Plant Soil (2017) 419:71–81
DOI 10.1007/s11104-017-3290-1

REGULAR ARTICLE

Temporal dynamics of ultraviolet radiation impacts on litter decomposition in a semi-arid ecosystem

Jing Wang · Sen Yang · Beibei Zhang · Weixing Liu · Meifeng Deng · Shiping Chen · Lingli Liu

Received: 21 November 2016 / Accepted: 18 May 2017 / Published online: 5 July 2017

Abstract
Background and aims The emerging consensus posits that ultraviolet (UV) radiation accelerates litter decomposition in xeric environments mainly by preconditioning litter for subsequent microbial decomposition. However, how UV radiation affects the interactions among litter chemistry, microbes, and eventually litter mass during different decomposition stages is still poorly understood.
Methods Here, we conducted a 29-month in situ decomposition experiment with litter exposed to ambient and reduced UV in a semi-arid grassland.
Results The decomposition rate for *Cleistogenes squarrosa* and *Stipa krylovii* under ambient UV was 82 and 111% greater than that under reduced UV, respectively. UV's positive effect showed three-stage temporal dynamics. During the early stage, UV had no impact on either litter chemistry or mass loss. During the intermediate stage, UV decreased litter carbon concentration and increased dissolved organic carbon concentration, but still had no effect on litter mass. During the late stage, UV exposure increased microbial population size in the surface soil and significantly increased litter mass loss.
Conclusions Overall, our study suggested that UV exposure accelerated litter decomposition first by improving litter biodegradability during the intermediate stage and then by enhancing microbial decomposition during the late stage. More long-term photodegradation experiments are needed to explore the biotic and abiotic interactions during different decomposition stages.

Keywords Arid and semi-arid ecosystems · DOC · Microbial decomposition · Photodegradation · PLFA · UV radiation

Responsible Editor: Elizabeth M Baggs.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-017-3290-1) contains supplementary material, which is available to authorized users.

J. Wang · S. Yang · B. Zhang · W. Liu · M. Deng · S. Chen · L. Liu (✉)
State Key Laboratory of Vegetation and Environmental Change, Institute of Botany|, Chinese Academy of Sciences, Beijing 100093, China
e-mail: lingli.liu@ibcas.ac.cn

J. Wang · S. Yang · B. Zhang · L. Liu
University of Chinese Academy of Sciences, Beijing 100049, China

Introduction

In arid and semi-arid regions, litter decomposition occurs much more rapidly than the predicted rate based on climate, litter quality, and available decomposers (Schaefer et al. 1985; Adair et al. 2008; Austin 2011). UV radiation has been recognized as a key driver accelerating litter decay via photodegradation in these regions (Austin and Vivanco 2006; Brandt et al. 2007, 2009). However, accumulating studies have shown that UV radiation has inconsistent impacts on litter decomposition (Uselman et al. 2011; Lambie et al. 2014; Almagro et al. 2015; Day et al. 2015). These

inconsistent responses may arise because UV exposure durations, the studied climate zones, and also the interactions between UV radiation and local environmental conditions were different (Brandt et al. 2010; Smith et al. 2010; Almagro et al. 2017). The impacts of UV radiation on litter chemistry and its interactions with microbial activity during different decomposition stages provide potential mechanisms to explain the discrepancy between studies, but such temporal dynamics is still not fully understood.

UV radiation may accelerate litter decomposition through abiotic photodegradation that directly mineralizes litter into gases, such as CO_2, CO, and CH_4 (Brandt et al. 2009; Rutledge et al. 2010; Lee et al. 2012), while simultaneously altering the chemistry of the remaining organic material (Lin et al. 2015; Zhou et al. 2015; Austin et al. 2016). Photosensitive compounds, such as lignin, may absorb UV radiation, resulting in a permanent change to the molecules, such as intramolecular rearrangement or electron transfer from or to the molecules (Kieber et al. 1989; Austin and Ballare 2010; King et al. 2012). Austin and Vivanco (2006) found that after inhibiting microbial decomposition by biocides, abiotic photodegradation by UV-B and total solar radiation accounted for 33 and 60% of litter decomposition in a semi-arid steppe, respectively. However, many other studies have suggested that the contribution of abiotic photodegradation may not be as high as described above (Lambie et al. 2014; van Asperen et al. 2015; Austin et al. 2016).

UV radiation also affects litter decomposition by altering microbial degradation. When microbes are directly exposed to UV radiation, it can retard microbial decomposition by suppressing microbial activity or changing microbial community composition (Johnson 2003; Pancotto et al. 2003; Robson et al. 2005). However, this negative effect does not necessarily occur. Baker and Allison (2015) found that microbial enzyme activity was higher and more effective under ambient UV radiation than under a reduced UV treatment because the microbes were better adapted to the ambient environment, even if the UV radiation was relatively higher.

Nevertheless, most previous studies focus only on litter mass loss under different UV treatments, with only a few studies simultaneously investigating the responses of microbes (Pancotto et al. 2003; Baker and Allison 2015). In contrast to microbes on the litter surface, soil microbes beneath the litter layer receive relatively less UV radiation. A previous study found that litter that was sheltered from direct UV exposure also decomposed faster under higher UV radiation, even when direct photodegradation was limited, possibly because microbial activity was stimulated by soluble leachates from the upper litter (Lin and King 2014). Microbes in the surface soil under the litter layer may also benefit from such conditions. It is therefore reasonable to expect that soil microbes under a litter layer could also be stimulated by higher litter biodegradability under UV radiation exposure. However, no experiment has directly assessed the effects of UV radiation on microbes on surface soil under the litter layer even though they are crucial for aboveground litter decomposition.

