (Gliksman et al., 2016; Day et al., 2018).

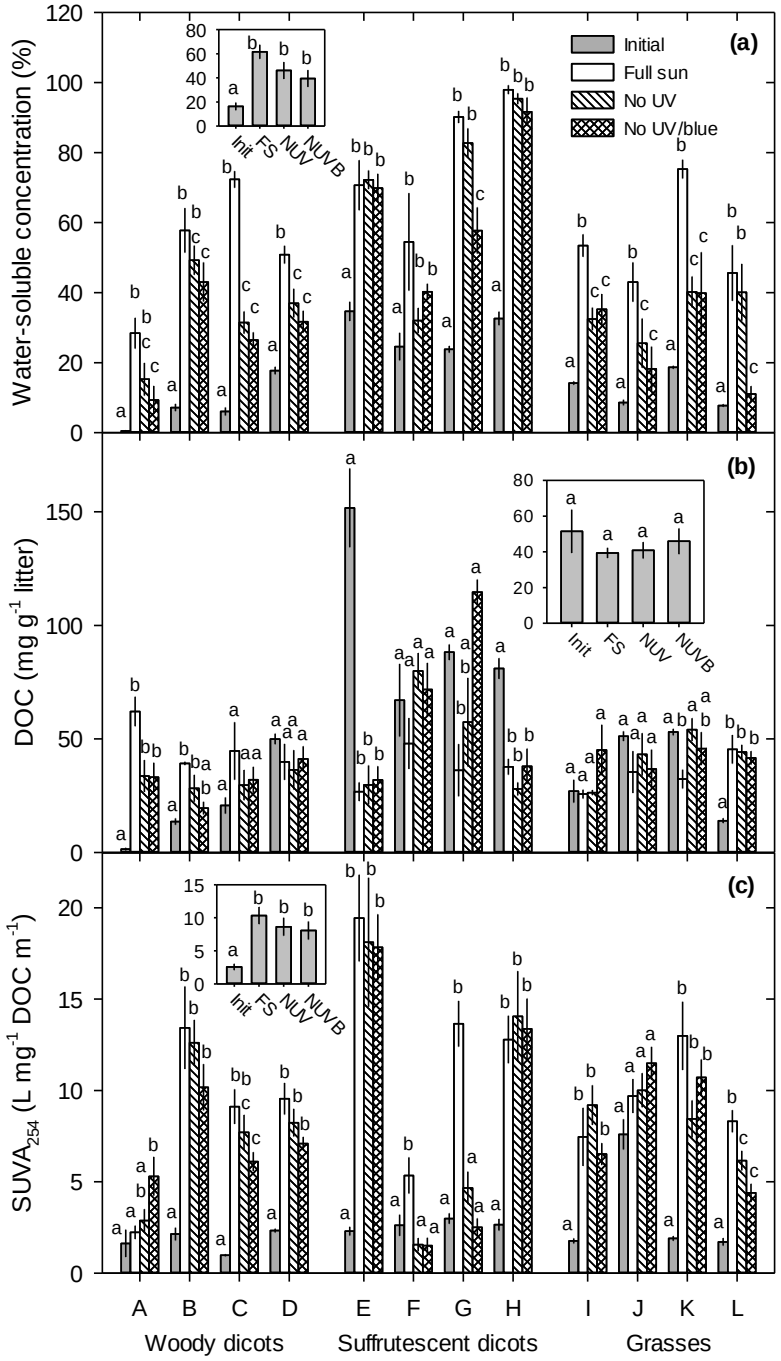

Figure 1 Water-soluble (a) and DOC concentration (b) of initial and decayed litter in the Full sun, No UV, No UV/blue treatments. Additionally, specific ultraviolet absorbance ($SUVA_{254}$) of leachates from initial and decayed litter in each treatment (c). Values are means (±*SE*, $n = 5$). Means within a litter type with different letters are significantly different ($p \leq 0.05$). See Figure 6 for the letter used as litter type codes. Insets are the mean for each treatment (±*SE*, $n = 12$). Init means initial litter, FS means Full sun, NUV means No UV, and NUVB means No UV/blue.

