Received: 29 March 2021 | Accepted: 11 January 2022

DOI: 10.1111/1365-2435.14053

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Photodegradation of plant litter cuticles enhances microbial decomposition by increasing uptake of non-rainfall moisture

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Funding information
Michigan State University; National Science Foundation

Handling Editor: Pablo García-Palacios

Abstract

1. Litter decomposition plays a central role in carbon cycling in terrestrial ecosystems worldwide. In drylands, which cover 40% of the Earth's land surface, photodegradation and biotic decomposition driven by non-rainfall moisture are important mechanisms of litter decay, though studies have only recently begun examining interactions between these two processes. We describe a novel priming mechanism in which photodegradation and biotic decay of the cuticle of plant litter increase litter absorption of non-rainfall moisture (fog, dew and water vapor), supporting greater microbial decomposition.
2. We used several field experiments in a coastal fog desert and a series of in situ observations to demonstrate a relationship between solar radiation, cuticle integrity, water absorption rates and mass loss.
3. Experimentally attenuating solar radiation for 36 months slowed mass loss, reduced cuticle degradation and decreased litter moisture uptake relative to litter under ambient sunlight controls. In a separate field experiment, removing the cuticle of recently senesced grass tillers increased mass loss fourfold over 6 months relative to controls. Tillers with degraded cuticles also absorbed 3.8 times more water following an overnight dew event than did those with intact cuticles. Finally, fungal growth was consistently greater on the sun-facing side of in situ tillers than on the shaded side, coincident with greater cuticle degradation.
4. We present a conceptual model where the cuticle of plant litter acts as a water-resistant barrier that is first degraded by solar radiation and surficial microbes, increasing litter's ability to absorb enough water during non-rainfall moisture events to support substantial biotic decomposition inside the tissue. Considering how photodegradation and non-rainfall moisture are both substantial drivers of litter decomposition in drylands, understanding how they interact under realistic field conditions will help us better predict how these systems are responding to changing climate regimes.

KEYWORDS
arid, carbon cycling, litter decomposition, non-rainfall moisture, photodegradation, plant traits

1 | INTRODUCTION

Plant litter decomposition is a critical component of the carbon cycle worldwide. While litter decay processes are fairly well understood in mesic systems (Adair et al., 2008), in drylands, litter decomposition involves the interaction of several less understood processes including photodegradation (Austin & Vivanco, 2006; Smith et al., 2010), biotic degradation by non-rainfall moisture (NRM; fog, dew and water vapour; Evans et al., 2020; Gliksman et al., 2017) and decomposer responses to intense abiotic stressors such as prolonged desiccation (Logan et al., 2021). This can lead to complex dynamics that do not fit neatly within classic paradigms. For example, while plant biomass production is tightly coupled with rainfall in drylands (Poulter et al., 2014; Seely & Louw, 1980), the decomposition of this biomass is rarely correlated with rainfall in these systems (Austin, 2011). Since arid and semi-arid lands cover 40% of Earth's land surface and can account for half of the interannual variability in global carbon storage (Poulter et al., 2014), this currently leaves a gap in our ability to describe terrestrial decomposition processes globally, especially as moisture regimes in drylands worldwide change (Dai, 2013; Forthun et al., 2006; Haensler et al., 2011; Kutty et al., 2019; Niu et al., 2010).

Compared to most mesic systems where rainfall-supported biotic activity is the primary driver of litter decomposition, in drylands, abiotic processes play a greater role in driving decomposition (Austin, 2011) and account for the majority of total litter decay in some ecosystems (Austin & Vivanco, 2006). Photodegradation—the direct or indirect decomposition of litter by solar radiation—is particularly important in drylands where ground-level solar irradiance is high and precipitation is low and erratic, reducing decomposer activity (Austin & Vivanco, 2006). Incorporating photodegradation into existing litter decay models can substantially improve model predictions (Adair et al., 2017; Chen et al., 2016), but more work is needed to understand the mechanisms by which photodegradation interacts with other litter decay processes.

Solar radiation influences litter decomposition through multiple mechanisms. Photolysis of organic compounds such as lignin, cellulose and hemicellulose directly accelerates litter mass loss (Brandt et al., 2009; Day et al., 2019) and also produces intermediaries such as peroxides and reactive oxygen species that can further degrade organic components of litter through indirect pathways (King et al., 2012; Messenger et al., 2009). By cleaving double bonds in recalcitrant compounds like lignin, solar radiation can make litter more susceptible to subsequent microbial degradation (King et al., 2012; Wang et al., 2017). This process, known as photopriming or photofacilitation, accelerates mass loss more than either abiotic photodegradation or microbial decomposition alone (Gliksman et al., 2017; Wang et al., 2015). Since photopriming links two major decomposition processes in drylands (biotic degradation and photodegradation), understanding the mechanisms underlying photopriming is essential to accurately describe carbon turnover in these systems.

In many drylands, NRM-driven biotic decomposition and photodegradation interact with one another through photopriming mechanisms. By manipulating nighttime humidity and daytime solar irradiance in a Mediterranean shrubland, Gliksman et al. (2017) found synergistic effects of NRM-supported microbial activity and photodegradation on diel time-scales. Lin et al. (2018) found that CO_2 production and lignin degradation were significantly greater when microcosms experienced an alternating cycle of UV radiation during the day and dark wet conditions at night. Since NRM can occur as often as 95% of nights in some grasslands (Ritter et al., 2019) and account for the majority of litter mass loss (Evans et al., 2020), interactions between NRM-driven biotic decay and photodegradation may be critical to dryland litter decay.

While many studies have focused on the classical photopriming mechanism by which solar radiation makes lignin more susceptible to biotic decay (Austin & Ballare, 2010; Austin et al., 2016; King et al., 2012), structural lignin is usually located within plant tissues where it is not exposed to solar radiation until the outer surface is broken or removed. Instead, photodegradation of compounds present in plant cuticles may be more important in the early stages of decay (Bruhn et al., 2014). Physical traits such as cuticle thickness can slow litter decay by blocking decomposer fungi and water (Zukswert & Prescott, 2017) and plant cuticles contain many photo-reactive compounds that are susceptible to degradation by solar ultraviolet (UV; 290–400 nm) radiation (Bruhn et al., 2014; Day et al., 2019; Messenger et al., 2009). Since cuticles are effective water barriers in living plants (Shepherd & Griffiths, 2006), they may affect how well litter absorbs water during NRM events after senescence.

We set out to test a novel mechanism of photopriming by which solar radiation degrades the cuticle of plant litter, increasing moisture uptake during NRM events, subsequently enhancing biotic decomposition. Since litter moisture content controls biotic activity during NRM events (Jacobson et al., 2015) and moisture content depends in part on cuticle permeability, we hypothesized that as solar radiation degrades the cuticle, it becomes more permeable to moisture, which enhances microbial decomposition during NRM events.

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted a series of field experiments and observations (Figure 1) at the Gobabeb Namib Research Institute (23°33.6′S 15°02.5′E) in the Namib Desert, Namibia, a hyperarid, coastal fog desert in southwestern Africa. The Namib Desert is an ideal site to study the interaction between NRM and photodegradation because it receives high solar irradiance (Soares et al., 2019) and supports substantial NRM-driven litter decomposition (Evans et al., 2020; Jacobson et al., 2015). We studied the decomposition of *Stipagrostis sabulicola*, a large hummock-forming grass that is the most dominant grass species in this system (Seely & Louw, 1980) and has widely distributed con-generics throughout Africa and Asia (Clayton et al., 2006).