The net effects of UV radiation on litter decomposition are complicated and are ultimately determined by the balance between its positive and negative impacts (King et al. 2012; Wang et al. 2015). UV radiation breaks the complex carbon structures into small molecular compounds (Gallo et al. 2009; Liu et al. 2014; Almagro et al. 2015; Lin et al. 2015), increasing litter dissolved organic carbon (DOC) concentration. The DOC concentration is an integrative indicator for the production rate of small-molecule carbon compounds during litter decomposition (Don and Kalbitz 2005). Indeed, a global meta-analysis suggested that when inhibiting microbial activities, elevated UV radiation significantly increased litter DOC concentration by 14% by abiotic photodegradation (Wang et al. 2015). Therefore, litter DOC concentration could act as an indicator to evaluate the net effects of UV on litter decomposition during different decomposition stages. Most photodegradation studies are confined to short-term observation results (King et al. 2012); long-term studies, especially those simultaneously measuring litter mass, litter DOC concentration, and decomposer communities during different decomposition stages, are needed to explore the temporal dynamics of UV net effects on litter decomposition.

In this study, a 29-month in situ experiment was conducted in the typical semi-arid grasslands of Inner Mongolia, China. We aim to test the following three hypotheses: (1) UV radiation will first increase litter biodegradability by stimulating DOC production; (2) the changes in litter biodegradability will later stimulate microbial activities in litter and surface soil; and (3) the impacts of UV radiation on litter mass loss will show significant temporal dynamics; that is, UV has a limited impact on litter decomposition during the early period,

but significantly accelerates it during the later stage, because the responses of microbial decomposition to UV radiation lag behind the changes in litter biodegradability.

Materials and methods

Study site

The study site was located at the Duolun Restoration Ecology Research Station, Inner Mongolia, China (42° 02′ N, 116° 17′ E, 1324 m a.s.l.). The mean annual precipitation is approximately 378 mm, with 90% falling between May and October. The mean annual temperature is 2.1 °C, with the highest mean monthly temperatures occurring in July (18.9 °C) and the lowest in January (−17.5 °C). The mean monthly temperatures, total monthly precipitation, and the amount of solar radiation (400–1100 nm) during the experimental years (2013–2015) at the study site are shown in Fig. 1a, b. The mean proportion of UV radiation (280–400 nm) to the solar radiation (400–1100 nm) at our study site was 0.18, which was derived based on the ground measurements during sunny days in June 2016. The amount of UV radiation (280–400 nm) at the study site was estimated by multiplying the actual measured solar radiation (400–1100 nm) with 0.18 (Fig. S1). According to FAO classification, the soils are Haplic Calcisols. The vegetation is classified as temperate steppe, and the dominant vegetation consists of perennial herbs such as *Stipa krylovii*, *Agropyron cristatum*, and *Cleistogenes squarrosa.*

Field experiment design

Standing dead, senesced *C. squarrosa* and *S. krylovii* litter was collected in September 2012. *C. squarrosa* had a higher initial N concentration (0.64%) and a lower initial C/N ratio (65.80) than *S. krylovii*, which were 0.55% and 79.48, respectively. The litter was oven-dried at 35 °C and mixed to achieve homogeneity before being used in the experiment. The dry weight per unit length or area of *S. krylovii* was higher than that of *C. squarrosa.* To ensure similar contact areas for litter and soil between the two species of litter, 2 g of dry *C. squarrosa* litter and 3 g of dry *S. krylovii* litter were placed separately into 1-mm × 1.5-mm nylon mesh litterbags (10 cm × 15 cm). Because we did not find more suitable material, we made the

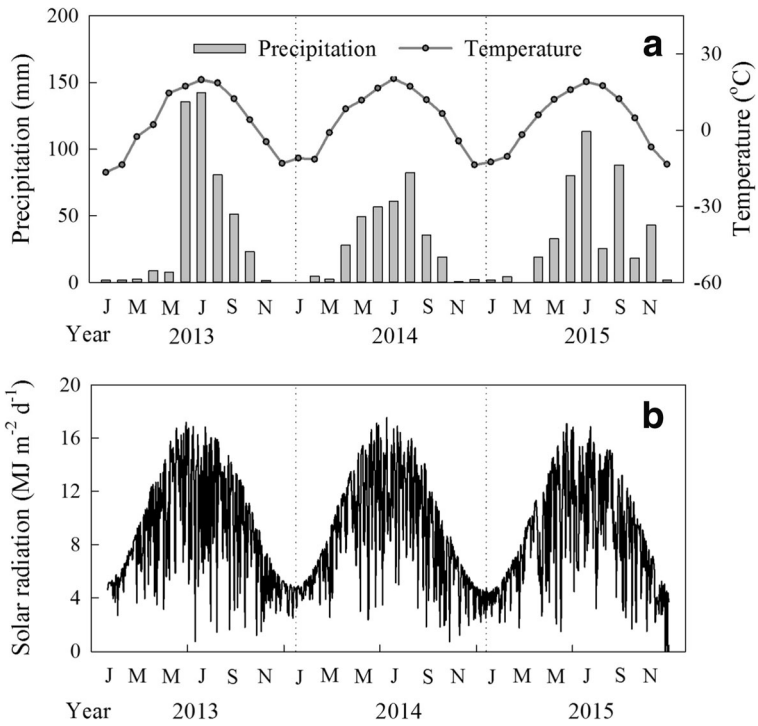

Fig. 1 **a** Total monthly precipitation (mm) and mean monthly temperature (°C) and **b** solar radiation (MJ m^{-2} day^{-1}) during the experimental years (2013–2015) at the study site