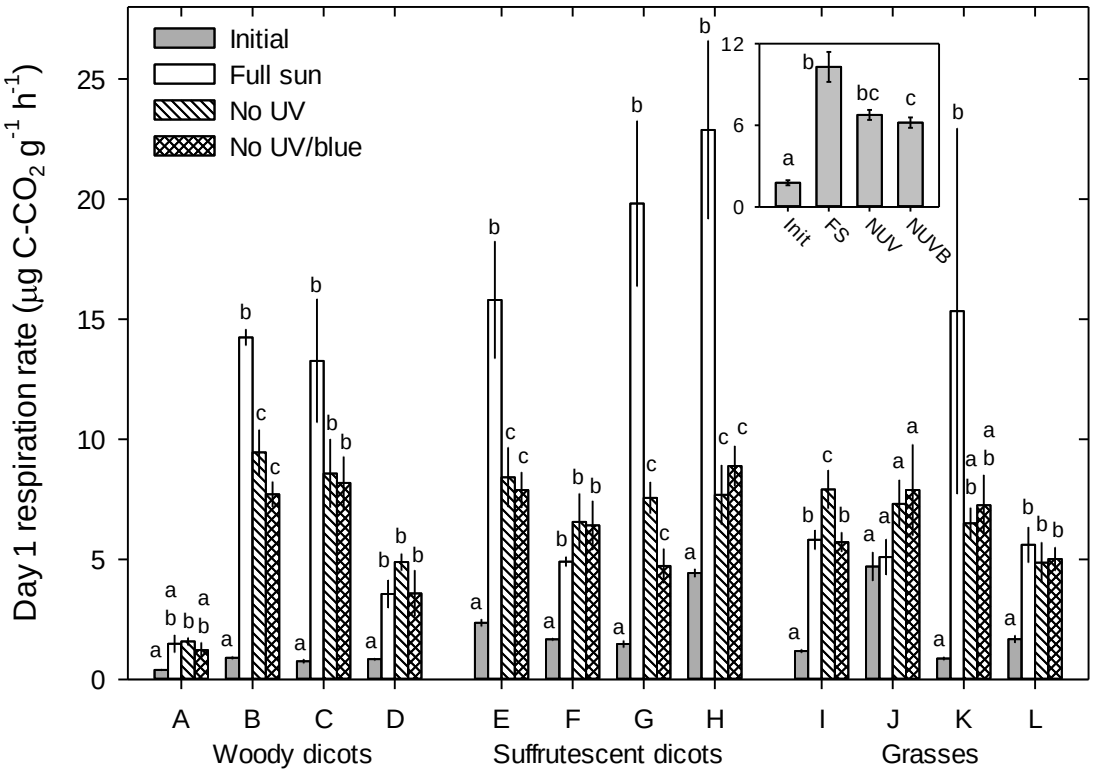

Figure 2 Microbial respiration rate on day 1 in initial and decayed litter in each radiation treatment. Values are means (±*SE*, $n = 5$). Means within a litter type with different letters are significantly different ($p < 0.05$). See Figure 6 for the letter used as litter type codes. Inset is the mean respiration rate for each treatment (±*SE*, $n = 12$). Init means initial litter, FS means Full sun, NUV means No UV, and NUVB means No UV/blue.