Gobabeb's meteorology has been described in detail elsewhere (Eckardt et al., 2013; Evans et al., 2020; Logan et al., 2021). Briefly, Gobabeb receives 25 mm mean annual rainfall, though it is highly variable (Eckardt et al., 2013). The site receives approximately 15.00 hr of wetness (presence of liquid water) per year and 99% of wet hours are attributable to NRM, not rainfall (Evans et al., 2020). During our study, the site received a total of 79.4 mm of rain, with 49.5 mm falling during three events in April and May 2018. Mean annual temperature is *c*. 20°C with mean daily maximum and minimum temperatures of 30°C and 13°C, respectively (Logan et al., 2021). Average daily unweighted ultraviolet-A (UVA; 315–400 nm) and ultraviolet-B (UVB; 280–315 nm) irradiances are 435.5 and 11.86 W/m, respectively (Figure S1).

2.2 | Exp 1: Solar radiation manipulation

To determine how solar radiation affected litter mass loss and cuticle integrity, we conducted a 36-month field manipulation of solar radiation (July 2016–July 2019). We collected recently senesced, standing *S. sabulicola* tillers (n = 240) from Gobabeb and deployed them under radiation filters. To eliminate microclimate variations inherent in litter bags, we placed tillers in litter racks, which are custom-made wooden frames covered with a dewaxed shellac for waterproofing (Figure S2G). Using tillers in litter racks, instead of fine litter in mesh bags, allowed us to secure tillers while keeping them exposed to ambient solar and moisture conditions (Evans et al., 2020; Logan et al., 2021). A subset of tillers was collected at roughly 6-month intervals for 36 months (Figure 1).

We established four treatments: a shade treatment which utilized plexiglass that was spray painted white to block direct solar radiation ('Shade'), a UV-attenuation treatment ('UVblock') using Lexan polycarbonate (SABIC Innovative Plastics) which blocks radiation below 400 nm but transmits 90% of radiation >400 nm, a 'UVpass' control made from clear Arkema G-UVT (Loop Acrylics) that has >70% transmittance of radiation above 300 nm and >80%

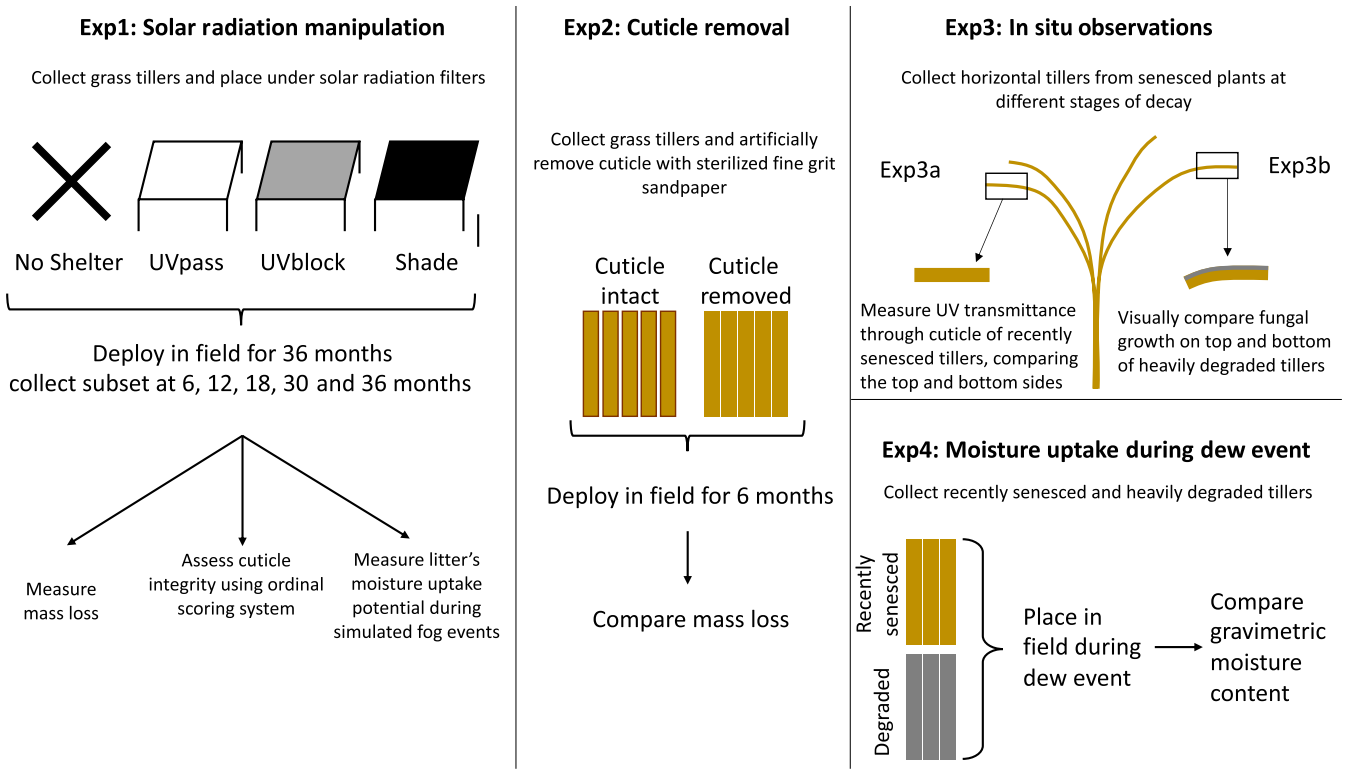


FIGURE 1 Study design identifying the four experiments. (Exp1) 36-month solar radiation manipulation; (Exp2) the cuticle removal experiment; (Exp3) in situ observations of grass tillers in the field comparing the sun-facing and shaded sides; (Exp4) measuring gravimetric moisture content following a dew event in the field. Different tillers were used for each experiment

above 400 nm, and a 'No Shelter' control to ascertain the effects of microclimate changes induced by the shelters. Details of shelter construction and microclimate measurements are described in the supplementary material. By comparing a UV-transparent control and a No Shelter control, we were able to determine whether the shelters themselves altered litter decomposition by changing the microclimate experienced by litter.

To determine whether mass loss was coincident with cuticle degradation, we assessed the integrity of the cuticle of tillers. Cuticular permeability to water is not strongly correlated with cuticle thickness or wax coverage (Riederer & Schreiber, 2001) but is related to physical characteristics like cracking, which can make leaf surfaces more porous (Pitcairn et al., 1986); hence, we visually assessed cuticles for physical damage to determine whether tillers under the radiation treatments differed in their degree of cuticle integrity. At each collection time, we photographed the top (sun-facing) and bottom (shaded) side of each tiller using a ProScope Micro Mobile microscope (Bodelin Technologies) attached to an iPhone 6S. We then created a 5-point ordinal scoring system to classify the tillers based on the degree of physical damage to their outer surface. Example photos of each stage as well as a detailed description of the scoring system are included in the supplementary material (Figure S6).

Finally, to determine whether the cuticle degradation we observed coincided with an increased ability of tillers to absorb atmospheric water, we placed tillers in an artificial fog chamber and measured gravimetric moisture content of the tiller segments following a simulated fog event. The fog chamber is an acrylic box that uses a reptile fogger to generate a spray of fine water droplets in a constant temperature and humidity environment (Figure S7). Tillers had their ends wrapped in parafilm (so water could only enter via the cuticle surface, not exposed vasculature) and were placed in the fog chamber for a set time, after which they were weighed to determine gravimetric moisture content; details of the procedure are described in the supplementary material. To control for variation in surface area among tillers with different diameters, we report moisture uptake values normalized to surface area (mg H_2O/mm^2).

2.3 | Exp 2: Direct cuticle removal

Since cuticle degradation in our solar radiation experiment could co-occur with photochemical-induced changes in litter quality, we sought to verify that the cuticle itself played a role in mass loss by physical removing the cuticle from a subset of tillers. We collected 48 standing, recently senesced *S. sabulicola* tillers and artificially removed the cuticle of half of them using sterilized, fine 220 grit sandpaper, leaving cuticles on the other tillers intact as controls (details described in supplementary material). We then weighed the tillers and deployed them in the field for 6 months underneath the same radiation shelters described above.