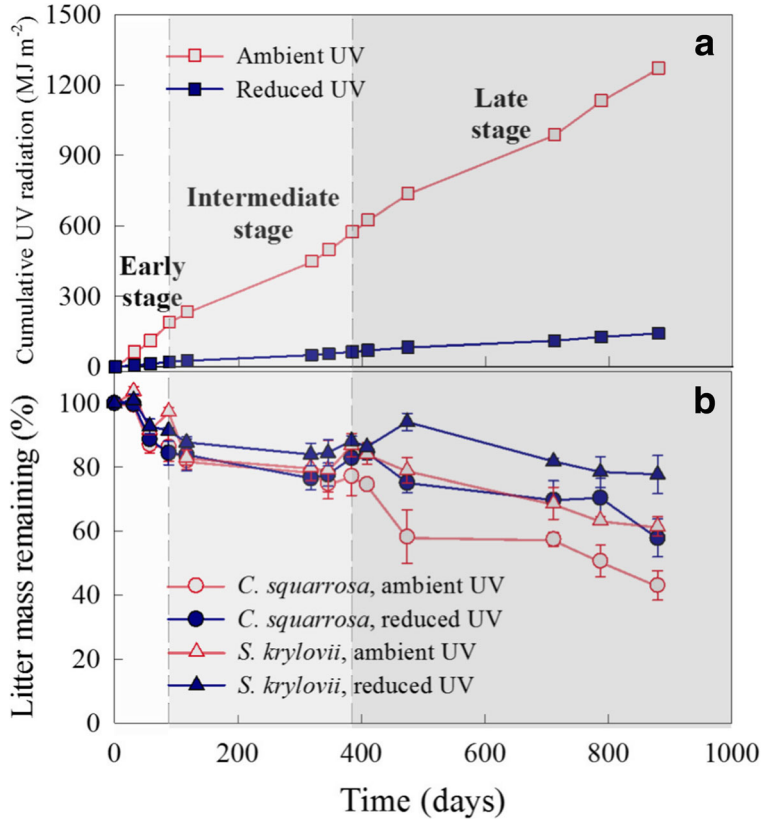

Fig. 2 **a** Cumulative UV radiation (MJ m^{-2}) at the litter surface under the two UV treatments and **b** effects of litter type and UV treatments on litter mass remaining (%) over the 29 months of decomposition. Values are means ± SE (n = 3)

litterbags with nylon mesh, which could have some impacts on litter N dynamics. We measured the penetration of UV radiation beneath the mesh at 10 spots, which were evenly distributed over the surface of a 10-cm × 15-cm mesh. The measurements indicated that the mesh allows 95.0 ± 1.6% of UV radiation to penetrate.

A two-by-two factorial experiment was conducted including two UV treatments (ambient UV and reduced UV) and two litter type treatments (*C. squarrosa* and *S. krylovii*). Steel frames, 50 cm × 50 cm × 10 cm ($l \times w \times h$), were erected on the ground, within which all aboveground vegetation was removed. During the growing season, the grasses were clipped periodically to avoid shading. The litterbags were deployed on the ground under the steel frames. To manipulate different levels of UV radiation, two types of plastic sheets (2 mm thick) were used: UV-transparent acrylic (ambient UV, which transmits 90% of UV-A and UV-B radiation) and UV-absorbing polycarbonate (reduced UV, which blocks 90% of UV-A and UV-B radiation). Both sheets allow the passage of more than 85% of the PAR. To avoid direct solar radiation from the southern face during noontime, we attached the plastic sheets on both the top and the southern faces of the frame. The spectral irradiance of the sheets was evaluated using a spectrometer (USB4000-UV-VIS, Ocean Optics, Dunedin, FL, USA). The background spectral distribution of solar radiation in summer at the study site and the spectral irradiance under the two types of plastic sheets used to create the different radiation treatments are shown in Fig. S2. To ensure the accuracy of their transmission properties, the sheets were cleaned frequently to remove any deposited dust. The sheets were also replaced every 3 months to avoid degradation over time. The UV transmission of the sheets was monitored periodically to ensure the differences in UV radiation (sum of UV-A and UV-B radiation) were maintained between the two treatments. For the two UV treatments, the cumulative UV radiation at the litter surface during the experimental years (2013–2015) is shown in Fig. 2a. At the beginning of the experiment, 24 perforations with a diameter of 5 mm were made in each plastic sheet to allow for water infiltration. Each treatment had three replicates, and 12 steel frames were constructed in total.

Litterbag collection

The experiment began on May 20, 2013. Three litterbags from each treatment (one from each replicate) were collected on days 31, 57, 88, 117, 318, 346, 384, 409, 474, 711, 787, and 880, with 12 collections in total. Because the area under each frame was basically occupied by the 12 litterbags, the edge effect can affect the results. To minimize the possible confounding effects caused by litterbag position, we randomly selected a position and collected the litterbags during each collection. The collected litterbags were stored in a refrigerator prior to weighing. Visible soil and green plants were removed from the litter. Litter samples were subsequently dried at 60 °C for 2 days after collection and then weighed.

Litter chemical analysis

Litter dissolved organic carbon was extracted by shaking 200 mg of a freshly collected litter sample with 30 ml of deionized water for 24 h at room temperature in the dark. The DOC concentration of the extract was analyzed with a total carbon analyzer (Multi N/C 3100; Analytik, Jena, Germany). The oven-dried litter samples were ground using a ball mill (Retsch MM400, Haan, Germany), and the litter C and N concentrations were analyzed with a CHNOS elemental analyzer (Vario EL III; Elementar Analysensysteme GmbH, Germany). The ash content of the decomposed litter was determined by combusting a subsample overnight in a muffle furnace at 500 °C. This estimate of ash content was used to correct all estimates of litter chemical composition and the remaining litter mass.