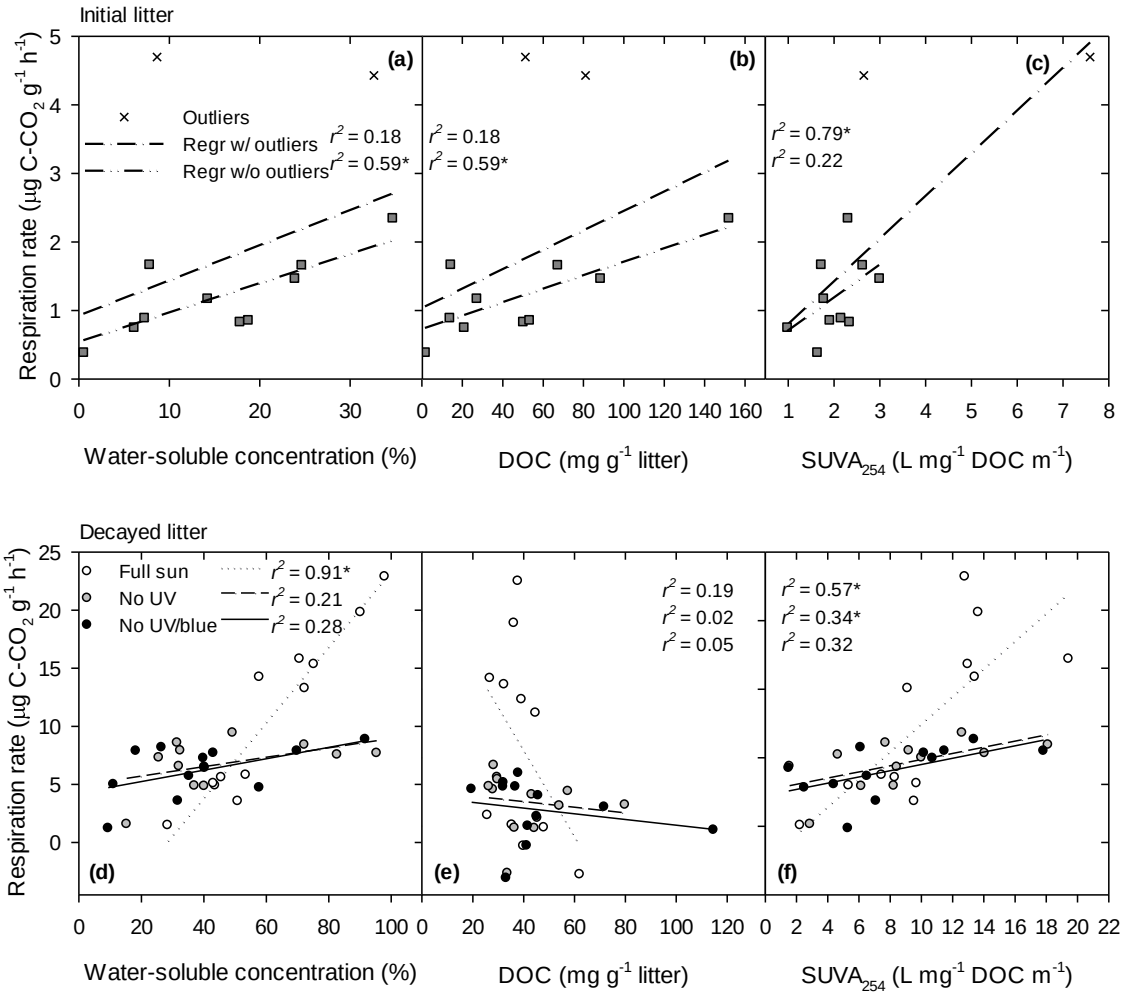

Figure 3 Relationship between concentrations of water-solubles (a and d) and DOC (b and e), and $SUVA_{254}$ (c and f), with day 1 respiration rates for initial (a-c) and decayed litter (d-f) in each treatment. Values are means in each litter type (n = 5). Lines are linear least-squares regressions; asterisks after r^2 values denote significant correlations ($p \leq 0.05$, n = 12, n =10 in regressions excluding outliers). Values denoted by the symbol "x" represent outliers.

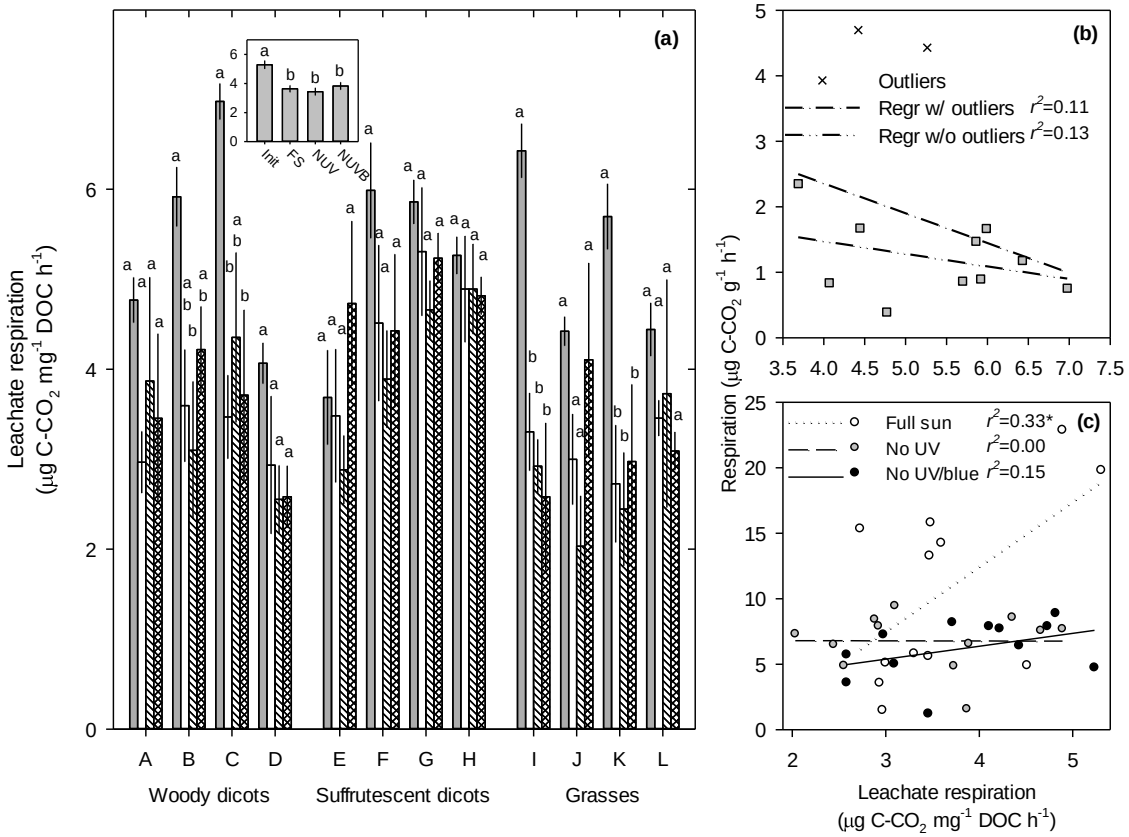

Figure 4 Leachate respiration **(a)** of initial and decayed litter in the Full sun, No UV, and No UV/blue treatments. Values are means (±*SE*, $n = 5$). Means within a litter type with different letters are significantly different ($p \leq 0.05$). See Figure 6 for the letter used for litter type codes. Inset is the mean leachate respiration rate for each treatment (±*SE*, $n = 12$). Additionally, relationships between leachate respiration and litter respiration of initial **(b)** and decayed **(c)** litter. Values are means in each litter type ($n = 5$). Lines are linear least-squares regressions; asterisks after r^2 values denote significant correlations ($p \leq 0.05$, $n = 12$, $n = 10$ in regressions excluding outliers). Values denoted with the symbol "x" in panel **(b)** represent outliers