2.4 | Exp 3a: In situ assessment of UV-driven cuticle degradation

We corroborated results from our experimental manipulations by assessing solar radiation-induced degradation of litter cuticles in the field using a fluorescence-based measure of cuticle transmittance of UV radiation. We used a UVA-PAM fluorometer (Bilger et al., 2014; Kolb et al., 2005), which was originally developed to non-invasively measure epidermal UV transmittance of leaves. The UVA-PAM measures fluorescence ($\lambda > 650$ nm) induced by UV (F_{UV}; $\lambda_{max} = 375$ nm) and normalizes it to fluorescence induced by blue-green light (F_{BG}; $\lambda_{max} = 470$ nm) to control for variation in underlying chlorophyll concentration (Barnes et al., 2015).

For this experiment, we collected an additional 24 horizontal *S. sabulicola* tillers and used the UVA-PAM to measure epidermal UV transmittance on both the upper (sun-facing) and lower (shaded) sides of the tillers. According to this technique, we inferred that higher F_{UV}:F_{BG} values represented greater UV penetration through the cuticle. Since all sides of the tillers were similar at the start of the experiment (because we collected identically looking, vertically oriented tillers), changes in their UV-absorption properties were inferred to be from a degradation of UV-absorbing compounds during decomposition. By comparing the upper and lower sides, we used F_{UV}:F_{BG} as a measure of UV-induced cuticle degradation, with higher values indicating greater UV damage. Since we did not calibrate our optical measurements against physical measurements of cuticle thickness or density, we use F_{UV}:F_{BG} only as a relative index of cuticle degradation by UV radiation.

2.5 | Exp 3b: Location of fungi on litter

To determine whether surficial fungi were more present on the sun-facing or shaded side of tillers, we collected a random sample of senesced tillers with pigmented fungal growth. We collected 51 tillers in January 2017 that showed anywhere from minor levels of dark-pigmented fungi to heavy colonization across their entire surface. We only collected tillers that were no more than 20° from horizontal and recorded whether they had visible fungal growth only on the top or bottom or both sides.

2.6 | Exp 4: Moisture uptake during a dew event

To verify whether tillers with degraded cuticles absorbed more water during actual NRM events in the field, we placed five late-stage decomposing tillers and five recently senesced tillers into litter racks in the field (Far East Dune; 23°47.0′S 15°46.9′E, 25 June 2015). Recently senesced tillers had intact cuticles, no visible signs of fungal growth and attached inflorescences (Figure S2C) while late-stage tillers were characterized by extensive dark-pigmented fungal growth and substantial cuticle degradation (Figure S2E), indicative of senescence having occurred over a year prior (Jacobson

et al., 2015; personal observation). We then weighed them to determine gravimetric moisture content after exposure to an overnight dew event.

2.7 | Statistical analysis

Since some tillers were measured multiple times over the course of our solar radiation manipulation (Exp1), we analysed the mass loss data using repeated measures ANOVAs using the 'lmer' function in the LME4 package in R (Bates et al., 2015; R Core Team, 2020), using time, treatment and initial mass as predictors of mass loss. Since we used an ordinal score to assess cuticle integrity, we used a Kruskal–Wallis test in the BASE package of R to determine whether scores changed over time and differed among the radiation treatments (though we used the arithmetic mean for ease of visualization when plotting figures). We conducted post-hoc pairwise comparisons among the treatments using a Wilcoxan rank-sum test with Bonferroni adjustments. We compared moisture uptake potential among the tillers using the 'ANOVA' function in the CAR package in R (Fox & Weisberg, 2019; R Core Team, 2020). We used a chi-squared test to determine whether fungi were more common on one side than the other in Exp3 and we used *t*-tests to compare mass loss in the cuticle removal experiment (Exp2) and to compare moisture content in the degraded and intact tillers (Exp4).

3 | RESULTS

3.1 | Exp 1: Solar radiation manipulation

The attenuation of solar UV radiation significantly reduced litter mass loss relative to both controls while subsequent shading to reduce visible light had no discernible effect on mass loss (Figure 2a). Decomposition in all treatments proceeded very slowly at first, accelerating over time, unlike the classical exponential decay typical of most mass loss curves (Figure 2a; Table 1). Mass loss under the UVblock and Shade treatments were 28.5% and 26.4% lower than in the No Shelter control receiving full spectrum solar radiation. Despite receiving similar levels of solar radiation, the UVpass control and the No Shelter control had different mass loss rates, suggesting that the shelters themselves induced at least some effect on mass loss (Figure 2a). Temperature and leaf wetness status underneath shelters tended to be slightly lower than in the open on some evenings, though microclimate measurements were limited to a few days due to equipment failure. Relative humidity did not show a clear difference beneath the shelters and controls, though we were only able to obtain data over a few nights (Figure S8).

Cuticle damage increased overtime in all treatments (Figure 2b) and the sun-facing sides had more damage than the shaded sides (Figure S9; $p_{wilcox} < 0.001$). Solar radiation treatment was significant only on the sun-facing side of the tillers ($p < 0.001$), not the downward-facing side ($p = 0.30$). Tillers in the Shade treatment had significantly lower cuticle damage scores than did those in the No Shelter control ($p < 0.001$) and the UVpass control ($p = 0.007$) but did not differ from the UVblock treatment ($p = 0.25$).

Tillers that had been decomposing in the field for longer, absorbed more water in simulated fog events and tillers under the Shade treatment tended to have lower moisture uptake than did the three treatments that received ambient visible light (Figure 2c; Table 2; Tukey's HSD test: $p_{shade\ vs\ no\ shelter} = 0.09$; $p_{shade\ vs\ UVpass} = 0.08$). None of the three treatments with ambient light had significantly different moisture uptake rates from one another ($p > 0.1$, Figure 2c). On average, tillers in the Shade treatment absorbed 17.7% less water (mg H_2O/mm^2) than did those from the three treatments receiving visible light.

Cuticle damage, moisture uptake potential and mass loss were all positively correlated with one another across all treatments. Tillers with more damaged cuticles absorbed more water under simulated NRM conditions (Figure 2d) and tillers with greater moisture uptake potential lost more mass by the end of the experiment (Figure 2e).

3.2 | Exp 2: Cuticle removal experiment

Tillers that had their cuticle artificially removed had 4.25 times greater mass loss than did control tillers with intact cuticles (Figure 3a), though mass loss did not differ among the UV treatments (Table 3). Tillers with removed cuticles absorbed 2.6 times more water during a simulated NRM event than did those with intact cuticles (Figure 3b).

3.3 | Exp 3: In situ observations of tillers

UV transmittance (F_{UV}:F_{BG}) across the cuticle of recently senesced tillers was higher on the upward sun-facing side than the downward shaded side (Figure 4a; $T_{paired} = 4.59$, $p < 0.001$). This signal was driven by variation in F_{UV}, not F_{BG}, indicating that this variation was due to differences in cuticle transmittance of UV radiation, not differences in the underlying chlorophyll concentration (Figure S10).

On older tillers, we observed in the field, pigmented fungi were consistently more likely to be found on the sun-facing side of stems than on the shaded side (Figure 4b,c; $\chi^2_2 = 49.1$, $p < 0.001$). Of 51 randomly sampled horizontal tillers that had visible fungal growth anywhere on them, 40 (78%) showed evidence of fungal growth only on the upward-facing side while only one tiller (2%) had visible fungal growth on the bottom but not the top.