Litter and soil microbial community analysis

To examine the changes in microbial biomass and community composition under different UV and litter type treatments, the phospholipid fatty acids (PLFAs) of the collected litter samples in July 2014 (day 409, the 8th collection) and 2015 (day 711, the 10th collection) were analyzed. The litter samples were freeze-dried and the PLFAs were extracted from 250 mg of ground sample. Samples of the top 5 cm of soil beneath the litterbags were also collected at the two sampling times using a boring auger (diameter 5 cm). The soil was immediately homogenized and sieved through a 2-mm mesh sieve to remove stones and large plant residues. The residual fine roots in the soil were then removed manually. Approximately 8 g of the soil sample from each collection was used to extract PLFAs. The PLFA analysis was based on the method of White et al. (1979), with modifications as in Wilkinson et al. (2002). Individual fatty acid methyl esters were identified and quantified using the MIDI Sherlock Microbial Identification System (MIDI, Newark, DE, USA) and a gas chromatograph (Agilent 6850, USA).

Twenty-four fatty acids were included in the analysis of microbial community composition: (1) fungi: 16:1 w5c, 18:3 w6c (6,9,12); (2) bacteria: 10:0 2OH, 12:00, 12:0 2OH, 14:00, 14:0 iso, 15:0 anteiso, 15:0 iso, 15:00, 15:0 3OH, 16:00, 16:1 iso, 16:1 isoG, 16:1 w7c, 17:00, 17:0 iso, 17:0 anteiso, 17:1 w8c, 17:0 cyclo, 19:0 cyclo w8c, 20:00; (3) actinomycetes: 17:0 10-methyl, 18:0 10-methyl TBSA.

Data analysis

In this study, the DOC concentration in both *C. squarrosa* and *S. krylovii* showed significant three-stage temporal dynamics. According to the temporal dynamics of litter DOC concentration, we divided litter decomposition into three stages, including the early stage (0–3 months), the intermediate stage (3–12 months), and the late stage (12–29 months). We evaluated UV's impacts on litter mass loss, chemistry, and microbial biomass and community composition for the whole decomposition period and also the three stages, respectively.

Litter decomposition rate (k) was calculated based on the equation $M_t = M_0 e^{-kt}$, where t = time (years), M_t = litter mass at time t, and M_0 = initial litter mass. For the whole litter decomposition process and each of the divided three stages, the remaining litter mass and litter chemistry data were analyzed using a repeated-measure ANOVA, with litter type and UV treated as between-subject factors and time as the within-subject factor. The total PLFAs were the sum of all the fungi, bacteria, and actinomycetes. The k value and microbial parameters were analyzed using a two-way ANOVA, with UV and litter type as the main factors. Treatment effects were considered to be statistically significant at $P < 0.05$. Statistical analysis was conducted using SAS (Version 9, SAS Institute Inc., Cary, NC, USA).

Results

Remaining litter mass and decomposition rate

The remaining litter mass of *C. squarrosa* was significantly lower than that of *S. krylovii* across the entire decomposition experiment (Fig. 2b; Table S1; $P < 0.001$). At the end of the experiment, UV exposure significantly decreased the remaining litter mass of both litter types (Fig. 2b; Table S1; $P = 0.002$). When the process of decomposition was divided into three stages, UV treatment had no impact on the remaining litter mass for both litter types during the early and intermediate stages (Fig. 2b; Table S1); the acceleration effect of UV radiation on litter decomposition occurred only at the late stage (Fig. 2b; Table S1; $P = 0.001$).

UV exposure significantly increased the litter decomposition rate (k) for both litter types (Fig. 3; $df = 1$, $F = 29.15$, $P = 0.001$). Compared with the reduced UV treatment, ambient UV radiation increased the litter decomposition rate (k) by 82 and 111% for *C. squarrosa* and *S. krylovii*, respectively.

Litter chemistry

There was no difference in DOC concentration between the two litter types during the whole experiment period (Fig. 4a; Table S1). However, *C. squarrosa* had a consistently lower C concentration, lower C/N ratio, and higher N concentration than *S. krylovii* during the 29 months of decomposition (Fig. 4b–d; Table S1; $P < 0.001$). Litter DOC concentrations showed distinct temporal dynamics: an initial decrease, followed by an increase, reaching the highest level during the intermediate stage, and a subsequent decrease during the late stage (Fig. 4a). Litter C concentration and C/N ratio significantly decreased, while litter N concentration increased over time (Fig. 4b–d; Table S1; $P < 0.001$).

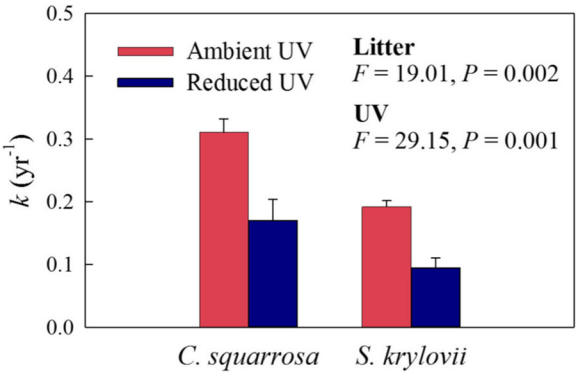

Fig. 3 Effects of litter type and UV treatments on litter decomposition rate, k (year^{-1}). Values are means ± SE ($n = 3$)

Overall, UV exposure decreased litter C concentration and C/N ratio, but had no impact on litter DOC concentration and N concentration (Fig. 4; Table S1). When the decomposition was divided into three stages, UV exposure had no impact on litter chemistry during the early stage (0–3 months), but significantly decreased litter C concentration during the intermediate stage (3–12 months) and decreased litter C concentration, C/N ratio, and the remaining litter N content during the late stage (12–29 months) (Fig. 4; Fig. S3; Table S1). Moreover, the impacts of UV exposure on litter DOC concentration were different between different stages. During the intermediate stage, the DOC concentration was significantly higher under the ambient UV treatment than under the reduced UV treatment (Fig. 4a; Table S1; $P = 0.050$), but this pattern was completely reversed during the late stage (Fig. 4a; Table S1; $P = 0.002$).