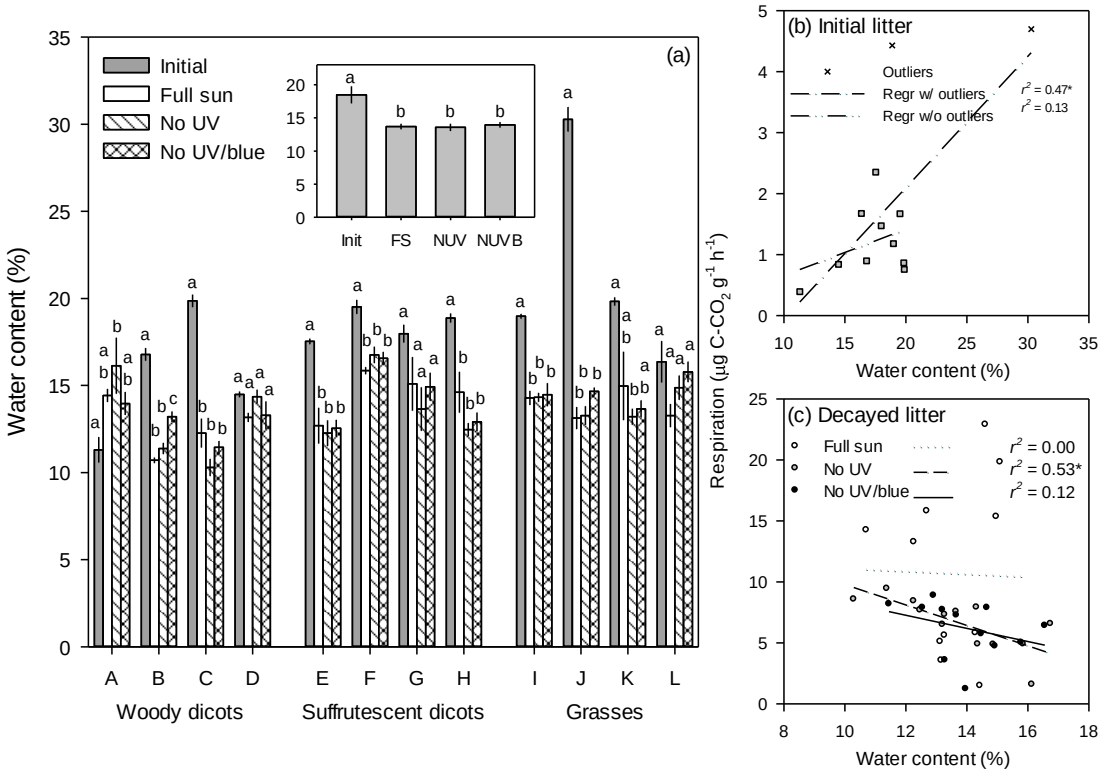

Figure 5 Water content on day 1**(a)** of initial and decayed litter in the Full sun, No UV, and No UV/blue treatments. Values are means (±*SE*, $n = 5$). Means within a litter type with different letters are significantly different ($p \leq 0.05$). See Figure 6 for the letter used for litter type codes. Inset is the mean water content on day 1 for each treatment (±*SE*, $n = 12$). Additionally, relationships between water content on day 1 and litter respiration of initial **(b)** and decayed **(c)** litter. Values are means in each litter type ($n = 5$). Lines are linear least-squares regressions; asterisks after r^2 values denote significant correlations ($p \leq 0.05$, $n = 12$, $n = 10$ in regressions excluding outliers). Values denoted with the symbol "x" in panel **(b)** represent outliers.