3.4 | Exp 4: Moisture uptake during a dew event

During an overnight dew event in the field, tillers with heavily degraded cuticles had gravimetric moisture content 3.8 times higher than did tillers with intact cuticles (Figure 5a; $p = 0.008$). In fact, even after a full night of exposure to dew, tillers with intact cuticles had an average water content (2.6% m/m) similar to that from a set

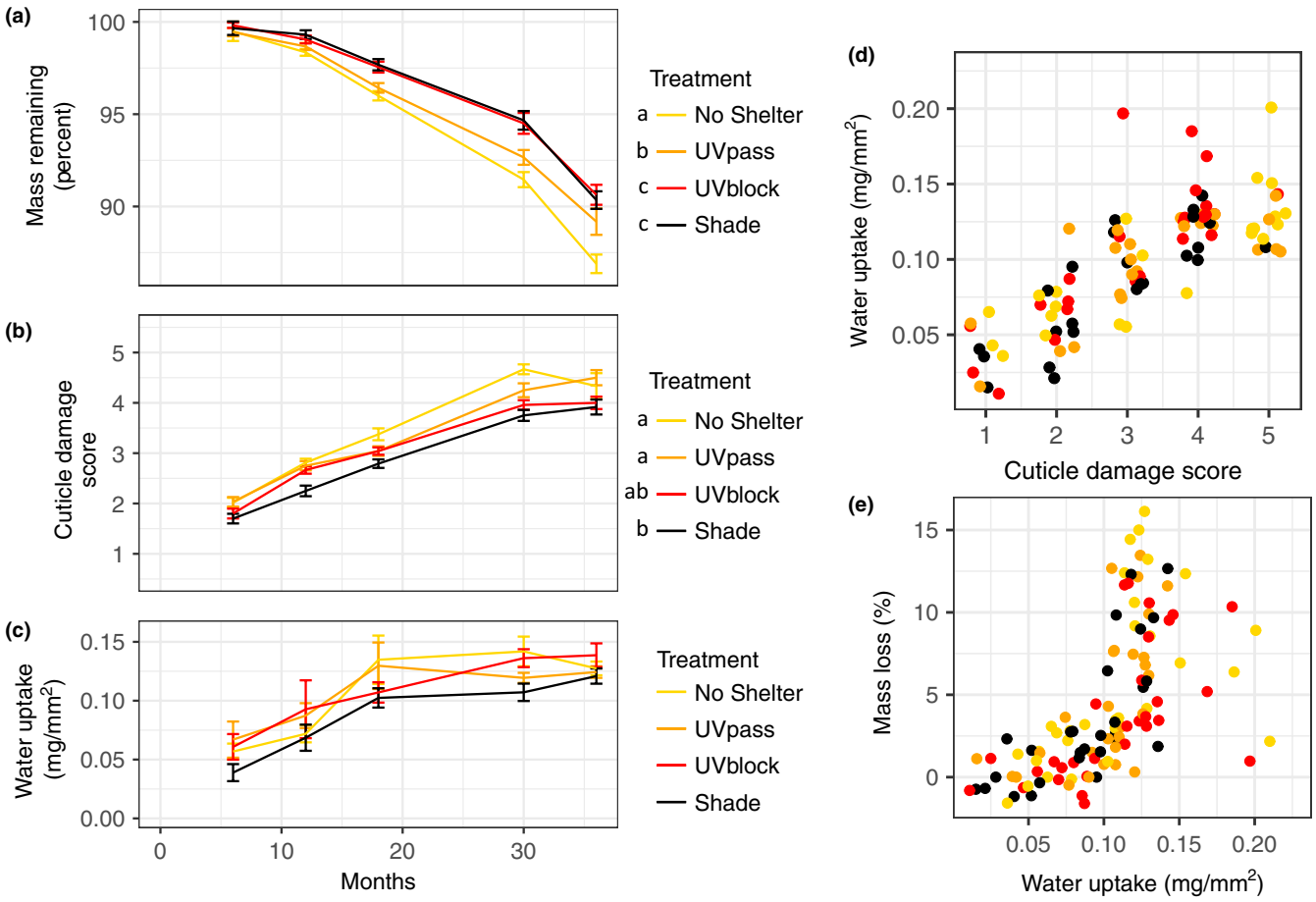


FIGURE 2 Results from the solar radiation manipulation (Exp1), showing changes in tiller properties over time. The three panels show progression of the same tillers. (a) mass loss; (b) cuticle damage (higher score denotes greater cuticle degradation; figure shows only the sun-facing side of tillers, see Figure S8 for the shaded side); (c) moisture uptake potential for tillers as measured during a simulated fog event. Plotted values are means ± 1 *SEM*. and significant differences are denoted by letters next to the legends; (d) moisture uptake potential as a function of cuticle damage score; (e) percent mass remaining as a function of moisture uptake potential. Panels d and e use the same data as shown in panels a–c

TABLE 1 ANOVA table for the mass loss model from the solar radiation manipulation (Exp1) with lowest AICc

Source	SS	*df*	*F*	*p*
Initial mass	0.22	1	0.174	0.677
Time	477	1	372	<0.001
Treatment	4.03	3	1.05	0.371
Initial mass × time	35.3	1	27.5	<0.001
Treatment × time	93.5	3	24.3	<0.001

TABLE 2 ANOVA table of moisture uptake (mg H_2O/mm^2) for the solar radiation manipulation (Exp1)

Source	SS	*df*	*F*	*p*
Treatment	3.77×10^{-9}	3	1.31	0.276
Time	2.49×10^{-8}	1	26.0	<0.001
Treatment × time	1.76×10^{-9}	3	0.611	0.609
Residuals	1.08×10^{-7}	112		

of recently senesced tillers collected during a dry period (2.2% m/m), both of which were considerably drier than tillers with degraded cuticles after the dew (10.1% m/m; Figure 5a), suggesting that tillers with intact cuticles absorbed almost no detectable water, even after several hours in a wet environment.

Finally, when we visually assessed tillers under wet conditions, intact cuticles prevented, or at least slowed, the absorption of liquid water. When we pipetted water onto recently-senesced tillers with intact cuticles, the water beaded up on the exterior and did not enter (Figure 5b) while tillers with heavily degraded cuticles absorbed water within 5 s of application (Figure 5c).

4 | DISCUSSION

Photodegradation and NRM-supported biotic decomposition are important components of litter decay in many dryland systems. We demonstrate a novel litter priming pathway where the cuticle of recently senesced grass tillers acts as a waterproof barrier, limiting

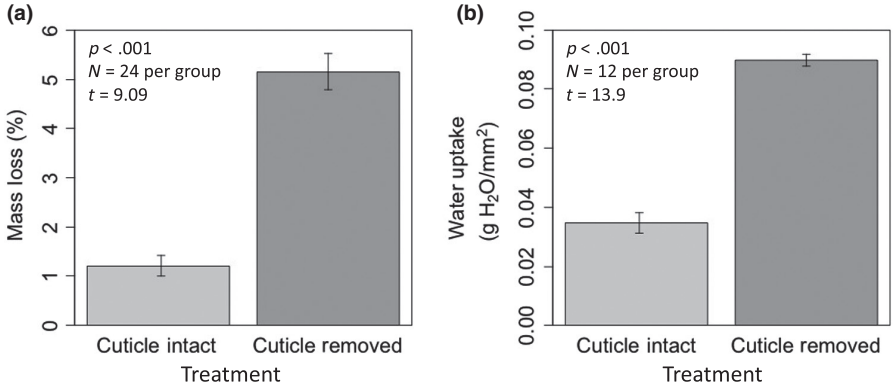


FIGURE 3 Results from the cuticle manipulation experiment (Exp2). (a) Mass loss after 6 months for tillers with intact cuticles and those with cuticles artificially removed by sanding. (b) Moisture uptake during a simulated fog event for tillers with intact cuticles and those with cuticles removed. Solar radiation treatment was not significant ($p > 0.05$), so we pooled samples by cuticle treatment for both plots. Plotted values are means ± 1 *SEM*