Microbial biomass and community composition

UV treatments did not affect microbial biomass and community composition in litter during both the intermediate and late stages (Fig. 5). The fungi/bacteria ratio was higher in *S. krylovii* litter than in *C. squarrosa* litter (Fig. 5c, d; $P < 0.050$). For soil microbes, there was no difference in total PLFAs or fungi/bacteria ratio between litter types or UV treatments during the intermediate stage (Fig. 6a, c). However, during the late stage, total PLFAs in soil were significantly higher under the ambient UV treatment than under the reduced UV treatment (Fig. 6b; $P = 0.005$). Moreover, there was significant interaction between UV and litter type treatments during the late stage (Fig. 6b; $P = 0.023$). The positive effect of UV exposure on total PLFAs in soil was higher in *S. krylovii* litter than in *C. squarrosa* litter.

Discussion

The photopriming effects of UV preconditioning litter for subsequent biological decomposition have been increasingly recognized (Wang et al. 2015; Austin et al. 2016). Our 29-month in situ experiment in a semi-arid grassland demonstrated that the positive effects of UV radiation on litter decomposition showed three-stage

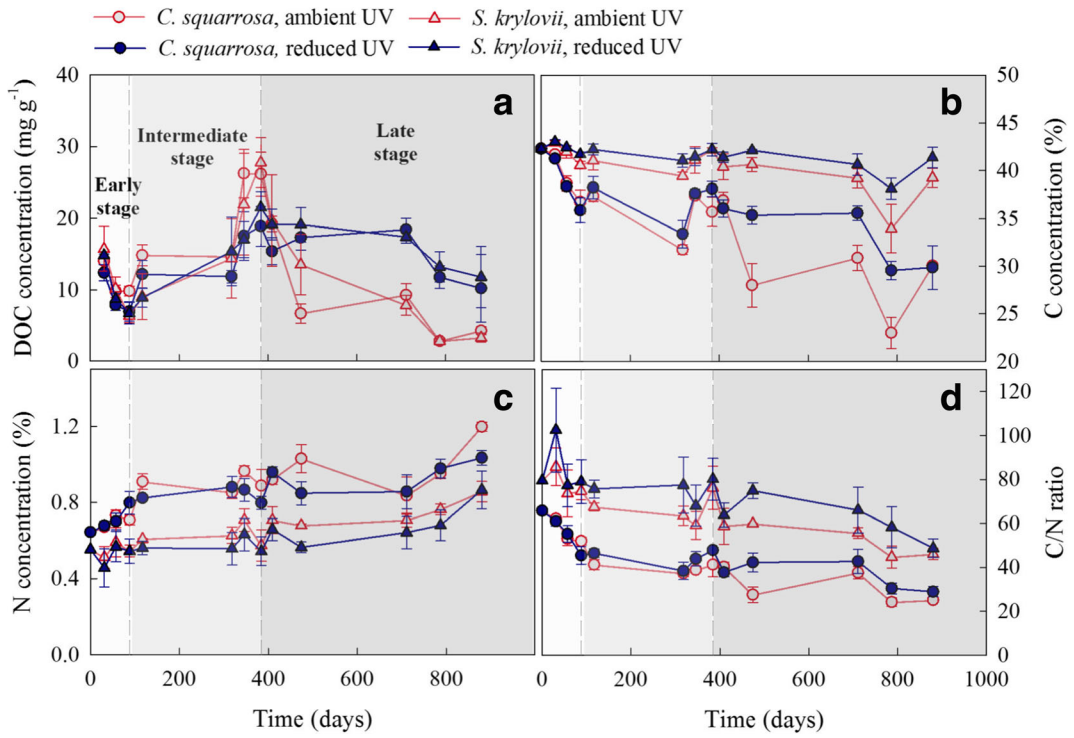

Fig. 4 Effects of litter type and UV treatments on **a** litter DOC concentration (mg g^{-1}), **b** litter C concentration (%), **c** litter N concentration (%), and **d** litter C/N ratio over the 29 months of decomposition. Values are means ± SE (n = 3)

temporal dynamics: UV radiation had no impact on litter chemistry and litter mass loss during the first 3 months (defined as the early stage). During the next 3–12 months, UV radiation significantly changed litter chemistry and increased litter biodegradability, but still had no impact on litter mass loss (defined as the intermediate stage). During the last 12–29 months, UV radiation significantly increased litter mass loss by increasing biological decomposition (defined as the late stage). Below, we discuss how the impacts of UV on litter chemistry interacts with microbial decomposition at the three stages and why this information is imperative to deepen our understanding of the mechanisms underlying litter decomposition dynamics in arid and semi-arid ecosystems.