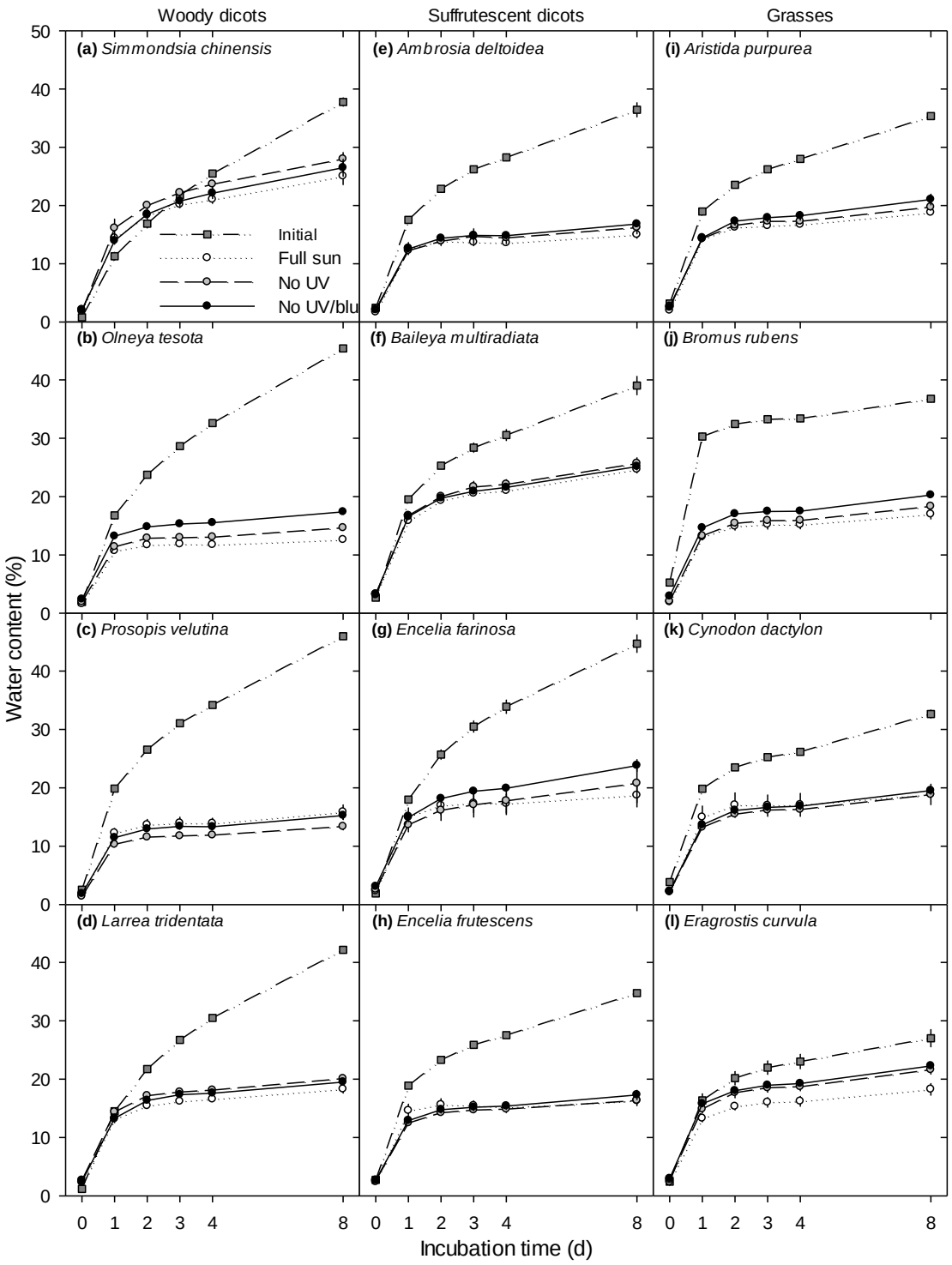

Figure 6 Water content of initial and decayed litter in each radiation treatment over an 8-day incubation in high relative humidity. Values are means (±*SE*, *n* = 5).