TABLE 3 ANOVA table of mass loss for the cuticle removal experiment (Exp2)

Source	SS	*df*	*F*	*p*
Cuticle treatment	186	1	88.1	<0.001
UV treatment	12.8	3	2.01	0.128
Cuticle × UV	6.25	3	0.985	0.410
Residuals	84.7	40		

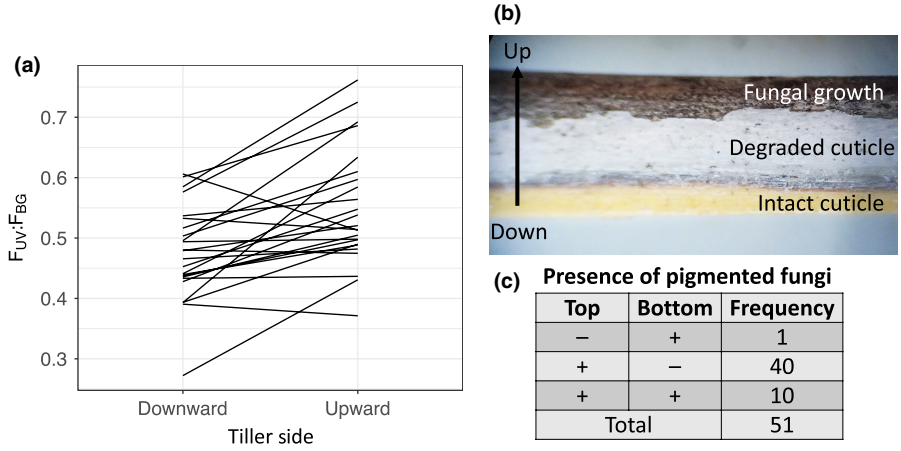
NRM-driven decomposition until it is degraded. Both photodegradation and NRM-driven biotic decay appeared to play significant roles in the early stages of litter decomposition by removing the cuticle, allowing greater moisture uptake by litter during subsequent NRM events.

Physical traits play important roles in controlling litter decay rates. Cuticle thickness and specific leaf area can predict litter mass loss rates as well as or better than chemical traits (Erdenebileg et al., 2020; Zukswert & Prescott, 2017). Here, we demonstrate an important mechanism of this process by showing that artificially removing the cuticle substantially increased both litter moisture uptake and mass loss and finding that tillers with degraded cuticles absorbed considerably more water during NRM events. Early- and late-stage decomposing *S. sabulicola* have differences in certain structural compounds, like lignin concentration (Logan et al., 2021), but these difference in gross chemistry cannot explain increases in moisture uptake as litter decays since they primarily describe the interior chemistry of litter, not the surface. More importantly, water pipetted onto tillers was only absorbed when cuticles were degraded and was repelled where cuticles were intact (Figure 5b,c). By demonstrating how the cuticle blocks moisture uptake and slows litter decay in an NRM-dominated system, we present a link between existing literature on plant traits in decomposition models and studies of photodegradation and NRM-driven litter decay.

Results from our study are consistent with others showing an interaction between photodegradation and NRM-supported microbial decomposition. Several studies have found that thermal and photochemical breakdown during the day can enhance NRM-driven microbial activity at night (Gliksman et al., 2017; Lin et al., 2018; Wang et al., 2015). In these previous studies, as with ours, solar radiation's primary contribution to mass loss was not thought to be from the production of volatiles or leachates through direct photochemical oxidation, but rather through a photopriming mechanism that enhanced biotic degradation. In our study, photodegradation played an important role in cuticle degradation for months prior to development of significant fungal decomposer communities. In this sense, the cuticular photopriming mechanism we describe here is more important early in the litter decay process and may decrease in importance over time, as biotic decomposition of inner tissues becomes less limited by litter moisture content.

One of the most striking patterns we observed in our field study was the peculiar shape of our mass loss curve, showing accelerating rather than decelerating mass loss over the 3-year study (Figure 2a). This could be explained in part by very low absolute rates of litter decomposition in the Namib Desert. Even after 3 years, tillers under our highest treatment (the No Shelter control) had an average mass loss of only 13.1% (Figure 2a). The accelerating mass loss likely reflects this being a snapshot of the initial phase of decomposition, highlighting a pattern that is not often seen in other studies that lack the temporal resolution necessary to see this shape when decomposition proceeds more rapidly. While we cannot know for certain, we may have seen a typical exponential decay curve had the experiment continued for several more years. The changes in cuticle integrity and moisture uptake potential we observed prior to the start of exponential decay highlight the importance of cuticle degradation early in the decomposition process.

While solar radiation was not the only cause of cuticle degradation, it played an important role in cuticle breakdown. Cuticle damage was greater for tillers exposed to ambient solar radiation than those receiving reduced UV radiation or visible light. Importantly, on in situ tillers in the field, fungi were more likely to be found on the sun-facing side than the shaded side of tillers, despite the potentially increased stress caused by direct exposure to solar radiation (Figure 4b,c). In other studies, UV radiation has been found to inhibit fungal growth or decomposition (Fourtouni et al., 1998; Pieristè et al., 2020) though this is not always the case as UV-A radiation can stimulate sporulation in many fungi (Manning & Tiedemann, 1995). It is unlikely that the stark contrast in fungal growth we observed between the upper and lower sides of tillers was a result of direct stimulation of fungal growth in response to UV radiation, especially when a more shaded portion of the exact same substrate was



Presence of pigmented fungi

Top	Bottom	Frequency
–	+	1
+	–	40
+	+	10
Total		51

FIGURE 4 Results for Exp3 showing (a) transmission of UV radiation through the cuticle for both the upward facing (sun-exposed) and downward (shaded) side of recently senesced horizontal stems that had no visual sign of fungal growth (paired *t*-test $p < 0.001$). Higher values reflect greater UV penetration into the tissue, consistent with greater UV-driven photodegradation. (b) Example of a late-stage tiller showing extensive fungal growth on the sun-facing side but not in the shade. Note photobleaching and cracking of the cuticle on the side. (c) Presence of pigmented fungi on randomly sampled horizontal tillers in the field, showing fungal growth is much more common on the upper side than on the lower side of horizontal tillers ($\chi^2_2 = 49.1$, $p < 0.001$)

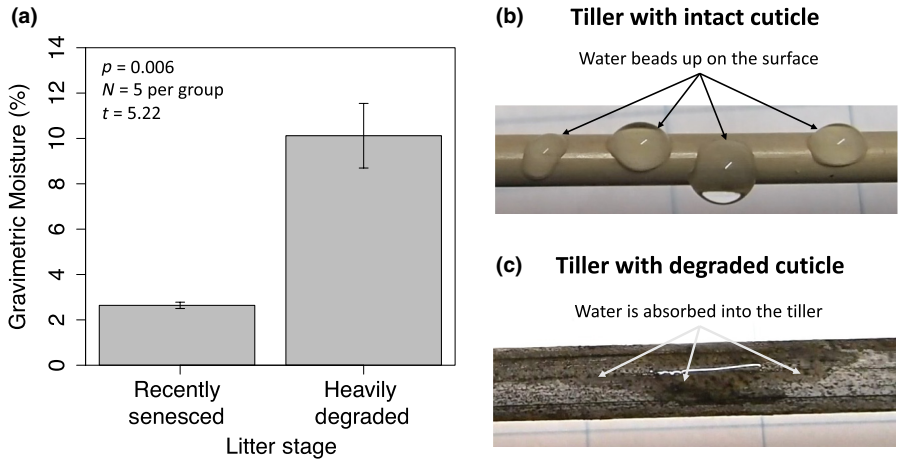


FIGURE 5 (a) Results from Exp4 showing gravimetric moisture content of recently senesced tillers (with intact cuticles) and older tillers (with heavily degraded cuticles) following a night of heavy dew deposition. Plotted values are means ± 1 *SEM*. (b) Photo of a recently senesced tiller with an intact cuticle, 5 s after water was pipetted onto it, showing water beading up on the surface. (c) Photo of a heavily degraded tiller with a degraded cuticle, 5 s after water was pipetted onto it, showing water is almost immediately absorbed into the tissue

available only millimetres away on the shaded side of the tillers. Of course, increased dew and fog deposition can sometimes occur on the upper side of tillers, which may also have contributed to the increased fungal growth there. Nevertheless, the degradation of UV-absorbing compounds in the sun-facing side of tillers (even in the absence of fungal growth in the early stages following senescence), and the observation that cuticle damage was greater when tillers received more solar radiation, demonstrate that UV radiation and biotic decomposition likely both played a role in cuticle breakdown in these early stages.