Early stage: litter mass loss predominantly driven by microbial decomposition

During the early stage, litter N concentration increased (Fig. 4c), while litter DOC concentration decreased over time (Fig. 4a). However, UV radiation did not alter either litter chemistry or mass loss for both litter types during this stage (Fig. 2b; Fig. 4; Table S1). Previous studies that exposed litter to UV radiation for only a few months have also found no positive effect of UV radiation on litter decomposition (Kirschbaum et al. 2011; Lambie et al. 2014). The non-significant impact of UV radiation on litter mass loss and chemistry during this stage could be possibly because the length of UV exposure was too short and the cumulative energy derived from the UV radiation was not sufficient to exert any impact. Considering that the mass loss rate was high but UV did not alter litter chemistry, we expect that litter decomposition during the early stage was predominately driven by microbial decomposition. However, because our field incubation started in May, the weather was warm and wet during the early stage (from May to August, Fig. 1a). The non-significant difference in litter DOC concentration between the two UV treatments may be due to the fact that DOC in litters was occasionally washed out by rainfall events or that microbial consumption contributed to a greater extension of litter DOC during the wet warm period.

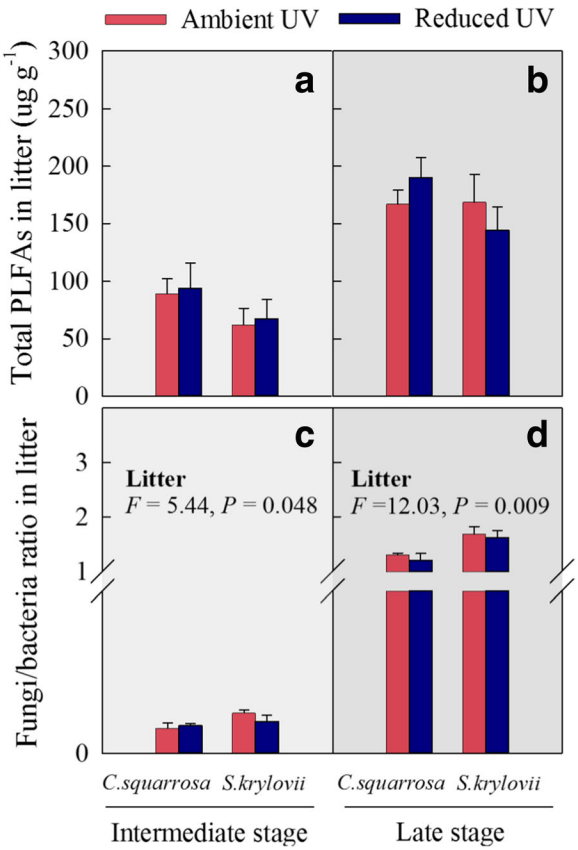

Fig. 5 Effects of litter type and UV treatments on microbial biomass and community composition in litter. **a** Total PLFAs in litter (μg g^{-1}) during the intermediate stage, **b** total PLFAs in litter (μg g^{-1}) during the late stage, **c** fungi/bacteria ratio in litter during the intermediate stage, and **d** fungi/bacteria ratio in litter during the late stage. Values are means ± SE (n = 3)

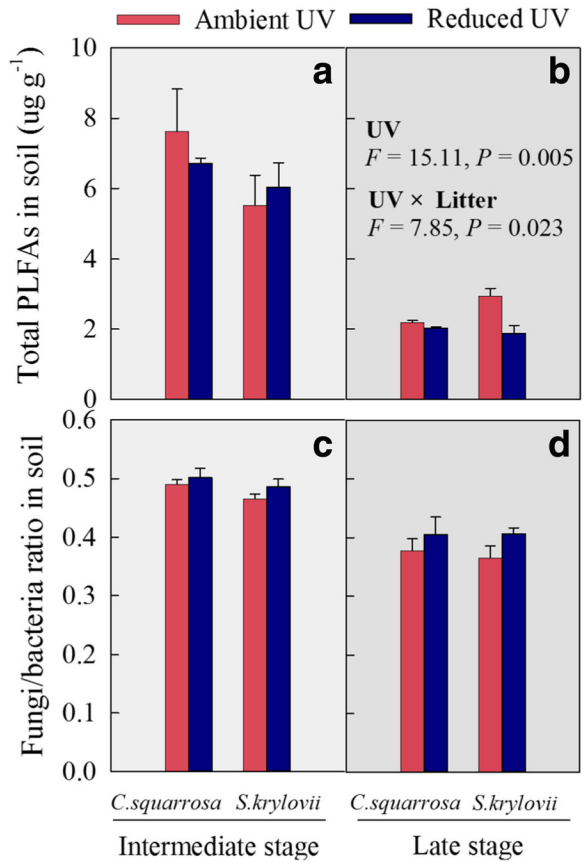

Fig. 6 Effects of litter type and UV treatments on microbial biomass and community composition in surface soil. **a** Total PLFAs in soil (μg g^{-1}) during the intermediate stage, **b** total PLFAs in soil (μg g^{-1}) during the late stage, **c** fungi/bacteria ratio in soil during the intermediate stage, and **d** fungi/bacteria ratio in soil during the late stage. Values are means ± SE (n = 3)

Intermediate stage: UV exposure increased litter biodegradability

During the intermediate stage, UV radiation still had no impact on litter mass loss, but decreased litter C concentration and increased litter DOC concentration (Fig. 4; Table S1). The high DOC concentration and low C concentration increased litter quality, and therefore also degradability for microbes (Liu et al. 2014; Wang et al. 2015; del Campo and Gómez 2016), which could stimulate microbial activities (Yanni et al. 2015; Austin et al. 2016). On the other hand, UV could also damage microbial nucleic acids and inhibit fungal growth (Johnson 2003; Pancotto et al. 2003). The significance of the photopriming effect on litter mass loss thus relies on the balance between those positive and negative impacts (King et al. 2012; Wang et al. 2015). However, we know little about whether, when, and how microbial population size and composition respond to the changed litter chemistry and the UV's direct damage simultaneously under UV radiation over the course of decomposition.