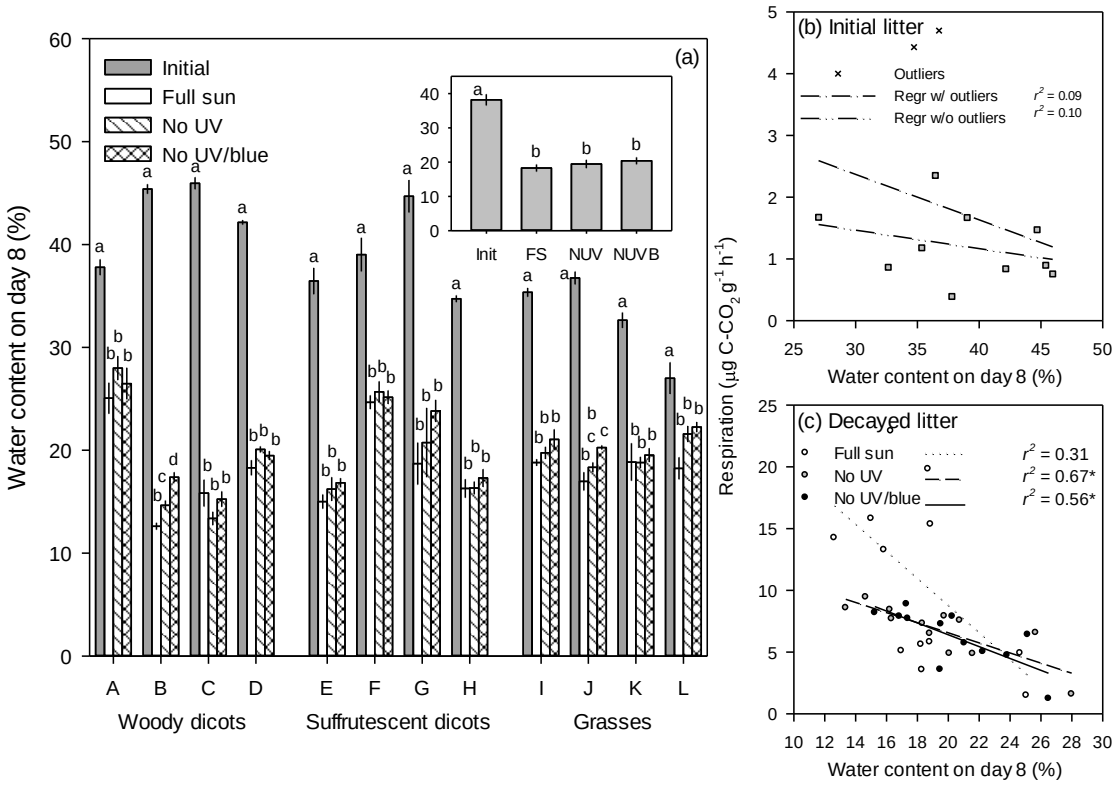

Figure 7 Water content on day 8 **(a)** of initial and decayed litter in the Full sun, No UV, and No UV/blue treatments. Values are means (±*SE*, $n = 5$). Means within a litter type with different letters are significantly different ($p \leq 0.05$). See Figure 6 for the letter used for litter type codes. Inset is the mean water content on day 8 for each treatment (±*SE*, $n = 12$). Additionally, relationships between water content on day 8 and litter respiration of initial **(b)** and decayed **(c)** litter. Values are means in each litter type ($n = 5$). Lines are linear least-squares regressions; asterisks after r^2 values denote significant correlations ($p \leq 0.05$, $n = 12$, $n = 10$ in regressions excluding outliers). Values denoted with the symbol "x" in panel **(b)** represent outliers.

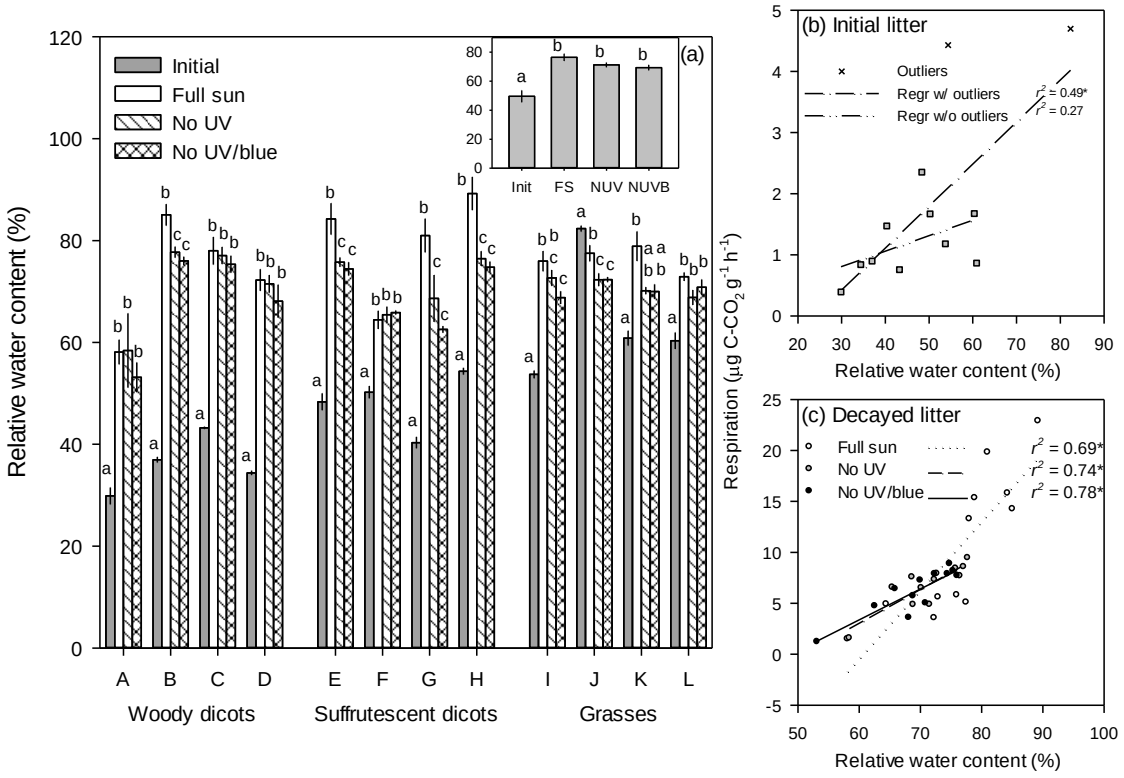

Figure 8 Relative water content on day 1 **(a)** of initial and decayed litter in the Full sun, No UV, and No UV/blue treatments. Values are means (±*SE*, $n = 5$). Means within a litter type with different letters are significantly different ($p \leq 0.05$). See Figure 6 for the letter used for litter type codes. Inset is the mean relative water content on day 1 for each treatment (±*SE*, $n = 12$). Additionally, relationships between relative water content on day 1 and litter respiration of initial **(b)** and decayed **(c)** litter. Values are means in each litter type ($n = 5$). Lines are linear least-squares regressions; asterisks after r^2 values denote significant correlations ($p \leq 0.05$, $n = 12$, $n = 10$ in regressions excluding outliers). Values denoted with the symbol "x" in panel **(b)** represent outliers.