While both UV radiation and visible light affected litter cuticle integrity, UV appeared to be the most important component of solar radiation responsible for cuticle degradation and mass loss. Once we attenuated UV radiation, the subsequent reduction of visible light did not have any noticeable effect on mass loss (Figure 2a). This is consistent with other studies that have shown that, while short wavelength visible light can accelerate litter decomposition (Pieristè et al., 2019), UV radiation is often a stronger driver (King et al., 2012). Our measurements of the optical properties of in situ tillers also implicate UV in cuticle degradation since our fluorescence-based measure found clear differences in UV transmittance through the cuticle. Future studies may examine the specific wavelengths responsible for cuticle degradation via this mechanism and how this may differ among plant species.

Mass loss and cuticle degradation occurred in all treatments, even under our shaded treatment, suggesting that photodegradation was not the only driver of cuticle degradation. By using two types of controls (a No Shelter control and our UVpass control that transmitted ~90% UV radiation), we were able to examine how changes in the microclimate and NRM frequency, induced by our shelters,

altered cuticle integrity and mass loss. The reduction in mass loss under the UVpass control relative to the No Shelter control was probably due to the shelter's interception of laterally transported fog droplets (since relative humidity was not as strongly altered by the shelters, but leaf wetness sensors detected less liquid water underneath a subset of shelters on some nights; Figure S8). Since we did not measure leachates, we are unable to attribute this effect to reduced leaching of soluble compounds early in the decay process or slowed biological decomposition due to moisture limitation under the shelters. While this limits our ability to precisely determine the relative contribution of leaching, biotic decay and photodegradation in our experiment, the fact that we saw consistent effects of solar radiation on mass loss and cuticle integrity while also observing significant decay even when solar radiation was substantially reduced, suggests that, both photodegradation and biotic decay contributed to cuticle breakdown.

Photodegradation and biotic decay may degrade cuticles in concert with one another. Many fungi and bacteria degrade cutin and suberin found in plant cuticles (Angst et al., 2016; Chen et al., 2008) and litter decomposition can proceed faster when photodegradation and microbial activity occur on diurnal scales rather than one following the other (Lin et al., 2018, though they looked at overall decomposition, not specifically plant cuticles). In the Namib, fog droplets can coalesce on the top of leaning grass tillers where solar radiation is more direct, potentially leading to a diurnal interaction between surficial fungi and photodegradation that could accelerate cuticle breakdown. Future studies can examine how the activity of yeasts and other fungi on the litter surface interact with solar radiation to degrade cuticles in the early stages of litter decomposition.

To date, most photopriming studies have focused on how solar radiation alters litter chemistry, making litter more easily degraded by microbial decomposers (Austin et al., 2016). We expand on this work by introducing a conceptual model that differentiates between this classical photopriming mechanism and the novel priming mechanism we describe in this study (Figure 6). According to the classical photopriming pathway (Figure 6, bottom half), solar radiation degrades recalcitrant structural components such as lignin through both direct photolysis and reactive intermediaries (King et al., 2012). These processes then accelerate decomposition by alleviating the lignin bottleneck and making litter components more available for biotic decomposition (Austin & Ballare, 2010; Austin et al., 2016). We present evidence of a simultaneous cuticular photopriming pathway, whereby solar radiation, along with biotic decay, degrades compounds in the cuticle of litter, increasing water absorption during wet events (Figure 6, top half).

While the cuticular photopriming process which we describe here likely goes hand-in-hand with classical photopriming, the relative importance of each mechanism likely varies among systems. For example, in mesic systems where water is less limiting and plant litter consists primarily of lignin-rich tissue (i.e. wood), microbial decomposition may be more limited by litter recalcitrance making alleviation of the lignin bottleneck a more important mechanism of photodegradation (Austin et al., 2016). Alternatively, in drylands, which are dominated by relatively labile grasses, photodegradation of the cuticle that we describe here may take on a more important role. Our study focused on one grass species; teasing out which of these mechanisms dominates in different systems will require studies that track how both physical and chemical properties of litter change during decomposition among species and across systems.

Future studies may build on this work by incorporating interactions between plant traits, NRM and photodegradation into existing litter decay models. For example, plant species vary in

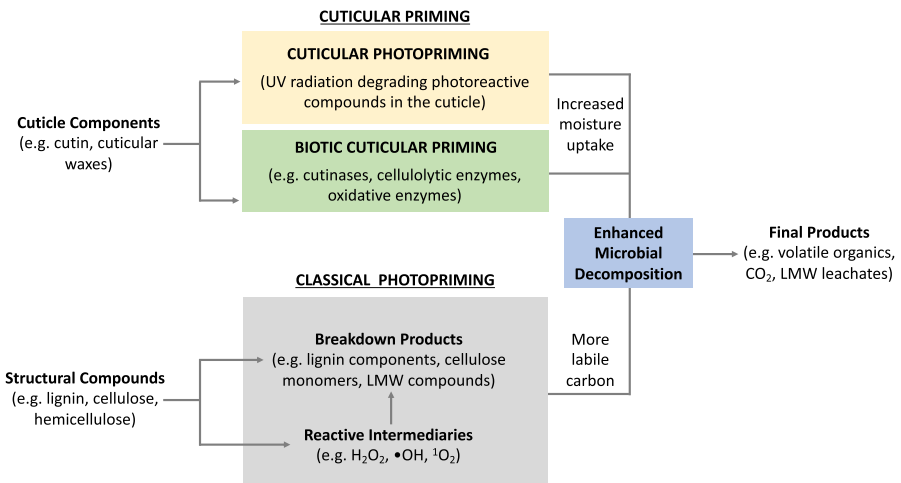


FIGURE 6 Conceptual model showing different priming mechanisms and how they enhance biotic decomposition. Classical photopriming is when solar radiation degrades recalcitrant compounds like lignin, producing more labile carbon sources that are more easily degraded (grey box). In our model, photodegradation (gold box) and biotic degradation of the cuticle (green box) also enhance microbial decomposition by increasing moisture uptake during NRM events. Yeasts, filamentous fungi and bacteria directly degrade both the cuticle and interior structural components of plant litter as well as the breakdown products of photodegradation. This simplified model does not preclude other processes such as thermal degradation, sand abrasion and insect herbivory that can also alter cuticle integrity and accelerate mass loss. LWM, low molecular weight

how long cuticles persist following senescence and this may affect their susceptibility to photodegradation (Throop & Archer, 2009). Attempts to incorporate photodegradation (Adair et al., 2017), NRM (Evans et al., 2020) and plant traits (Cornwell et al., 2008) into litter decay models have improved carbon loss estimates, but so far, these efforts have typically focused on only one of these drivers at a time. Combining data from plant trait databases such as the TRY Database (Kattge et al., 2020) and solar radiation networks (NOAA Global Monitoring Laboratory, 2021) may provide the opportunity to study interactions between these different drivers using existing datasets, improving our understanding of carbon loss in dryland systems.