In this study, we assessed the responses of microbes both in litter and in surface soil beneath the litter. We found that UV radiation did not alter microbial biomass and community composition in litter during the intermediate stage. This may be due to the fact that the positive effects of the increased DOC concentration (Wang et al. 2015) were offset by the negative impacts of UV exposure on microbial activities (Johnson 2003; Pancotto et al. 2003; Robson et al. 2005). Consistently, previous studies that were conducted for less than 1 year have also found that UV radiation breaks down complex

compounds, but had no significant impact on litter mass loss (Uselman et al. 2011; Liu et al. 2014; Lin et al. 2015; Yanni et al. 2015).

Late stage: UV's preconditioning effect stimulated microbial decomposition

During the late stage, we found that UV radiation significantly increased litter mass loss, and the positive effects were similar between the two litter types (Fig. 2b; Table S1). Generally, UV photodegradation could increase litter DOC concentration (Liu et al. 2014; Almagro et al. 2015; Lin et al. 2015). However, during the late stage, the litter DOC concentration was lower under ambient UV treatment than that under reduced UV treatment (Fig. 4; Table S1), which might be related to microbial consumption. Moreover, the litter C/N ratio was lower under ambient UV treatment (Fig. 4; Table S1), which was not beneficial to photodegradation but to microbial decomposition (Day et al. 2015). We also found that the remaining nitrogen content was lower under ambient UV treatment than that under reduced UV treatment (Fig. S3), which suggested higher N release by microbial activities under ambient UV treatment. Although no significant UV impact was found for microbes in litter during the late stage of decomposition, the size of the microbial community in surface soil was significantly higher under ambient UV treatment than that under reduced UV treatment (Fig. 6b). Considering the higher soil microbial biomass under the ambient UV treatment, the synchronously decreased litter mass and DOC concentration at this stage were likely associated with higher levels of microbial decomposition but not higher photodegradation (Wang et al. 2015). However, UV treatment had no significant impacts on microbial community composition such as the fungi/bacteria ratio, probably because the balance between the negative effect of UV exposure and the positive effect from litter chemistry change exerted similar impacts on fungi and bacteria.

Nevertheless, our findings demonstrate that the responses of the microbes to UV radiation varied with vertical depth from the litter layer to the surface soil beneath the litter layer. This is most likely because from the litter layer to the surface soil, the negative effects of direct UV exposure on microbial activity were offset, or even reversed, by the photopriming effects of UV radiation. Few studies have evaluated the responses of soil microbes when exploring UV's impact on litter decomposition. Further efforts should be made to evaluate whether UV radiation alters the contribution of soil microbes to litter decomposition, rather than merely concentrating on the changes in litter mass and chemistry under UV radiation.

Conclusion and prospects for photodegradation studies

Our study demonstrated that UV radiation can accelerate litter decomposition; however, this positive effect requires a period of UV accumulation, by increasing litter DOC concentration and decreasing litter C concentration during the intermediate stage and priming subsequent microbial decomposition. Other than local climatic conditions or litter quality, the temporal dynamics of UV's impact can be one possible reason to explain the inconsistent findings in photodegradation studies: the neutral or even negative responses of litter decomposition to UV exposure were mostly found in the short-term experiments (Kirschbaum et al. 2011; Uselman et al. 2011; Lambie et al. 2014), whereas positive responses were often derived from long-term experiments (Austin and Vivanco 2006; Brandt et al. 2007; Brandt et al. 2010). Taking into account such temporal dynamics of UV impacts will greatly increase the predictability of litter decomposition models in arid and semi-arid ecosystems.

Whether the photopriming effect of UV radiation has an overall positive effect on litter decomposition is also largely dependent on microbial activity, which is greatly driven by environmental conditions such as precipitation and temperature. Indeed, previous studies suggested that water availability significantly interacted with UV photodegradation during the litter decomposition process (Brandt et al. 2010; Smith et al. 2010; Almagro et al. 2017). Also, recent studies showed that the photopriming effect occurs not only in arid lands but also in ecosystems where organic material may be exposed to solar radiation for some period of time (Cory et al. 2014; Austin et al. 2016). Few studies have assessed the magnitude of how great microorganisms could benefit from the increased litter biodegradability caused by UV exposure under different climate conditions. The poorly explored interactions between UV radiation and environmental conditions may largely impact the predictability of litter C turnover in a wide range of ecosystems. More studies are needed to further investigate the mechanisms driving the dynamics of

photodegradation under different environmental conditions.

Acknowledgements This study was financially supported by the National Natural Science Foundation of China (31522011), the Chinese National Key Development Program for Basic Research (2013CB956304, 2014CB954003), and the National 1000 Young Talents Program.