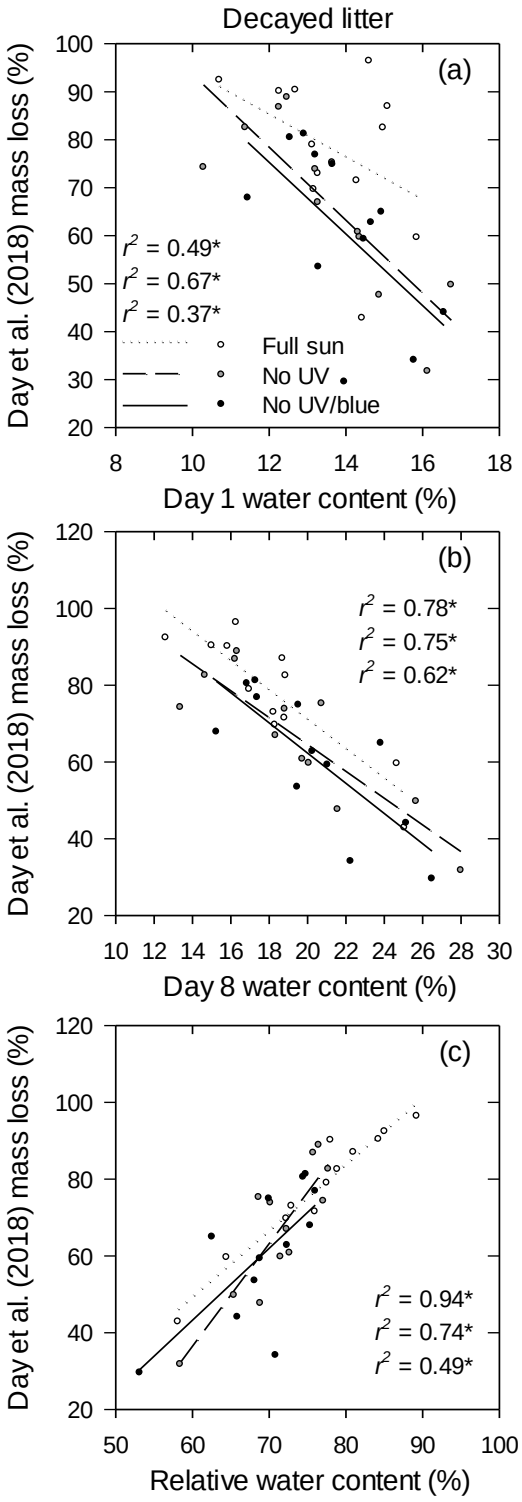

Figure 9 Relationships between mass loss in field experiment after 34 months and day 1 water content (a), day 8 water content, and relative water content on day 1 (c) of decayed litter. Values are means (n = 8 for mass loss, n = 5 water content parameters). Lines are linear least-squares regressions; asterisks after r^2 values denote significant correlations ($p \leq 0.05$, n = 12).