We demonstrate a novel priming mechanism that links an important plant litter physical property with two increasingly well understood litter decay mechanisms: photodegradation and NRM-driven biotic decay. As climate regimes change in dryland systems worldwide, carbon cycling is likely to be altered by shifts in plant communities as well as microbial communities' response to altered temperature and moisture conditions. Understanding how NRM-driven litter decomposition is constrained by leaf litter properties, and how abiotic drivers can alleviate these constraints, will allow us to better understand how drylands are responding to global change, enabling us to better manage these globally important ecosystems.

ACKNOWLEDGEMENTS

We would like to thank the Namibian Ministry of Environment and Tourism, the National Commission on Research, Science, and Technology, and the Gobabeb Namib Research Institute for their permission and support in the Namib-Naukluft Park (permit numbers 2116/2016, 2228/2016 and RPIV000102017). Special thanks to Martin Handjaba and Ritha Kapitango, for their support and maintenance of the UV experiment throughout the study and to Kathy Jacobson and Peter Jacobson for stimulating discussions about litter decomposition in the Namib Desert, litter racks, shelter design tips and helpful comments on the manuscript. Thank you to Roland Vogt and the Baseline Surface Radiation Network for solar radiation data. We would like to thank two anonymous reviewers for their helpful feedback on this paper. The fog chamber was constructed and loaned by Kyle Jaynes at the W. K. Kellogg Biological Station. Additional thanks to Tyler Scifres, Hannah Shireman, Angela Curtis, Steve Hamilton, the KBS Writing Group and the Evans Lab members. Funding was provided by the NSF Graduate Research Fellowship Program; Michigan State University's Ecology, Evolution, and Behavior program; the MSU African Studies Center; the MSU International Studies & Programs Office's Dr Charles and Marjorie Gliozzo Dissertation Research Scholarship; the W. K. Kellogg Biological Station through its T. Wayne and Kathryn Porter Graduate Fellowship and the George H. Lauff Scholarship; and the taxpayers of the United States and Michigan. This paper is KBS Contribution Number 2281.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

J.R.L. and S.E.E. conceived the ideas and designed the methodology; J.R.L. collected the data; J.R.L., P.B. and S.E.E. analysed the data; J.R.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data were deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.b2rbnzsh8 (Logan et al., 2022).

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REFERENCES

Adair, E. C., Parton, W. J., Del grosso, S. J., Silver, W. L., Harmon, M. E., Hall, S. A., Burke, I. C., & Hart, S. C. (2008). Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. *Global Change Biology*, *14*, 2636–2660. https://doi.org/10.1111/j.1365-2486.2008.01674.x

Adair, E. C., Parton, W. J., King, J. Y., Brandt, L. A., & Lin, Y. (2017). Accounting for photodegradation dramatically improves prediction of carbon losses in dryland systems. *Ecosphere*, *8*. https://doi.org/10.1002/ecs2.1892

Angst, G., Heinrich, L., Kögel-knabner, I., & Mueller, C. W. (2016). The fate of cutin and suberin of decaying leaves, needles and roots – Inferences from the initial decomposition of bound fatty acids. *Organic Geochemistry*, *95*, 81–92. https://doi.org/10.1016/j.orggeochem.2016.02.006

Austin, A. T. (2011). Has water limited our imagination for aridland biogeochemistry? *Trends in Ecology & Evolution*, *26*, 229–235. https://doi.org/10.1016/j.tree.2011.02.003

Austin, A. T., & Ballare, C. L. (2010). Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 4618–4622. https://doi.org/10.1073/pnas.0909396107

Austin, A. T., Méndez, M. S., & Ballaré, C. L. (2016). Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 4392–4397. https://doi.org/10.1073/pnas.1516157113

Austin, A. T., & Vivanco, L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*, *442*, 555–558. https://doi.org/10.1038/nature05038

Barnes, P. W., Throop, H. L., Archer, S. R., Breshears, D. D., Mcculley, R. L., & Tobler, M. A. (2015). Sunlight and soil–litter mixing: Drivers of litter decomposition in drylands. *Progress in Botany*, 273–302. https://doi.org/10.1038/1941023a0

Bates, D., Mächler, M., Bolker, B., & Walk, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Bilger, W., Johnsen, T., & Schreiber, U. (2014). UV-excited chlorophyll fluorescence as a tool for the assessment of UV-protection by the epidermis of plants. *Journal of Experimental Botany*, *52*, 2007–2014. https://doi.org/10.1093/jexbot/52.363.2007

Brandt, L. A., Bonnet, C., & King, J. Y. (2009). Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. *Journal of Geophysical Research: Biogeosciences*, *114*, 1–13. https://doi.org/10.1029/2008JG000772

Bruhn, D., Mikkelsen, T. N., Rolsted, M. M. M., Egsgaard, H., & Ambus, P. (2014). Leaf surface wax is a source of plant methane formation under UV radiation and in the presence of oxygen. *Plant Biology*, *16*(2), 512–516. https://doi.org/10.1111/plb.12137

Chen, M., Parton, W. J., Adair, E. C., Asao, S., Hartman, M. D., & Gao, W. (2016). Simulation of the effects of photodecay on long-term litter decay using DayCent. *Ecosphere*, *7*. https://doi.org/10.1002/ecs2.1631

Chen, S., Tong, X., Woodard, R. W., Du, G., Wu, J., & Chen, J. (2008). Identification and characterization of bacterial cutinase. *Journal of Biological Chemistry*, *283*, 25854–25862. https://doi.org/10.1074/jbc.M800848200

Clayton, W. D., Vorontsova, M. S., Harman, K. T., & Williamson, H. (2006). *GrassBase – The online world grass flora*. Retrieved from http://www.kew.org/data/grasses-db.html

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., … Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, *11*, 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*, 52–58. https://doi.org/10.1038/nclimate1633

Day, T. A., Bliss, M. S., Placek, S. K., Tomes, A. R., & Guénon, R. (2019). Thermal abiotic emission of CO_2 and CH_4 from leaf litter and its significance in a photodegradation assessment. *Ecosphere*, *10*. https://doi.org/10.1002/ecs2.2745

Eckardt, F. D., Soderberg, K., Coop, L. J., Muller, A. A., Vickery, K. J., Grandin, R. D., Jack, C., Kapalanga, T. S., & Henschel, J. (2013). The nature of moisture at Gobabeb, in the central Namib Desert. *Journal of Arid Environments*, *93*, 7–19. https://doi.org/10.1016/j.jaridenv.2012.01.011

Erdenebileg, E., Wang, C., Ye, X., Cui, Q., Du, J., Huang, Z., Liu, G., & Cornelissen, J. H. C. (2020). Multiple abiotic and biotic drivers of long-term wood decomposition within and among species in the semi-arid inland dunes: A dual role for stem diameter. *Functional Ecology*, *34*, 1472–1484. https://doi.org/10.1111/1365-2435.13559

Evans, S. E., Todd-brown, K. E. O., Jacobson, K. M., & Jacobson, P. J. (2020). Non-rainfall moisture: A key driver of microbial respiration from standing litter in arid, semiarid, and mesic grasslands. *Ecosystems*, *23*, 1154–1169. https://doi.org/10.1007/s10021-019-00461-y

Forthun, G. M., Johnson, M. B., Schmitz, W. G., Blume, J., & Caldwell, R. J. (2006). Trends in fog frequency and duration in the southeast United States. *Physical Geography*, *27*, 206–222. https://doi.org/10.2747/0272-3646.27.3.206

Fourtouni, A., Manetas, Y., & Christias, C. (1998). Effects of UV-B radiation on growth, pigmentation, and spore production in the phytopathogenic fungus *Alternaria solani*. *Canadian Journal of Botany*, *76*, 2093–2099.