References

Adair EC, Parton WJ, Del Grosso SJ, Silver WL, Harmon ME, Hall SA, Burke IC, Hart SC (2008) Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. Glob Change Biol 14:2636–2660

Almagro M, Maestre FT, Martinez-Lopez J, Valencia E, Rey A (2015) Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands. Soil Biol Biochem 90:214–223

Almagro M, Martínez-López J, Maestre FT, Rey A (2017) The contribution of photodegradation to litter decomposition in semiarid mediterranean grasslands depends on its interaction with local humidity conditions, litter quality and position. Ecosystems 20:527–42

Austin AT (2011) Has water limited our imagination for aridland biogeochemistry? Trends Ecol Evol 26:229–235

Austin AT, Ballare CL (2010) Dual role of lignin in plant litter decomposition in terrestrial ecosystems. Proc Natl Acad Sci 107:4618–4622

Austin AT, Méndez MS, Ballaré CL (2016) Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. Proc Natl Acad Sci 113:4392–4397

Austin AT, Vivanco L (2006) Plant litter decomposition in a semiarid ecosystem controlled by photodegradation. Nature 442: 555–558

Baker NR, Allison SD (2015) Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. Ecology 96:1994–2003

Brandt LA, Bohnet C, King JY (2009) Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. J Geophys Res 114: G02004

Brandt LA, King JY, Hobbie SE, Milchunas DG, Sinsabaugh RL (2010) The role of photodegradation in surface litter decomposition across a grassland ecosystem precipitation gradient. Ecosystems 13:765–781

Brandt LA, King JY, Milchunas DG (2007) Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. Glob Change Biol 13:2193–2205

Cory RM, Ward CP, Crump BC, Kling GW (2014) Sunlight controls water column processing of carbon in arctic fresh waters. Science 345:925–928

Day TA, Guenon R, Ruhland CT (2015) Photodegradation of plant litter in the Sonoran Desert varies by litter type and age. Soil Biol Biochem 89:109–122

del Campo R, Gómez R (2016) Exposure of wood in floodplains affects its chemical quality and its subsequent breakdown in streams. Sci Total Environ 543(Part A):652–661

Don A, Kalbitz K (2005) Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. Soil Biol Biochem 37:2171–2179

Gallo ME, Porras-Alfaro A, Odenbach KJ, Sinsabaugh RL (2009) Photoacceleration of plant litter decomposition in an arid environment. Soil Biol Biochem 41:1433–1441

Johnson D (2003) Response of terrestrial microorganisms to ultraviolet-B radiation in ecosystems. Res Microbiol 154: 315–320

Kieber DJ, McDaniel J, Mopper K (1989) Photochemical source of biological substrates in sea water: implications for carbon cycling. Nature 341:637–639

King J, Brandt L, Adair EC (2012) Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. Biogeochemistry 111:57–81

Kirschbaum MUF, Lambie SM, Zhou H (2011) No UV enhancement of litter decomposition observed on dry samples under controlled laboratory conditions. Soil Biol Biochem 43: 1300–1307

Lambie SM, Kirschbaum MUF, Dando J (2014) No photodegradation of litter and humus exposed to UV-B radiation under laboratory conditions: no effect of leaf senescence or drying temperature. Soil Biol Biochem 69:46–53

Lee H, Rahn T, Throop H (2012) An accounting of C-based trace gas release during abiotic plant litter degradation. Glob Change Biol 18:1185–1195

Lin Y, King J (2014) Effects of UV exposure and litter position on decomposition in a California grassland. Ecosystems 17: 158–168

Lin Y, King JY, Karlen SD, Ralph J (2015) Using 2D NMR spectroscopy to assess effects of UV radiation on cell wall chemistry during litter decomposition. Biogeochemistry 125: 427–436

Liu SR, Hu RG, Cai GC, Lin S, Zhao JS, Li YY (2014) The role of UV-B radiation and precipitation on straw decomposition and topsoil C turnover. Soil Biol Biochem 77:197–202

Pancotto VA, Sala OE, Cabello M, López NI, Matthew Robson T, Ballaré CL, Caldwell MM, Scopel AL (2003) Solar UV-B decreases decomposition in herbaceous plant litter in Tierra del Fuego, Argentina: potential role of an altered decomposer community. Glob Change Biol 9:1465–1474

Robson TM, Pancotto VA, Scopel AL, Flint SD, Caldwell MM (2005) Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland. Soil Biol Biochem 37:2205–2215

Rutledge S, Campbell DI, Baldocchi D, Schipper LA (2010) Photodegradation leads to increased carbon dioxide losses from terrestrial organic matter. Glob Change Biol 16:3065–3074

Schaefer D, Steinberger Y, Whitford WG (1985) The failure of nitrogen and lignin control of decomposition in a North-American desert. Oecologia 65:382–386

Smith WK, Gao W, Steltzer H, Wallenstein MD, Tree R (2010) Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. Glob Change Biol 16:484–495

Uselman SM, Snyder KA, Blank RR, Jones TJ (2011) UVB exposure does not accelerate rates of litter decomposition in a semi-arid riparian ecosystem. Soil Biol and Biochem 43: 1254–1265

van Asperen H, Warneke T, Sabbatini S, Nicolini G, Papale D, Notholt J (2015) The role of photo- and thermal degradation for CO_2 and CO fluxes in an arid ecosystem. Biogeosciences 12:4161–4174

Wang J, Liu L, Wang X, Chen Y (2015) The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. Glob Change Biol 21:2095–2104

White DC, Davis WM, Nickels JS, King JD, Bobbie RJ (1979) Determination of the sedimentary microbial biomass by extractable lipid phosphate. Oecologia 40:51–62

Wilkinson SC, Anderson JM, Scardelis SP, Tisiafouli M, Taylor A, Wolters V (2002) PLFA profiles of microbial communities in decomposing conifer litters subject to moisture stress. Soil Biol Biochem 34:189–200

Yanni SF, Suddick EC, Six J (2015) Photodegradation effects on CO_2 emissions from litter and SOM and photo-facilitation of microbial decomposition in a California grassland. Soil Biol Biochem 91:40–49

Zhou GX, Zhang JB, Mao JD, Zhang CZ, Chen L, Xin XL, Zhao BZ (2015) Mass loss and chemical structures of wheat and maize straws in response to ultraviolet-B radiation and soil contact. Scientific Reports 5:14851