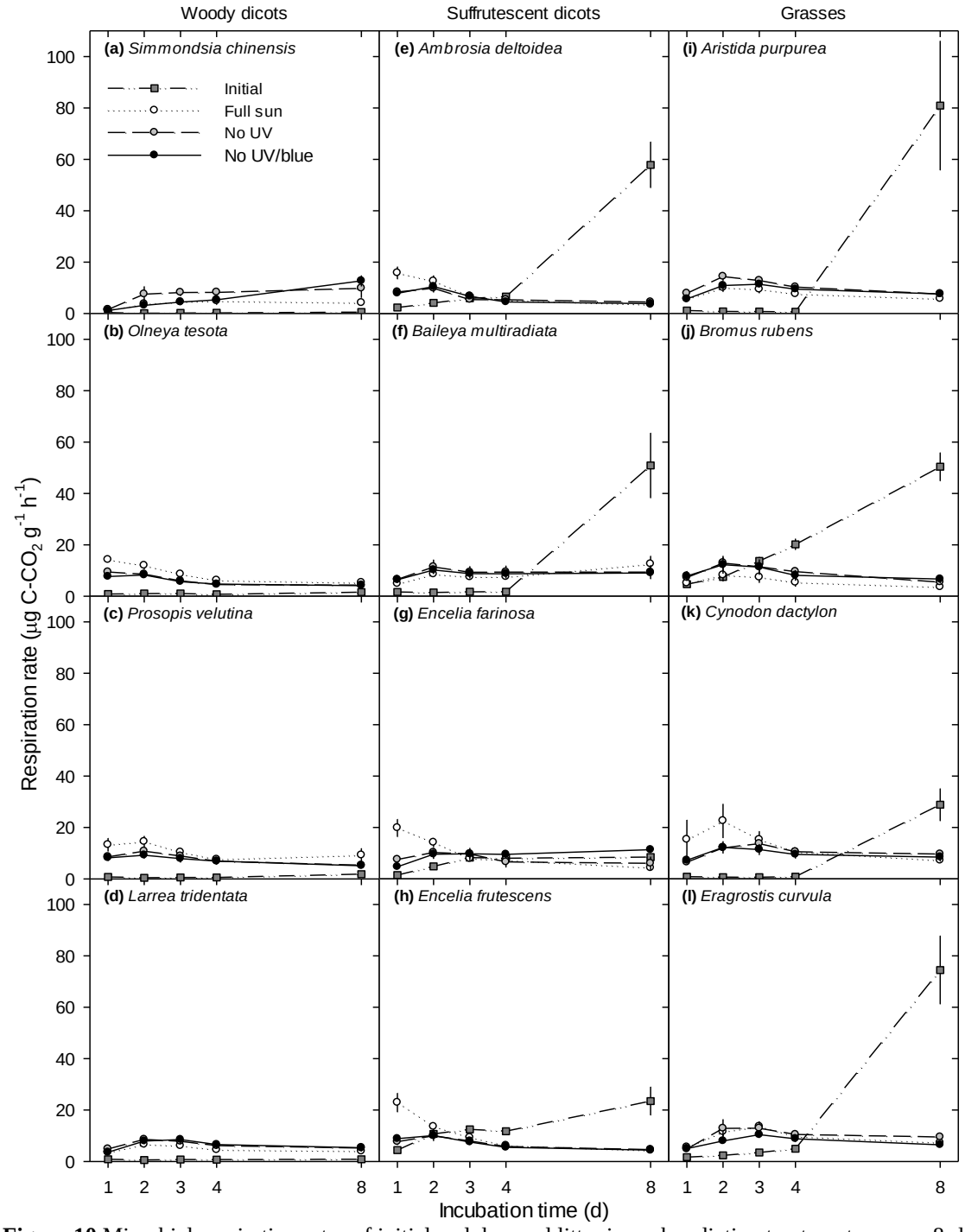

Figure 10 Microbial respiration rates of initial and decayed litter in each radiation treatment over an 8-day incubation at high relative humidity. Values are means (±*SE*; $n = 5$). The panel letter in front of each litter type name is used as a litter type code in other Figures and Tables.

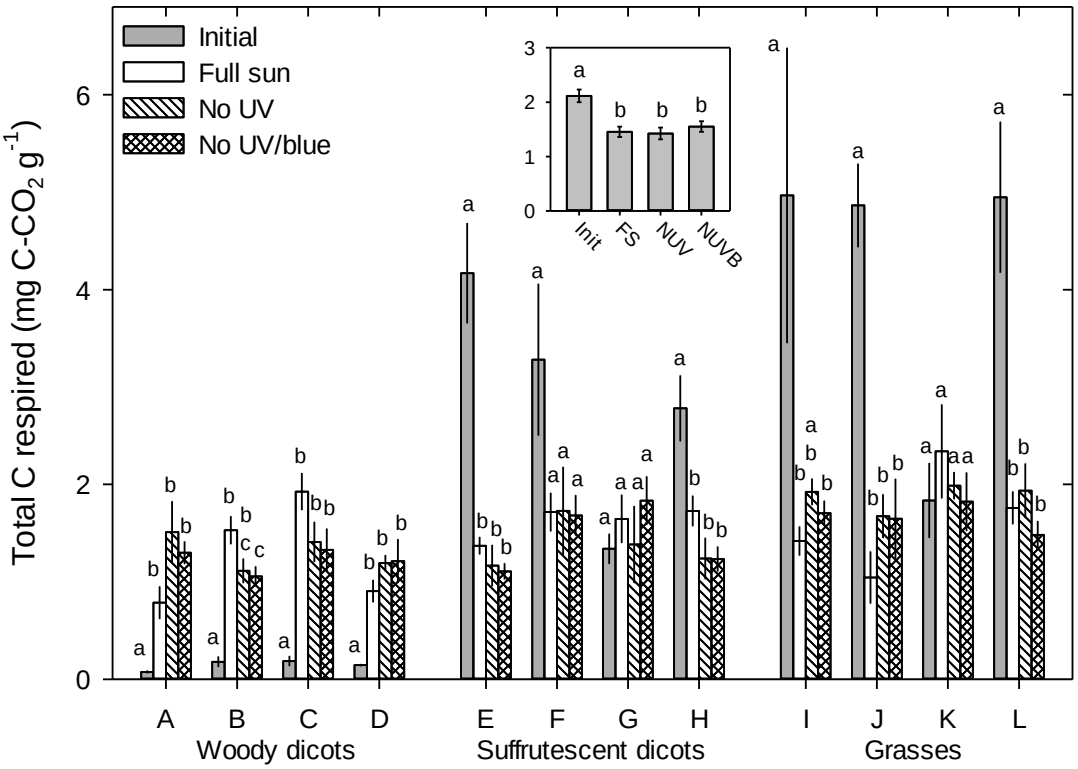

Figure 11 Total microbial respiration measured over 8-day incubation in initial and decayed litter in each radiation treatment. Values are means (±*SE*, *n* = 5). Means within a litter type with different letters are significantly different ($p < 0.05$). See Figure 6 for the letter used as litter type codes. Inset is the mean respiration for each treatment (±*SE*, *n* = 12). Init means initial litter, FS means Full sun, NUV means No UV, and NUVB means No UV/blue.

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