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Gliksman, D., Rey, A., Seligmann, R., Dumbur, R., Sperling, O. R., Navon, Y., Haenel, S., De Angelis, P., Arnone, J. A., & Grünzweig, J. M. (2017). Biotic degradation at night, abiotic degradation at day: Positive feedbacks on litter decomposition in drylands. *Global Change Biology*, *23*, 1564–1574. https://doi.org/10.1111/gcb.13465

Haensler, A., Cermak, J., Hagemann, S., & Jacob, D. (2011). Will the southern African west coast fog be affected by future climate change? *Erdkunde*, *65*, 261–275. https://doi.org/10.3112/erdkunde.2011.03.04

Jacobson, K., van Diepeningen, A., Evans, S., Fritts, R., Gemmel, P., Marsho, C., Seely, M., Wenndt, A., Yang, X., & Jacobson, P. (2015). Non-rainfall moisture activates fungal decomposition of surface litter in the Namib Sand Sea. *PLoS One*, *10*, e0126977. https://doi.org/10.1371/journal.pone.0126977

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database – Enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

King, J. Y., Brandt, L. A., & Adair, E. C. (2012). Shedding light on plant litter decomposition: Advances, implications and new directions in understanding the role of photodegradation. *Biogeochemistry*, *111*, 57–81. https://doi.org/10.1007/s10533-012-9737-9

Kolb, C. A., Schreiber, U., Gademann, R., & Pundel, E. E. (2005). UV-A screening in plants determined using a new portable fluorimeter. *Photosynthetica*, *43*, 371–377. https://doi.org/10.1007/s11099-005-0061-7

Kutty, S. G., Dimri, A. P., & Gultepe, I. (2019). Climatic trends in fog occurrence over the Indo-Gangetic plains. *International Journal of Climatology*, 1–14. https://doi.org/10.1002/joc.6317

Lin, Y., Karlen, S. D., Ralph, J., & King, J. Y. (2018). Short-term facilitation of microbial litter decomposition by ultraviolet radiation. *Science of the Total Environment*, *615*, 838–848. https://doi.org/10.1016/j.scitotenv.2017.09.239

Logan, J. R., Barnes, P., & Evans, S. E. (2022). Photodegradation of plant litter cuticles enhances microbial decomposition by increasing uptake of non-rainfall moisture. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.b2rbnzsh8

Logan, J. R., Jacobson, K. M., Jacobson, P. J., & Evans, S. E. (2021). Fungal communities on standing litter are structured by moisture type and constrain decomposition in a hyper-arid grassland site descriptions and climatic data. *Frontiers in Microbiology*, *12*, 1–15. https://doi.org/10.3389/fmicb.2021.596517

Manning, W. J., & Tiedemann, A. (1995). Climate Change: Potential effects of increased atmospheric carbon dioxide (CO_2), ozone (O_3), and ultraviolet-B (UV-B) radiation on plant diseases. *Environmental Pollution*, *88*, 219–245. https://doi.org/10.1016/0269-7491(95)91446-R

Messenger, D. J., Mcleod, A. R., & Fry, S. C. (2009). The role of ultraviolet radiation, photosensitizers, reactive oxygen species and ester groups in mechanisms of methane formation from pectin. *Plant, Cell and Environment*, *32*, 1–9. https://doi.org/10.1111/j.1365-3040.2008.01892.x

Niu, F., Li, Z., Li, C., Lee, K. H., & Wang, M. (2010). Increase of wintertime fog in China: Potential impacts of weakening of the Eastern Asian monsoon circulation and increasing aerosol loading. *Journal of Geophysical Research*, *115*. https://doi.org/10.1029/2009JD013484

NOAA Global Monitoring Laboratory. (2021). *SURFRAD: Other surface radiation networks*. Retrieved from https://gml.noaa.gov/grad/surfrad/netlinks.html

Pieristè, M., Chauvat, M., Kotilainen, T. K., Jones, A. G., Aubert, M., Robson, T. M., & Forey, E. (2019). Solar UV-A radiation and blue light enhance tree leaf litter decomposition in a temperate forest. *Oecologia*, *191*, 191–203. https://doi.org/10.1007/s00442-019-04478-x

Pieristè, M., Neimane, S., Solanki, T., Nybakken, L., Jones, A. G., Forey, E., Chauvat, M., Ņečajeva, J., & Robson, T. M. (2020). Ultraviolet radiation accelerates photodegradation under controlled conditions but slows the decomposition of senescent leaves from forest stands in southern Finland. *Plant Physiology and Biochemistry*, *146*, 42–54. https://doi.org/10.1016/j.plaphy.2019.11.005

Pitcairn, C. E. R., Jeffree, C. E., & Grace, J. (1986). Influence of polishing and abrasion on the diffusive conductance of leaf surface of *Festuca arundinacea* Schreb. *Plant, Cell and Environment*, *9*, 191–196. https://doi.org/10.1111/j.1365-3040.1986.tb01731.x

Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G., Chevallier, F., Liu, Y. Y., Running, S. W., Sitch, S.,

& van der Werf, G. R. (2014). Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature*, *509*, 600–603. https://doi.org/10.1038/nature13376

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Riederer, M., & Schreiber, L. (2001). Protecting against water loss: Analysis of the barrier properties of plant cuticles. *Journal of Experimental Botany*, *52*, 2023–2032. https://doi.org/10.1093/jexbot/52.363.2023

Ritter, F., Berkelhammer, M., & Beysens, D. (2019). Dew frequency across the US from a network of in situ radiometers. *Hydrology and Earth System Sciences*, *23*, 1179–1197. https://doi.org/10.5194/hess-23-1179-2019

Seely, M. K., & Louw, G. N. (1980). First approximation of the effects of rainfall on the ecology of a Namib Desert dune ecosystem. *Journal of Arid Environments*, *3*, 25–54.

Shepherd, T., & Griffiths, D. W. (2006). The effects of stress on plant cuticular waxes. *New Phytologist*, *171*, 469–499. https://doi.org/10.1111/j.1469-8137.2006.01826.x

Smith, W. K., Gao, W., Steltzer, H., Wallenstein, M. D., & Tree, R. (2010). Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. *Global Change Biology*, *16*, 484–495. https://doi.org/10.1111/j.1365-2486.2009.01973.x

Soares, P. M. M., Brito, M. C., & Careto, J. A. M. (2019). Persistence of the high solar potential in Africa in a changing climate. *Environmental Research Letters*, *14*, 124036. https://doi.org/10.1088/1748-9326/ab51a1

Throop, H., & Archer, S. (2009). Resolving the dryland decomposition conundrum: Some new perspectives on potential drivers. *Progress in Botany*, *70*, 171–194.

Wang, J., Liu, L., Wang, X., & Chen, Y. (2015). The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. *Global Change Biology*, *21*, 2095–2104. https://doi.org/10.1111/gcb.12812

Wang, J., Yang, S., Zhang, B., Liu, W., Deng, M., Chen, S., & Liu, L. (2017). Temporal dynamics of ultraviolet radiation impacts on litter decomposition in a semi-arid ecosystem. *Plant and Soil*, *419*, 71–81. https://doi.org/10.1007/s11104-017-3290-1

Zukswert, J. M., & Prescott, C. E. (2017). Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. *Oecologia*, *185*, 305–316. https://doi.org/10.1007/s00442-017-3951-z

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How to cite this article: Logan, J. R., Barnes, P., & Evans, S. E. (2022). Photodegradation of plant litter cuticles enhances microbial decomposition by increasing uptake of non-rainfall moisture. *Functional Ecology*, 00, 1–12. https://doi.org/10.1111/1365-2435.14053